# Seventy-five Years of Mammalogy (1919–1994)

ELMER C. BIRNEY
AND
JERRY R. CHOATE
Editors

# SEVENTY-FIVE YEARS OF MAMMALOGY

# (1919–1994)

ELMER C. BIRNEY

AND

JERRY R. CHOATE

Editors

## SPECIAL PUBLICATIONS

This series, published by the American Society of Mammalogists, has been established for papers of monographic scope concerned with some aspect of the biology of mammals.

Correspondence concerning manuscripts to be submitted for publication in the series should be addressed to the Editor for Special Publications, Michael A. Mares (address below).

Copies of Special Publications of the Society may be ordered from the Secretary-Treasurer, H. Duane Smith, 501 Widtsoe Bldg., Dept. Zoology, Brigham Young University, Provo, UT 84602.

---

## COMMITTEE ON SPECIAL PUBLICATIONS

# SEVENTY-FIVE YEARS OF MAMMALOGY (1919–1994)



EDITED BY

ELMER C. BIRNEY
Bell Museum of Natural History
100 Ecology Building
University of Minnesota
St. Paul, Minnesota 55108

JERRY R. CHOATE
Sternberg Museum of Natural History
Fort Hays State University
Hays, Kansas 67601

SPECIAL PUBLICATION NO. 11
THE AMERICAN SOCIETY OF MAMMALOGISTS
PUBLISHED 27 MAY 1994

Library of Congress Catalog Card No. 97-71464



ISBN No. 0-935868-73-9

# *LIST OF AUTHORS*

**Sydney Anderson**
American Museum of Natural History
Central Park West at 79th Street
New York, NY 10024

**David M. Armstrong**
Department of Evolutionary, Population, and Organismic Biology
University of Colorado
Boulder, CO 80309

**Robert J. Baker**
Department of Biological Sciences and the Museum
Texas Tech University
Lubbock, TX 79409

**Elmer C. Birney**
Bell Museum of Natural History
100 Ecology Building
University of Minnesota
St. Paul, MN 55108

**James H. Brown**
Department of Biology
University of New Mexico
Albuquerque, NM 87131

**Guy N. Cameron**
Department of Biology
University of Houston
Houston, TX 77004

**Jerry R. Choate**
Sternberg Museum of Natural History
Fort Hays State University
Hays, KS 67601

**Mark D. Engstrom**
Department of Mammalogy
Royal Ontario Museum
100 Queen's Park
Toronto, Ontario, CANADA M5S 2C6

**John F. Eisenberg**
Florida Museum of Natural History
Department of Natural Sciences and School of Forest Resources and Conservation
University of Florida, Gainesville, FL 32611

**Gregory L. Florant**
Department of Biology
Temple University
Philadelphia, PA 19122

**Hugh H. Genoways**
University of Nebraska State Museum
University of Nebraska–Lincoln
Lincoln, NE 68588

**Ayesha E. Gill**
Institute of Health Policy Studies
University of California
1388 Sutter Street, 11th Floor
San Francisco, CA 94109
*Present Address*
2308 Jefferson Avenue
Berkeley, CA 94703

**Mark S. Hafner**
Museum of Natural Science and
Department of Zoology and Physiology
Louisiana State University
Baton Rouge, LA 70803

**Robert S. Hoffmann**
Smithsonian Institution
Washington, D.C. 20560

**Donald F. Hoffmeister**
Museum of Natural History
University of Illinois
Urbana, IL 61801

**Rodney L. Honeycutt**
Department of Wildlife and
Fisheries Sciences and
The Faculty of Genetics
210 Nagle Hall
Texas A&M University
College Station, TX 77843

**Murray L. Johnson**
501 N. Tacoma Avenue
Tacoma, WA 98403

**G. J. Kenagy**
Department of Zoology
University of Washington
Seattle, WA 98195

**Gordon L. Kirkland, Jr.**
The Vertebrate Museum
Shippensburg University
Shippensburg, PA 17257

**James N. Layne**
Archbold Biological Station
P.O. Box 2057
Lake Placid, FL 33852

**William Z. Lidicker, Jr.**
Museum of Vertebrate Zoology
University of California
Berkeley, CA 94720

**Jason A. Lillegraven**
Departments of Geology/Geophysics and
Zoology/Physiology
The University of Wyoming
Laramie, WY 82071

**Michael A. Mares**
Oklahoma Museum of Natural History
University of Oklahoma
Norman, OK 73019

**Bruce D. Patterson**
Field Museum of Natural History
Roosevelt Road at Lake Shore Drive
Chicago, IL 60605

**Oliver P. Pearson**
Museum of Vertebrate Zoology
University of California
Berkeley, CA 94720

**Randolph L. Peterson** (Deceased)
Royal Ontario Museum
100 Queen's Park
Toronto, Ontario, CANADA M5S 2C6

**Carleton J. Phillips**
Department of Biological Sciences
Illinois State University
Normal, IL 61790

**Duane A. Schlitter**
Edward O'Neil Research Center
Carnegie Museum of Natural History
5800 Baum Blvd
Pittsburgh, PA 15206

**David J. Schmidly**
Texas A&M University
P.O. Box 1675
Galveston, TX 77553

**James H. Shaw**
Department of Zoology
Oklahoma State University
Stillwater, OK 74078

**H. Duane Smith**
Department of Zoology
Brigham Young University
Provo, UT 84602

**Keir Sterling**
324 Webster Street
Bel Air, MD 21014

**J. Mary Taylor**
Cleveland Museum of Natural History
Wade Oval, University Circle
Cleveland, OH 44106

**B. J. Verts**
Department of Fisheries and Wildlife
Oregon State University
Corvallis, OR 97331

**John O. Whitaker, Jr.**
Department of Life Science
Indiana State University
Terre Haute, IN 47809

**Don E. Wilson**
National Museum of Natural History
Smithsonian Institution
Washington, D.C. 20560

**Jerry O. Wolff**
Department of Fisheries and Wildlife
Oregon State University
Corvallis, OR 97331

**W. Chris Wozencraft**
Division of Natural Sciences
Lewis-Clark State College
Lewiston, ID 83501

**Bruce A. Wunder**
Department of Biology
Colorado State University
Fort Collins, CO 80523

**Terry L. Yates**
Department of Biology and
Museum of Southwestern Biology
University of New Mexico
Albuquerque, NM 87131

**Richard J. Zakrzewski**
Department of Geosciences and
Sternberg Museum of Natural History
Fort Hays State University
Hays, KS 67601

# *PREFACE*

1919-1994

The ad hoc committee to plan the 75th anniversary of the American Society of Mammalogists (abbreviated ASM here and throughout this book), was established by President Hugh Genoways, seemingly only a short time after we celebrated our 50th anniversary. The first meeting of that committee that we recall was at the annual gathering of ASM in Madison, Wisconsin, in 1986, and was chaired by Craig Hood. The coeditors of this book volunteered early in that meeting to oversee the preparation of a book covering the 75 years that ASM had been in existence, 1919–1994, admitting at the time that we had no specific plan but that we thought we could get something of this nature done in the 8 years available.

We are not the first, nor will we be the last, to learn that every job expands to consume all available time. Certainly, this book was no exception. It was remarkably easy for authors to agree to participate and for editors to develop "firm" deadlines when the target dates were such a long time in the future. Today, 10 February 1994, as we are drafting this final note to accompany the 21 chapters in this book, we still lack and shall never see one important chapter, and Allen Press is bending over backwards to get page proofs to the authors. Managing Editor Joe Merritt and Special Publications Editor Michael Mares are probably the only authors and editors who did not have time to procrastinate! Nevertheless, production presently is on schedule to have this book in the hands of ASM members at the anniversary meeting in Washington, D.C., as promised so long ago.

As we employ the latest in word-processing software to draft this document, send e-mail messages between Kansas and Minnesota in seconds, fax manuscripts between authors and editors, and generally make the most of this electronic era and its information superhighways, we contemplate 1919, the year ASM was founded. The First World War had just ended, Woodrow Wilson was President of the United States, and Mexico was experiencing a revolution. What was the state of the discipline of mammalogy, and what has ASM done in its 75-year existence to promote and facilitate the science? That is the topic of this book, which was conceived without much forethought in an otherwise forgotten committee meeting, and which underwent early embryogenesis along the banks of Lake Mendota on the beautiful University of Wisconsin campus, then survived a lengthy period of delayed development following some rapid growth that took place while the list of chapters was finalized and authors were recruited. A few individual cells underwent mitosis now and then, but real gestation began in the spring and summer of 1992. Subsequently, all chapters were subjected to two reviews by peers, mostly during the spring of 1993, and final revisions of most chapters were completed that summer.

The book is in two parts, one on the society and its members (the first eight chapters) and the other on the intellectual growth and development of the discipline of mammalogy during the past 75 years. The charge to authors of the two parts was different. Those writing chapters for Part I were asked simply to treat the topic, and in all cases the emphasis was on ASM, its members, its growth, and its activities to promote mammalogy. Thus, those chapters address history, and their topics are less about science than its facilitation.

Authors writing chapters for Part II were given the following, much more specific, guidelines: "We envision that chapters in this section will briefly review the pre-1919 state of knowledge of the assigned subdiscipline, if appropriate, then trace the intellectual development of the field through the 75-year period that ASM will have been in existence. Chapters in Part II are expected to take a global perspective of the history, with no special emphasis on either ASM or its members, of the field's development." We judge that all authors have more than adequately fulfilled the charge.

Authors originally were selected in pairs with an eye toward diversity. In some pairs our strategy was to select collaborators representing different eras, in others different schools of thought, and in still others we sought authors whose expertise encompassed the extremes of a broad or complex subdiscipline. A few prospective authors resigned for one reason or another, one died, one pair decided their chapter was not necessary, and for a host of other reasons author lines changed. We attempted to maintain the two-author-per-chapter philosophy throughout in order to get the best ideas of at least two individuals into every chapter, but in three instances that was not possible and in one a third author was recruited. Historical details of author selection pale in comparison to the heartfelt thanks we extend to all authors—it was our very real pleasure to work with each of them.

We are equally appreciative of the considerable effort donated by Jane Waterman, who drew the vignettes used on the first pages of chapters. We like each one very much, Jane. Our thanks go also to a long list of reviewers, some of whom dropped everything in order to help us meet our deadline, then employed fax and e-mail as necessary to provide nearly instantaneous turn-around of excellent, insightful reviews. We greatly appreciate the time and efforts of all reviewers, several of whom reviewed more than a single chapter: Sydney Anderson, David M. Armstrong, Robert J. Baker, Patricia J. Berger, James H. Brown, William A. Clemens, Mark D. Engstrom, James S. Findley, G. Lawrence Forman, Erik K. Fritzell, Hugh H. Genoways, Sarah B. George, Donald W. Kaufman, Gordon L. Kirkland, Jr., Thomas H. Kunz, Norman C. Negus, Bruce D. Patterson, Anne E. Pusey, O. J. Reichman, Eric A. Rickart, Duke S. Rogers, Robert K. Rose, William D. Schmid, Robert S. Sikes, Donald B. Siniff, Norman A. Slade, H. Duane Smith, Robert H. Tamarin, Robert M. Timm, Michael R. Voorhies, Jane M. Waterman, Michael R. Willig, Don E. Wilson, and Robert M. Zink.

Finally, we thank three people who made our jobs easy, and without whose untiring energies at crucial times this book would not have been completed in time for the anniversary celebration: Joseph F. Merritt, Managing Editor for Mammalian Species and Special Publications, put a prodigious amount of time and energy (with occasional lapses into jocularity) into making certain that no important detail of production was slighted; Michael A. Mares, Editor for Special Publications, processed manuscripts as fast as the two of us could send them to him; and Ken Blair at Allen Press adopted this project and simply made it happen on time no matter what the obstacle.

The proof of the pudding, as always, is in the eating. We hope that you, the reader, like our idea of pudding.

ELMER C. BIRNEY
St. Paul, Minnesota

JERRY R. CHOATE
Hays, Kansas
February 1994

# CONTENTS

# PART I

## HISTORY OF ASM AND ITS MOST PROMINENT MEMBERS

# *ORIGIN*

Donald F. Hoffmeister and Keir B. Sterling

## *Introduction*

Early in the 20th century, groups of scientists with common interests were banding together to share their mutual research and activities. Some of these groups organized themselves to form scientific societies. Among vertebrate zoologists this was especially true of the ornithologists, but much field work and research on mammals also was being conducted during this period. For example, the United States Bureau of Biological Survey had field workers studying and collecting mammals in many parts of North America, and by 1919 this group had published 44 monographs on mammals in the *North American Fauna* series. Universities and museums in the United States also were becoming increasingly more active in mammalian research. Thus, it is not surprising that in 1919 a group at the United States Bureau of Biological Survey would consider forming a scientific society for mammalogists (Hoffmeister, 1969).

This chapter summarizes the historical details of the formation of this society, which became known as The American Society of Mammalogists (ASM). To accomplish this, it is necessary first to review briefly some of the earlier developments of mammalian research, collections, and societies in the Old World, as well as the work conducted with mammals in North America prior to the formation of the ASM.

## *The Development of Scientific Societies in Europe in the 18th and 19th Centuries*

In the Middle Ages, interest in mammals was directed more to their economic importance—as a source of food and furs, as beasts of burden, as animals that could be domesticated. People were most familiar and concerned with those mammals they could readily observe, especially those that were diurnal or of large size. As interest in identifying and describing all of the mammals developed, it was advantageous and even necessary to collect and preserve them. With more parts of the world being explored and colonized and new and unusual mammals being encountered, these needed to be collected and described. The naturalists involved in research on these new discoveries were slow in joining together to form scientific societies. However, as their numbers increased and printing became possible and affordable, they formed groups with common interests which were the forerunners of our scientific societies.

Already in the late 1600s, collections of animals and plants increased so much that museums, usually called cabinets, were being developed, especially by wealthy individuals. In Paris alone there reportedly were over 200 private cabinets and a visitor's guide to Paris, published in 1787, listed 45 notable cabinets of natural history for that year. It was said that every member of the leisured class felt it necessary to have a cabinet of natural curiosities. The owners of such cabinets and collections usually were not scientists or naturalists. Some sponsored collecting expeditions, both locally and to distant places, and hired persons to do the collecting for them. Among the European collections in the 1700s were those of the English East India Company, the cabinets of Becoeur and Mauduyt de la Varenne, Sir Hans Sloane, Lady Margaret Cavendish Bentinck, Comte de Reaumur, Coenraad Jacob Temminck, William Yarrel, Lord Stanley, Rene-Antoine Ferchault de Reaumur, and the Cabinet du Roi. Most of these were private cabinets or collections, although some were opened to the public for a fee.

In the 1700s the preservation of mammal and bird specimens was haphazard and poor (Farber, 1982). Many specimens were without adequate data. Specimens obtained from foreign travelers were often of even poorer quality. Attempts were made to improve the quality of the materials. Some of the larger private collections hired curators. Many of these were trained in universities or apprenticed under medical doctors. Often those persons working with the collections published catalogues of the specimens in their cabinets. For example, Mathurin-Jacques Brisson's *Ornithologie* of 1760 has been referred to as a collection-catalogue of natural history, and Etienne Geoffroy Saint-Hilaire's work of 1803 was a *Catalogue des Mammiferes du Museum.* Some of the wealthy cabinet owners sought to advance their prestige by producing lavishly illustrated books, based in part upon their collections. Because of the great expense, such works were not widely distributed or available. There were exceptions, such as the volumes of *Histoire Naturelle* by Buffon (Georges Louis Leclerc, Comte de Buffon), starting in 1749.

In the early 1700s, natural history societies were practically non-existent. By the latter half of that century, groups of literary and scientific men frequently met for informal discussions. Natural history was further stimulated by the publicity Carl Linnaeus was receiving. In England, James Edward Smith and a few friends formed a "Society for the Investigation of Natural History" and a group that was the forerunner of the Linnean Society of London was started in 1782 by William Forsyth and nurtured by James Smith. In France, several local or provincial societies started, as in Caen, Cherbourg, Lyons, Nancy, and others, but most lasted only for a short time and not beyond the French Revolution.

At the end of the 18th century, natural history became increasingly noteworthy because many turned to improving upon Linnaeus' *Sytema Naturae.* Lamarck's ideas stirred interest, as did the debates of Georges Cuvier and Etienne Geoffroy Saint-Hilaire (Appel, 1987). This was the period when 18th-century natural history was changing to 19th-century biology. With such interest, local and national governments became more involved with making collections for the scientific communities. Government ships were sent to chart distant seas and coasts and to survey overseas holdings, as well as to trade with the new colonies. These were outfitted with naturalists whose intents were to bring back specimens. Examples of such voyages are those of Maximilan Prinz von Wied-Neuwied in 1815 to the New World, John Natterer to Brazil in 1817, sponsored by the Imperial Natural History

Museum of Vienna, Robert Herman Schomburgh to British Guiana in 1835, sponsored by the Royal Geographical Society of London, Johann Jacob von Tschudi in 1838 to Peru, the voyages of the *Beagle,* and the explorations of Captain Cook.

Museums and collections maintained by government agencies grew in size and importance, became available to the public, and began to incorporate some of the private collections (McClellan, 1985). The British Museum in its infancy was located in the Montagu House and was not open to the public. Sir Hans Sloane's large collection was turned over to the museum and in 1830 it moved to a new building, was recognized as the national museum, and soon additional private collections were acquired. For example, James Edward Smith bought Carl Linnaeus' library, manuscripts, herbarium, and specimens in 1788. Shortly thereafter the Linnean Society was formed, with Smith as president. Collections of the Society went to the British Museum, as did those of some other British societies. In the ensuing parts of the 19th century, the British Museum was curated by such mammalogists as George Robert Waterhouse, Richard Lydekker, and William Henry Flower.

The Jardin du Roi became the French Museum National d'Histoire Naturelle in 1793. Buffon had built the Cabinet at the Jardin into an outstanding collection during the mid-1700s. Etienne Geoffroy Saint-Hilaire continued this endeavor when, at age 21, he was placed in charge of the newly established national museum. Other persons with mammalogical interests associated with the Muséum d'Histoire Naturelle were Georges Cuvier, Georges Duvernoy, Henri Milne Edwards, and Etienne's son, Isidore Geoffroy St-Hilaire. Anselme-Gaëtan Desmarest served part-time as a preparator for Cuvier.

Germany had fewer private collections in the 1700s, but a museum was included with the establishment of the Universitat zu Berlin in 1810. Johann Carl Wilhelm Illiger was the first curator. Incorporated into this museum was the Pallas Collection and the Cabinet of Count Johann Centurius von Hoffmannsegg.

In Holland, there were many collectors (reportedly more than in all the rest of Europe) and many private collections in the late 1700s. In 1820, the Rijksmuseum van Natuurlijke Histoire was started in Leiden and many of these private collections were incorporated. This included the private collection of Coenraad Jacob Temminck, who became the first director of the new museum. The Dutch government provided specimens from its possessions. Max Wilhelm Carl Weber, known for numerous studies on mammals including *Die Saugetiere,* was associated with the University of Amsterdam.

The beginning of the 19th century saw the birth of many new scientific societies and the beginning of many new scientific journals. As collections and museums grew, so did the international community of scholars. At about the same time, it became possible to publish one's findings more readily. For example, before 1802 there were few permanent journals in Europe for publishing research in natural history. However, the development of steam-driven printing presses in the early 1800s made it possible to produce up to 20 times as many impressions in a given time span. The price of production of periodicals and books declined. Also, the wars that had ravaged parts of Europe from about 1790 greatly subsided after 1815.

As the number of scholars interested in natural history and biology grew, they began to associate into mutually beneficial groups or societies. There are many examples of societies and journals started in the late 1700s and early 1800s. The Zoological Society of London was founded in 1826, incorporated in 1829, and shortly thereafter started publishing the *Proceedings.* The Linnean Society of London began in 1788 and published its *Transactions* in 1789 and its *Zoological Journal* in 1824. The Scottish counterpart of the Linnean Society, the

Wernerian Society of Edinburgh, was founded in 1808. Although the Royal Society of London began at an earlier time, it was in 1820 that it reportedly threw off its social club aura and became a society of professional scientists. In 1823, the Plinian Society of Edinburgh, and in 1836 the Botanical Society of Edinburgh, were founded, and soon they started the *Magazine of Natural History.* The British Association for the Advancement of Science was founded in 1831 and the British Ornithological Union in 1858.

In France, the numerous provincial societies that had been established began to wane; during the French Revolution, a decree was issued in 1793 that eliminated all societies patented or endowed by the nation. The Paris Academy of Sciences was revived in 1795; in 1822, the Societe d'Histoire Naturelle de Paris was founded and in 1824 began publishing the *Annals des Sciences Naturelles*; and the French journal *Magasin de Zoologie* was founded in 1831.

In Germany and northern Europe, societies and academies were only beginning to emerge in the late 1700s. Most were associated with universities. One of the early societies was the Berlin Gessellschaft Naturforschender Freunde, first established as a private society in 1742. In 1812, the Akademie der Wissenschaften became aligned with the University of Berlin. In 1822, the Deutsche Naturforscher Versammlung was organized; in 1831, the Gesellshaft Deutscher Naturforscher und Artze. The *Archiv fur Naturgeschichte* began publication in 1835. The Society for Finnish Zoology and Botany, later called the Societas pro Fauna et Flora Fennica, was founded in 1821, and published *Fauna Fennica.* The Society of Naturalists of the Imperial University of Moscow initiated publishing in 1811 the *Memoires Moskovskoe Olshchestov Ispytatelei Prierody,* which was republished in Paris as *Memoires de la Societe Imperiale des Naturalistes de Moscou.*

During the 18th and 19th centuries, numerous factors contributed to the evolving study of mammals. The scientific exploration of many parts of the world and the growth of collections were early factors. The development of private collections that later became public or university museums was significant. The growth of numerous scientific societies and the proliferation of scientific journals encouraged the study of fauna and flora. Numerous persons during this time made an imprint on scientific thought and research, especially Carl Linnaeus, Georges Cuvier, Geoffroy Saint-Hillaire, Jean Baptiste de Lamarck, Alfred Russel Wallace, and Charles Darwin.

## *North American Mammalogy Before the 20th Century*

The fauna and flora of North America were of considerable interest to the naturalists, travellers, colonists, and other visitors who arrived there beginning in the late 15th century. Mammals they encountered were either eaten or had their fur or hides utilized for clothing, decoration, and other purposes. Thomas Hariot's *Briefe and True Report of the New Found Land of Virginia,* published in London in 1588, was the first scientific effort to describe the natural resources of any part of what is now the United States. Hariot accompanied Sir Walter Raleigh's 1585 expedition to North Carolina. His 44-page account mentioned deer, rabbits, opossum, raccoons, squirrels, bears, "lyon," wolves, and "Wolfish Dogges," although he did not personally observe all of these. Hariot's book underwent 17 editions before the 1620s.

Spanish observers, notably Gonzalo Fernandez de Oviedo y Valdez, whose *Historia general y natural de las Indias, Islas y Tierra-Firme del Mar Oceano* (a natural history of the West Indies) was published in 1526, had preceded Hariot in reporting on the mammals of the New World, but these earlier writers were active in the Spanish colonies of the Caribbean and in Central and South America from the beginning of the 16th century. The first person to give concentrated attention to the natural history of Canada was Samuel de Champlain. However, his studies at the end of the 16th century were principally concerned with plants.

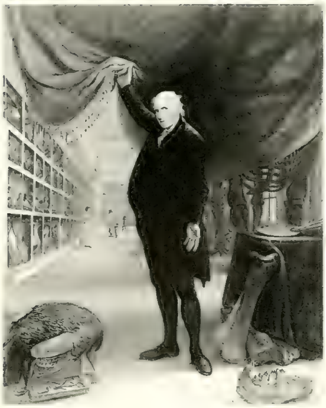
Other notable travelers and observers who mentioned the mammals of the English colonies in their writings before the 18th century included Ralph Hamor, author of *A True Discourse of the Present State of Virginia* (1615); Captain John Smith, in his *General Historie of Virginia, New England, and Summer Isles* (1624); William Wood, author of *New Englands Prospect* (1634), with a listing of New England mammals in verse; Thomas Morton's *New English Canaan* (1637); and John Josselyn's *New England's Rarities Discovered* (1672) and *An Account of Two Voyages to New England* (1674).

John Lawson, surveyor general of the North Carolina Colony from 1708 until his death at the hands of Indians in 1711, provided a full and detailed account of the mammals of that region. Pehr (or Peter) Kalm (1715–1779), a protegé of Linnaeus, traveled in the American colonies between 1748 and 1751 and was a principal contributor to his mentor's understanding of North American species for successive editions of the *Systema Naturae.* His *En Resa Til Norra America,* published in Stockholm between 1753 and 1761, was translated by John Reinhold Forster in 1770–1771. The narrative provided ethological information for some species, and he mentioned fossil elephants found in the Ohio country.

Undoubtedly the single most outstanding work to appear before the American Revolution was Mark Catesby's *The Natural History of Carolina, Florida, and the Bahama Islands,* which first appeared between 1729 and 1747. A later revision was completed by Catesby's friend George Edwards in 1754. Although a popular as opposed to a scientific account, Catesby's was the first attempt at a detailed description of the mammals he observed. His two volumes contained illustrations of only nine mammals, as compared with 113 birds, 33 amphibians, 46 fish, and 31 insects, most of them set against a background of plant life, but these combinations introduced for the first time many American ecological associations. Not until the early 19th century would there be any further notable advances in general descriptive mammalogy.

The Revolutionary and post-Revolutionary period offered some useful details about North American mammals in the works of such men as the Marquis Francois de Chastellux, a French army officer whose *Travels in North America* (1786) included a detailed account of opossum gestation written by a friend, and William Bartram's *Travels Through North and South Carolina, Georgia, . . .* (1791), which included a short descriptive narrative of the mammals encountered on his travels. When Buffon published his account of New World fauna in 1769, detailing principally mammals, he was clearly unimpressed by his subject (Peden, 1955). He implied that American species were "shrivelled and diminished" both in size and variety because of excessive moisture and less heat than was to be found in Europe. In Thomas Jefferson's *Notes on the State of Virginia,* written during the American Revolution and later revised, the future president went to considerable pains to amass statistical data with which he effectively demolished the French savant's views. Buffon appeared to be convinced by the weight of Jefferson's evidence, and promised that suitable corrections would be published in the next volume of his Histoire Naturelle. However, he died before this could be accomplished.

Philadelphia was the first important center of research in natural history in the United States, and it maintained its dominance in the field from the late 1790s until the late 1830s. There were a number of reasons for this. Curious naturalists in the Quaker city had closer ties with their English and French colleagues than did naturalists in any other part of the country. Here, the American Philosophical Society, the oldest scholarly

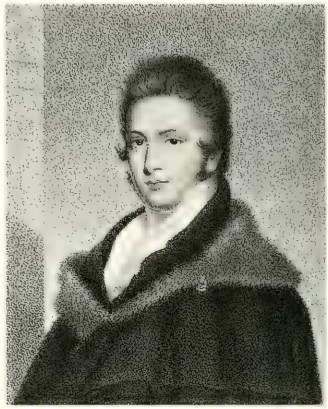


Charles Willson Peale*
(1741–1826)

Courtesy of the Pennsylvania Academy of Fine Arts, Philadelphia. Gift of Mrs. Sarah Harrison (The Joseph Harrison, Jr. Collection)

John D. Godman
(1794–1830)

Courtesy of the Library, College of Physicians of Philadelphia



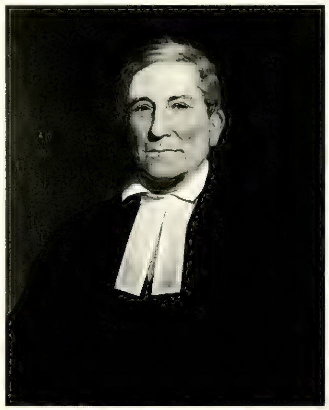
Richard Harlan
(1796–1843)

Courtesy of the Library, College of Physicians of Philadelphia

Elliott Coues, M.D.
(1842–1899)

Spencer F. Baird
(1823–1887)

Courtesy of the Smithsonian Institution, Washington, D.C.



Rev. John Bachman
(1790–1874)

Courtesy of the Charleston Museum, Charleston, N.C.

FIG. 1.—Eminent early North American mammalogists.

* The self-portrait of 1822, showing his museum on the second floor of Independence Hall, Philadelphia. A mastodon skeleton exhumed and mounted by Peale stands to the right, partially obscured by the curtain.

organization in America, had been founded in 1743. Here too, other organizations, including Peale's Museum, begun in 1784, the Academy of Natural Sciences, founded in 1812, and several medical colleges were in operation. Philadelphia also led the rest of the nation both in the number of libraries and in the numbers of books they contained. At least 40% of all scientific periodicals published in the United States were published in Philadelphia by 1832, at a time when none was being published in New York City.

Art and medicine were the two major avenues through which Americans approached the study of mammals in the 19th century. The Maryland-born Charles Willson Peale (1741–1826) was a largely self-taught artist whose interest in natural history began to manifest itself when he was in his mid-40s (Fig. 1). The museum he founded in his Philadelphia home in 1784 was not the first in the country, but was the first successful one to be started north of the Mason and Dixon Line. It survived for more than 60 years (Sellers, 1980). The Charleston Museum in South Carolina had begun operations in 1773, and still operates today, but was slower to develop its natural history collections. Peale's was the focal point for those working on mammals in Philadelphia. Most books on the subject published from about 1815 until the early 1840s were largely based on specimens examined there. Peale's Museum operated for many years on the top floor of Independence Hall, and he was probably the first to supply painted backgrounds suggestive of habitat for the cases in which many of his specimens were mounted. The natural history specimens in Peale's Museum were exhibited as a unit by Charles' sons and grandsons until forced to sell, with most going to P. T. Barnum and some to the Boston Museum. Peale also attempted a series of public lectures on what was then (1799–1800) known concerning the mammals and birds of the world. Peale's Museum housed specimens brought back by the leaders of the Lewis and Clark Expedition of 1805–1807, the first federally-sponsored scientific expedition. It cost the government about $2,500, and produced 39 new species and subspecies of mammals. Most of the specimens were later lost in a fire, but a few survive to this day.

The first attempt at a comprehensive compilation of mammals by an American was George Ord's "North American Zoology," which appeared anonymously in the third edition of William Guthries' *A New Geographical, Historical, and Commercial Grammar, and Present State of the Several Kingdoms of the World* (1815). Of the 167 species listed, Samuel Rhoads determined in 1894 that "fifteen are undeterminable, twenty-four are Mexican and South American species, eighteen are synonyms of other names on the list and ten are old world forms having no specific affinities with those of America" (Baird, 1859). Nevertheless, Ord's 24-page contribution was the first effort by an American to place American species in some scientific arrangement.

Two Philadelphia physician-naturalists (Fig. 1), Richard Harlan (1796–1843) and John Godman (1794–1830), produced notable works focusing on American mammals in the 1820s. Harlan's *Fauna Americana* (1825) was largely a compilation, although he added 10 new American species and discussed the role of tooth structure in speciation. Godman's *American Natural History: Part I: Mastology,* appeared in three volumes (1826–1828), and was the first essentially original work on mammals completed by an American. The illustrations were based on mounted specimens in Peale's Museum. The first part of the English explorer-naturalist Sir John Richardson's *Fauna Boreali Americana* dealing with mammals was published in London in 1829. Richardson focused on Canadian forms, some of them native to the United States, and his descriptions were still considered authoritative at the end of the 19th century.

With the creation of the various state geological and natural history surveys in the 1830s, and a rapid increase in new information, a greater degree of specialization entered into American natural science. A number of studies centered on particular states were published, such as Ebenezer Emmons' *Report on the Quadrupeds of Massachusetts* (1840) and James De Kay's five-volume *Zoology of New York* (1842–1844), which included a volume on mammals. Such publications helped expand the horizons of Americans interested in their native mammalian fauna.

The famous collaboration of John James Audubon (1785–1851) and his colleague, the New York-born Charleston-Lutheran clergyman John Bachman (1790–1874), resulted in the brilliant three-volume *Quadrupeds of North America* (1845–1854) (Fig. 1). Bachman supplied much of the scientific information in this work, while Audubon (until his mind and eyes failed him in 1846) and his sons Victor Gifford (1809–1860) and John Woodhouse Audubon (1812–1862) completed the excellent mammal paintings. Audubon and Bachman tried to deal with all known species from the Tropic of Cancer north to Canada and Alaska. The work was intended for the widest appeal, necessitated in some measure by the costs of producing this very expensive set of books. As a consequence, there was no particular sequence of orders, families, and genera, although this weakened the finished product from a scientific standpoint. Today, the 155 forms described in the Imperial Folios of 1845–1848 have been reduced to about 118.

In June 1840, the 17-year-old Spencer Fullerton Baird (1823–1887) (Fig. 1), on the point of graduating from Dickinson College, Pennsylvania, diffidently wrote Audubon for help in identifying a flycatcher, which proved to be a new species. Audubon was kind, agreed that the bird was probably undescribed, and asked Baird's help in capturing small mammals. Baird gave up the study of medicine, taught natural history at Dickinson, and in 1850, was named the first Assistant Secretary of the new (1846) Smithsonian Institution at the comparatively young age of 27. Baird, a seminal figure in American zoology, brilliantly orchestrated the collecting talents of eager but unpaid civilian naturalists who accompanied the field parties exploring railroad surveys sent out by Secretary of War Jefferson Davis in the mid 1850s. From the materials thus derived, Baird wrote and published his famous report on the mammals of the expeditions in 1857, which was commercially reprinted 2 years later as *Mammals of North America.* This substantial volume listed 52 new species and 18 previously described forms not mentioned by Audubon and Bachman. Baird also listed 37 other species and varieties he had not personally seen or identified, together with 16 species of squirrels and skunks, which he thought might be located in the United States. This totaled 273 forms, although Baird was careful to state that some might prove invalid. Baird's work was a model of accuracy for its time, with emphasis placed upon morphological detail and geographical range.

As Baird had been encouraged by Audubon and Bachman, so he in turn provided all possible support to his contemporaries and to the next generation of individuals just beginning their professional careers. A wise and patient official, he doled out the limited practical assistance at his command and carefully gathered many of the specimens and field observations that form the basis of the excellent government collections of today (Lindsay, 1993; Rivinus and Youssef, 1992). Among his protegés may be mentioned Elliott Coues (Fig. 1), Joseph Leidy, Robert Kennicott, Robert Ridgway, and C. Hart Merriam.

The last several decades of the 19th century coincided with a period of ferment in American intellectual life and in American natural science. A few American and Canadian colleges and universities began to offer modern biological training after the American Civil War. At the same time, the federal government became increasingly concerned with scientific research and exploration. The creation of a federal Department of Agriculture in 1862 (which achieved cabinet status in 1889) provided the needed home for a number of research components. These included an Entomological Commission, established in 1877, and the antecedents of work in animal industry, begun in 1879. These and several other agencies separately organized, including the Fish Commission in 1871 (placed in the Commerce Department in 1903) and the U.S. Geological Survey in 1878 (placed in Interior), all helped to create a large group of professions interested in various kinds of scientific activity in Washington (Dupree, 1957). The capitol city rapidly became an important center of scientific inquiry. Indeed, Congress gave some consideration to the establishment of a Department of Science in the early 1880s. One authority has pointed out that the 1,812 members of the Agriculture Department employed in scientific research in the year 1913 was larger than the number of American scientists known to be active in the first 5 decades of the 19th century.

A number of professional organizations in zoology began making their appearance in the 1880s. The American Society of Naturalists and the American Ornithologists' Union were founded in 1883, the Entomological Society of America in 1889, and the American Morphological Society, and later the American Society of Zoologists, in 1890. These organizations and others that followed helped bring about a rise in scientific standards. The articles and reviews appearing in their journals made possible the dissemination of modern scientific information.

Mammalian paleontology, in which Harlan and Godman had been early American pioneers, prospered with the work of Joseph Leidy (1823–1891), the first of whose two most famous works was published under the aegis of the Smithsonian. This was his *Ancient Fauna of Nebraska* (1854). The other, *On the Extinct Mammalia of Dakota and Nebraska,* was published by the Academy of Natural Sciences of Philadelphia in 1869. Other leading paleontologists who made contributions to the study of fossil mammals included Othniel Charles Marsh (1831–1899), including his studies on fossil horses; Edward Drinker Cope (1840–1897), including work with mammals of the Paleocene, and Henry Fairfield Osborn (1857–1935), whose *Age of Mammals in Europe, Asia, and North America* (1910) and later works on the Equidae, on titanotheres, and on the Proboscidea were important additions to the literature.

A good number of late 19th century leaders in ornithology were simultaneously active in studying mammals, both in the field and in the laboratory. They included Baird at the Smithsonian and Joel Asaph Allen (1838–1921) at Harvard, who moved in 1885 to the American Museum of Natural History in New York City as its first curator of ornithology and mammalogy. Two protegés of Baird also began making substantial contributions to mammalogy in the 1860s and 1880s, respectively. One was Elliott Coues (1842–1899), an Army physician involved with several of the federal geographical and geological surveys of the west, and later a free-lance naturalist. The other was Clinton Hart Merriam (1855–1942), trained as a medical doctor (Columbia University, 1879), who wrote *Mammals of the Adirondacks* (1882 and 1884) at an early age.

In 1888, the Federal government established an agency in the Department of Agriculture called the "Division of Economic Ornithology and Mammalogy," under the direction of C. Hart Merriam. This division, later to evolve into the Bureau of Biological Survey, developed in a most indirect way. The American Ornithologists' Union in 1883 created a committee concerned with the migration and geographical distribution of birds. Merriam was the chairman, and his group was so successful at gathering data that they soon had more on their hands than they could handle. Into this emergency stepped Spencer F. Baird and Senator Warner Miller of New York, an old Merriam family friend. In 1884, they pushed a bill through Congress calling for a $5,000 subvention for the establishment of an Office of Economic Ornithology to be placed within the Entomological Commission at the Agriculture Department. As head of this division, Merriam invited Albert Kenrick Fisher (1856–1948), a friend and fellow alumnus of the College of Physicians and Surgeons in New York, to join the fledgling agency as his assistant. They began operations in July, 1885 (Cameron, 1929; Sterling, 1977, 1989). Their task was to research "the interrelation of birds and agriculture [and] an investigation of the food, habits and migration of birds in relation to plants, and publishing report[s] thereon . . . . " The intent of this operation was to benefit American agriculture by collecting data and developing information that farmers could use in fending off the depredations of harmful species. The relationship between birds and insects was to be an important element in this work. Within a year, Merriam's responsibilities had been expanded to include mammals and birds as they related to agriculture, horticulture, and forestry.

By 1886, Merriam's agency had achieved emancipation from the parent Entomological Commission; within 10 years, it had been redesignated the Division of Biological Survey, and by 1906, it had become the Bureau of Biological Survey, the name it would retain until 1940. In that year, it was combined with the old Fish Commission, then in the Commerce Department, to form the U.S. Fish and Wildlife Service, which was placed in the Interior Department. The United States National Museum was established in 1879 as an adjunct of the Smithsonian. It is reported that the National Museum started back-handedly when an unauthorized sign "National Museum of the United States" appeared in the hall with the collections of the Smithsonian.

## *The Early History of the American Society of Mammalogists*

The United States Biological Survey flourished under the direction of C. Hart Merriam (Fig. 2). Merriam's personal agenda involved nothing less than a continent-wide biogeographical reconnaissance, and Congress officially incorporated this in its authorization of his agency's expenditures in 1894. Merriam assembled an impressive cadre of young workers in Washington, D.C. Some of these came college-trained, but many had only a high school education. Merriam was critical of the educational philosophies of some American universities that stressed laboratory work to the exclusion of field work. He preferred to give his men on-the-job training, using field methods he had developed (Cameron, 1929; Sterling, 1977, 1989). Included in those associated in the early history of the Biological survey were Vernon Bailey, Clarence Birdseye, A. K. Fisher, Frederick Funston, Edward A. Goldman, Ned Hollister, Arthur H. Howell, Hartley H. T. Jackson, John Alden Loring, Marcus Ward Lyon, Jr., Waldo Lee McAtee, Gerrit S. Miller, Jr., Edward M. Nelson, Wilfred H. Osgood, T. S. Palmer, Edward Preble, Walter P. Taylor, W. E. Clyde Todd, and Stanley P. Young.

Another event that gave great impetus to the study of mammals at this time was the invention and adoption of the cyclone mouse trap in the late 1880s. This trap and its various modifications, including the Museum Special and live traps, opened up new vistas in the study of mammals.

In the early 1900s an increasing number of persons outside of the Washington, D.C., area were publishing or lecturing about mammals. Some of these were associated with universities and others with large museums. Included in this group were Joel A. Allen, Glover M. Allen, Rudolph Anderson, Joseph Grinnell, W. D. Matthew, Ernest Thompson Seton, and Alfred H. Wright.

Many important events mentioned above led to the formation of the American Society of Mammalogists: 1) the establishment and objectives of the U.S. Bureau of Biological Survey with its cadre of enthusiastic, eager mammalogists; 2) the formation and growth of the U.S. National Museum with curators in mammalogy, including Elliott Coues, Gerrit S. Miller, Jr.,

FIG. 2.—Bureau of Biological Survey members working at the U.S. National Museum at the turn of the century. From left to right: Vernon O. Bailey, Wilfred H. Osgood, Edward W. Nelson, Albert K. Fisher. Photograph from the files of the U.S. Fish and Wildlife Service.

and Frederick True; 3) the formation and growth of successful scientific societies for the other "ologies"; 4) the use of the museum-special trap and the associated increase in numbers of specimens of mammals in collections with uniform, standard data; and 5) the increased interest in teaching mammalogy at the college level.

One young mammalogist working at the Bureau of Biological Survey had often thought about a society of persons interested in mammals. This was Hartley H. T. Jackson (Fig. 3). In 1902, when a junior at Milton College, Wisconsin, young Jackson discussed such a society with his admired mentor, Professor Ludwig Kumlien, and his boyhood friend, Ned Hollister. Although the others were somewhat skeptical, Jackson was not. In 1910, Jackson who by then was working for the Bureau of Biological Survey in Washington, D.C., attended the annual meeting of the American Ornithologists' Union held in that city. This meeting enforced his earlier views and "I became more thoroughly convinced that we could make a success of a mammal society" (H. H. T. Jackson letter, 1968, in archives of ASM). For the next few years, Jackson "muddled along with ideas, worked on a possible constitution or bylaws, figured on possible sources of members" (*ibid*). He discussed such an organization with Edward Goldman when in the field on Horseshoe Cienega, Arizona, in 1915, and again with Goldman and Walter Taylor on the Nantan Plateau, Arizona, in 1916. Walter Taylor was enthusiastic about such an organization.

The Bureau of Biological Survey was under the leadership of Edward W. Nelson in 1918, Merriam having stepped down in 1910. The Survey, by custom, held staff meetings periodically, but they gradually had become disorganized, according to Jackson.

FIG. 3.—Hartley Harrad Thompson Jackson, the one person whose dream, dedication, and perseverance contributed the most to the successful origin of the American Society of Mammalogists.

To rectify this situation, a committee of three—A. K. Fisher, Vernon Bailey, and Walter Taylor—was appointed to plan such meetings. Among other things, this committee recommended that the scientific staff hold evening meetings monthly at the home of different staff members.

At the third such meeting, held at Vernon Bailey's home on 5 December 1918, Jackson wrote (*ibid*) that he "thought there might not be too much to talk about at the December meeting, and suggested to Mr. Bailey [who would preside] ahead of the meeting that it might be a good time to bring up the matter of a mammal society." Dr. Jackson continued to write that "near the close of a busy session the question as to the advisability of launching a new organization for the promotion of mammal study was brought up for discussion by Chairman Bailey. I had already appraised Bailey of some of my ideas such as that [A. H.] Howell, [Ned] Hollister, [E. A.] Preble, and [W. P.] Taylor should be on the committee, and that it would be advisable to have five other representatives, one from each of five other institutions outside of Washington. I had already done considerable work such as outlining a constitution or by-laws, searching lists for possible members, etc." At this meeting it was moved that a committee be appointed to canvas the situation, and this committee consisted of Dr. Jackson as chairman and the other recommended members. It was further suggested that a report be made at the next meeting on working plans for the proposed organization.

Eight days after the committee was appointed, on 13 December 1918, the five Washington members met, discussed a constitution for the proposed society, suggested a first regular meeting in the spring of 1919, and added these non-Washingtonians to the committee: G. M. Allen, J. A. Allen, J. Grinnell, W. H. Osgood, and later, Witmer Stone. On 21 December the Washington-members of the committee met again and, quoting from Walter Taylor's notes (in ASM archives), "decided upon the following recommendations: (1) That there be organized a society for mammal study to be known as the American Society of Mammalogists. (2) That the constitution attached hereto be proposed as a basis for further consideration. (3) That the report of the Committee on Organization appointed by the Chairman of the meeting of the Scientific Staff of the Biological Survey on Dec. 5, 1918, be received and the Committee discharged, it being understood that the Committee would be immediately reorganized as a permanent Committee on Organization independent of the Survey. (4) That plans be made for holding a formal organization meeting of the new Society if possible in March, 1919."

At the next staff meeting at the home of Walter Henderson, 9 January 1919, the report of the committee was approved, the committee was discharged, and Jackson as chairman appointed a new committee consisting of the same ten persons. Also, the original notice of "A proposed American

## A PROPOSED AMERICAN SOCIETY OF MAMMALOGISTS

You are cordially invited to join in a movement to organize a society for the promotion of the interests and study of mammalogy. It is intended that the society shall devote itself to the subject in a broad way, including studies of habits, life histories, evolution, ecology, and other phases. Plans call for the publication of a journal in which both popular and technical matter shall be presented, for holding meetings, both general and sectional, aiding research, and engaging in such other activities as may be deemed expedient. It is hoped that you will actively participate, and, if possible, attend the organization meeting which will be held in the New National Museum, Washington, D. C., April 3 and 4, 1919, sessions commencing at 10.00 A. M. and 2.00 P. M. No program of papers has been planned for this meeting.

Prevalent opinion indicates that annual dues for members will be about three dollars.

Kindly bring this notice to the attention of others who may be interested in the movement.

Respectfully submitted,

Committee on Organization

HARTLEY H. T. JACKSON, Chairman,
U. S. Biological Survey.
WALTER P. TAYLOR, Secretary,
U. S. Biological Survey.
GLOVER M. ALLEN,
Boston Society of Natural History.
J. A. ALLEN,
American Museum of Natural History.
JOSEPH GRINNELL,
University of California.
N. HOLLISTER,
National Zoological Park.
ARTHUR H. HOWELL,
U. S. Biological Survey.
WILFRED H. OSGOOD,
Field Museum of Natural History.
EDWARD A. PREBLE,
U. S. Biological Survey.
WITMER STONE,
Academy of Natural Sciences of Philadelphia.

The following blank properly filled and sent to the Chairman or Secretary of the Committee, Biological Survey, U. S. Department of Agriculture, Washington, D. C., will constitute application for charter membership.

I desire to become a charter member of the American Society of Mammalogists. I shall.................attend the organization meeting.

Name (in full)..............................................................

Address ..............................................................

..............................................................

..............................................................

..............................................................

...............................1919.

FIG. 4.—This announcement of the proposed Society was sent to prospective members in the United States and other countries.

A PROPOSED AMERICAN SOCIETY OF MAMMALOGISTS

A COMMITTEE of representative American mammalogists, including men from different parts of the country in its membership, has recently been at work on plans to organize a society for the promotion of interest in the study of mammalogy. It is intended that the society shall devote itself to the subject in a broad way, including investigations of habits, life histories, evolution and ecology. The plans call for the publication of a journal in which both popular and technical matter will be presented, for holding meetings both general and sectional, aiding research, and engaging in such other activities as may be deemed expedient. It is hoped to secure the active participation of all interested. The organization meeting will be held at the New National Museum, Washington, D. C., April 3 and 4, 1919, sessions commencing at 10:00 A.M. and 2:00 P.M. No program of papers has been planned for this meeting. The organization committee includes the following: Hartley H. T. Jackson, Chairman, U. S. Biological Survey; Walter P. Taylor, Secretary, U. S. Biological Survey; Glover M. Allen, Boston Society of Natural History; J. A. Allen, American Museum of Natural History; Joseph Grinnell, University of California; N. Hollister, National Zoological Park; Arthur H. Howell, U. S. Biological Survey; Wilfred H. Osgood, Field Museum of Natural History; Edward A. Preble, U. S. Biological Survey; Witmer Stone, Academy of Natural Sciences of Philadelphia. Further information will be furnished by either the chairman or the secretary, to whom applications for charter membership should be transmitted.

FIG. 5.—Account of the proposed American Society of Mammalogists as it appeared six weeks before the first meeting in *Science,* n.s., XLIX, 21 February 1919.

Society of Mammalogists" was printed and mailed in early February, 1919, to prospective members (Fig. 4). A notice of the forthcoming organizational meeting was published in *Science,* n.s., 49:189, 21 February 1919 (Fig. 5).

With an official committee set up for the organization of a society of mammalogists, five meetings were held in late January to March, 1919. The out-of-town members were usually unable to attend. Jackson was busily drawing up a list of prospective members, gathering funds to start such an organization, and drafting the by-laws. These, Jackson said, were modeled after the constitution and by-laws of the A. O. U., American Society of Naturalists, Wisconsin Natural History Society, Wisconsin Academy of Sciences, and the Biological Society of Washington. Jackson learned that under the laws of the District of Columbia, where the Society was to be incorporated, the phraseology of "bylaws and rules, had to be used, not constitution." On 23 January 1919, a most important meeting of the "Committee on the Organization of Mammal Society" was held in Room 61 of the "New Museum," Washington, D.C. Four typescript pages of this meeting are in the ASM archives. Jackson chaired the meeting with other committee members consisting of A. H. Howell, Ned Hollister, and Walter Taylor. Other "resident mammalogists" who were present included J. W. Gidley, E. W. Nelson, H. H. Sheldon, Charles Sheldon, C. Birdseye, William Palmer, T. S. Palmer, Vernon Bailey, C. Hart Merriam, George Field, W. C. Henderson, W. D. Bell, and M. W. Lyon, Jr. Most of the meeting was devoted to a discussion of the by-laws. Merriam "advocated simplicity in the constitution as the best way to promote effective business administration and permanence." He also opposed "the division of the membership into different classes and favoring one general class of members, with possibly an honorary class composed of foreign members." Thereby a section on "Fellows" was deleted by committee action, but a section on Honorary Members was included. The suggestion of meeting with other societies was discussed but remained undecided. Persons in the Washington area were encouraged to make voluntary contributions of $2.00 for preliminary operations, and Jackson said the response was good. A total of $52 had been collected by the time of the first meeting, and of this $47.31 had been spent for 1,000 circulars and stamped envelopes, 500 printed membership cards, and 100 printed programs. The first annual meeting started with a balance of $4.69.

The organizational meeting was held on 3 and 4 April 1919 at the U.S. National Museum (Fig. 6). Eight members of the original organizing committee were elected to top positions in the new society. Although many persons were anxious for J. A. Allen to be the first president, he declined because of failing health. C. Hart Merriam was elected President, E. W. Nelson and Wilfred H. Osgood Vice-presidents, H. H. T. Jackson Corresponding Secretary, W. P. Taylor Treasurer, H. H. Lane Recording Secretary, and Joel A. Allen Honorary Member. Ten members were elected to the Council (now Board of Directors), five for a 1-year term—R. M. Anderson, M. W. Lyon, Jr., W. D. Matthew, T. S. Palmer, E. A. Preble—and five for a 2-year term—G. M. Allen, J. Grinnell, J. C. Merriam, G. S. Miller, Jr., and W. Stone. Every person who joined before or during the first meeting or the first year was regarded as a charter member and received a card signed by Jackson and Merriam. About 60 persons attended the meeting.

At the first meeting, often referred to as the Organizational Meeting, there were three sessions of the Council (Fig. 7). These were held at 8 p.m., April 3; 9 a.m., April 4; and 11:15 a.m., April 4. The original By-laws and Rules had a "Council or Board of Managers" (*Journal of Mammalogy,* 1:50, 1919). Before the society was incorporated in the District of Columbia, this was changed to Directors (*Journal of Mammalogy,* 1, inside cover of No. 4, 1920).

At the first session of the organizational meeting, Marcus W. Lyon was elected temporary chairman, H. H. Lane, temporary secretary. Two hundred and forty persons were accepted as charter members. The original list is on file in the ASM archives. At the afternoon session the officers and "councillors" were elected. Wilfred H. Osgood gave an "illustrated lecture on North American Mammals" at the evening session (1919 minutes, ASM archives).

The business that transpired at the third (Friday morning) session can be summarized thus: 1) J. A. Allen unanimously elected Honorary Member; 2) persons qualified for charter membership if they enroll before the next annual meeting; 3) incorporation of the Society under the laws of the District of Columbia; 4) plans to issue a quarterly publication known as the *Journal of Mammalogy*; 5) appointed a Committee on Membership; 6) J. C. Merriam was elected "Councillor" to replace Ned Hollister, who was appointed Editor of the *Journal*; 7) established a Committee on the Study of Game Mammals; 8) next annual meeting in New York City.

There was "quite a difference of opinion regarding the name of the Journal. Some favor a short name, like 'Bison', 'Puma', or something of that sort. Others like 'Bairdia', but I think that most of us here, at least, agree with you that 'American Journal of Mammalogy' is the most appropriate name suggested to date. Or, more simply 'Journal of Mammalogy' [letter from Walter P. Taylor to Glover Allen on 11 March 1919]." On 11 July 1919, Williams and Wilkins Company of Baltimore, Maryland, solicited the new society through President C. Hart Merriam and Glover Allen to print the *Journal of Mammalogy.* The report of the "Committee on Publications," chaired by Ned Hollister, pointed out that Williams and Wilkins was the only company to submit a bid.

By January 1920, there were 11 life members with their membership fees invested in United States Liberty and Victory bonds. By the end of the second annual meeting, there were 441 members (Fig. 8), of which 25 resided outside of the United States and Canada. Income for this period amounted to $3,003.58; expenses for printing and mailing the *Journal* and all other expenses were $748.44; monies invested in bonds and in the bank, $2,255.14. A memorandum of

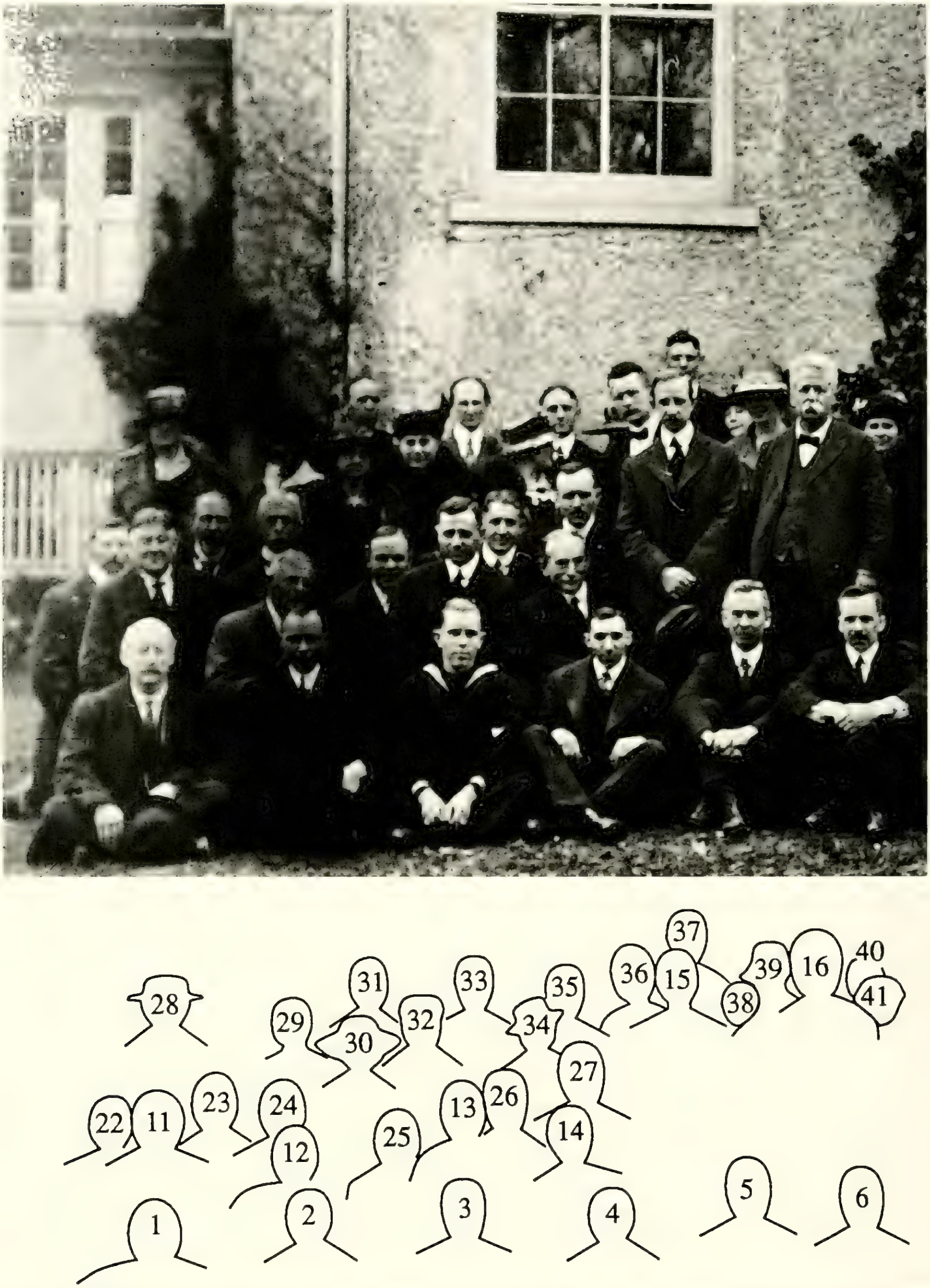



FIG. 6.—This is the only known photograph of the first (organizational) meeting of the American Society of Mammalogists, 4 April 1919, taken at the Administration Building, National Zoological Park, Washington, D.C. 1. C. H. M. Barrett; 2. Walter P. Taylor; 3. Charles M. Hoy; 4. Arthur J. Poole; 5. Vernon Bailey; 6. Ned Hollister; 7. Marcus W. Lyon, Jr.; 8. George A. Lawyer; 9. Frank M. Jarvis; 10. H. H. T. Jackson; 11. A. K. Fisher; 12. Leo D. Miner; 13. W. B. Bell; 14. Witmer Stone; 15. Wilfred H. Osgood; 16. C. Hart Merriam; 17. J. W. Gidley; 18. W. H. Cheesman; 19. James S. Gutsell; 20. C. C. Adams; 21. G. W. Field; 22. Ned Dearborn; 23. T. S. Palmer; 24. Charles Batchelder; 25. Charles Sheldon; 26. E. A. Preble; 27. Rudolph M. Anderson; 28. Mrs. Witmer Stone;


29. Mrs. T. S. Palmer; 30. Mrs. E. A. Preble; 31. A. B. Baker; 32. Mrs. C. H. Merriam; 33. Harry Oberholser; 34. Mrs. F. M. Bailey; 35. B. H. Swales; 36. Waldo L. Schmitt; 37. Alexander Wetmore; 38. Mrs. Leo D. Miner; 39. Mrs. Waldo Schmitt; 40. Miss Catherine Baird; 41. Miss May T. Cooke; 42. Mrs. G. W. Gidley; 43. J. W. Scollick; 44. Jonathan Dwight; 45. Mrs. Ned Hollister; 46. Mrs. Jane Elliott; 47. John P. Buwalda; 48. Leland C. Wyman; 49. H. W. Henshaw; 50. Warren Craven; 51. Mrs. Marcus W. Lyon; 52. Remington Kellogg; 53. Viola S. Schantz; 54. Mrs. Anna Jackson; 55. E. W. Nelson; 56. H. H. Lane; 57. W. C. Henderson.

# American Society of Mammalogists

## ORGANIZATION MEETING

## NEW NATIONAL MUSEUM
WASHINGTON, D. C.

## APRIL 3 AND 4, 1919

ALL BUSINESS SESSIONS WILL BE HELD IN ROOMS 42 AND 43

### Program

April 3. Business session . . . . . 10:00 A. M.

Luncheon for members . . . . 1:00 P. M.

Members are asked to assemble at 12.45 P. M. at B Street or North entrance of the Museum and proceed in a body to Maynard Cafe, formerly Tea Cup Inn, 611 12th Street, N. W.

Business session . . . . . 2:00 P. M.

Informal program and conversazione . 7:30 P. M.

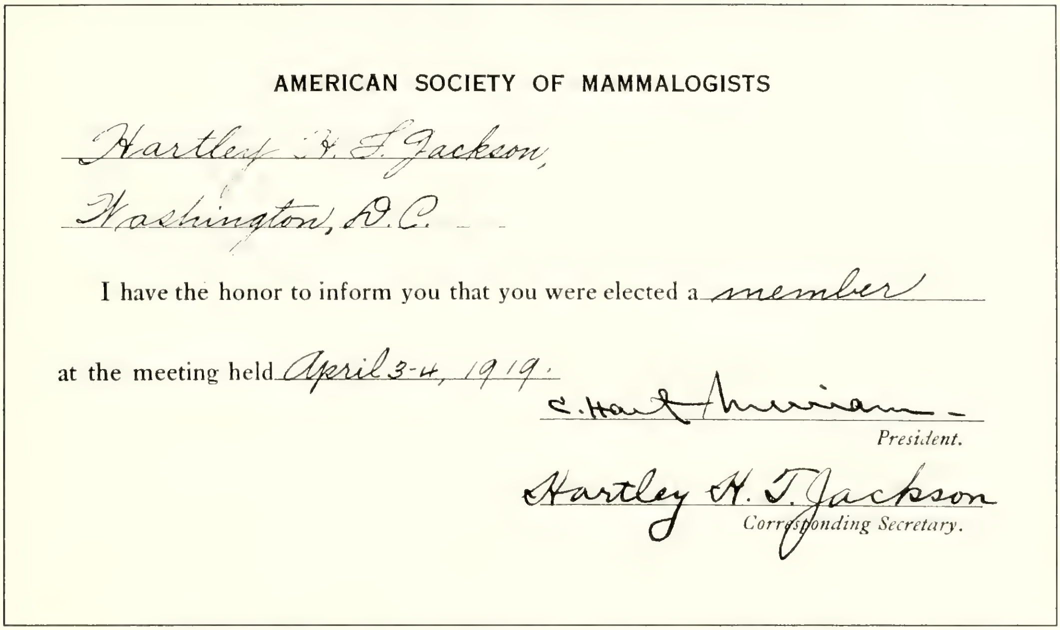
Auditorium, New National Museum.

April 4. Business session . . . . . 10:00 A. M.

Luncheon for members and their wives 12:30 P. M.

National Zoological Park, Administration Building. Members are asked to assemble at the B Street entrance of the Museum at 12:00 o'clock sharp. Following the luncheon there will be a tour of National Zoological Park, under direction of N. Hollister, Superintendent.

FIG. 7.—Program of the first meeting of the American Society of Mammalogists. Note that this was called the "organization" meeting.



AMERICAN SOCIETY OF MAMMALOGISTS

Hartley H. T. Jackson,

Washington, D.C.

I have the honor to inform you that you were elected a member

at the meeting held April 3-4, 1919.

C. Hart Merriam

President.

Hartley H. T. Jackson

Corresponding Secretary.

FIG. 8.—Original membership card of Hartley H. T. Jackson. Cards so dated represented charter membership. The first four lines are in the hand-writing of Anna Marcia Jackson.

H. H. T. Jackson's (ASM archives) of 3 May 1920, states that "After many distressing circumstances the Journal of Mammalogy is started. . . . A written agreement was made with Williams and Wilkins Company, Baltimore, to print the first volume. . . . It seems to the corresponding secretary [Jackson] that an endowment—a publication fund—is essential if the Society is to live up to standards worthy of its membership. The income from such a fund would nourish the Journal through its precarious infancy, and could later be utilized for publishing monographs or for whatever worthy cause the Society might deem desirable."

On 3 May 1921, Jackson re-emphasized this request in the Second Annual Report of the Corresponding Secretary. He wrote: "The Society can take pride in having established a creditable magazine without a single financial donation toward its publication or general expenses. This has been done at a critical period in industrial history and at a time when printing costs were almost prohibitive. It has been possible, however, largely through the Charter Members, who willingly paid membership dues for the year 1919, yet received only one number of the Journal during that year. With a normal increase in the number of members and subscribers we can hope to continue to publish under present conditions between 200 and 250 pages, and 10 halftones a year. The actual costs of printing and distributing our present edition averages a trifle less than $8.00 per page. Indications are that we shall soon be receiving first class manuscript in quantity sufficient to publish 400 pages a year. Is the Editor to be placed in a position where it will be necessary for him to refuse valuable contributions? It would seem that the Society could ill afford to sanction such a predicament. Diffusion of knowledge is as essential as its creation. Immense endowments are given to be devoted to research, investigations, and explorations. Comparatively small sums set aside as permanent publication funds would make available some of the results now buried in manuscripts. It is, therefore, essential to the best interests of the Society, the Journal, and everybody concerned, that definite and positive action be immediately taken to raise a Permanent Publication Fund. Any amount raised would actually be worth double the amount to the Journal because of the assured increase in the number of subscriptions which would follow the improvement in the Journal."

The Board of Directors, on 17 May 1922, heard and approved the report of the Committee on the Allen Memorial, chaired by Harold E. Anthony. This report recommended that: 1) a permanent fund be created to be known as the J. A. Allen Memorial Fund; 2) this fund be invested and the income used for the publication of such memorial numbers of the *Journal of Mammalogy* or other publications dedicated to the memory of Dr. J. A. Allen; 3) a committee be appointed to raise such funds; 4) a minimum of $10,000 be raised in 2 years. By the end of 1924, the Fund had acquired $7,606. At the 1925 meeting, John Rowley, noted taxidermist, offered to apply all royalties from his book towards this Fund until $10,000 had been secured from all sources. By 10 July 1928, the goal had been reached. Also at the meeting in 1922, it was proposed that the by-laws be amended to provide for a board of three trustees. These trustees continue to manage the society's reserve fund.

The new society received considerable early publicity. *Science* in its 21 February 1919 issue carried a report of "A Proposed American Society of Mammalogists" and a follow-up account on 18 April 1919, of the organizational meeting, with elected officers and "councilors," committees, and reference to a forthcoming *Journal of Mammalogy.*

Concerning the Fourth Annual Meeting, *Science* reported in its 16 May 1922 issue that "among the many interesting papers that were given before the mammalogists was the 'Symposium on the Anatomy and Relationships of the Gorilla.' At this session the attendance was probably greater than at any of the others, and representatives of the press were present to make the most of a subject in which the public is at present so keenly interested [the infamous Scopes trial]."

Of the Sixth Annual Meeting of the Society, the *Boston Evening Transcript* had an interesting story. It began: "Mammalogists take their electioneering seriously. Twenty-five of them, all members of the American Society of Mammalogists, spent an hour and a half at the Harvard Museum in Cambridge this morning, making up a slate of six officers and as many directors. The hitch came in choosing the directors. On the first ballot the names of twenty-four candidates appeared, one fewer than the number of men in the room. Eight ballots were taken before the choice was made."

At the beginning of the 20th century, there was a marked increase in the study of mammals in the United States. Museums and universities were training young people in mammalogy, both in the laboratory and field. Sooner or later there surely would be an organization of such scientists. However, this would not have come about as rapidly, effectively, and successfully without the dreams and determination of Hartley Jackson and a group of dedicated fellow workers in Washington, D.C. Their work toward the formation of a new society is attested to in a small part by the fact that between 5 December 1918 and 13 March 1919, Jackson and his colleagues held a recorded nine organizational meetings, and undoubtedly many other private discussions. Once the ASM was started, many persons continued unselfishly to devote much time to the operations of the society. For the first 14 years, Henry H. Lane of the University of Kansas served as Recording Secretary. For 23 years, Viola S. Schantz served as Treasurer. Anna M. Jackson, Hartley's wife, did most of the record-keeping and typing during the formative period and during the years that Hartley served as Corresponding Secretary. The work of these and many others provided a sound basis for the rapidly growing society.

The foregoing paragraphs have briefly reviewed the events and circumstances that led to the formation of a scientific society of mammalogists in the Americas in the early 1900s. A group of energetic and farsighted mammalogists working in the United States National Museum seized the moment to spearhead the organization of the ASM. As stated in Article 1, Section 2, of their by-laws, it was their intention that: "The object of the Society shall be the promotion of the interests of mammalogy by holding meetings, issuing a serial or other publications, aiding research, and engaging in such other activities as may be deemed expedient." The following chapters review how these aims and goals of 1919 have been accomplished during the ensuing 75 years, both through activities of the ASM and the growth and intellectual development of the discipline of mammalogy.

## Additional Readings

One volume of an international history of mammalogy has been published (Sterling, 1987) and another is in progress. Historical accounts of mammalogy in the USA include contributions by Hamilton (1955) and Gunderson (1976); Allen (1916) provided insights into the career of a major American mammalogist and founder of the ASM.

## Literature Cited


Allen, J. A. 1916. Autobiographical notes and a bibliography of the scientific publications of Joel Asaph Allen. American Museum of Natural History, New York, 215 pp.

Appel, T. A. 1987. The Cuvier-Geoffroy debate: French biology in the decades before Darwin. Oxford University Press, New York, 305 pp.

Baird, S. F. 1859. Mammals of North America. J. B. Lippincott, Philadelphia, 764 pp.

Cameron, J. 1929. The Bureau of Biological Survey. Johns Hopkins University Press, Baltimore, 339 pp.

Dupree, A. H. 1957. Science in the federal government; a history of policies and activities to 1940. Harvard University Press, Cambridge, 460 pp.

Farber, P. L. 1982. The emergence of ornithology as a scientific discipline, 1760–1850. Dordrecht, Holland, 191 pp.

Gunderson, H. L. 1976. Mammalogy. McGraw-Hill Book Company, New York, 483 pp.

Hamilton, W. J., Jr. 1955. Mammalogy in North America. Pp. 661–688, *in* A century of progress in the natural sciences, 1853–1953 (E. L. Kessel, ed.). California Academy of Sciences, San Francisco, 807 pp.

Hoffmeister, D. F. 1969. The first fifty years of the American Society of Mammalogists. Journal of Mammalogy, 50:794–802.

Lindsay, D. 1993. Science in the subarctic: trappers, traders, and the Smithsonian Institution. Smithsonian Institution Press, Washington, D.C., 176 pp.

McClellan, J. R. 1985. Science reorganized: scientific societies in the Eighteenth Century. Columbia University Press, New York, 413 pp.

Peden, W. (ed.) 1955. Thomas Jefferson's notes on the state of Virginia. University of North Carolina Press, Chapel Hill, 315 pp.

Rhoads, S. N. (ed.) 1894. A reprint of the North American zoology, by George Ord. . . . George Stokely Printer, Haddonfield, New Jersey, 290–361; 1–90 pp.

Sellers, C. C. 1980. Mr. Peale's museum: Charles Willson Peale and the first popular museum of science and art. W. W. Norton, New York, 370 pp.

Sterling, K. B. 1977. Last of the naturalists: the career of C. Hart Merriam (revised edition). Arno Press, New York, 478 pp.

———. (ed.) 1987. An international history of mammalogy. One World Press, Bel Air, Maryland, Vol. 1, 198 pp.

———. 1989. Builders of the Biological Survey, 1885–1930. Journal of Forest History, 30:180–187.

# *PRESIDENTS*

James N. Layne and Robert S. Hoffmann

*Sec. 9. The President is empowered to speak for the Society...*

### *Introduction*

The President is one of four elective officers of the ASM, the others being the First and Second Vice-presidents and the Recording Secretary. The President is the official representative of the Society. His or her duties include presiding over the meetings of the Board of Directors and the general business meeting, appointment of chairs and members of standing committees, establishing ad hoc committees to carry out specific tasks, designating representatives to other organizations, and preparation of an annual budget proposal with the help of the Secretary-Treasurer. Past-presidents are automatically members of the Board of Directors.

The term of office of the President and other elective and appointed officers of the society extends from the end of the annual meeting at which elected or appointed to the end of the following annual meeting, normally from June of one year to June of the next. Prior to 1973, the President was elected for a 1-year term and was eligible for reelection. In 1974, the By-laws and Rules were revised to extend the term of office to 2 years, with no provision for reelection.

Unlike many scientific societies in which election of officers is by mail ballot, the ASM has followed the practice of holding elections at the annual general business meeting. Nominations are made from the floor and voting is by written ballot. The pros and cons of this policy have been debated over the years, but it has survived successive revisions of the By-laws and Rules. The prevailing view has been that members who regularly attend annual meetings and take an active part in the affairs of the society are best qualified to judge the qualifications of candidates. The long succession of presidents who have ably served the society attests to the effectiveness of this system.

The 38 presidents of the society during its 75-year history and their terms of office are as follows (living individuals indicated with an asterisk):

1. C. Hart Merriam (1919–1921)
2. Edward W. Nelson (1921–1924)
3. Wilfred H. Osgood (1924–1926)
4. William D. Matthew (1926–1927)
5. Glover M. Allen (1927–1929)
6. Witmer Stone (1929–1931)
7. Marcus W. Lyon, Jr. (1931–1933)
8. Vernon Bailey (1933–1935)
9. Harold E. Anthony (1935–1937)

10. Joseph Grinnell (1937–1938)
11. Hartley H. T. Jackson (1938–1940)
12. Walter P. Taylor (1940–1942)
13. A. Brazier Howell (1942–1944)
14. E. Raymond Hall (1944–1946)
15. Edward A. Goldman (1946–1947)
16. Remington Kellogg (1947–1949)
17. Tracy I. Storer (1949–1951)
18. William J. Hamilton, Jr. (1951–1953)
19. William H. Burt (1953–1955)
20. William B. Davis* (1955–1958)
21. Robert T. Orr* (1958–1960)
22. Stephen D. Durrant (1960–1962)
23. Emmet T. Hooper, Jr. (1962–1964)
24. Donald F. Hoffmeister* (1964–1966)
25. Randolph L. Peterson (1966–1968)
26. Richard G. Van Gelder* (1968–1970)
27. James N. Layne* (1970–1972)
28. J. Knox Jones, Jr. (1972–1974)
29. Sydney Anderson* (1974–1976)
30. William Z. Lidicker, Jr.* (1976–1978)
31. Robert S. Hoffmann* (1978–1980)
32. James S. Findley* (1980–1982)
33. J. Mary Taylor* (1982–1984)
34. Hugh H. Genoways* (1984–1986)
35. Don E. Wilson* (1986–1988)
36. Elmer C. Birney* (1988–1990)
37. James H. Brown* (1990–1992)
38. James L. Patton* (1992–1994)

## *Presidential Profile*

Several of the early presidents played a key role in the prehistory of the ASM. Grinnell was one of the founders, in 1903, of the short-lived Pacific Coast Mammalogical Club, apparently the first attempt to form a professional mammalogy society in North America (Jackson, 1948). The major figure in the establishment of the ASM was Jackson. As early as 1902, he discussed with Ned Hollister the formation of a mammal society (Hoffmeister, 1969). More serious consideration of the idea took place while Jackson and Goldman were collecting in the White Mountains of Arizona in the summer of 1915 and when Jackson, Goldman, and Taylor were working on the Natanes Plateau in Arizona in 1916 (Hoffmeister, 1969). Jackson, together with three others (Bailey, Nelson, and W. Taylor) destined to become ASM presidents, was a member in 1918 and 1919 of the informal group from the Washington area known as the Biological Survey Association that formally proposed the formation of the ASM; and he served as chairman, with W. Taylor as secretary, at the first meeting of the society in April 1919. Four presidents (Bailey, Jackson, Merriam, Nelson) were signatories to the articles of incorporation of the society in April 1920 (Anon., 1923). With the exception of Hall, who became a member of the society in 1923, all of the first 17 presidents, from Merriam to Storer, were charter members. Nelson and Osgood, the second and third presidents, were the first vice-presidents, serving in that capacity from 1919 to 1921 and 1924, respectively.

Typical of other scientific organizations, the sex ratio of the elective officers of ASM has been strongly male-biased; and it was not until 1982 that the first woman, J. Mary Taylor, was elected president. Prior to that time, Viola S. Schantz and Caroline A. Heppenstall were the only women to hold office, that of treasurer, which together with secretary, was the traditional post of women in scientific and other organizations in earlier days.

Most presidents (excluding charter members) joined the society in their early 20s (average age 23), with Findley and Jones the youngest (18) and Davis and Durrant the oldest (32). Presidents who were charter members averaged 46 years of age at the time ASM was formed. Storer (27) and Anthony (29) were the youngest and Merriam and Nelson the oldest (64). Van Gelder was the youngest president (40) at the time of election, followed by Wilson (42), Jones (43), and Genoways, Layne, and Lidicker (44). Goldman (73) was the oldest, followed by Bailey (69), Nelson (66), and Merriam (64). Considering only non-charter members, Durrant (58) was the oldest president at the time of election. As a group, ASM presidents have been relatively long-lived, with an average life span of 76 years, with Jackson holding the record for longevity (95) and Matthew being the youngest at time of death (59). The average age of living presidents (as of June 1993) was 64, ranging from 49 (Wilson) to 91 (Davis). With six exceptions, all presidents have served for 2 years. Goldman died within a few months of election, Matthew and Grinnell served only 1 year, and Nelson and Davis were elected for 3 years. Davis's extended tenure was the result of a desire of the membership to maintain administrative continuity during a period of reorganization of the society's finances.

The usual path to the presidency of the society has been through membership in standing committees, service as a director, and election to the vice-presidency. Matthew, Allen, Stone, and Lyon were members of the original Council. With the exception of Merriam, Bailey, and Anderson, presidents have served from 1 (Nelson, Jackson, Kellogg, Van Gelder) to 9 (Patton) terms as vice-president, with a mean of 3 years. Ten presidents have held other elective offices in the society besides those of Director and Vice-president. Jackson, Howell, Burt, Hooper, and Hoffmeister served as Corresponding Secretary and Orr, Peterson, Van Gelder, and Anderson as Recording Secretary. W. Taylor was Treasurer. Anthony, Davis, and Anderson served as Trustees of the Reserve Fund. Thirteen presidents held editorial posts. These included Jackson (*Journal of Mammalogy*), Howell (*Journal of Mammalogy*), Burt (*Journal of Mammalogy, Special Publications*), Davis (*Journal of Mammalogy*), Van Gelder (Recent Literature), Layne (*Special Publications*), Jones (Managing Editor, Review Editor, *Journal of Mammalogy*), Anderson (*Mammalian Species*), Hoffmann (Review Editor), Genoways (*Journal of Mammalogy, Special Publications*), Wilson (*Mammalian Species, Special Publications*), Birney (Managing Editor, *Journal of Mammalogy, Special Publications*), and Patton (Review Editor).

With the exception of Matthew, who was born in New Brunswick, Canada, all ASM presidents have been born in the United States. Nine were born in the Northeast (Maryland [1], New Hampshire [3], New York [4], Pennsylvania [1]), 18 in the Middle West (Illinois [4], Iowa [1], Kansas [4], Michigan [1], Missouri [1], Nebraska [2], Ohio [1], Oklahoma [2], Wisconsin [2]), and 8 in the West (Arizona [1], California [2], Idaho [1], Oregon [2], Texas [1], Utah [1]). There is a historical trend in the geographic origins of the presidents, with the Northeast and Middle West predominating in the period up to the 1940s and increasing representation of western states in subsequent years. Interestingly enough, the Southeast has produced no presidents thus far in the history of the society.

Slightly more than half (55%) of the presidents were born and spent at least their early childhood in a rural setting, while the remainder, with the exception of Lyon, who spent his youth on different army posts around the country, were born in larger cities. The proportion of presidents born and raised in cities increases after the late 1940s. Regardless of the environment of their youth, almost all of the presidents developed a consuming interest in natural history at an early age, sometimes through an interest in collecting objects or in hunting or other outdoor activity such as falconry (Layne). Birney and J. Taylor divided their interests between natural history and sports, football and tennis, respectively; and Hamilton was a champion boxer during his undergraduate years.

Almost all presidents were strongly influenced in their pursuits of natural history by their mothers or fathers; particular friends; high school, college, and, in the case of Hamilton, Sunday school teachers; or museum curators or keepers in zoological parks. The majority of presidents focused on mammalogy as a career during their college years as a result of the influence of an undergraduate or graduate professor or, in some cases, a fellow student. Seven presidents have had students who themselves became president. These include (students in parentheses) Grinnell (Burt, Davis, Hall, Hooper, Orr), Hall (Hoffmeister, Durrant, Jones, Anderson, Findley), Jones (Genoways, Birney), Hooper (Brown), Hoffmeister (Lidicker, Van Gelder), Hamilton (Layne), and Findley (Wilson). A more-detailed "family tree" of ASM presidents and other North American mammalogists is given in the chapter by Whitaker (1994) in this volume. Major influences on the careers of the earliest presidents were Spencer Fullerton Baird, second Secretary of the Smithsonian Institution, who encouraged Merriam as a youth and supported Nelson at an early stage in his career, and the famous ichthyologist and president of Stanford University, David Starr Jordan, who advised Osgood to take a position under Merriam in the Bureau of Biological Survey while he was still an undergraduate. Osgood was not only one of "Merriam's Men" in the Survey but also lived in Merriam's home. Merriam also played an important role in the career of Bailey, purchasing specimens from him when he was a youth and later bringing him into the Bureau of Biological Survey. The famous team of Nelson and Goldman was born when Nelson, who needed a field assistant for a survey of the southern San Joaquin Valley of California, happened to stop at the Goldman ranch to have his wagon repaired. Goldman's father told him of his son's interest in natural history and suggested that Nelson might like to hire him, which he did.

Nelson and Osgood were bachelors. Of the presidents who were married, six (Stone, Jackson, Storer, Burt, W. Taylor, Patton) had no children. The remainder had from one to five children, with an average of 2.7.

Except for Matthew, a geologist and paleontologist, all ASM presidents have been neomammalogists, although some, such as Anthony and Kellogg, also published on fossil mammals. Other than Howell, who was primarily a mammalian anatomist, the major research fields of the remainder of the presidents can be broadly defined as either taxonomy or ecology. This categorization is, however, rather arbitrary, as one of the hallmarks of the work of many presidents has been the wide scope of their interests. Thus, persons who might be classed as taxonomists on the basis of the major body of their research may well have published significant papers in the area of life history, ecology, behavior, morphology, or physiology; and workers whose major research has been in ecology and life history have often done taxonomic or distributional studies as well. Given this qualification, the presidency of ASM has been dominated by taxonomists (67%). The early presidents were exclusively taxonomists, W. Taylor being the first president whose interests were in areas of ecology and life history, which in the present day would probably be defined as "wildlife biology." Although beginning with Storer and Hamilton, ecology and life history interests have been more strongly represented in the ASM presidency, taxonomy still prevails as the major field.

In addition to the wide recognition of the research of ASM presidents among mammalogists at the national and international levels, the work of several of the presidents has had an impact beyond the field of mammalogy in the broader areas of evolution, ecology, and education. Examples include Merriam's life zone concept, Matthew's volume *Climate and Evolution,* Storer's classic text *General Zoology,* Burt's work on territoriality and home range, and Brown's research on desert ecology.

In addition to the diversity of their mammalian research, most presidents have published on other taxonomic groups or in other fields. Merriam and Nelson, for example, conducted ethnographic research and Matthew published many papers on geology. Of the other taxonomic groups of interest to

ASM presidents, birds predominate. Allen, Grinnell, and Stone are as well known as ornithologists as they are mammalogists, and at least 17 other presidents have published one or more papers on birds. Also appearing in the bibliographies of presidents are publications on fishes, amphibians and reptiles, insects and other invertebrate groups, botany, plant ecology, conservation, and a wide range of other topics. One of the most versatile researchers among ASM presidents was Hamilton, who, besides work on a broad range of mammalian subjects, published extensively on the ecology and life histories of other vertebrates.

In addition to their service to ASM in many capacities, presidents have played an active role in over 20 other scientific societies as president or other elective officer. These include the Ecological Society of America (W. Taylor, Hamilton, Brown), American Society of Naturalists (Brown), Wildlife Society (Storer, W. Taylor), Paleontological Society (Matthew), Biological Society of Washington (Osgood, Bailey, Jackson, Wilson), Texas Academy of Science (W. Taylor), Florida Academy of Sciences (Layne), Society of Systematic Zoology (Durrant, Hoffmann, Peterson), Midwest Museums Conference (Hoffmeister), Texas Mammal Society (Jones), Organization of Biological Field Stations (Layne), Southwest Association of Naturalists (Genoways), Nebraska Museum Association (Genoways), Nuttall Ornithological Club (Allen), American Ornithologists' Union (Merriam, Grinnell), Cooper Ornithological Society (Osgood, Storer), New York Academy of Sciences (Anthony), New York Explorers Club (Anthony), Organization of Tropical Studies (Jones), American Society of Ichthyologists and Herpetologists (Storer), and Association of Science Museum Directors (J. Taylor). ASM presidents have also served as editors of journals of other organizations, including the *Auk* (Allen, Stone), *Condor* (Grinnell), *Ecological Monographs* (Hamilton), *The American Midland Naturalist* (Hoffmeister, Birney), *Evolution* (Jones), *The Journal of Wildlife Management* (Storer), and *The Texas Journal of Science* (Jones). In addition to these activities, presidents have served as board members of numerous conservation, academic, and museum organizations, as well as scientific consultants or advisors to various local, state, federal, and international agencies.

ASM presidents have frequently received recognition from the society for their research, service to the society, and other contributions to the field of mammalogy. Merriam and Jackson have been memorialized through the creation of the C. Hart Merriam and the H. H. T. Jackson awards. Seven (Layne, Jones, Lidicker, Findley, Genoways, Brown, Patton) of the 12 presidents since the establishment of the Merriam Award have been recipients; and the Jackson Award has gone to Jones and Anderson. Honorary Membership has been bestowed on Merriam, Nelson, Lyon, Anthony, Jackson, W. Taylor, Howell, Hall, Storer, Hamilton, Burt, Davis, Orr, Durrant, Hooper, Hoffmeister, Peterson, Layne, Jones, and Anderson. Early in their careers, Anderson and Layne received ASM Graduate Student Honoraria.

ASM presidents also have been the recipients of numerous honors and awards from other professional organizations as well as from academic institutions, governmental bodies, and environmental groups. Merriam is the only president to have been elected to the National Academy of Sciences.

Ten of the 38 presidents have served with distinction in the armed forces of the United States. These include Lyon, Anthony, Goldman, Kellogg, and Storer who served in various branches of the army in World War I; Hamilton and Findley (army) and Peterson, Hooper, and Layne (air force) during or just after World War II; Jones (army) in the Korean War; and Birney (navy) in the 1960s.

The educational backgrounds of the earlier ASM presidents were more diverse than those of later years. Merriam and Lyon were MDs, and Stone had an honorary D.Sc. Nelson, Bailey, Howell, and Goldman were largely self-trained scientists, and were known by some of their contemporaries as "range-raised naturalists and biologists" (Young, 1947). With these exceptions, presidents have invariably had bachelor's and Ph.D.s, and a large percentage has also received master's degrees. Presidents have attended 25 different undergraduate institutions, with the University of California at Berkeley, University of Kansas, and Cornell each having been attended by four future presidents; the University of Arizona, Yale, and Stanford by two; and the remaining 17 colleges or universities by a single president. The list of institutions from which presidents have received their doctorates is much shorter (12), with over half (58%) of the degrees having been awarded by the University of California (11) and University of Kansas (6) and a maximum of two by other institutions.

The careers of ASM presidents have covered a broad spectrum of employment, and summarization of their professional posts is complicated by the fact that in many cases persons have held a number of appointments, either concurrently or successively, during the course of their careers. Thus, the following breakdown, based upon the predominant, if not exclusive, type of positions held by ASM presidents during their careers is of neccessity somewhat arbitrary. Seven presidents have been employed in various agencies or organizations of the federal government, including the original Biological Survey (Merriam, Nelson, Bailey, Jackson, Goldman, Kellogg), U.S. Fish and Wildlife Service (W. Taylor, Wilson), and the Smithsonian Institution (Kellogg, Hoffmann). Over half (55%) of the presidents are identified primarily with museums. Nine of these have been associated with public museums, including the American Museum of Natural History (Anthony, Van Gelder, Anderson), Field Museum of Natural History (Osgood), Academy of Natural Sciences of Philadelphia (Stone), California Academy of Sciences (Orr), Cleveland Museum of Natural History (J. M. Taylor), and the Royal Ontario Museum (Peterson). Twelve more have been members of the curatorial staffs, and with professorial appointments in academic departments as well, of museums affiliated with universities, including the Museum of Comparative Zoology at Harvard (Allen), Museum of Vertebrate Zoology at the University of California, Berkeley (Grinnell, Lidicker, Patton), Museum of Natural History at the University of Kansas (Hall, Jones, Hoffmann), Museum of Natural History at the University of Illinois (Hoffmeister), Museum of Zoology at the University of Michigan (Burt, Hooper), Museum of Southwestern Biology at the University of New Mexico (Findley), The Museum of Texas Tech University (Jones), University of Nebraska State Museum (Genoways), and the Bell Museum of the University of Minnesota (Birney).

Five presidents have been teachers and researchers in academic departments at the University of California at Davis (Storer), Cornell University (Hamilton), Texas A&M University (Davis), University of Utah (Durrant), and University of New Mexico (Brown). One president (Layne) left academia (Cornell) to spend a major portion of his career as a research biologist at the Archbold Biological Station, one (Howell) was a professor in a medical school (Johns Hopkins), and one (Lyon) did much of his research while a practicing physician in Indiana.

In addition to their research, teaching, and other professional activities, many (74%) ASM presidents have held administrative posts during the course of their careers. Merriam, Nelson, Bailey, Jackson, W. Taylor, and Wilson served as heads of sections or programs of federal agencies, including the Biological Survey and U.S. Fish and Wildlife Service Cooperative Research Units. Anthony, Peterson, Van Gelder, and Anderson were chairmen of museum mammal departments; Osgood, Matthew, and Allen were chief curators at museums; Orr and Patton were associate directors of museums; and Stone, Grinnell, Hall, Kellogg, Hoffmeister, Jones, Findley, M. J. Taylor, Birney, and Genoways served as museum directors. Hall, Davis, Hoffmann, and Findley served stints as university department chairman. Layne was director of research and executive director of the Archbold Biological Station. Kellogg and Hoffmann held the post of assistant secretary for science at the Smithsonian, and Jones served as graduate school Dean and Vice-President for research at Texas Tech University.

## *Biographic Sketches*

Following are brief biographies, arranged chronologically by term of office, of the 38 persons who have served as presidents of the ASM during the 75 years of the society's history. Published source materials used in preparation of the accounts of deceased presidents are given at the end of the accounts.

### *Clinton Hart Merriam: 1919–1921*

C. Hart Merriam (Fig. 1) was a founding member and the first president of the ASM. His selection as the founding president of the new society was a logical choice, given the preeminence he had attained in the field of mammalogy by age 64 when he assumed the presidency. His career spanned the formative period of the science of mammalogy. He was born on 5 December 1855 at Locust Grove, New York, and at age 16 joined the Hayden Survey of the American West. Throughout a long and extremely productive career that ended with his death in 1942, he helped shape the modern science of mammalogy. His parents lived in comfortable circumstances, in a "rural mansion surrounded by ample acres and shadowed by the Adirondack Mountains," (Osgood, 1943). His early schooling appears to have been routine, and it is likely that he was much influenced by his natural surroundings. In his teens he began to collect birds and eggs and early came under the influence of Spencer Fullerton Baird, the second Secretary of the Smithsonian Institution. At age 17, he was sent to a day preparatory school, Pingry Military, in Elizabeth, New Jersey. After 2 years, he enrolled at Yale University to study medicine. However, his interest in natural history continued unabated, and he had already accumulated a significant series of publications when he enrolled at age 24 in medical school at Columbia University. While still a medical student, he was involved in organizing the Linnaean Society of New York and chosen its first president, having previously been involved in the organization of the Nuttall Ornithological Club. Graduating from medical school in 1879, he returned home to Locust Grove to practice, but continued to pursue his natural history avocation; at this time his increasing interest in mammals became evident. Through the early 1880s, most of his publications were devoted to mammals, and this early phase culminated with publication of *Mammals of the Adirondacks* in 1884. Nevertheless, his interest in birds had not flagged, and he was also active in the formation of the American Ornithologists' Union, becoming the first secretary of that organization.

By 1885 Merriam was ready to give up his medical practice and accepted the position of ornithologist in the Division of Entomology of the Department of Agriculture. His position soon became a division and in 1888 was expanded to include mammalogy, at the same time separating itself from entomology. This new scientific bureau of the government provided the vehicle for his principal life work; Merriam's name is synonymous with the Bureau of Biological Survey, and with the "life zone" concept he pioneered. He inaugurated the *North American Fauna* series and in the first four numbers (1889–1890) described 71 new species and several new genera of mammals. He developed an ambitious program of field collecting throughout North America, aided


C. Hart Merriam
(1919–1921)

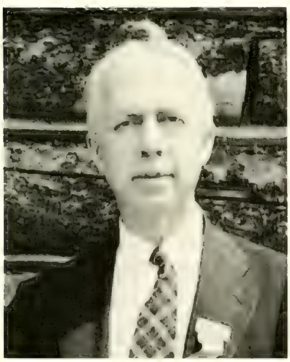

Edward W. Nelson
(1921–1924)

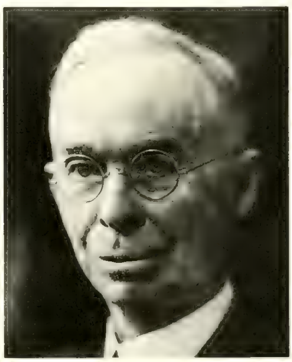

Wilfred H. Osgood
(1924–1926)


William D. Matthew
(1926–1927)


Glover M. Allen
(1927–1929)


Witmer Stone
(1929–1931)


Marcus W. Lyon
(1931–1933)


Vernon O. Bailey
(1933–1935)


Harold E. Anthony
(1935–1937)

FIG. 1.—Presidents of the ASM from 1919 to 1937.

by people such as Vernon Bailey, A. K. Fischer, T. S. Palmer (Fig. 5), and the incomparable duo of Nelson and Goldman. Equally important was the recent invention of a cheap portable "mouse trap," the Cyclone.

The avidity with which Merriam named new species ultimately led him to write a revision of the brown and grizzly bears of North America in which he described a total of 84 species, including one of separate generic rank. However, from about 1900, at the age of 55, he began to devote most of his time to the ethnology of California Indians, having become the beneficiary of the Harriman Trust. His work on bears was thus published when he no longer was devoting himself primarily to mammalogy. Paradoxically, the nearly universal rejection of his systematic concept was balanced by his reputation, which resulted in his systematic arrangement nevertheless being employed even after his death.

Among his many honors was election to the National Academy of Sciences in 1902. He married Elizabeth Gosnell in 1886 and they had two daughters (Sources: Grinnell, 1943; Osgood, 1943).

## *Edward William Nelson: 1921–1923*

The second president of the ASM and an Honorary Member, E. W. Nelson (Fig. 1) was born near Manchester, New Hampshire, on 8 May 1855 and, like his predecessor, Merriam, is said to have been interested in the out-of-doors as a child. During the Civil War he lived with his grandparents on a farm in the northern Adirondacks while his father served in the Union Army and his mother nursed in a hospital in Baltimore. He attended a one-room rural school until 1886 when his mother, now widowed, moved to Chicago and enrolled him in schools there. His formal education appears to have been somewhat spotty, but continued until 1875. However, even by 1872 he had participated in a field collecting expedition to the western United States and after assuming a teaching position in Dalton, Illinois, in 1875 began to publish on birds. Like Merriam, he also went to Washington, met Spencer Baird at the Smithsonian, and was sent on a government expedition to Alaska. During this trip he carried out a variety of observing and collecting activities, including geography, ethnography, and zoology. Other expeditions to Alaska followed, resulting in a series of ethnographic and biological publications; although not trained as a scientist, Nelson was obviously an excellent self-trained natural historian.

By 1890 he was working for the Bureau of Biological Survey, as a special agent on the Death Valley Expedition. Thereafter, he and Edward A. Goldman began a series of field studies in Mexico, which continued almost unabated until 1929 when he retired. During his later years, he became increasingly involved in administration of the Survey, being named Assistant Chief in 1914 and Chief in 1916, and serving until 1927. For the next 4 years, he continued his research as a Principal Biologist for the Survey. Subsequent to his retirement, he spent some time in California, but died in Washington, D.C. on 19 May 1934 (Sources: Goldman, 1935; Lantis, 1954).

## *Wilfred Hudson Osgood: 1924–1926*

W. H. Osgood (Fig. 1) was born 8 December 1875 in Rochester, New Hampshire; he was the first of five children. When the family moved to California in 1888, they settled in the Santa Clara Valley in a rural area at the south end of San Francisco Bay. Osgood's primary schooling was in Rochester, and he attended three years of high school in Santa Clara, but the family then moved into the city of San Jose. Osgood had become interested in birds and egg collecting and was involved in the organization of the Cooper Ornithological Club in San

Jose, which has subsequently become a major professional organization.

After graduating from high school, Osgood accepted a teaching position in a small school in Wilcox, Arizona, for a year and then entered Stanford University shortly after its founding. Here he came within the orbit of the eminent zoologist David Starr Jordan, then president of the university. It was Jordan's suggestion that he leave Stanford before completing his BA degree in order to take a position in C. Hart Merriam's Bureau of Biological Survey, but he was eventually awarded his degree in 1899. He spent over a decade with the Survey, publishing a number of papers in the *North American Fauna* series, culminating in his monographic revision of the genus *Peromyscus* in 1909. In that year he joined the staff of the Field Museum of Natural History in Chicago, the second of his two posts. He was Assistant Curator of Mammals and Birds, receiving his Ph.D. from University of Chicago in 1918 for a dissertation entitled "A Monographic Study of the American Marsupial, *Caenolestes,*" which was published a few years later by the Field Museum. He served as Chief Curator of Zoology for 20 years, until his retirement in 1941. During his career at the Field Museum, he alternated between studying collections, both at the Field and in museums in other parts of the world, and conducting field expeditions. He participated in about 20 expeditions, 8 of which were major foreign ventures. As a result, the Field Museum mammal collections grew greatly in size and importance during his tenure. From his retirement until his death 6 years later on 20 June 1947, he remained fully engaged in publishing scientific papers. He was active not only in scientific societies, including the Biological Society of Washington, the Chicago Zoological Society, the American Ornithologists' Union, and the British Ornithologists' Union, but also in a number of other clubs such as the Explorers Club.

Like Nelson, his predecessor, he remained a bachelor (Source: Sanborn, 1948).

## *William Diller Matthew: 1926–1927*

William D. Matthew (Fig. 1) was born on 19 February 1871 in St. John, New Brunswick. He acquired his interest in the natural sciences from his father, Dr. George F. Matthew, who was a well-known and highly skilled amateur paleontologist and an authority on the geology, paleobotany, and fossil amphibian tracks of New Brunswick.

In graduate work at Columbia University, he studied geology, mineralogy, and metallurgy, which provided a solid background for his subsequent research in paleontology. He received the doctorate in 1895 and the same year joined the staff of The American Museum of Natural History as an assistant in the Department of Vertebrate Paleontology. He rose to Assistant Curator and then Curator in the department and Curator-in-chief of the Division of Geology, Mineralogy, and Paleontology. In 1927, after 32 years service with the Museum, he left to become Professor of Paleontology and Curator of the Paleontological Museum of the University of California at Berkeley. His courses in paleontology, despite their reputation as difficult, were taken by hundreds of students, many of whom went on to distinguished careers in the field.

Although his early publications were in the field of geology, for example, crystallography and the structure of rocks in New Brunswick, the main body of Matthew's research dealt with mammalian paleontology. His first major project after coming to the American Museum was to catalog, pack, and ship to the Museum the extensive collections of E. D. Cope. This task introduced him to the mammal fauna of the Basal Eocene of New Mexico, which he later designated as the Paleocene. In the course of his career he was to work on fossils of nearly every major group of mammals, including carnivores, insectivores, primates, marsupials, rodents, edentates, and ungulates. He played a leading role in fossil collecting expeditions to many localities in the western states and Florida, as well as Mongolia, China, and Java. In addition to his basic studies on the phylogeny of various groups, he also contributed to general theories concerning the arboreal origin of mammals, the mode of formation of the mammal fossil-bearing strata in the western United States, and the major patterns of the origin and dispersal of the mammalian fauna of the world. It was the latter subject, treated in his book *Climate and Evolution,* published in 1915, for which he was most widely known outside the field of paleontology. The book was a healthy antidote to the tendency at the time of erecting hypothetical land bridges to explain the distribution of related groups separated by ocean barriers. Although some of the major conclusions have not stood the test of time, the book remains one of the classic works in biogeography.

In addition to his technical writing, Matthew contributed many articles to *Natural History* magazine and authored handbooks and guide leaflets on various fossil exhibits at the museum. He was active in preparation of public exhibits. He was especially concerned with mounting fossils in a life-like posture and was a pioneer in the use of comparative myology and osteology for this purpose.

His scholarship and solid contributions to paleontology brought him numerous honors from scientific societies during the course of his career, including election as a Fellow of the Royal Society of England. He was a Charter Member of ASM and, in addition to his term as president, also was a member of the original Council and Vice-president. He also served as President of the Paleontological Society in 1929.

He was married and had two daughters and a son. He died on 24 September 1930, following an illness of several months (Source: Gregory, 1930*a,* 1930*b,* 1931).

## *Glover Morrill Allen: 1927–1929*

Glover M. Allen (Fig. 1), son of Reverend Nathaniel Allen and Harriet Ann (Schouler) Allen, was born on 8 February 1879, in Walpole, New Hampshire. He developed a keen interest in natural history at an early age and by the time he was in high school had become an expert in bird identification and an authority on local mammals. He attended Harvard College on a John Harvard Scholarship, was elected to Phi Beta Kappa in his junior year, and graduated magna cum laude in 1901. He remained at Harvard for graduate studies, receiving an A.M. in 1903 and a Ph.D. in 1904. His doctoral thesis was on the heredity of pelage color in mice. In addition to scientific subjects, he studied several foreign languages and acquired broad knowledge of classical European and Russian literature. He was married in 1911 to Sarah Moody Cushing, and they had one daughter, Elizabeth Cushing Allen (Mrs. Arthur Gilman).

Upon receiving his doctorate, he was appointed Secretary, Librarian, and Editor of the Boston Society of Natural History. He returned to the Harvard Graduate School in 1906 and 1907 and in the latter year began work on the mammal collections of the Museum of Comparative Zoology. In 1924, he became Lecturer in Zoology at Harvard and Curator of Mammals in the Museum of Comparative Zoology, where he remained for the remainder of his career.

His research involved both mammals and birds. He had a keen interest in the fauna of New England and also conducted research in the Bahamas, Labrador, Africa, West Indies, Brazil, and Australia. Although small and slight of build, he had unusual stamina and capacity for work when in the field. His mammal research was primarily concerned with taxonomy and distribution, and he also published a number of papers on fossil sirenians, cetaceans, and bats. Among his major contributions were the books *Bats, Checklist of African Mammals, Mammals of China and Mongolia,* and *Extinct and Vanishing Mammals of the Western Hemisphere with Marine Species of all Oceans.* His ornithological work included *The Birds of Massachusetts* coauthored with R. H. Howe, Jr., and *Birds and Their Attributes.* He also published numerous distributional records and regional checklists of birds and was a prolific reviewer of ornithological works.

He was a charter and life member of the ASM and, in addition to the presidency, was Vice-president, a Director, and member of a number of standing committees. The Life Histories and Ecology, Conservation of Land Mammals, and Nomenclature committees were established during his presidency. He was a Fellow of the American Ornithologists' Union and Editor of the *Auk* and also served as Editor of the *American Naturalist* and Secretary and President of the Nuttall Ornithological Club.

Glover Allen was known for his modest nature, kindly presence, diplomacy, and accessibility to all who wished his advice or help. Although not given to "hearty camaraderie," as one of his friends put it, when encouraged he would greatly entertain listeners with whimsical and humorous tales of his travels, often enhancing his accounts with appropriate quotes drawn from his vast knowledge of literature. W. M. Tyler (1943) cited an example of Allen's ability to come up with a quote from the classics to fit the occasion. After they had gone to bed in a hotel on Cape Cod after a day in the field, someone in the room above tramped heavily across the floor. Allen, nearly asleep, muttered: "The Wild Ass stamps o'er his Head, but cannot break his Sleep." Glover Allen died on 14 February 1942 in Cambridge, Massachusetts (Sources: Barbour et al., 1943; Tyler, 1943).

## *Witmer Stone: 1929–1931*

Witmer Stone (Fig. 1) was born in Philadelphia, Pennsylvania, on 22 September 1866. His parents were Frederick D. Stone and Anne E. Witmer. He developed an interest in natural history at an early age and as a small boy was a regular visitor to the Academy of Natural Sciences of Philadelphia, where he was later to spend his entire career. While a student at the Germantown Academy in 1877, he and several schoolmates founded the Wilson Natural Science Association. Regular meetings were held at which formal papers were presented, and scientific collections were maintained. Included among the mammals were specimens he collected during summers spent at his uncle's home in Chester County, Pennsylvania. He was married to Lillie May Lafferty in 1904.

He received A.B. and A.M. degrees from the University of Pennsylvania in 1887 and 1891, respectively. His first position following graduation was that of assistant in the library of the Historical Society of Pennsylvania, where his father was librarian. In 1888, he became affiliated with the Academy of Natural Sciences of Philadelphia where he served in many capacities until his death on 23 May 1939. He was Conservator of the Ornithological Section (1891–1918); Assistant Curator (1893–1908) and Curator (1908–1918) of the Museum; Executive Curator (1918–1925); Director (1925–1929); Emeritus Director (1929–1939); Curator of Vertebrates (1918–1936); Honorary Curator of Birds (1938–1939); and Vice-president of the Academy (1927–1939).

Although Stone authored 19 publications on mammals, he was primarily an ornithologist. Reflecting his broad interest in natural history, he also conducted research on plants, reptiles, amphibians, insects, and land molluscs. He published two books on mammals: *American Animals* coauthored with W. E. Cram and *The mammals of New Jersey.* His other mammal publications included descriptions of several new taxa; reports on collections from Alaska, Sumatra, western United States, and Ecuador; and studies of the Hawaiian rat and pumas in western United States. One of his best known ornithological works is *Bird Studies of Old Cape May,* which earned him comparison with Thoreau and Burroughs as a writer. A major botanical contribution was *The Plants of Southern New Jersey with Especial Reference to the Flora of the Pine Barrens.*

One of his major accomplishments as curator of the bird and mammal collections at the Philadelphia Academy was rescuing many valuable historic specimens that had been exposed to moisture, mold, and insects and the dust and grime of the city while on exhibit. He also performed the monumental task of salvaging and rehabilitating E. D. Cope's large collection of reptiles, which came to the Academy after Cope's death. The state of preservation of many of the valuable specimens was questionable and the alcohol had to be poured off carefully before the condition of the specimens could be determined. J. A. Rhen, who assisted him in the task, wrote that "the tedium of this work was greatly enlivened by Stone's vivid classification and nomenclature of the various color shades and consistencies referred to as 'gorum,' 'gee,' and 'goo,' to be found in the five-gallon glass jars used to receive the discarded solution."

Witmer Stone was a Charter Member of the ASM. He was a member of the original Council and served as Vice-president prior to assuming the presidency. Two important standing committees established during his tenure as President were the Editorial and Membership committees. He also was an active member of the American Ornithologists' Union, serving as Editor of the *Auk* from 1912 to 1937. Among honors he received was an Honorary Sc.D. and the Alumni Award of Merit from the University of Pennsylvania (Source: Huber, 1940).

## *Marcus Ward Lyon, Jr.: 1931–1932*

Marcus Ward Lyon, Jr. (Fig. 1), was born at Rock Island Arsenal, in Illinois, to Captain Lyon and his wife on 5 February 1875. Little appears to be known of his early life, which was spent at Army posts in various parts of the country. One of these was Watertown Arsenal near Boston, Massachusetts. His scientific interests apparently stem from his childhood days there when he began to make collections of insects and other animals. Later, his father apparently was again posted to Rock Island, because Lyon graduated from high school there in 1893 and entered Brown University that same year, receiving his bachelor's degree in 1897. His college training in biology led to his being offered an instructorship in bacteriology at North Carolina Medical College in 1897. After serving in that post for a year, he moved to Washington, D.C., where he was appointed an Aid in the Division of Mammals, U.S. National Museum (USNM), Smithsonian Institution. Concurrent with this part-time position, he began graduate studies at George Washington University, obtaining his M.S. degree in 1900 and his M.D. in 1902. In that same year he married Martha Maria Brewer of Lanham, Maryland. Lyon continued to work in the National Museum, but embarked upon a parallel teaching career in the Howard University Medical School in Washington. He taught physiology, bacteriology, and pathology there until 1917. With the outbreak of World War I, he joined the U.S. Army and served as pathologist in Walter Reed Army Hospital from 1917 to 1919, attaining the rank of Major. At the same time, he taught veterinary zoology and parasitology at the Medical School of George Washington University. During that 18-year stretch of medical teaching and practice, his wife also obtained an M.D. from Howard University, and in 1919 they jointly accepted an invitation to join the staff of the South Bend Clinic in Indiana. This decision resulted in a major change of direction for Lyon. Previously while associated with the Division of Mammals at USNM, he had published a series of significant papers on the morphology, systematics, and zoogeography of wild mammals. Most notable among these are his paper on the classification of the hares and their allies (1904) and an account of the mammalian family Tupaiidae (1913), for which he was awarded a doctorate by George Washington University. Although his formal relationship with the USNM ended in 1912, he continued to publish broadly in mammalogy until his move to Indiana. In addition, he published a number of basic medical studies during that period.

After he and his wife set up their medical practice in South Bend, Indiana, his scientific contributions were almost all devoted to Indiana subjects, focusing particularly on the region around South Bend. His medical publications also drew from his practice more frequently than during his time in Washington. Perhaps the most significant publication from this period is his book, *Mammals of Indiana*, published in 1936. In this last period of his life, he became an ardent conservationist and spokesman for wildlife protection. His last paper was in press when he died on 19 May 1942; it described the changes, mostly negative, that had occurred in the Kankakee Region along the Indiana border near his home as a result of human activities (Source: Anon., 1942).

## *Vernon Orlando Bailey: 1933–1934*

Vernon Bailey (Fig. 1) was born of pioneer parents, the fourth child of Hiram and Emily Bailey, on 21 June 1864 in Manchester, Michigan. His father had learned the mason's trade, but was by preference a woodsman and hunter, and when Vernon was about 6 years old the family moved west to Elk River, Minnesota, on the western frontier. This move was accomplished in a horse-drawn wagon and must have taken some months to cover the 700 miles. The only opportunity for schooling in a frontier homestead such as his parents established was at home, but late in 1873 the families of the adjacent homesteads built a schoolhouse and formal coursework began. Like most early mammalogists, Bailey began by collecting the organisms in his surroundings. Self-taught in taxidermy, he began to prepare museum specimens, which he sold to firms in Ontario, Canada, and in Halle, Germany. Some of these specimens were in turn purchased by C. Hart Merriam, leading him to contact Bailey who was then 19. This was prior to Merriam's being named to his government position, eventually in the Bureau of Biological Survey, and their lifelong association gained Bailey entreé into the Bureau. In 1887 Bailey was appointed as a field naturalist and sent to the northern Great Plains and Rocky Mountains. For virtually every year thereafter, until his final trip to Nevada in 1937, he collected for the Bureau and for the U.S. National Museum. However, he found time to take course work at the University of Michigan in 1893 and at George Washington University in 1894–1895.

He retired from the Biological Survey in 1933, having gained the rank of Chief Field Naturalist, but continued to work until his death in Washington on 20 April 1942. He was survived by his wife, Florence Merriam Bailey, herself a biologist, whom he married in 1904. In addition to the presidency of the American Society of Mammalogists, he served as President of the Biological Society of Washington (Sources: Smithsonian Institution Archives, Record Unit 7098; Zahniser, 1942).

## *Harold Elmer Anthony: 1935–1937*

Harold E. Anthony (Fig. 1) was born in Beaverton, Oregon, on 5 April 1890. His father was a well-known Pacific Coast ornithologist and collector. From an early age, he hunted and trapped and loved the outdoors and, although his primary field came to be mammalogy, he retained a broad interest in natural history throughout his life. He was married in 1916 to Edith Demerell, who died shortly after their son, Alfred Webster Anthony, was born. Four years later he married Margaret Feldt, and they had a daughter, Margery Stuart, and a son, Gilbert Chase. He was an officer (1st Lieutenant and Captain) in the field artillery during World War I (1917–1919) and saw action in France.

He attended Pacific University for 2 years (1910–1911) and received B.S. and M.A. degrees from Columbia University in 1915 and 1920, respectively.

He began his career as a field collector for the Biological Survey in 1910 and in the same year was employed by The American Museum of Natural History as naturalist on the Albatross Expedition to Lower California. The following year he joined the Mu-

Joseph Grinnell
(1937–1938)

Hartley H. T. Jackson
(1938–1940)


Walter P. Taylor
(1940–1942)

A. Brazier Howell
(1942–1944)

E. Raymond Hall
(1944–1946)

Edward A. Goldman
(1946–1947)

Remington Kellogg
(1947–1949)

Tracy I. Storer
(1949–1951)

William J. Hamilton, Jr.
(1951–1953)

FIG. 2.—Presidents of the ASM from 1937 to 1953.

seum staff full-time as a cataloger and general handyman in the Department of Mammals and Ornithology. He was appointed Associate Curator in the Department of Mammalogy in 1919, Curator in 1926, and Emeritus Curator upon his retirement in 1958. In addition to serving as Chairman of the Department of Mammalogy from 1942 to 1958, he held the posts of Dean of the Scientific Staff (1942–1948) and Deputy Director (1952–1957) of the Museum. After retirement, he was Appointed Curator of the Frick Laboratory, a paleontological research laboratory at the Museum supported by the Charles Frick Foundation, and served in that capacity until 1966.

Anthony's research involved both Recent and fossil mammals, with an emphasis on the Caribbean and Central and South American regions. In addition to his work in the Neotropics, he participated in expeditions to various regions of western United States, Alaska and the Arctic Ocean, Canada, Africa, and Burma. Among his major contributions were the two volume *Mammals of Puerto Rico, Living and Extinct* and *Field Book of North American Mammals,* which for many years was the major guide to mammals of the region. He was active in the Museum's exhibition program, playing a key role in the creation of the Hall of North American Mammals, the Akeley Hall of African Mammals, and the Hall of South Asiatic Mammals. An ardent conservationist, he served as Chairman of the Committee on Preservation of Natural Conditions of the National Research Council's Division of Biology and Agriculture.

Anthony was a Charter Member of the ASM. Besides the presidency, he served as a Councillor, Trustee, and Vice-president. He also was a director of both the New York Explorers Club and National Audubon Society, Treasurer of the New York Academy of Sciences, and an Honorary Life Member of the Sociedad Colombiana de Ciencias Naturales.

In addition to his scientific interests, Anthony was a financial expert. As was once stated in an article in an American Museum employee newsletter "he knew that a bear market wasn't always a place where grizzlies and kodiaks are sold, and that there are two kinds of bulls." His financial expertise made him a particularly valuable member of the Museum's Pension Board and Welfare Committee.

As a youth, he discovered the pleasure and satisfaction of growing plants and this became a lifetime avocation. Orchids were his specialty. He served as President of the Greater New York Orchid Society and Treasurer of the American Orchid Society, from which he received a gold medal in recognition of his contributions. Cooking was another of his long-time interests, and his culinary skills were attested to by his induction into the Society of Amateur Chefs.

He died of a heart attack on 29 March 1970, while on a family outing in Paradise, California (Sources: Anon., 1958*a,* 1958*b,* 1970).

## *Joseph Grinnell: 1937–1938*

Joseph Grinnell (Fig. 2) was born on 27 February 1877, at Ft. Sill (then Indian Territory) in what is now Oklahoma. His family was of New England origin, but his father, a physician, moved the family to California when Grinnell was still young. Joseph's schooling through college was in Pasadena. He attended Pasadena High School and then enrolled in what was known as Throop Polytechnic Institute (now the California Institute of Technology) where he received a bachelor's degree in 1897. He began his graduate studies at Stanford University shortly thereafter, receiving his M.A. degree in 1901. Even as a high school student he had displayed an interest in natural history and had begun to amass a collection of vertebrates. In 1896, while only 19 years old, he made his first visit to Alaska, where he collected around Sitka. Two years later he returned to Kotzebue and the Bering Sea Region where he not only collected vertebrates but also apparently prospected for gold. An apocryphal tale suggests that he found a rich claim but was robbed of it by claim jumpers; however, this cannot be substantiated. Between these early expeditions, he served as instructor at Throop Polytech, teaching assistant at Stanford, and instructor in the Palo Alto High School. He received an appointment at the University of California, Berkeley, in 1905, and almost all of his subsequent field collecting was carried out within the state of California. Shortly after joining the Berkeley faculty, however, he returned to coastal Alaska in 1907 on an expedition headed by Annie M. Alexander, who became his life-long benefactor. In 1908 she founded the California Museum of Vertebrate Zoology at the University of California, Berkeley, of which Grinnell was named Director. Together with Louise Kellogg, Alexander supported the Museum and Grinnell until his death at age 63 on 29 May 1939. During those 31 years as Director of the Museum of Vertebrate Zoology, Grinnell developed a highly organized approach to field collecting, which has had an influence far beyond the state of California, to which he restricted not only his own efforts, but if possible, those of his students. Most of his many publications were devoted to birds, but 76 treat wholly or in part of mammals.

In addition to his systematic and ecological work, he played a significant role in the developing field of conservation. His impact on teaching biology at Berkeley was profound, as is suggested by the fact that 15 years after his death his principal course "Zoology 113" and his graduate seminar "Vertebrate Review" were still essentially Grinnellian (Source: Hall, 1939).

## *Hartley Harrad Thompson Jackson: 1938–1939*

Although Hartley H. T. Jackson (Fig. 2) was only the eleventh president of the ASM, he was one of those Biological Survey scientists who first developed the idea of such a society, and he chaired the first Organizing Committee. He served first as Corresponding Secretary (1919–1925), was elected Vice President in 1937, and in addition held a number of committee posts. Hartley Jackson was born in Milton, Wisconsin, on 19 May 1881, the son of English immigrants to the United States. He was the last of their eight children and the only one born in this country. Like so many other field biologists, he began when still young to collect birds, and his first scientific paper on screech owls appeared when he was 16 years old. Jackson attended primary and secondary schools in Milton, and then enrolled in Milton College, where he received his bachelor's degree in 1904. Upon graduating, he taught at Carthage Collegiate Institute in Missouri, where he met Anna Marcia Adams who he married in 1910, having already entered the University of Wisconsin 2 years earlier for graduate work. His master's degree was awarded in 1909, and the following year he joined the Bureau of Biological Survey in Washington. He also enrolled in George Washington University, and attained a doctoral degree in Zoology in 1914.

In 1917, E. W. Nelson, Chief of the Survey, arranged with the State of Wisconsin for a cooperative study of the fauna. Jackson was designated principal investigator from the Biological Survey, with the state supplying a field assistant and other support. Jackson had, even prior to this formal agreement, carried out field work in Wisconsin, but thereafter field work was conducted regularly each summer by a team directed by Jackson until 1922 when the agreement became inactive. It was, however, reactivated in 1940, and eventually led to one of Jackson's most important works, *The Mammals of Wisconsin,* published in 1954.

Increasing administrative duties curtailed Jackson's field research, and he became more involved in wildlife management as Chief of the Division of Wildlife Research, later renamed Wildlife Surveys. This unit sponsored a great many important studies of game birds and mammals in the period just prior to World War II, during which Jackson served on several War Production Board committees. After a 41-year period of government service, Hartley Jackson retired in 1951. He continued to utilize his office in the National Museum of Natural History after retirement, but worked primarily on a history of the Bureau of Biological Survey, which apparently was never published. His wife Anna died in 1968, but 2 years later he married Mrs. Stephanie Hall of Durham, North Carolina, whose father was the former president of Milton College in Wisconsin. He died at age 95 in Durham (Source: Aldrich, 1977).

## *Walter Penn Taylor: 1940–1942*

Walter P. Taylor (Fig. 2) was born 31 October 1888 near Elkhorn, Wisconsin, to Benton Ben and Helen West Taylor. No information could be found concerning the family or Taylor's childhood and early education. That the family had moved by the time he reached his teens can be inferred from the fact that he received his secondary education from Throop Polytechnic Institute in Pasadena, California, between 1902 and 1908. This was the same school attended by Joseph Grinnell a few years previously. He then spent one semester at Stanford University before transferring to the University of California at Berkeley, where he received a bachelor's degree in 1911. He continued on at Berkeley in graduate school, marrying Mary E. Fairchild in 1912, and completing his doctorate in zoology in 1914. Both at Throop and at the University of California he was employed while a student.

His first post-doctoral appointment was as Assistant Curator and then Curator of Mammals at the University of California Museum of Vertebrate Zoology under its director, Joseph Grinnell. In 1916, as so many of his colleagues had, he joined the U.S. Biological Survey first as Assistant and subsequently Senior Biologist. He remained full time with the Survey until 1932, when he joined the faculty of the University of Arizona under a cooperative arrangement with the Survey. From 1935 to 1947 he occupied a comparable position at Texas A&M College; during this time, the Biological Survey was transformed to the U.S. Fish and Wildlife Service, and he headed one of the first Cooperative Wildlife Research Units within the Service. He then transferred to Oklahoma State University in Stillwater (then the Agricultural and Mechanical College) where he served as Wildlife Research Unit Leader until 1951, when he retired from federal service. In 1954 he was appointed Professor of Conservation Education and Biology at the Claremont Graduate School of the Claremont Colleges group in southern California. During this time he also taught at LaVerne College, Murray State College, and Southern Illinois University. He retired from this position in 1962, but entered on a second career in politics, serving on the City Council and as Vice-mayor of Claremont.

He was the recipient of many honors, including the Distinguished Service Medal of the Department of the Interior, and the Leopold Award of The Wildlife Society. He was President of The Wildlife Society, Ecological Society of America, and Texas Academy of Sciences, as well as of the ASM.

Although Taylor held a number of different appointments in the course of a long career, his principal focus after he joined the Biological Survey in 1916 was on what would now be called wildlife biology. He was a prolific writer, authoring about 300 scientific and technical papers and pamphlets, and was co-author or editor of several books, including *The Birds of the State of Washington* (1953) and *Deer of North America* (1956).

He died on 29 March 1972, and was survived by his wife, Clara, two sons, and two daughters, one of whom, Elizabeth, married Randolph Peterson (Sources: Cottam, n.d.; Lehmann, 1972; E. Peterson, pers. comm.).

## *Alfred Brazier Howell: 1942–1944*

A. Brazier Howell (Fig. 2) was born on 28 July 1886 in Catonsville, Maryland. His parents were Darius Carpenter and Katherine Hyatt Howell. As a youngster, Howell became interested in birds and egg collecting. At age 13 his mother gave him a bird book by William E. D. Scott inscribed "A. Brazier Howell from Mother," which may have been the reason he later dropped his first name from most of his publications. He married Margaret Gray Sherk in 1914, and they had three daughters and a son. His wife enjoyed the out-of-doors and frequently accompanied him in the field. He died on 23 December 1961 at his home in Bangor, Maine.

Howell's formal college education was limited to a year at Yale after graduation from the Hill Preparatory Boys School in 1905. In 1908 he and his mother moved to Pasadena, California. There he developed a serious interest in research, which began with a study of the birds of the Channel Islands off the southern California coast. In 1911, having sufficient financial means, he purchased a home and small orange grove in Covina, California, where he housed his expanding collections and library. He could afford to spend considerable time in the field, and from time to time he employed collectors, among whom were A. J. Van Rossem, Chester Lamb, and Laurence Huey. In 1918, under the direction of E. W. Nelson, he and Luther Little conducted a collecting expedition in southern Arizona. They were kept out of one area by an uprising of Yaqui Indians. From 1922 to 1928, the Howells lived in Washington, D.C., and Brazier worked as a "dollar-a-year-man" in the Division of Biological Survey with the title of Scientific Assistant. In 1928, he accepted a position in the Department of Anatomy of Johns Hopkins Medical School. He taught gross human anatomy, in which he had never had a formal course, until his retirement in 1943.

Although Howell is best known for his work on mammalian anatomy, his early research was primarily on the distribution, taxonomy, and life histories of birds and mammals. His first anatomical paper, "On the alimentary tracts of squirrels with diverse food habits," appeared in 1925. His best known contribution to mammalian anatomy was the volume *Anatomy of the Woodrat,* which appeared as the first monograph of the ASM in 1926 and remains one of the classics in the field. Among his other important contributions to mammalogy were a revision of the genus *Phenacomys* and the life history of the red tree mouse and a revision of the genus *Synaptomys* published in the *North American Fauna* series.

Howell was a Charter Member of the ASM, and, in addition to the presidency, was a Director, Corresponding Secretary, and member of various committees. He also served on the Council for the Conservation of Whales and other Marine Mammals organized in 1929 under the ASM. A few years before his death he provided an endowment to the ASM for a graduate student award, now designated the A. Brazier Howell Graduate Student Honorarium. He also was active in the Cooper Ornithological Society, serving for some time as an aid to the Business Manager and in managing the endowment fund.

Brazier Howell was a talented artist, as reflected in his anatomical illustrations, a gifted musician, and an accomplished wood worker. Among his other interests were refurbishing old cars, stamp collecting, raising tropical fish, and collecting antiques. He was a quiet, friendly man, but as a result of an inherited hard-of-hearing condition tended to avoid meetings and large groups of people. One of the Bill Hamilton anecdotes concerns A. Brazier Howell. As a graduate student, the well-known Cornell anatomist and shark expert, Perry Gilbert, was greatly impressed by the work of Howell. Thus he was delighted when he came to Hamilton's office one day and found him with a man Bill introduced as his old friend Brazier Howell. After going to great lengths to display his knowledge of anatomy and Howell's research, Gilbert was disappointed that Howell remained silent and seemingly unimpressed. It was not until later that he learned that "Brazier Howell" was a local farmer who had come to ask Hamilton how to get rid of some mammal pest (Source: Little, 1968).

## *Eugene Raymond Hall: 1944–1946*

E. Raymond Hall (Fig. 2) (students and colleagues never called him Eugene) was born on 11 May 1902, in the small town of Imes, in eastern Kansas, a town that no longer appears on most maps. He grew up on the family farm in nearby Le Loup and spent his boyhood helping in farming activities and in fur trapping. After an initial education in rural schools, he spent his final year of high school in Lawrence, Kansas, and then enrolled in the University of Kansas. His first scientific publication, "The First Record of a Golden-Winged Warbler from Kansas," was published in 1921 while he was still an undergraduate majoring in zoology. During his KU years, he was influenced by Remington Kellogg, who, 10 years his senior, had graduated from the university and was then working in the Bureau of Biological Survey in Washington. Kellogg urged him to enroll in graduate studies at the University of California at Berkeley, as Kellogg had. Hall did so, first marrying Mary Harkey, also a University of Kansas undergraduate. At Berkeley, he worked under the direction of Joseph Grinnell, who was to become president of ASM and was Director of the Museum of Vertebrate Zoology. In 1927, still a year short of earning his Ph.D., he became Curator of Mammals in the museum. During the next decade, expanding beyond Grinnell's preoccupation with California, Hall carried out intensive field work on mammals in Nevada. This led to what many regard as his most notable publication, *The Mammals of Nevada,* in 1946. In 1938 he became Acting Director of the Museum of Vertebrate Zoology upon the resignation of the founding director, Grinnell, who died the next year. Hall served as acting director until 1944; in that year he abruptly left Berkeley to return to the University of Kansas as Chairman of the Department of Zoology and Director of the Museum of Natural History, holding the latter position until he retired in 1967. Many have speculated that his sudden departure from Berkeley was occasioned by the failure of the university to name him as Director of the Museum of Vertebrate Zoology during the 6 years he served there in an acting capacity.

At Kansas, he took a museum with a strong tradition and built it into one of the leading research and graduate education museums of natural history in the country. His own productivity was prodigious, resulting in an output of 350 publications before his death at age 84 in 1986. In addition to his other contributions to mammalogy, his major work was *The Mammals of North America,* first published in 1959 and revised in 1981.

He attracted a large number of students to Kansas, many of whom have gone on to make major contributions to the ASM. Hall was respected by many, disliked by some, and feared by a few. He had an exceptionally strong personality, through which he inspired respect and loyalty among his graduate students. Few ever saw Hall's human side, but for those who did, he was a proud father and husband, and loyal friend. "E. Raymond Hall was a farmer, trapper, and naturalist at heart, and a prodigiously successful scientist by profession. He was a uniquely prominent and tremendously influential figure in twentieth century mammalogy" (Findley and Jones, 1989) (Sources: Findley and Jones, 1989; Jones, 1990).

## *Edward Alphonso Goldman: 1946*

Edward A. Goldman (Fig. 2) was born to Jacob and Laura Goltman in Mount Carroll, Illinois, in 1873. His parents were farmers, and little is known about his childhood, although he was presumably educated in rural schools. When he was around 10 years old, his parents left Illinois for Falls

City, in eastern Nebraska, driving 300 head of cattle seeking "greener pastures." Two signal events marked their short residence in Nebraska; Jacob Goltman changed the family name to Goldman and a grasshopper plague resulted in the family losing most of its livestock to starvation. In 1888, the family again resettled, this time in Tulare County, California. No details concerning his schooling in either Nebraska or California could be found, but as was the case with some other early presidents of the society, he was thoroughly self-tutored as a naturalist. His interest in natural history appears to have come from his father, who was himself an amateur student of nature. Goldman was taught to shoot a shotgun while on the Nebraska ranch and began then to collect specimens of birds and mammals, a hobby he continued after the move to California. At age 17 Goldman left home to accept a job as vineyard foreman near Fresno, about 120 km north of the family ranch at Earlimart in the southern San Joaquin Valley. In that same year, there came his fateful meeting with E. W. Nelson, who had been in California participating in the famous Death Valley Expedition of the Bureau of Biological Survey. Nelson had been asked by the survey director, C. Hart Merriam, to conduct a survey of the southern San Joaquin Valley and needed an assistant. He stopped at the Goldman ranch for help in repairing his wagon, learned of Jacob Goldman's interest in natural history, and received the suggestion that son Edward might serve as a field assistant. From this fortuitous meeting came the famous collecting team of Nelson and Goldman.

The first joint expedition was a short one, of about 3 months duration, but it was followed by Merriam's order to collect in western Mexico. What was planned as a 3-month stay in Mexico lengthened to 4 years, during which time Goldman worked his way up from the status of temporary field assistant to a permanent position in the Biological Survey. Together Nelson and Goldman collected in every state and territory in Mexico, obtaining a combined total of nearly 23,000 mammal specimens by the time of Nelson's death in 1934. In addition to Mexico, Goldman worked in many parts of the United States, as well as in Panama, where his results were published as *Mammals of Panama* by the Smithsonian in 1920.

During World War I he entered the U.S. Army, attaining the rank of Major in the Sanitary Corps in France. After the war, he retained his rank in the Sanitary Reserve Corps of the U.S. Army Medical Department until 1937. Although the war had interrupted his work with Nelson, this was resumed until Nelson's retirement in 1929 terminated the active collaboration. The previous year, however, Goldman had been relieved of all administrative duties so that he could carry on the Mexican work, which he did very productively until his retirement at the end of 1944. He continued to work on the "Mammals of Mexico" manuscript until his untimely death from a heart attack on 2 September 1946, which cut short his service as President of the American Society of Mammalogists. He was survived by his widow, Emma May Chase, and three sons, Nelson, Orville, and Luther. The latter followed his father's interest in natural history.

Edward Goldman was one of the small group who had the vision to organize an American Society of Mammalogists during the years immediately following World War I. He published over 200 scientific papers, among them classic volumes on the puma and gray wolf (Sources: Jackson, 1947; Taylor, 1947; Young, 1947).

## *Arthur Remington Kellogg: 1946–1949*

Another midwesterner, Remington Kellogg (Fig. 2), was born in Davenport, Iowa, on 5 October 1892, the son of Claire and Rolla Remington Kellogg. His father was a printer by profession and his mother taught school. When young Remington was 6 years old, his parents moved to Kansas City, Missouri, where, after grammar school, he completed Westport High School, and then enrolled at the University of Kansas in 1910. As an undergraduate at the university, he was strongly influenced by two men, Charles Dean Bunker, who was then Curator of Birds and Mammals in the Museum of Natural History, and Alexander Wetmore, a Kansan who was an upper division student in zoology and who was to become an eminent American ornithologist. While initially interested in insects, Kellogg shifted his focus to marine mammals and paleontology during the course of his undergraduate work. After graduation, he enrolled at the University of California, Berkeley, in 1916. It had taken him 6 years to graduate from Kansas because of the necessity of working to support his college career, but in California he was awarded a teaching fellowship under Dr. John C. Merriam, who was to be another important influence in Kellogg's life. His graduate work was interrupted by World War I, and he enlisted in late 1917. Several months later he was promoted to sergeant and transferred to the Central Medical Department Laboratory, whose commander was Major Edward Goldman and whom he succeeded as President of the American Society of Mammalogists, serving not only Goldman's unexpired term but a regular 2-year term subsequently. Receiving a discharge from the Army in 1919, he returned to the University of California to complete his residence requirements for the doctoral degree and at the end of the fall semester was appointed Assistant Biologist in the Biological Survey. Later that year he married fellow student Marguerite Henrich, and they spent their entire married life in Washington, D.C., until his death from a heart attack at age 77, in 1969.

Around the same time that Kellogg joined the Biological Survey, his former mentor John C. Merriam accepted appointment as President of the Carnegie Institution in Washington. Merriam arranged for Kellogg to be made a Research Associate of the Institution, a position he held from 1921 until 1943. This arrangement allowed Kellogg to receive funding from Carnegie to pursue his research on marine mammals at the same time that he carried out assigned projects for the Biological Survey. This in turn allowed Kellogg to complete the research necessary to write his dissertation, which completed the requirements for his Ph.D.from the University of California in 1928. That same year, Kellogg left the Biological Survey to fill a position of Assistant Curator of Mammals at the U.S. National Museum. Under Gerritt S. Miller's supervision, Kellogg was able to devote more time to marine mammals, and he became recognized as the American authority. As a result he found himself in 1937 with an appointment by the Department of State as U.S. Delegate to the International Conference on Whaling, the forerunner of the International Whaling Commission (IWC). Further appointments followed in 1944–1946, and he served as Commissioner of the IWC from 1949 until 1967, being Chairman from 1952 to 1964.

In 1948, Kellogg was appointed Director of the U.S. National Museum, and 10 years later, Assistant Secretary for Science of the Smithsonian Institution. His heavy administrative burdens deprived him of the time he was used to spending on research, but he still attempted to spend several hours a day on his own research projects. As an administrator, his tenure in both the museum and the Office of the Assistant Secretary were characterized by an innate negativism that led him to be referred to at times as the "abominable no man" (Source: Setzer, 1977).

## *Tracy Irvin Storer: 1949–1951*

Like many presidents of the ASM, Tracy I. Storer (Fig. 2) had a wide array of interests beyond the study of mammals. He was also well known as an ornithologist and herpetologist, published in the field of wildlife management and animal control, and authored the most successful general zoology text of its time. He was born in San Francisco, California, on 17 August 1889 and grew up in Elmhurst, south of Oakland. He and his brother were raised by their father, his mother having died when he was 9 years old. Tracy went to local public schools, and in 1908 at the age of 18 entered the University of California at Berkeley. He received his bachelor's degree in zoology with honors in 1912 and his master's degree the next year. He worked his way through college as a printer, primarily of handbills and cards, and his well known frugality was undoubtedly instilled by the often straitened financial circumstances of his motherless boyhood. Upon completion of his master's degree he was hired as an assistant by Charles Koford in Berkeley's Department of Zoology but transferred the next year to the staff of the Museum of Vertebrate Zoology, established five years previously and directed by Joseph Grinnell. With the financial support of Annie M. Alexander, Grinnell had mapped out several ambitious projects. Storer's first assignment was to work with Grinnell and Harold Bryant on a project that resulted in the publication of *The Game Birds of California* in 1918. While this was going on, Storer, along with Walter P. Taylor and a number of others, began field work on an ambitious transect survey across the Sierra Nevada in the region of Yosemite National Park. This field work was interrupted by World War I, during which Storer served in the U.S. Army Sanitary Corps in Texas; his commanding officer was his former employer, Koford. Upon his return from the Army he resumed the Yosemite survey, completing field work in 1920 and then drafting the report, which he and Grinnell completed as *Animal Life in the Yosemite* in 1924.

Storer had married Ruth Risdon just before his Army tour. His wife, one of the first women graduates of the University of California Medical School, suffered from tuberculosis during the first years of their marriage, which further strengthened Storer's habits of frugality. In order to fund field work for his doctoral dissertation, Storer accumulated vacation time for 6 years, and his doctoral dissertation on *Amphibia of California* earned him a Ph.D. in 1924, just as he and Grinnell completed the Yosemite work.

With these two milestones achieved, Storer accepted a position at the University of California at Davis as the first member of its new Division of Zoology. The appointment was not only as Assistant Professor but also as Assistant Zoologist in the Experiment Station, and his research henceforth focused on control and manipulation of vertebrate population densities—wildlife management and pest control. After a decade, undergraduate enrollment in zoology at Davis had increased so much that additional faculty could be added to his one-person division. When a program in wildlife management that he had sought for the expanding division was instead awarded to the Berkeley campus, Storer turned his attention to undergraduate teaching and wrote a text first published in 1943 with the title *General Zoology*. The book, with its systematic organization, profuse illustration, and large information content, quickly came to dominate the freshman zoology market, and made Storer relatively wealthy. At the same time, the book and its many subsequent editions and associated teaching aids came to usurp much of his time. He nevertheless continued to produce a steady flow of short papers and reviews, as well as several major monographs, most notably those on the California grizzly in 1955 and on Pacific Island rat ecology in 1963.

The Storers were childless. While he was frugal, Tracy Storer was generous. In addition to gifts to U.C. Davis, he also remembered the ASM in his will with a large bequest, which has become a major portion of the trust funds administered by the society. He died from a heart attack on 25 June 1973 at age 84 (Source: Salt and Rudd, 1975).

## *William John Hamilton, Jr.: 1951–1953*

William J. Hamilton, Jr. (Fig. 2), was born on 11 December 1902 in Corona, New York, the son of William J. Hamilton and Charlotte Richardson Hamilton. Bill, as he was known to all, was a quintessential naturalist, whose interest in natural history stemmed from the experience of caring for a plant he received as a gift when he was 7 years old. Gardening and horticulture remained a major avocation throughout his life. Bill met his future wife, Nellie Rightmyer, when she took a class in which he was an instructor. They were married in 1928 and had three children, Ruth, June, and William J. III, who also is a well-known zoologist. Bill was commissioned a captain in the U.S. Army Medical Corps in 1942 and worked on rodent and typhus control problems and as one of the military governors of Manheim, Germany, after the war. He was discharged in 1945 with the rank of Major.

He received all of his degrees from Cornell University, including a B.S. in 1926; M.S. in entomology in 1928; and a Ph.D. in vertebrate zoology in 1930. His major professor for the doctorate was the herpetologist Albert H. Wright, and his doctoral thesis was on the life history of the star-nosed mole.

In 1930, he was appointed Instructor in Zoology in the New York State College of Agriculture at Cornell, where he remained for his entire career. He became Assistant Professor in 1937, Associate Professor in 1942, Professor in 1947, and Professor Emeritus upon his retirement in 1963. At various times he was a member of the departments of Entomology, Zoology, and Conservation (now Natural Resources). He taught vertebrate zoology, mammalogy, herpetology, literature of vertebrate zoology, economic zoology, and conservation and served as major professor of over 60 graduate students in mammalogy and herpetology.

Bill's principal research interests were the ecology and life history of mammals. Much of his work was done in New York, reflecting his belief that one did not have to go to far off places to find interesting and significant problems to study. Among his major contributions were studies on microtine cycles, food habits of mammals and other vertebrates, and various aspects of reproductive biology. He also published life history accounts for a substantial proportion of eastern United States mammals. In addition to over 200 papers, he authored *American Mammals,* the first textbook in mammalogy, and *Mammals of Eastern United States* and was coauthor of *Conservation in the United States.*

His professional honors included election as an Honorary Member of the ASM and as a Fellow of the American Association for the Advancement of Science, New York Academy of Sciences, and the Royal Horticultural Society of England. He also was the recipient of the LePiniec Award from the American Rock Garden Society and the Outstanding Alumni Award from Cornell University.

He joined the American Society of Mammalogists in 1924. In addition to the presidency, he was Vice-president, a Director, and a member of numerous committees. He was also Secretary and President of the Ecological Society of America and Zoological Editor of *Ecological Monographs.* He served on the Environmental Biology Panel of the National Science Foundation and as Chairman of the Scientific Advisory Committee of the E. N. Huyck Preserve and for many years was a Research Associate in the Department of Mammalogy of the American Museum of Natural History.

Bill Hamilton was one of the most colorful of the mammal society presidents. His sense of humor, which earned him the title "Wild Bill," was legendary. He was able to weave the most outlandish tall tales into a conversation with such apparent sincerity that the listener often did not realize he was joking. He died at his home in Ithaca, New

York, on 27 July 1990 (Source: Layne and Whitaker, 1992).

## *William Henry Burt: 1953–1955*

Like several other presidents of the ASM, William H. Burt (Fig. 3) was born and raised in Kansas. He was born on 22 January 1903 in Haddam, near the border with eastern Nebraska. His parents were Frank and Hattie Burt, and no references to siblings have been found. He grew up on the Burt farm, but was reticent to talk about his early years. He did, however, comment once that his observations of prairie dogs on the family farm were the basis of his later thoughts on territoriality and home range in mammals, the field in which he made a singular contribution to biology. He attended the University of Kansas, graduating in 1926; he was thus an undergraduate together with E. Raymond Hall. He completed a master's degree at Kansas in its Museum of Natural History in 1927, after which, like Hall, he enrolled in graduate school at the University of California, Berkeley. He began graduate work in paleontology, even though his earlier interest had been in ornithology and mammalogy. In 1928 and 1929, he was awarded a research fellowship at the California Institute of Technology, which allowed him to complete his doctoral dissertation on the morphology and evolution of woodpeckers, and he was awarded a Ph.D. by the University of California in 1930. While in graduate school, he married Leona Suzan Galutia.

His doctorate was awarded at the beginning of the Great Depression, and Burt remained at Cal Tech as a research fellow for 6 years working on a variety of projects. In 1935, he was awarded a tenure-track position at the University of Michigan, where he remained for the rest of his career. He also held a joint appointment as Curator of Mammals in the Museum of Zoology there. His career at Michigan was marked by the mentoring of over 20 graduate students, many of whom have become important mammalogists in their own right. He successfully guided the growth of the mammal collections of the Museum of Zoology to their current level of excellence. He also published pioneering studies on territorial behavior and home range in mammals. In addition to his scientific publications, he authored *A Field Guide to the Mammals,* which with its illustrations by Richard Grossenheider, became a best-selling classic.

Burt retired in 1969 and took up residence in Boulder, Colorado, where he continued his scientific studies as Honorary Curator and Lecturer at the University of Colorado Museum. He and his wife also were able to indulge in the foreign travel they both loved until her death in 1973. He died in 1987 at the age of 84. His alma mater, the University of Kansas, was bequeathed the royalties from his field guide (Source: Muul, 1990).

## *William B. Davis: 1955–1958*

William B. Davis (Fig. 3) was born to Bennoni Washington Davis and Mary Ann Matilda (Owens) Davis on 14 March 1902 in Rexburg, Idaho, a small agricultural and lumber community on the Snake River about 50 miles southwest of Yellowstone National Park. His father and grandfather operated a small sawmill east of Rexburg. When Bill was 3 years old his father was killed in an accident at the sawmill. This tragedy left Bill's mother with two small children and no visible means of support. Fortunately she was a competent cook so she spent the next 2 years cooking for mining crews in northern Utah. In 1907 she found employment as a cook in a new boarding house and hotel in Rupert, Idaho, a small community in an irrigation project on the north side of the Snake River. Bill received all of his elementary and high school education there and graduated in February 1920.

At that time Idaho law permitted high


William H. Burt
(1953–1955)


William B. Davis
(1955–1958)


Robert T. Orr
(1958–1960)


Stephen D. Durrant
(1960–1962)


Emmet T. Hooper
(1962–1964)


Donald F. Hoffmeister
(1964–1966)


Randolph L. Peterson
(1966–1968)


Richard G. Van Gelder
(1968–1970)


James N. Layne
(1970–1972)

FIG. 3.—Presidents of the ASM from 1953 to 1972.

school graduates to qualify for a teaching certificate upon completion of two summer school courses at a normal college. Bill was not enthused with the labor involved in farming, so he followed the suggestion of his fiancée and qualified for a grade three teaching certificate. That autumn he began his teaching career in a rural school near St. Anthony, Idaho. During the next 13 years he alternated going to summer school and teaching in elementary schools in Idaho, Washington, and California, ranging from a single-room school with seven students in six grades to a three-room school where he was principal and teacher of the sixth to eighth grades. On 21 April 1923 he married Pearl Kathryn Tansey, and they have two children, a daughter, LaNell, and a son, Robert Lee.

In 1932, Bill matriculated at Chico State College in California, where he received a B.A. in Education in 1933. However, even before entering college, he had developed a professional interest in ornithology. His first paper is dated 1923, and by the time he had finished at Chico State he had published 10 papers, all but one on birds, based on observations made during the course of his teaching career.

His association with the University of California at Berkeley began the summer after he completed his B.A., when he served as a field assistant to E. R. Hall in Nevada, a position also held by Bob Orr. Dr. Joseph Grinnell agreed to chair Bill's graduate committee if he switched his research to the field of mammalogy. This appears to have been the stimulus that turned him from birds to mammals, and in the following four summers he conducted his graduate field work in Idaho, collecting mammals throughout the state, while supporting himself by working as a graduate assistant in the Department of Zoology. His dissertation, *The Recent Mammals of Idaho,* was published in 1939, 2 years after he received his Ph.D. By that time he had also published an additional 26 papers, mostly based on work done while a graduate student. It is interesting to see the increasing emphasis on mammals in his scholarly output during this period.

Upon completing his doctorate, Bill accepted a professorship in the Department of Wildlife Science at Texas A&M University. The following year (1938) he became Curator of the Texas Cooperative Wildlife Collections. He also served as Head of the Department from 1947 to 1965. During his academic career, he supervised the theses and dissertations of many well-known mammalogists. Upon his retirement from administration, he received the Governor's Award for Outstanding Service in Conservation Education.

He first became active as an officer of the ASM in 1937, as Corresponding Secretary, which he held for 3 years. He was elected President in 1955, and re-elected in 1956 and 1957. He was appointed Chairman of the Board of Trustees, strong evidence of his colleagues' confidence in his judgment and financial acumen. Bill remained active in research following his retirement in 1967, and to date has published a total of 188 scholarly contributions. Failing eyesight finally forced him to curtail his scholarly activities, but his interests remain strong. He now lives quietly with his second wife of 8 years, Leola, in Bryan, Texas. She has two children by a former marriage.

## *Robert Thomas Orr: 1958–1960*

Robert T. Orr (Fig. 3) recently told a friend and colleague that he has always considered himself "a real naturalist, not a specialist." He attributed his initial interests in the out-of-doors to his physician father who took the whole family camping and encouraged him to hunt and fish. Bob was born on 17 August 1908 in San Francisco, California, to Robert H. and Agnes K. Orr; he was one of three children. His grandfather had a ranch in Tehama County, and Bob spent many vacations while growing up collecting vertebrates on the ranch, although it is not clear where those specimens were deposited, if they still survive. After grammar and high school in San Francisco, he enrolled in the University of San Francisco, receiving a Bachelor of Science in 1929. One of his teachers there, George Haley, was a personal friend of Joseph Grinnell at the University of California, Berkeley, to whom he introduced Orr. It was natural then that Bob should enroll in graduate school at Berkeley, receiving a master's degree in 1931. At this time, E. Raymond Hall was also in the Museum of Vertebrate Zoology, and employed him in field studies on the mammals of Nevada, which Hall later published through the U.C. Press. He also was befriended there by Alden Miller, the highly respected ornithologist who was to become director of MVZ after Grinnell's death. Bob accompanied Miller on collecting trips, and credited Miller with teaching him the fundamentals of field ornithology, whose study he pursued throughout his career.

His doctoral research was on the rabbits of California and was supervised by Grinnell. He received the Ph.D. in 1937, 2 years after he had accepted a position as Wildlife Biologist with the National Park Service with assignments at various places in central California. In 1936 he began a lifetime association with the California Academy of Sciences when he was appointed Assistant Curator in the Department of Ornithology and Mammalogy, ultimately being awarded its Fellow's Medal in 1973.

Although his work prior to his doctoral dissertation was primarily on terrestrial mammals, his research interests at the Academy began to focus on marine mammals, although he continued to publish widely in both ornithology and mammalogy. His advancement at the California Academy of Sciences was steady, and he was named Full Curator in 1945, a rank he held for 30 years until his retirement. He also assumed the additional administrative duty of Associate Director in 1964 at the request of George Lindsay, whom he had supported for the directorship. Those additional duties finally forced him to terminate his courtesy teaching appointment at the University of San Francisco, which he had begun as an Assistant Professor of Biology in 1942, again rising through the ranks to Full Professor in 1955. Upon his retirement in 1975, he was named Senior Scientist and Curator Emeritus at the Academy. He has continued to publish, and his total bibliography now amounts to 267 titles. Only about one in ten were co-authored, one with his wife, Margaret C. Orr. They have one daughter.

Bob has been honored as a Fellow and Honorary Member by a number of scientific societies and conservation organizations, including the American Association for the Advancement of Science, American Ornithologists' Union, and Explorers Club of New York.

## *Stephen David Durrant: 1960–1962*

Stephen D. Durrant (Fig. 3) was born 11 October 1902 in Salt Lake City, Utah, the son of Stephen Thomas and Martha Harman Durrant. Following graduation from high school he spent several years (1922–1925) in Europe, mainly in Switzerland, on a mission for the Church of Jesus Christ of Latter-day Saints. During the summer of 1933 while taking a course at the University of California at Berkeley, he met Sylvia Jane Burt, who was vacationing there from Salt Lake. They were married that December. They had two children, a daughter, Sue Marilyn, and a son, Stephen Carl.

Steve began his undergraduate work at Weber Junior College, then transferred to the University of Utah, where he received the A.B. degree, with a major in Modern Languages (French), in 1929. As a result of courses taken with William W. Newby, who also taught him to prepare mammal skins, he decided to major in zoology for his Master's degree, which he received in 1931. He began doctoral work at the University of Minnesota but after a year (1931–1932) accepted an offer to return to the University of Utah as an instructor in comparative anatomy. While a full-time faculty member, he began doctoral work in mammalogy with E. R. Hall, first at the University of California at Berkeley (1938–1939) then at the University of Kansas when Hall moved there. He received his doctorate in 1950 and remained at the University of Utah for his entire career, rising from Assistant Professor to Professor.

Steve's research dealt primarily with the distribution and systematics of Utah mammals. The genus *Thomomys* was a favorite subject. Of 37 new subspecies named by him and collaborators, 15 were pocket gophers. He spent most of his summers in the field, often traveling by horseback. He participated in the Upper Colorado River Basin Surveys from 1958 to 1962, serving as Field Director and mammalogist. His years of field work, during which he and graduate students amassed some 27,000 specimens, and his intimate knowledge of the mammalian fauna of Utah were reflected in his book *Mammals of Utah, Taxonomy and Distribution.*

Steve excelled as a teacher and, although a tough taskmaster, was revered by his students. His comparative anatomy course had the reputation of being both one of the best and hardest courses on campus. Mammalogy was offered once a year and was such a popular course that enrollment had to be limited. He had 36 graduate students, a number of which earned both master's and doctorates under his direction.

Steve joined the ASM in 1934. In addition to the presidency, he was a Director and Vice-president. The International Relations Committee, one of the most productive in the Society, was formed during his tenure as president. He also served as a member, often chairman, of six standing committees. He participated in other scientific societies, including serving as President of the Pacific Division of the Society of Systematic Zoology in 1956. Among honors received during his career were election as Honorary Member of the ASM; the Distinguished Teaching Award from the University of Utah; the Distinguished Service Award from the Utah Academy of Sciences, Arts and Letters; and the establishment of the Stephen D. Durrant Memorial Scholarship at the University of Utah. Perhaps his most cherished honor was a bronze casting of a pocket gopher presented to him by graduate students and members of his last classes in comparative anatomy and mammalogy.

Steve was a warm and jovial person and a superb raconteur—a skill honed during many hours around a campfire with students and colleagues. He was an ardent duck hunter and a crack shot. He died on 11 November 1975, and his remains after cremation were deposited near his favorite blind on Salt Lake where he had hunted for many years (Source: Behle, 1977).

## *Emmet Thurman Hooper, Jr.: 1962–1964*

Emmet T. Hooper (Fig. 3) was another of the many mammalogists inspired by Joseph Grinnell to pursue a professional career in biology. He was born 19 August 1911 in Phoenix, Arizona, the eldest of two children, to Emmet Thurman and Frances Jewell (McDonald) Hooper. His elementary schooling was in Phoenix, but after he had finished a year of high school, the family moved to San Diego, California. Completing high school in that city, Emmet then enrolled in San Diego State University at the somewhat precocious age of 17. For his senior year, however, he transferred to the University of California at Berkeley where he came within the sphere of Joseph Grinnell and the Museum of Vertebrate Zoology. Completing his bachelor's degree in 1933, he then continued his graduate studies, receiving a master's degree in 1936 and his Ph.D. in 1939. His doctoral dissertation focused on geographic variation in woodrats of the San Francisco Bay region. While at Berkeley, he also worked as a part-time assistant in the U.S. Bureau of Fisheries.

He married Helen Bacon while a graduate

student, and they had two sons, Alan and Kim. Shortly before completing his doctorate, Emmet accepted what appears to have been a non-tenured position at the University of Michigan Museum of Zoology, where he began a long professional association with fellow U.C. Berkeley graduates Bill Burt and Lee Dice. His tenure at the University of Michigan was interrupted by World War II, and he spent 4 years in the U.S. Army Air Corps, attaining the rank of Captain by the time of his discharge in 1946. He returned to the University of Michigan in that year and remained at the Museum of Zoology as Professor and Curator until his retirement in 1978. During those 3 decades, he served as major professor for many graduate students who have gone on to distinguished careers in mammalogy. His own research, published in 85 papers and monographs, was principally on the muroid rodents, especially their morphology and systematics.

Having lost his wife of 40 years in 1976, Emmet made the decision to relocate following his retirement from the University of Michigan and accepted a position as leader of the sea otter research program of the U.S. Fish and Wildlife Service at the Center for Marine Studies, University of California, Santa Cruz. He was very active in retirement, not only scientifically but in public service as well, serving as Commissioner of the Santa Cruz Museum and member of the Citizens Advisory Committee for Nisenemarks State Park. In 1983 he remarried, to Leanore Theriot, and they resided in Aptos, California, until his death on 28 June 1992 (Sources: Anon., 1988, 1992).

## *Donald Frederick Hoffmeister: 1964–1966*

Donald F. Hoffmeister (Fig. 3) was born in San Bernardino, California, on 21 March 1916, and spent his youth in southern California. Although his parents moved to California from Iowa in 1906, his paternal grandfather had gone to California in the gold rush of 1849. Don and his wife, the former Helen Kaatz, were married in 1938 and have two sons, Robert and Ronald.

Don took his first 2 years of undergraduate work at San Bernardino Junior College and received his A.B. from the University of California, Berkeley, in 1938. Following in the footsteps of his grandfather and encouraged by his parents, Don originally intended to become a medical doctor. However, as the result of the influence of Dr. Elton R. Edge, one of his instructors in junior college who had taken a field trip in Nevada with E. R. Hall, and a course in vertebrate zoology taught by Joseph Grinnell and Hall, which he took in his senior year, Don decided to switch from medicine to mammalogy even though he had already been accepted to medical school. He remained at Berkeley for graduate study with E. R. Hall, who had a profound influence on his scientific career. He received the M.A. in 1940 and the Ph.D. in 1944. During his graduate work, he held a Teaching Assistantship and also served as Technical Assistant and Research Assistant in the Museum of Vertebrate Zoology.

In 1944 he was appointed Assistant Professor and Assistant Curator of Modern Vertebrates at the University of Kansas, and in 1946 went to the University of Illinois as Assistant Professor and Assistant Curator in the Museum of Natural History, where he remained for the remainder of his career. He became Associate Professor in 1956, and Professor in 1959. He was promoted to Curator, with responsibility as director, in the Museum of Natural History in 1948 and was given the official title of Director of the museum in 1964. Upon his retirement in 1984, he was appointed Emeritus Director and Professor. In addition to his research, administration, and teaching, he served as chairman of 14 Ph.D. and 18 master's students. Two of his students are themselves past-presidents of ASM.

Don's research has dealt primarily with the distribution and taxonomy of mammals, with emphasis on Arizona and Illinois. However, his publications include a distributional note and study of growth and development of birds and papers on life history and ecology, pelage coloration, and various aspects of anatomy of mammals. He has also described a number of mammalian taxa. He is the author or coauthor of a number of semipopular and technical books on mammals, including *Mammals/A Guide to Familar American Species* with H. S. Zim, *Handbook of Illinois Mammals* with C. O. Mohr, *Fieldbook of Illinois Mammals* with C. O. Mohr, *Mammals of the Grand Canyon, Mammals of Illinois,* and the monumental *Mammals of Arizona.* Sources of support for his work include the National Science Foundation, National Institutes of Health, Illinois Department of Conservation, Arizona Fish and Game Department, and the Max McGraw Wildlife Foundation.

Don became a member of the ASM in 1938. Other elective offices he held in addition to the presidency include Director, Corresponding Secretary, and Vice-president. He was appointed in 1966 as the society's first Historian and continues to serve in that capacity. He was a member of five, and chairman of three, standing committees and also chaired special committees on Subscriptions to the *Journal of Mammalogy* and Reprinting of the *Journal of Mammalogy.* Offices he has held in other professional organizations include President of the Midwest Museums Conference, Chairman of the Zoology Section and Councillor of the Illinois State Academy of Science, Councillor of the American Association of Museums, and Associate Editor of *The American Midland Naturalist.*

In recognition of his outstanding service to the ASM, Don was awarded Honorary Membership in 1982 and the Hartley H. T. Jackson Award in 1986. Among his other professional honors are Honorary Membership, Midwest Museums Conference; appointment to the Governor's Board of the Illinois State Museum; and appointment as Research Associate of both the Museum of Northern Arizona and the Northern Arizona Society of Science and Art.

The second meeting of the society outside the United States was held in Winnipeg, Canada, during Don's presidency, and in what was probably a first for an ASM president he was made an Honorary Citizen of Winnipeg by Royal proclamation.

## *Randolph Lee Peterson: 1966–1968*

Randolph L. Peterson (Fig. 3) was born on 16 February 1920 in Roanoke, Texas, one of five children of Omas and Margaret Francisco Peterson. Pete, as he was known to his friends and colleagues, spent his youth on the family farm, where he developed an interest in natural history, particularly mammals, plants, and ecology. In 1942 he married Elizabeth Fairchild Taylor, the daughter of the well-known mammalogist Walter P. Taylor, who was Pete's mentor. They had one daughter, Penny Elizabeth. In addition to her role as wife and mother, Elizabeth participated with Pete in running a biological supply business and helped as his research assistant. During World War II, Pete served in the U.S. Air Force as pilot and instructor and Operations Officer with the Mediterranean Allied Air Force.

He obtained his B.Sc. in 1941 in the Department of Fish and Game at Texas A&M University. During his undergraduate years he served as Assistant Curator of the Texas Cooperative Wildlife Research Collection under William B. Davis. He began graduate studies at Texas A&M, but went into service before completing his degree. After the war, he entered the graduate program of the University of Toronto under J. R. Dymond and received the Ph.D. in 1950.

While at the University of Toronto, Pete served as Acting Curator in Charge of the Mammal Division of the Royal Ontario Museum and upon receiving his degree was appointed Curator-in-Charge of the Department of Mammalogy of the Museum, a position he held until retirement in 1985. He was also on the faculty of the University of Toronto, as Special Lecturer in the Department of Zoology (1949–1962), Associate Professor (1962–1968), and Professor (1968–1985). Upon retirement he was appointed Curator Emeritus in the museum and Professor Emeritus in the university. He died on 29 October 1989.

Pete's doctoral research was on the biology of the moose and was published as the book *North American Moose* in 1955. This was one of the most definitive studies of the species and has been reprinted several times. He also directed a survey of the mammals of Ontario and Quebec, which culminated in his second book, *Mammals of Eastern Canada,* in 1966. Bats became a consuming research interest later in his career and over a third of his publications deal with the taxonomy, distribution, habitats, and habits of bats, including descriptions of five new species. He led expeditions to many areas in North America and Mexico and abroad and built one of the largest and most complete collections of bats in the world at the Royal Ontario Museum.

As Curator-in-Charge of mammalogy at the museum, he supervised the renovation and expansion of the department's office and collection space. He also served as Editor and Chairman of the Life Sciences Publications and was a member of the Promotion and Tenure Committees. As Professor of Zoology he taught mammalogy and directed the work of eight doctoral and eight master's students, in addition to serving on the graduate committees of many others.

Pete joined the ASM in 1940 and attended 50 consecutive meetings. Besides the presidency, he was a Director, Recording Secretary, and Vice-president, in addition to serving as chairman and member of numerous committees. He played a key role in the establishment of the Future Mammalogists Fund and in 1986 was awarded Honorary Membership. His participation in other scientific organizations included serving on the boards of the Metropolitan Toronto Zoological Society and the Metropolitan Toronto Zoo and as Councillor of the Society of Systematic Zoology.

In addition to his active and productive professional life, Pete pursued interests in gardening, farming, wood-working, and oenology. In the 1950s, he and Elizabeth started a thriving biological supply company and operated it until 1974. He also invented such items of equipment as automated calipers for measuring specimens, a cider press, and a large skeleton cleaning apparatus.

Pete was a man of contrasts. When necessary, he was rough and ready, as might be expected given his Texas origins, but on other occasions he was the perfect country gentleman (Source: Eger and Mitchell, 1990).

## *Richard George Van Gelder: 1968–1970*

Richard G. Van Gelder (Fig. 3) was born in New York City on 17 December 1928, the son of Joseph and Clara DeHirsch Van Gelder. Despite growing up in an urban environment, he developed an avid interest in natural history at an early age. Upon graduation from the Horace Mann School in New York with honors in biology and Spanish, he entered Colorado A&M College. He received a B.S. with honors in 1950, then attended graduate school at the University of Illinois at Urbana, where he worked with Donald F. Hoffmeister. Dick received the M.S. in 1952 and Ph.D. in 1958. During graduate school, he spent one summer at the Marine Biological Laboratory at Woods Hole. He was married in 1962 to Rosalind Rudnick, and they have three children: Russell Neil, Gordon Mark, and Leslie Gail. His son Russell probably holds the record of being the youngest person ever to join ASM, as Dick took out a life membership for him when he was a baby.

Dick served as Curator in the Natural History Museum of Colorado A&M College in 1948–1949 and was an Assistant in the Mammal Department of the American Museum of Natural History in 1952. He was a Research Assistant in the Museum of Natural History of the University of Kansas from 1954 to 1956 and an Assistant Professor in 1955–1956. In 1956, he was appointed Assistant Curator in the Department of Mammals of the American Museum of Natural History and was promoted to Associate Curator in 1961 and Curator in 1969. He also served as Acting Chairman of the Mammal Department in 1958–1959 and as Chairman from 1959 to 1974. He retired in 1986. During his tenure at the American Museum, Dick also held appointments as Instructor and Assistant Professor at Columbia University; Adjunct Graduate Advisor at Albert Einstein Medical College, Columbia University, New York University, and City College of New York; and Professorial Lecturer at Downstate Medical Center of the State University of New York.

Dick's areas of research reflect his broad interests in mammals, including mammal populations and physiology; taxonomy of carnivores, marine mammals, bats, artiodactyls; behavior; hybridization and speciation; color patterns, and mammals of New Jersey. He also has published on other vertebrates, including amphibians, reptiles, and birds. He has conducted field work in many parts of North America, as well as Mexico, Uruguay, Bolivia, Bahamas, Mozambique, Botswana, and South West Africa. Skunks were one of his favorite groups, and he published a definitive revision of the spotted skunks in 1959, as well as a number of other papers and semipopular articles on the taxonomy, morphology, behavior, and habits of skunks. In later years, he worked on the behavioral ecology of African ungulates and directed a cooperative study of the status of mammals of New Jersey. He was author of the books *Biology of Mammals, Mammals of the National Parks,* and *Animals and Man, Past, Present, Future*; coauthor of *Animals in Winter*; and coeditor of *Physiological Mammalogy* volumes I and II. In addition to research, he directed graduate students in areas of mammalian anatomy, behavior, and history and was active in the Museum's exhibits program, playing a lead role in the design, construction, and installation of the blue whale model that dominates the Hall of Fishes. He recounted his experience with the latter project in the humorous article "Whale on my back" published in *Curator.* Dick also taught adult education courses at the museum for many years.

Dick joined the ASM in 1948. Besides the presidency, he served as Director, Vice-president, and Recording Secretary. As chairman of the Committee on Recent Literature, he edited the Recent Literature section of the *Journal of Mammalogy* from 1965 to 1968. He also was a member of many other committees. The office of Historian was established during his presidency.

Among other appointments, Dick was a member of the Board of Directors of Archbold Expeditions; a Director of the Quincy Bog Natural Area in New Hampshire; a member of the Board of Education, Harrington Park, New Jersey; and a member of the Technical and Editorial Advisory Board of the Population Reference Bureau.

## *James Nathaniel Layne: 1970–1972*

James N. Layne (Fig. 3) was born on 16 May 1926 in Chicago, Illinois, to Harriet (Hausman) and Leslie J. Layne. He grew up in what Chicagoans call the "near north side," Irving Park and Rogers Park. When he was 6 years old, his father left the family, and he and his younger brother were raised by his mother through the difficult days of the Great Depression. Despite the hard times, his mother encouraged his growing interest in natural history. By age 12 he had become an enthusiastic falconer, and his high school years were spent capturing and training hawks, and spending many hours observing raptors in the Cook County Forest Preserves. His high school biology teachers Doris Plapp and Susan Arenberg also encouraged his passion for raptors, taking him on field trips and, together with his English teacher Fred Thompson, encouraging him to write. His first scientific paper, published in 1943 in the *Illinois Audubon Society Bulletin,* was completed while he was still in high school.

Upon his graduation in 1944, Jim enlisted in the Army Air Force and served until after World War II, being discharged in 1946. While stationed in the southeastern U.S., he met Philip S. Humphrey, the well-known ornithologist who now directs the University of Kansas Museum of Natural History. Through his influence, Jim developed a broad interest in birds and was committed to ornithology when he enrolled in Cornell University in 1947 after a freshman year at Chicago City Junior College. However, during his sophomore year he took the vertebrate zoology course taught by Ed Raney and Bill Hamilton, and henceforth fishes and mammals also competed for his interest. He completed his B.A. degree in 1950 still uncommitted to a particular vertebrate group, until Hamilton offered him an assistantship to work on mammals. In that year, he not only acquired a mentor, but also a wife when he was married to Lois Linderoth; they have five children, all daughters: Linda, Kimberly, Jamie, Susan, and Rachel.

Jim continued to publish during his Air Force and undergraduate as well as graduate careers, producing 15 more papers by the time he completed his Ph.D. in 1954. His dissertation on the biology of the red squirrel was published in that year, and he accepted an assistant professorship in the Department of Zoology and the Cooperative Wildlife Research Laboratory at Southern Illinois University in Carbondale. The next year he moved to the University of Florida in Gainesville where he held both an academic and a curatorial appointment (Assistant and Associate Professor of Biology and Assistant and Associate Curator in Charge of Mammals in the Florida State Museum) until 1963. This was a productive period for him, with papers in a number of different disciplines of mammalogy, and supervision of graduate students. Nonetheless, in 1963 he heeded the call from his alma mater and returned to Cornell for 4 years as Associate Professor of Zoology, only to reverse his course in 1967 and return to Florida as Director of Research at the Archbold Biological Station in Lake Placid, Florida, with a concurrent appointment as Archbold Curator of Mammals in the American Museum of Natural History. From 1976 to 1985 he served as Executive Director of the station, and now continues as Senior Research Biologist there. His research has continued unabated, not only over a broad field of mammalian topics, but extended to all aspects of the natural history of Florida.

His contributions to the ASM, beginning with his service on the Committee on Marine Mammals in 1959, are many and varied, including membership and chairmanship of many other committees, long service on the Board of Directors, and Editor of *Special Publications.* In 1976, he received the C. Hart Merriam Award and in 1993 was elected an Honorary Member. His activities in other professional organizations include the presidency of the Organization of Biological Field Stations and Florida Academy of Sciences. He has also served on a number of boards of environmental organizations and advisory committees of the Florida Game and Fresh Water Fish Commission, U.S. Fish and Wildlife Service, and other governmental agencies.

## *J. Knox Jones, Jr.: 1972–1974*

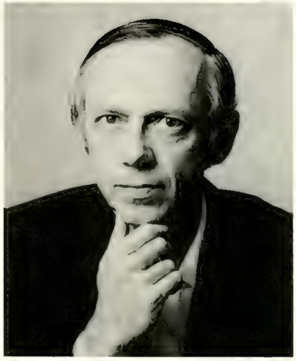
J. Knox Jones, Jr. (Fig. 4) was born in Lincoln, Nebraska, on 16 March 1929. He was married to Marijane Rountree Davis in 1989. Knox had three daughters, Amy, Sarah, and Laura, from an earlier marriage to Janet Glock. He was an officer, with terminal rank of Captain, in the U.S. Army and served on active duty in Korea and Japan from 1953 to 1955 and in the reserve from 1956 to 1965.

Knox received his B.S. in 1951 from the University of Nebraska and both his M.A. (1953) and Ph.D. (1962) degrees under E. R. Hall from the University of Kansas.

In 1962 he was appointed Assistant Professor of Zoology and Assistant Curator of Mammals in the Museum of Natural History, University of Kansas, and was promoted to Associate Professor and Associate Curator in 1965 and Professor and Curator in 1968. While at Kansas, he also served as

J. Knox Jones, Jr.
(1972–1974)

Sydney Anderson
(1974–1976)



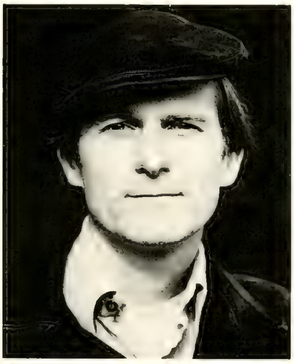
William Z. Lidicker, Jr.
(1976–1978)

Robert S. Hoffmann
(1978–1980)

James S. Findley
(1980–1982)

J. Mary Taylor
(1982–1984)

Hugh H. Genoways
(1984–1986)



Don E. Wilson
(1986–1988)

Elmer C. Birney
(1988–1990)

FIG. 4.—Presidents of the ASM from 1972 to 1990.

Assistant (1965–1967) and Associate (1967–1971) Director of the Museum. In 1971 he became Professor of Biological Sciences at Texas Tech University and in 1986 was appointed Paul Whitfield Horn Professor of Biological Sciences and Museum Science. He also served as Dean of the Graduate School (1971–1984), Associate Vice President for Research (1972–1974), and Vice President for Research and Graduate Studies (1974–1984). Additional appointments he held at Texas Tech included Adjunct Professor of Veterinary and Zoological Medicine and Director of Academic Publications. He was Acting Director of the Texas Tech Museum in 1971–1972, a Research Associate in 1971–1984, and was Curator and Editor of Museum Publications at the time of his death.

Knox taught a wide range of courses at both the University of Kansas and Texas Tech and served as major professor to 16 doctoral and 15 master's students in mammalogy. His primary areas of research were mammalian systematics, evolution, biogeography, and natural history, with a focus on the Great Plains and the Neotropics. His more than 300 publications include original descriptions of over 30 mammalian taxa, as well as three invertebrate species. He was the author or editor and contributing author of 13 books, including *Distribution and Taxonomy of Mammals of Nebraska, Recent Mammals of the World—a Synopsis of Families, Pleistocene and Recent Environments of the Central Great Plains, Mammals of the Northern Great Plains,* and *Handbook of Mammals of the North-central States.*

Knox became a member of the ASM in 1947 and played an active role in the affairs of the society. Other offices he held in addition to the presidency include Director, Vice-president, Managing Editor, and Editor for Reviews. He served on many of the standing committees of the society. Major initiatives he undertook as president included organizing, together with Bob Hoffmann, the transportation for, and leading the ASM contingent to, the 1st International Theriological Congress in Moscow in 1974; establishing the geographic rotation plan for annual meeting sites; initiating the establishment of the Merriam Award; and obtaining National Science Foundation support for a committee to evaluate systematic resources in mammalogy. The Information Retrieval, Index, and Systematic Collections committees were established during his presidency.

Offices he held in other scientific organizations included Director and Treasurer, Organization of Tropical Studies; Managing Editor, Society for the Study of Evolution; Councillor, Society of Systematic Zoology; Editor, *The Texas Journal of Science* of the Texas Academy of Science; and President, Texas Society of Mammalogists.

Knox received the three highest honors bestowed by the ASM: the C. Hart Merriam Award (1977), the H. H. T. Jackson Award (1983), and Honorary Membership (1992). Among the other honors that came to him during the course of his career were the Outstanding Research Award from the College of Arts and Sciences, Texas Tech University, the Barnie E. Rushing Award for outstanding research, and election as Fellow of the Texas Academy of Science. Knox died at his home in Lubbock, Texas, on 15 November 1992. His outstanding contributions to science and education have been recognized by Texas Tech University through the creation of the J. Knox Jones Memorial Scholarship.

## *Sydney Anderson: 1974–1976*

Sydney Anderson (Fig. 4) was born in Topeka, Kansas, on 11 January 1927. His early years were spent in Kansas. As a child, he was fascinated with collecting things, foreshadowing his later career as a museum curator, and at age five he began to include natural history objects in his collections. His decision to become a mammalogist came while completing his undergraduate work at the University of Kansas and was strongly influenced by the environment of the Museum of Natural History under E. Raymond Hall and summer field work directed by Rollin H. Baker. Syd met Justine Klusmire, also a native Kansan, while both were students at the University of Kansas, and they were married in 1951. Justine has shared Syd's professional interests, working with him at the museum and in the field. She is a familiar figure at the annual meetings. They have three children, Evelyn Lee, Charles Sydney, an ichthyologist, and Laura Lynnette.

Syd attended Baker University for 3 years and completed his A.B. degree at the University of Kansas in 1950. He remained at Kansas for graduate work, receiving the M.A. in 1952 and the Ph.D. in 1959. He spent the summer of 1952 at the Friday Harbor Oceanographic Laboratory of the University of Washington.

He joined the staff of The American Museum of Natural History as Assistant Curator of Mammals in 1961 and was promoted to Associate Curator in 1965 and Curator in 1969. He was appointed Emeritus Curator upon retirement in 1992. He also served as Chairman of the Mammalogy Department from 1975 to 1981 and as Adjunct Professor at the City University of New York from 1968 to 1988. He became a Research Associate of the University of New Mexico in 1988.

Syd's research has dealt broadly with natural history, ecology, distribution, evolution, and systematics of mammals and has also included work on such diverse topics as areography of North American fishes, amphibians, and reptiles; food habits of owls; and patterns of geographic distribution of birds. He also was one of the pioneers in the development of information retrieval systems for natural history museums and has pursued interests in history of science and the literature of natural history. He has conducted field work in a number of regions in the eastern and western United States, as well as Mexico, Uruguay, and, most recently, Bolivia. In addition to his other publications, Syd is author or coauthor of numerous book chapters and symposium papers as well as coeditor and coauthor of four books: *Recent Mammals of the World, a Synopsis of Families*; *Readings in Mammalogy*; *Selected Readings in Mammalogy*; and *Orders and Families of Recent Mammals of the World.*

He was awarded a National Science Foundation Graduate Fellowship in 1952–1954 and received an ASM Graduate Student Honorarium in 1954. He is a Fellow of the American Association for the Advancement of Science. For his contributions to the ASM and mammalogy in general, he received the H. H. T. Jackson Award in 1986 and was elected to Honorary Membership in 1992.

Syd has been a member of ASM since 1952 and has served the society in a number of capacities in addition to the presidency. These include Vice-president, Recording Secretary, Director, Trustee (Chairman), Editor of *Mammalian Species,* and membership in many standing and ad hoc committees. The Merriam Award was formally established during Syd's presidency. He was a prime mover in the creation of the *Mammalian Species* series and played a key part in the establishment of the society's standing committees on systematic collections and information retrieval and in clarifying the role of the Trustees and management of the Reserve Fund. As a member of the committee on revision of the Rules and By-laws in 1974, he proposed the expansion of the elected directors from 10 to 15 and the retention of past presidents on the Board. He also has served as the society's unofficial parliamentarian. Syd has been active in a number of other scientific, educational, and conservation organizations as well, including serving as trustee and officer of the Closter Nature Center Association and the Bergen Museum of Art and Science in New Jersey.

### *William Zander Lidicker, Jr.: 1976–1978*

William Z. Lidicker, Jr. (Fig. 4) was born in Evanston, Illinois, on 19 August 1932, to William Z. Lidicker and Frida Schroeter Lidicker; his father is a civil engineer. Bill is the eldest of three sisters and one brother. As a child, he lived successively in Iowa, Missouri, Minnesota, New Mexico, Minnesota, The Republic of Panama, Texas, and finally New York. Bill attended Forest Hills High School in the Borough of Queens, New York City, by which time he had already developed a serious interest in natural history. He recalls that this was probably a result of his experiences beginning with his residence in Panama. The family lived close to swamps along the Panama Canal and he had opportunities to visit tropical rain forests, including Barro Colorado Island, already a famous tropical research center, as well as cloud forests in northern Panama near the Costa Rican border. When the family returned to the United States to live in Galveston, Texas, he was an active member of a Boy Scout troop that regularly hiked and camped along the coast. By the time he was a sophomore in high school in New York, he had become an active bird watcher, and his developing professionalism was encouraged by biologists such as H. M. Van Deusen, then at the American Museum of Natural History.

He enrolled at Cornell University with the intention of studying ornithology under Arthur A. Allen, but quickly was swayed by the powerful personality of William J. Hamilton, Jr., to broaden his horizons to mammals. As an undergraduate, he had a series of summer jobs in biology, including work with Jess Low in Utah, Paul S. Martin in northeastern Mexico, and finally as a biologist on an oceanographic expedition along the coast of Newfoundland and Labrador. He received his bachelor's degree from Cornell in 1953, and immediately enrolled in the graduate program at the University of Illinois, having been accepted as a student by Donald F. Hoffmeister. He progressed through graduate school in near-record time, being awarded a master's in 1954 and his Ph.D. in 1957 from the University of California, Berkeley. He progressed regularly through the professorial/curatoral ranks at Berkeley, where he has remained. His career appears to depict a linear trajectory without interruption or deviation; it also reveals a fundamental and continuing expansion of his scientific interests. His publication record shows him to be focused in his student years on taxonomy and distribution of mammals. In his first years at Berkeley he was influenced by a number of colleagues, particularly Paul K. Anderson and Frank A. Pitelka, to expand his horizons to ecology, and particularly population ecology and genetics, where he became a leader in establishing the inter-disciplinary field of genetic ecology. This shift was clearly recognizable in 1962, when he published two papers in this field that continue to be cited. In that same year, he accompanied a field expedition to New Guinea, which led him to expand his interests beyond North America. All of his later publications reflect a progressive broadening of his research interests (social behavior, landscape ecology, conservation biology) as does the work of most of the 21 doctoral and 10 master's students who have received their degrees under his supervision.

In addition to mammalogy, his passion is international folk dancing, which he shares with his wife, Louise. He has two sons, Jeffrey and Kenneth, by his former wife Naomi Ishino.

### *Robert Shaw Hoffmann: 1978–1980*

Robert S. Hoffmann (Fig. 4) was born in Evanston, Illinois, a northern suburb of

Chicago, on 2 March 1929. By the time he was in grade school his family had moved to a more rural town, and he was spending much of his time in the woods and fields around his home and in a nearby forest preserve. He frequently journeyed by streetcar to the Field Museum in downtown Chicago and haunted the Brookfield Zoo. At age 11 he got a summer job at the zoo selling peanuts, which gave him the opportunity of getting to know all the keepers and animals. A fifth grade teacher, Nell Hashagen, also strongly encouraged his interest in natural history, and by the time he reached high school he had decided on a career in some field of biology. Phil Wright, his advisor during a year he spent at the University of Montana as an undergraduate, was a major influence in his selection of mammalogy as his major field of specialization. Bob and his wife, the former Sally Ann Monson, have four children: Karl, John, David, and Brenna.

As an undergraduate, Bob attended the University of Illinois Extension in Moline (1946–1947), University of Montana (1947–1948), and Utah State University (1948–1950), from which he received the B.S. He did his graduate work (M.A. in 1954, Ph.D. in 1955) at the University of California, Berkeley, where he was awarded two National Science Foundation Predoctoral Fellowships and the Alexander Museum of Vertebrate Zoology Scholarship. His major professor was A. Starker Leopold, and he was also strongly influenced by Frank A. Pitelka and O. P. Pearson.

In 1955, Bob was appointed Instructor in the Department of Zoology, University of Montana. He was promoted to Assistant Professor in 1957, Associate Professor in 1961, and Professor in 1965. He also served as Curator of the Zoological Museum of the University of Montana. He joined the faculty of the University of Kansas in 1968 as Curator of Mammals in the Museum of Natural History and Professor in the Department of Zoology. For varying periods during his tenure at the University of Kansas, he also served as Chairman of the Department of Systematics and Ecology, Acting Chairman of the Division of Biological Sciences, and Associate Dean and Acting Dean of the College of Liberal Arts and Sciences. In 1986, he became Director of the National Museum of Natural History and since 1988 has served as Assistant Secretary for Science at the Smithsonian Institution.

Bob's research has dealt with birds and wildlife management, as well as both fossil and Recent mammals. A major focus in his work has been on various groups of Holarctic mammals and the Pleistocene history of Beringia. He is coauthor of *Selected Readings in Mammalogy.*

He became a member of the ASM in 1955. In addition to the presidency, he has served as a Director, Vice-president, Review Editor of the *Journal of Mammalogy,* and member or chairman of a number of committees. He has been especially active in the Committee on International Relations, which he chaired in 1964–1968 and 1972–1978. Because of his research in Russia, familiarity with Russian scientists, and knowledge of the language, he played an important role in establishing liaison between the ASM and Russian mammalogists and laying the groundwork for the 1st Theriological Congress. The Education and Graduate Students Committee was formed during his presidency.

Bob is a member of a number of other professional societies and has served as a consultant to, or member of, many national and international scientific bodies, including the U.S.-U.S.S.R. Joint Commission of Science Policies of the U.S. National Academy of Sciences and the Board of Editors of *Acta Zoologica Sinica* (Beijing). He is a member of Phi Kappa Phi, Sigma Xi, and Phi Sigma and a Fellow of the American Association for the Advancement of Science. Included among other honors he has received are an Honorary Doctor of Science from Utah State University, the Summerfield Distinguished Professorship from the University of Kansas, and Honorary Membership in the All-Union (U.S.S.R.) Theriological Society.

## *James Smith Findley: 1980–1982*

James S. Findley (Fig. 4) was born in Cleveland, Ohio, on 28 December 1926. He grew up in a well-forested suburb of the city, an environment that fostered his early interest in birds, which was further nurtured by his membership in the Kirtland Bird Club at the Cleveland Museum of Natural History. When in seventh grade, he met Norman Negus, who shared his interest in natural history and fishing. Together they began to collect mammals, birds, herps, and insects and discovered Hamilton's *Mammals of Eastern United States,* which greatly influenced Jim's later decision to become a mammalogist. When 13 years old, he became acquainted with Phil Moulthrop and B. P. Bole, Jr., mammalogists at the Cleveland Museum of Natural History, and they and other museum staff members introduced him to the possibilities of a career in natural history. Jim's father wrote to Harold E. Anthony at the American Museum of Natural History asking advice on what to do with a son with such interests. Anthony replied that the financial rewards of a career in biology would be modest and emphasized the importance of attending a good university with broad offerings in biology and a rich local flora and fauna, recommending Berkeley as such a place.

Jim served in the U.S. Army in 1945 and 1946, and saw duty in Japan. He and and wife, Helen Muriel Thomson ("Tommie"), were married in 1949 and spent their honeymoon surveying mammals in Jackson Hole, Wyoming. They have four children, sons Stuart and Douglas and daughters Heidi and Joan.

Jim took undergraduate courses at Kobe Central School during the year he was stationed in Japan and spent the summer of 1947 at the Rocky Mountain Biological Laboratory. He received the B.A. *cum laude* from Western Reserve University in 1950. He attended the University of California, Pacific Grove, in 1951, and completed his graduate work (Ph.D., 1955) at the University of Kansas, with E. R. Hall as his major professor.

From 1954 to 1955, he was an Instructor in the Zoology Department of the University of South Dakota. In 1955 he joined the staff of the Biology Department of the University of New Mexico as Assistant Professor. He became Associate Professor in 1961 and Professor in 1970. He served as Chairman of the Biology Department from 1978 to 1982 and was Director of the Museum of Southwestern Biology from 1983 to 1992. He retired in July 1992.

The main focus of Jim's research has been on zoogeography, distribution, and taxonomy of mammals of southwestern United States, with emphasis on bats and shrews. He pioneered in the study of ecological correlates of morphology of bats and other mammals and has made important contributions to knowledge of the patterns and processes of small mammal community formation. Besides journal papers and other publications, he is an author of chapters in *Recent Mammals of the World, Contributions to Mammalogy, Ecology of Bats, Patterns in the Structure of Mammalian Communities*; and *The Butterflyfishes: Success on the Coral Reef* (with Tommie Findley). He coauthored *Mammals of New Mexico* and is the author of *Natural History of New Mexican Mammals* and *Bats: a Community Perspective.* In addition to his research with mammals, Jim has published on distribution of such diverse taxa as birds, amphibians, and river crabs and in recent years has been investigating patterns of community organization in reef fishes around the world.

He has directed the work of 33 master's and 24 doctoral students, and under his direction the Museum of Southwestern Biology grew in the size and significance of its collections and production of scholarly research. Together with Terry L. Yates, he was instrumental in obtaining National Science Foundation funding to upgrade the Museum's mammal collection.

Jim became a member of the ASM in 1944 and besides the presidency has served as a Director and Vice-president. During his tenure as president, the decision was made for the society to participate in producing the first edition of *Mammal Species of the World.* In 1978, Jim was presented the C. Hart Merriam Award from the Society in recognition of his outstanding contributions to mammalogy. Among other honors he has received is the Leopold Conservation Award of the Nature Conservancy. Two species and one subspecies of mammals also have been named in his honor.

## *Jocelyn Mary Taylor: 1982–1984*

J. Mary Taylor (Fig. 4) (she decided before entering kindergarten not to use her first given name) was born in Portland, Oregon, on May 30, 1931, to Kathleen and Arnold L. Taylor. She has an older brother, John Stewart Taylor. Growing up in that area, she had early and regular contacts with the out-of-doors through daily walks with her mother, which instilled in her a love of nature. However, being tall and athletic, she also developed a love of tennis, and toured the junior circuit, playing in a prestigious British tournament at age 17. She also played the piano and became devoted to chamber music.

However, instead of pursuing the sport, she went East to Smith College, intending to study music. A biology course in her senior year of high school led her to take further biology courses in college and she switched her major to zoology, with an honors thesis in protozoology. Mary received her bachelor's degree from Smith in 1952 and enrolled the same year at the University of California at Berkeley. She completed her master's degree the next year, again specializing in protozoology, and accepted a position in the Department of Zoology at Connecticut College. In 1954, upon receiving a Fulbright Fellowship, she spent a year in Australia, which formed the basis for her life-long interest in Australasian mammals. Returning from her pre-doctoral fellowship, she enrolled again at Berkeley, completing her doctorate in mammalogy in 1959 and then accepting a position at Wellesley, not too far from her alma mater. She remained at Wellesley until 1965, collaborating with Betty Horner on research on Australian rodents and small marsupials. While at Wellesley she also began a long-term collaboration with Dr. Helen Padykula of Harvard Medical School on placentation in marsupials.

In 1965 she heeded the call of the great Northwest, and returned across the continent to the University of British Columbia in Vancouver, where she was the first woman to hold a professorial appointment in the Department of Zoology, and a curatorial one as Director of the Cowan Vertebrate Museum. This was scientifically a particularly productive period of her career with many published papers and 10 graduate students. However, changing priorities at the university resulted in decreasing support for vertebrate zoology, and in 1982 Mary resigned her appointments and moved back to Portland, this time with her husband, Dr. J. William Kamp, an entomologist whom she met in British Columbia.

She became a scientist at the Oregon Regional Primate Research Center in Beaverton, Oregon, and in addition held an honorary professorship at Oregon State University in Corvallis. Her move to Oregon also coincided with her election to the presidency of the ASM, the first woman to be so honored.

In 1987, she became the first woman to become Director of the Cleveland Museum of Natural History. In 1989 she became Chairman of the Rodent Specialist Group, SSG/IUCN, and the following year was elected Vice-president of the Association of Science Museum Directors. A few years ago, she shepherded to completion a major addition to the Museum that included expanded housing for the mammal collections (Source: Snow, 1987).

## *Hugh Howard Genoways: 1984–1986*

Hugh H. Genoways (Fig. 4) was born on 24 December 1940 at Scottsbluff, Nebraska, and grew up in the town of Bayard, Nebraska, and on farms in the vicinity. As a youth he was active in the Boy Scouts of America with his father, and the scouting experience was a strong influence on his eventual decision to pursue a career in the field of biology. As an undergraduate at Hastings College in Nebraska, he was introduced to the science of biology by Professor Wendell Showalter. His interest in mammals was first awakened by another undergraduate professor, Gilbert Adrian, and it later matured under the guidance of Knox Jones, his major professor in graduate school. Hugh and Joyce Elaine Cox were married in 1963 and have a daughter, Margaret Louise, and son, Theodore Howard.

Hugh received his A.B. in 1963 from Hastings College and his Ph.D. from the University of Kansas in 1971. While in graduate school, he was a part-time Instructor in the Department of Systematics and Ecology and a Research Assistant in the Museum of Natural History. He also spent a year at the University of Western Australia.

From 1971 to 1976 he held various appointments on the faculty of Texas Tech University. These included Research Associate, Lecturer, Acting Coordinator of Research, and Curator of Mammals in the Museum and Adjunct Assistant Professor of Veterinary and Zoological Medicine and Pathology in the School of Medicine. He was Curator of Mammals at the Carnegie Museum of Natural History from 1976 to 1986. He assumed his present post as Director of the University of Nebraska State Museum in 1986. He also holds appointments as Professor of the Museum and Museum Studies, Chair of the Museum Studies Program, Courtesy Professor in the School of Biological Sciences, and Faculty Fellow of the Graduate College.

Hugh's research has centered on the systematics, biogeography, and ecology of New World mammals, with emphasis on rodents, particularly heteromyids and geomyids, and bats. He has conducted field work in most regions of the United States and throughout the Caribbean, as well as Suriname, Mexico, Nicaragua, Venezuela, India, and Australia. In addition to numerous journal papers and other publications, he is author, coauthor, or editor of eight volumes, including *Systematics and Evolutionary Relationships of the Spiny Pocket Mice of the Genus* Liomys; *Biological Investigations in the Guadalupe Mountains National park, Texas*; *Mammalian Biology in South America*; and *Contributions in Quaternary Vetebrate Paleontology.* He also has been active in the development of techniques for use of computers in data analysis and retrieval and in museum collections management.

Hugh became a member of the ASM in 1963. In addition to the presidency, he has served as a Director, Vice-president, Managing Editor of the *Journal of Mammalogy,* and Editor of *Special Publications,* as well as chair/member of seven standing committees. One of his major actions as president was the establishment of the Future Mammalogists Fund. He also focused on strengthening the committees and broadening their membership. The decision for ASM participation and the planning for an international meeting with the Mexican Mammal Society also took place during his term.

Offices he has held in other scientific organizations include the presidency of both the Southwestern Association of Naturalists and the Nebraska Museums Association. He also served as Publications Editor of the Carnegie Museum of Natural History and Editor of *Museology* published by Texas Tech University and is presently Editor-in-chief of *Current Mammalogy.*

Hugh is a recipient of the C. Hart Merriam Award from the society and other honors include a Fulbright Grant while a graduate student, selection by the United States Jaycees as one of the Outstanding Young Men in America, and election as a Fellow of the Center for Great Plains Studies of the University of Nebraska.

## *Don Ellis Wilson: 1986–1988*

Don E. Wilson (Fig. 4) was born 30 April 1944 in Davis, Oklahoma, and during his youth lived in Nebraska, Texas, Oregon, Washington, and Arizona. He developed an interest in natural history at an early age, and by the time he entered college had decided on a career in biology. While an undergraduate he worked for the National Park Service in Grand Canyon National Park and made his first trip to the tropics. He also spent a summer as a naturalist for the U.S. Forest Service in the Sandia Mountains of New Mexico. In 1962 he married Kathleen Hayes, and they have two daughters, Wendy and Kristy.

Don received a B.S. in Wildlife Management from the University of Arizona in 1965 and did his graduate work (M.S., 1967; Ph.D., 1970) at the University of New Mexico under the direction of James Findley. He held a Postdoctoral Fellowship in Ecology from the University of Chicago in 1970–1971 and also obtained advanced training in statistics, computer systems, automatic data processing, editing, and personnel and financial management through programs in the U.S. Fish and Wildlife Service, Smithsonian Institution, and the U.S. Department of Agriculture Graduate School.

In 1971 he was appointed Zoologist in the Bird and Mammal Laboratories of the U.S. Fish and Wildlife Service at the National Museum of Natural History and in 1973 became Chief of the Mammal Section of the National Fish and Wildlife Laboratory. In 1978, he became Chief of the Museum Section of the Denver Wildlife Research Center and in 1984 was promoted to Chief of the Biological Survey. He was appointed to his present post, Director of the Biodiversity Programs of the Smithsonian Institution, in 1990. He also has appointments as Visiting Professor at the University of Maryland, George Mason University, and the Organization for Tropical Studies—Universidad de Costa Rica.

Don's principal research interests have been the biology of neotropical bats and tropical ecology in general. His studies of bats have ranged over a broad spectrum of topics, including taxonomy, distribution, community ecology, physiology, and reproductive biology. He has also worked on a variety of other mammals, including rodents, lagomorphs, carnivores, ungulates, and marsupials. In addition to mammal research, he has conducted studies on birds, amphibians, and reptiles, as well as seed predation, tropical strand plants, and insects. He is a coauthor of *Mammals of New Mexico* and author or coauthor of chapters in a number of volumes, including *Biology of Bats of the New World Family Phyllostomatidae, Wild Mammals of North America, Advances in the Study of Mammalian Behavior, Costa Rican Natural History, Biology and Management of the Cervidae, Ecological and Behavioral Methods for the Study of Bats,* and *Tropical Rain Forest Ecosystems.* He also coedited the second edition of the ASM-sponsored *Mammal Species of the World* published in 1993.

Don became a member of the ASM in 1966. Besides the presidency, he has served the society as a Director, Vice-president, Journal Editor, and Managing Editor of *Mammalian Species* and *Special Publications.* Offices held in other professional organizations include President of the Association for Tropical Biology; Councilman and Treasurer of the Biological Society of Washington; Board of Managers, Vice-president, and President of the Washington Field Biologists Club; Board of Scientific Directors of Bat Conservation International; and Board of Directors of Integrated Conservation Research. He also serves on the Chiroptera Specialists Group of the IUCN Species Survival Commission and is Associate Editor of *Revista de Mastozoologia Mexicana* and a member of the editorial boards of *Acta Zoologica Mexicana, Current Mammalogy,* and *Anales del Instituto de Biologia.* In addition, he has served as a consultant to many U.S. and foreign governmental agencies and nongovernmental organizations.

Among his professional honors and awards are membership in Phi Sigma; National Science Foundation Predoctoral and Postdoctoral Fellowships; the Smithsonian Institution Award for Excellence in Tropical Biology; Outstanding Publication Award from the Denver Wildlife Research Center; Reconocimiento, Asociacion Mexicana de Mastozoologia, and the Centennial Distinguished Alumni Award from the University of New Mexico.

## *Elmer Clea Birney: 1988–1990*

Elmer C. Birney (Fig. 4) was born on 26 March 1940 at Satanta, Kansas, and grew up on a wheat farm and cattle ranch in a staunchly conservative family with a strong work ethic and belief in education as a key to one's future. Sports were his major interest as a youth, and the closest he came to a biological interest was crossbreeding rare breeds of chickens to determine what combination of phenotypic traits were produced in the hybrids. The possibility of obtaining a football scholarship got him thinking seriously about attending college. After his first year as an agriculture major, he enlisted in the Naval Reserve and served 2 years on active duty on a destroyer in the Pacific. While on leave in 1960, he met Marcia Fayla McVey, and they were married in 1961, a day after his release from active duty. They have a daughter, Amelia Joleen, and son, Clayton Eugene.

Elmer received his B.S. in 1963 and M.S. in 1965 from Fort Hays State University, where he developed his interest in mammals under the influence Gene Fleharty. He obtained his Ph.D. in 1970 from the University of Kansas. His major professor at Kansas was Knox Jones, who played a strong role in his professional development. His doctoral research was supported by a National Science Foundation Traineeship and a Watkins Natural History grant.

Elmer served as instructor of biology at Kearney State College in Nebraska in 1965–1966. After receiving the Ph.D., he joined the faculty of the University of Minnesota, where he is presently Curator of Mammals in the Bell Museum of Natural History and Professor in the Department of Ecology, Evolution, and Behavior. In addition, he has served as Director of Graduate Studies in both the Ecology Graduate Program and Zoology Graduate Program of the Department of Ecology, Evolution, and Behavior. He was Director of the Bell Museum from 1990 to 1992.

Elmer's research has spanned a broad range of topics, including distribution, life history, ecology, systematics, physiology, and biochemistry. Among his important contributions are studies on the evolution of the enzyme systems involved in ascorbic acid biosynthesis in vertebrates conducted jointly with Robert Jenness and investigations on the relationship of vegetative cover to microtine cycles and other aspects of grassland mammal communities with W. E. Grant, D. D. Baird, N. R. French, and others. The geographic focus of his work has been on mammals of central and western United States, and he was a participant in the U.S.I.B.P. Grassland Biome studies. He also has conducted substantial field work in Mexico, Argentina, Australia, and Antarctica. His publications include coauthorship of two books, *The True Prairie Ecosystem* and *Handbook of Mammals of the North-central States,* the chapter Community Ecology in *Biology of New World* Microtus, and the section on mammals in *Minnesota's Endangered Flora and Fauna.* His work has been supported by grants from many sources, including the National Science

Foundation, Society of Sigma Xi, Nongame and Minerals divisions of Minnesota Natural Resources, Institute of Museum Services, and the Legislative Commission on Minnesota Resources.

Elmer became a member of the ASM in 1963 and, besides the presidency, has served as a Director, Vice-president, Managing Editor, Journal Editor, and Editor for *Special Publications.* He has been a member of a number of standing committees and chaired the Membership, Editorial, and Development committees. Among his goals as president were to facilitate more open discussion of matters of concern to the membership, increase participation of women on committees and in other business of the society, and encourage election of younger members to the Board of Directors. He is a Life Member of the Southwestern Society of Naturalists and member of a number of other international, national, and regional scientific and environmental organizations.

## *James Hemphill Brown: 1990–1992*

James H. Brown (Fig. 5) was born on 25 September 1942 at Ithaca, New York, and grew up in rural upstate New York. His mother fostered his early interest in keeping pets and making natural history collections and when he was 8 or 9 years old introduced him to W. J. Hamilton, Jr. His association with Bill Hamilton during his elementary, high school, and university undergraduate years greatly influenced his development as a scientist. Between the ages of 10 and 12, he became acquainted with Kyle Barbehenn, then a graduate student of W. Robert Eadie, and regularly accompanied him in his field work on small rodent populations near the Browns' home. This experience, particularly Kyle's patience in answering questions and treatment of him as a fellow scientist, contributed greatly to shaping Jim's interests in mammalogy and ecology. Jim and his wife, the former Astrid R. Kodric, were married in 1965 and have a son, Kevin, and daughter, Karen. Astrid is a scientific colleague as well as wife, and she and Jim have collaborated in a number of studies. They have mutual interests in hiking; camping; reading; and collecting American Indian baskets, rugs, and pottery.

Jim did his undergraduate work at Cornell, receiving the B.A. (with honors in zoology) in 1963. He received the Ph.D. in zoology from the University of Michigan in 1967. Emmet Hooper was his major professor, but he also worked closely with Bill Burt and William Dawson. Supported by a Rackham Postdoctoral Fellowship from the University of Michigan, he did physiological ecology research with George A. Bartholomew at the University of California at Los Angeles in 1967–1968.

He held faculty positions at the University of California at Los Angeles (1968–1971), the University of Utah (1971–1975), and the University of Arizona (1975–1987). In 1987 he was appointed Professor of Biology at the University of New Mexico. During his university career he has directed the work of 12 master's students, 29 Ph.D. students, and 7 postdoctoral students. Jim's primary research interests are the patterns and processes that influence the abundance, distribution, and diversity of species. Although mammals, particularly desert rodents, have been the principal subjects of his research, he has also worked on birds, fishes, insects, and plants. Among his studies that have received broad recognition is the long-term experimental field investigation of the interactions between granivorous mammals, birds, ants, and seed-producing plants in the Chihuahuan Desert of southeastern Arizona. He also has worked in many other parts of the Southwest, as well as Mexico. In addition to numerous journal papers and chapters in books, he is coauthor of *Biogeography* and coeditor of *Foundations of Ecology* and *Biology of the Heteromyidae.*

He became a member of ASM in 1965 and, in addition to the presidency, has served as a Director, Vice-president, and member

James H. Brown
(1990–1992)

James L. Patton
(1992–1994)

FIG. 5.—Above: Presidents of the ASM from 1990 to 1994, James H. Brown and James L. Patton. Below (l–r): Early ASM presidents V. O. Bailey and C. H. Merriam with fellow members of the Bureau of Biological Survey, T. S. Palmer and A. K. Fischer, in the field at Lone Pine, Owens Valley, California, 13 June 1891.

of a number of standing committees. As president he promoted a thorough reorganization of the editorial policies and format of the *Journal of Mammalogy* and initiated the policy of evaluating presentation of student papers at the annual meeting. He has been an active participant in other scientific societies, serving as Vice-president of the Ecological Society of America, President of the American Society of Naturalists, Council member of the Society for the Study of Evolution, and in editorial capacities for *Ecology, Evolutionary Ecology,* and the *Journal of Biogeography.* He served as a member of the Scientific Advisory Board of the American Museum of Natural History's Southwestern Research Station and on the Population Biology and Physiological Ecology panels of the National Science Foundation.

He is a recipient of the C. Hart Merriam Award from the ASM and a Fellow of the American Association for the Advancement of Science. In addition, he was awarded a Certificate of Merit from the Southwestern and Rocky Mountain Division of the American Association for the Advancement of Science and a Guggenheim Fellowship in 1991–1992.

## *James Lloyd Patton: 1992–1994*

James L. Patton (Fig. 5) was born in St. Louis, Missouri, on 21 June 1941. His father was a physician who served in the U.S. Army during World War II and the Korean War. Jim spent much of his early years as an "army brat" at various military bases in the United States and Germany. He was married to Carol Porter in 1966. They combined their honeymoon with the ASM meeting in Long Beach, which was both his first national meeting and the first time he presented a professional paper.

Jim's initial scientific interest was anthropology, which was his undergraduate major at the University of Arizona. He planned to continue on in anthropology for his master's, but after being exposed to a course in evolutionary genetics taught by William Heed he switched from anthropology to zoology and began work on chromosomal inversion polymorphisms in desert fruit flies (*Drosophila*). During this period, he met and began to interact with Al Gardner, one of Lendell Cockrum's graduate students at the time, and as a result "discovered" small desert mammals and went on to complete both his master's and doctorate on cytogenetics of pocket mice.

He received all of his degrees from the University of Arizona: the B.A. (with distinction) in 1963, M.S. in 1965, and Ph.D. in 1969. During his doctoral work, he held a National Defense Education Act Title IV Fellowship.

In 1969, he was appointed Assistant Professor in the Department of Zoology and Assistant Curator in the Museum of Vertebrate Zoology of the University of California, Berkeley. He was promoted to Associate Professor and Associate Curator in 1974 and Professor and Curator in 1979. He has been Associate Director of the Museum of Vertebrate Zoology since 1982 and was Acting Director in 1988–1989 and 1992.

Jim's research has had two major themes: population genetics and geographic divergence in pocket gophers in western United States and systematics of neotropical mammals. However, he has also published on such diverse topics as chromosome evolution in caecilians, biochemical relationships of Galapagos giant tortoises, genetic variation in Galapagos finches, and distribution patterns of amphibians and reptiles in southern Peru. In addition to numerous journal papers, he is the author or coauthor of numerous papers and chapters in symposium volumes and books, including *Mammal Studies of South America, Patterns of Evolution in Galapagos Organisms, Annual Review of Ecology and Systematics, Evolution in the Galapagos,* and *Mammalian Dispersal Patterns.*

Jim became a member of the ASM in

1963. In addition to the presidency, he served on the Board of Directors, as First and Second Vice-president, and as Editor for Reviews of the *Journal of Mammalogy.* Posts held in other scientific societies include Councilor and member of the Editorial Board, Society of Systematic Zoology; Second Vice-president of the Society for the Study of Evolution and Associate Editor of *Evolution*; and Associate Editor of *Genetica.* He also has served on the Board of Directors of the Charles Darwin Foundation; Board of Overseers of the Museum of Comparative Zoology; several National Science Foundation panels and committees; as well as the editorial boards of the *University of California Publications in Zoology, Current Mammalogy,* and *Israel Journal of Zoology.* He is a Charter Member of the Society for Conservation Biology.

Jim received the C. Hart Merriam Award from the ASM in 1983 in recognition of his outstanding contributions to mammalogy and is a Fellow of both the California Academy of Sciences and American Association for the Advancement of Science. His honors also include a Distinguished Teaching Award from the University of California, Berkeley, and appointment as Distinguished Visiting Scientist in the Museum of Zoology of the University of Michigan and Miller Professor in the Miller Institute for Basic Research of the University of California, Berkeley. He is a Research Associate in the Department of Mammalogy of the American Museum of Natural History and the Museum of Southwestern Biology of the University of New Mexico.

## Acknowledgments

We especially thank the living past-presidents of ASM for providing us with background material on their careers in mammalogy and regret that space limitations prevented us from including many of the interesting details in the biographical sketches. However, all material supplied will be placed in the society archives. We also thank Judith Eger for reviewing the account for R. L. Peterson; Elizabeth Peterson for providing information on her father, W. P. Taylor; the Mammal Department of the American Museum of Natural History for the source materials for the accounts of H. E. Anthony and R. G. Van Gelder; K. Grimes, Public Affairs Office, American Museum of Natural History, and W. Deiss and E. Glenn, Smithsonian Institution Archives, for providing photographs; and the editors of this volume for their patience in awaiting completion of the manuscript.

## Literature Cited

ALDRICH, J. W. 1977. In memoriam: Hartley Harrad Thompson Jackson (1881–1976). Journal of Mammalogy, 58:691–694.

ANONYMOUS. 1923. American Society of Mammalogists articles of incorporation. Journal of Mammalogy, 4:271–272.

———. 1942. Marcus Ward Lyon, Jr. 1875–1942. The American Midland Naturalist, 27(3):i–xv.

———. 1958*a*. Chairman of museum's mammal department retires after forty-seven years on staff. American Museum of Natural History (news release), 13 April 1958.

———. 1958*b*. Harold Anthony retires. The Grapevine (American Museum of Natural History), 15: 1–2.

———. 1970. Noted mammalogist dies in California. American Museum of Natural History (news release), 30 March 1970.

———. 1988. Emmet T. Hooper. Peromyscus Newsletter, No. 6:9–11.

———. 1992. Emmet T. Hooper. [unidentified newspaper obituary, July 2, 1992].

BARBOUR, T., B. LAWRENCE, W. E. SCHEVILL, S. L. WASHBURN, AND M. B. COBB. 1943. Glover Morrill Allen 1879–1942. Journal of Mammalogy, 24:297–304.

BEHLE, W. H. 1977. In memoriam: Stephen David Durrant (1902–1975). Journal of Mammalogy, 58: 111–118.

COTTAM, C. 1971. TAYLOR, WALTER PENN (1888–). Pp. 317–318, *in* Leaders of American Conservation (H. Clepper, ed.). Ronald Press, New York, 353 pp.

EGER, J., AND L. MITCHELL. 1990. Randolph Lee Peterson: 1920–1989. Journal of Mammalogy, 71:707–713.

FINDLEY, J. S., AND J. K. JONES, JR. 1989. Eugene Raymond Hall: 1902–1986. Journal of Mammalogy, 70:455–458.

GOLDMAN, E. A. 1935. Edward W. Nelson—naturalist, 1855–1934. Auk, 52:135–148.

GREGORY, W. K. 1930*a*. William Diller Matthew 1871–1930. Natural History, 30:664–666.

———. 1930*b*. William Diller Matthew, paleontologist (1871–1930). Science, 1878:642–645.

———. 1931. A review of William Diller Matthew's contributions to mammalian palaeontology. American Museum Novitates, 473:1–22.

GRINNELL, H. W. 1943. Bibliography of Clinton Hart Merriam. Journal of Mammalogy, 24:436–457.

HALL, E. R. 1939. Joseph Grinnell (1877 to 1939). Journal of Mammalogy, 20:409–417.

HOFFMEISTER, D. F. 1969. A history of the American Society of Mammalogists. Program of the 50th Anniversary Celebration of the American Society of Mammalogists, pp. 8–12.

HUBER, W. 1940. Witmer Stone (1866–1939). Journal of Mammalogy, 21:1–4.

JACKSON, H. H. T. 1947. Association and correspondence with Goldman. Journal of Mammalogy, 28: 109–113.

———. 1948. An earlier American mammal society. Journal of Mammalogy, 29:1–4.

[JONES, C.]. 1990. Additions to the obituary of E. Raymond Hall. Journal of Mammalogy, 71:117.

LANTIS, M. 1954. Edward William Nelson. Anthropological Papers of the University of Alaska, 3(1): 5–16.

LAYNE, J. N., AND J. O. WHITAKER, JR. 1992. William John Hamilton, Jr.: 1902–1990. Journal of Mammalogy, 73:693–706.

LEHMANN, V. W. 1972. Walter P. Taylor, 1888–1972. Journal of Wildlife Management, 36:1379–1380.

LITTLE, L. 1968. Alfred Brazier Howell, 1866–1961. Journal of Mammalogy, 49:732–742.

MUUL, I. 1990. William Henry Burt: 1903–1987. Journal of Mammalogy, 71:113–116.

OSGOOD, W. H. 1943. Clinton Hart Merriam—1855–1942. Journal of Mammalogy, 24:421–436.

SALT, G. W., AND R. L. RUDD. 1975. Tracy Irvin Storer (1889–1973)—an appreciation. Journal of Mammalogy, 56:538–552.

SANBORN, C. C. 1948. Wilfred Hudson Osgood: 1875–1947. Journal of Mammalogy, 29:95–112.

SETZER, H. W. 1977. A. Remington Kellogg—1892–1969. Journal of Mammalogy, 58:251–253.

SNOW, J. C. 1987. The road taken by a woman of science. Beacon [magazine], Sept. 20. Pp. 7–8,10.

TAYLOR, W. P. 1947. Edward A. Goldman. Journal of Mammalogy, 28:114.

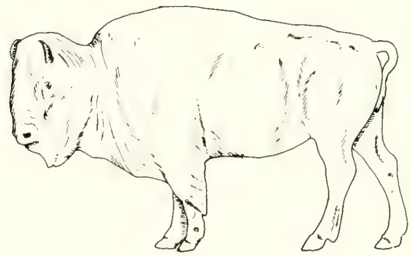
TYLER, W. M. 1943. In memorium: Glover Morrill Allen. Auk, 60:163–168.

YOUNG, S. P. 1947. Edward Alphonso Goldman: 1873–1946. Journal of Mammalogy, 28:91–109.

ZAHNISER, H. 1942. Vernon Orlando Bailey. 1894–1942. Science, 96:6–7.

# *AWARDEES*

J. Mary Taylor and Duane A. Schlitter



### *Introduction*

Recognition by the ASM of outstanding persons in the field of mammalogy began in the first year of the society's existence with establishment of Honorary Membership. A second award, the C. Hart Merriam Award, was created 54 years later with the goal of recognizing exceptional contributions to the discipline of mammalogy within the past decade. This award was the first to bear the name of an earlier ASM member, himself an exemplar of the intent of this award. The Hartley H. T. Jackson Award, also named for a pre-eminent mammalogist, was established only 3 years later to honor ASM members who have provided long and outstanding service to the society. Today, the H. H. T. Jackson Award is by its very nature the only one of the three awards whose recipients must be ASM members. The awardees of these three prestigious forms of recognition and their many contributions to mammalogy and the ASM are discussed in the following accounts.

### *Honorary Members*

Honorary Membership, the most esteemed recognition by the ASM, was first bestowed on Joel Asaph Allen in the same year that the society was founded. This award was established to acknowledge a "distinguished record of achievement" to the science of mammalogy. The recipient receives a certificate signed by the President of the society. In 1957 the procedure was formalized by the establishment of an Honorary Membership Committee consisting of the five most recent past presidents. The committee member in his or her 7th year after leaving office chairs the committee for two years. A successful nominee requires unanimous approval by the Committee, recommendation by the Board of Directors, and majority approval by the members present at the annual meeting.

Although not awarded every year, 58 mammalogists have had this honor conferred on them through 1992, and on occasion more than one person may be recognized in a given year. Of these, 20 are past presidents, 7 are also recipients of the Jackson Award, and 1 of the Merriam Award. Recipients come from the following countries: United States (38), England (4), Germany (3), Russia (3), France (2), Norway (1), Spain (1), Japan (1), Denmark (1), China (1), Poland (1), Finland (1), and Mexico (1).

The average age at which recipients have received Honorary Membership is 70, ranging from 48 (Sokolov) to 86 (Stejneger).

## *Joel Asaph Allen, 1919*

Born 19 July 1838 in Springfield, Massachusetts; A.B., Lawrence Scientific School, Cambridge; Ph.D. (honorary), University of Indiana; died 29 August 1921 (*Journal of Mammalogy,* 3:254–258, 1922) (Fig. 1).

J. A. Allen descended from families who traced their New England origins to the early 17th Century. Raised on a farm, Allen showed an early interest and aptitude for studies of nature. At each higher level of academic opportunity, Allen was fortunate enough to study with someone who encouraged his interest in nature until, finally, he won a position at Lawrence Scientific School in Cambridge, Massachusetts, where he studied under Professor Louis Agassiz. This relationship with Agassiz and the Museum of Comparative Zoology (MCZ) was the beginning of 70 years of museum associations.

The first of numerous field trips was an expedition to Brazil with Agassiz in 1865. After nearly a year in northern and eastern Brazil, and in possession of large quantities of all orders of vertebrates, mollusks and other invertebrates, as well as samples of the flora, Allen returned to Cambridge. After a short break on the farm to recover his health, Allen left again for the field to collect on Lake Ontario and in Michigan, Indiana, and Illinois. He returned to the MCZ to become curator of birds and mammals. Within a year he left for a collecting trip to Florida, and in 1871 he took a nine-month swing through the Great Plains and Rocky Mountains as far as the Great Salt Lake. Again, Allen's collections included large numbers of mollusks, insects, crustaceans, Recent and fossil fishes, as well as the usual birds, bird eggs, and mammals. In 1873 he was appointed scientific chief of the survey of the Northern Pacific Railroad in North Dakota and Montana on behalf of MCZ and the Smithsonian Institution. Because of the presence of hostile Indians, use of firearms and side trips were prohibited and collecting was difficult. On one occasion, he was escorted by General George Custer and 1,400 troops. With the exception of a short trip to Colorado in 1882, primarily for purposes of restoring his health, his return from the railway survey to Cambridge in late 1873 marked the end of field work for Allen.

In 1885 Allen accepted a position as Curator of birds and mammals at the American Museum of Natural History. The museum had entered a period of scientific focus intended to match the already famous exhibitions. During the next 36 years, Allen was to become an outstanding scientist and editor. From a combined 14,300 specimens of birds and mammals in 1885, Allen saw the collection grow to nearly 250,000 specimens by 1920. At the same time, he edited 37 volumes of the *Bulletin* and 22 volumes of the *Memoirs,* a total of 21,368 pages, between 1885 and 1917. During this interval, Allen published 23 papers on birds and 168 on mammals, describing and naming a total of 724 new taxa.

Allen was a leader in the founding of the American Ornithologists' Union and edited *The Auk* for 30 years. He virtually wrote *The Code of Nomenclature of the American Ornithologists' Union* and was a member of the Commission for Zoological Nomenclature from its formation in 1910 until his death. He founded the Audubon Society. Receiving numerous medals and honors, Allen was a member of nearly all of the leading scientific societies of the world. He was a member of the National Academy of Sciences and an honorary member of the Zoological Society of London, British Ornithologists' Union, and the New Zoological Society.

Although plagued by periods of poor health, Allen continued his incredible pace until his death. His erudition and productivity inspired universal affection and reverence. No more suitable person could have been honored as the first honorary member

Joel Asaph Allen
(1919)

Max Weber[a]
(1928)

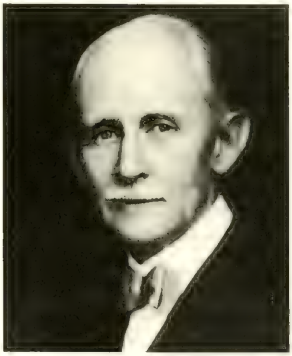
M. R. Oldfield Thomas
(1928)

Henry Fairfield Osborn[b]
(1929)

William Berryman Scott[c]
(1936)

Alfred W. Anthony[d]
(1936)

Leonhard Stejneger[e]
(1937)



Gerrit S. Miller, Jr.[f]
(1941)

Angel Cabrere Latorre[g]
(1947)

FIG. 1.—Honorary members of the ASM, 1919–1947. Courtesy of: [a]Artis Library, University of Amsterdam; [b]Department of Library Sciences, American Museum of Natural History; [c]Department of Geological and Geophysical Sciences, Princeton University; [d]Natural History Museum, San Diego, California; [e]Photographic Collection, Smithsonian Institution; [f]Biographical Files, Smithsonian Institution; [g]National University of La Plata, Argentina.

of the newly formed American Society of Mammalogists. He was also a Charter Member. Following his death, the American Museum of Natural History named its new mammal hall the Allen Hall of North American Mammals.

## *Edouard-Louis Trouessart, 1921*

Born 25 August 1842 in Angers, France; undergraduate degree, University of Poitiers, 1864; M.D., University of Paris, 1870; died 30 June 1927 (*Journal of Mammalogy*, 8:352, 1927).

Trouessart was born into an academic family. His father, Joseph, was a professor of physics in the Faculty of Sciences at Poitiers. From the beginning, Edouard-Louis was interested in zoology and medicine. Upon graduation, he was sent with the French army as a physician to the 36th Regiment, 1st Battalion of the Vienne Mobile Guard, in the war with Germany (1870–1871). When peace was declared, he returned to the Maine-et-Loire district to hospital practice and work with the relief committee. At the same time, he began his studies of natural history. As a result of these activities, he was asked to collaborate in the production of a Parisian journal of medicine and zoology, serving in this role from 1871 to 1882.

In 1882, he was appointed Director of the Museum of Natural History of Angers. He expanded activities of the museum in Angers to include new public programs and natural history courses in the public schools. As such, he had a great impact on this town with his energy and advanced ideas. However, budget cuts ultimately caused Trouessart to leave Angers in 1885. He moved to Paris, where he began to produce a series of memoir volumes in natural history on a variety of subjects, including parasites, marine biology, mammals, birds, and medicine.

In 1906, Trouessart was named Professor of mammalogy and ornithology at the National Museum of Natural History, Paris. In Paris he was able to continue production of monographs on a variety of subjects. The government also charged him with other duties, among them a study of the organization and utilization of zoos in Belgium, Germany, and Holland, and a review of hunting in the colonies.

Trouessart was a prolific author on a variety of subjects in medicine and zoology. Among his best know works are the multivolume *Les Mammifères vivants et fossiles* (1879–1907), series of papers entitled *Les Acariens parasites et les acariens marins* (1880–1907), *La Faune des Mammifères de France* (1885), *Les Microbes, les ferments et les moisissures* (1886), *La Géographie Zoologique* (1890), *Catalogue des Mammifères vivants et fossiles* (3 vols.) (1898, 1904), *La Faune des Mammifères de l'Algerie, du Maroc et de la Tunisie* (1905), *La Faune de Mammifères d'Europe* (1909), and *Catalogue des Oiseaux d'Europe* (1912). He collaborated on the *Grand Encyclopédie, Revue Scientifique, Nature,* and *Revue Générale des Sciences.*

Among the many honors and awards given to Trouessart were the Knight of the Legion d'honneur and Knight of the Mérite Agricole. He was a corresponding member of the Zoological Society, London, and an officer of the Academy of Paris. He was awarded the Gold Medal from the Exposition Universelle de Paris (1889) and the Dollfus Prize from the Société Entomologique de France (1895). Although mammalogists know Trouessart best for his many contributions on mammals, his breadth of study and level of productivity in both medicine and zoology were even more impressive and unequalled in the modern day.

## *Michael Rogers Oldfield Thomas, 1928*

Born 21 February 1858 in Millbrook, Bedfordshire, England; no university degrees; died 18 June 1929 (*Journal of Mammalogy,* 10:280, 1929) (Fig. 1).

Oldfield Thomas began his career at age

18 as a clerk at the British Museum, which then housed the natural history collections. After taking two years of lectures given by Thomas H. Huxley, Thomas' hopes were realized in 1878 when he was appointed Assistant in the Department of Zoology at the Museum, a position he held for 45 years.

It was Dr. Albert Gunther, Keeper of Zoology, who steered Thomas to work on mammals. He spent most of his working life building up the collections of mammals in the Museum, taking them over from John Edward Gray, his predecessor from 1837 to 1874. During Oldfield Thomas' career, the biological collections were moved from the British Museum at Bloomsbury to the new Natural History Museum in South Kensington. It was then that Thomas started the enormous task of cataloging the mammal collections, beginning in 1888 with the Marsupialia and Monotremata.

Thomas became receptive to the new concept (developed in the 1890s by C. Hart Merriam and other American mammalogists) regarding the importance of series of specimens rather than the typological approach. He responded accordingly by acquisition and study of widespread collections. Thomas and his wife supported mammal collectors from all over the world and also financed collecting expeditions.

Thomas is the author of almost eleven hundred published works, mostly descriptions of mammals, for which he proposed 2,900 new taxa. Most of his publications appeared in the *Annals and Magazine of Natural History* or the *Proceedings of the Zoological Society of London.* He was elected a Fellow of the Royal Society in 1901.

Although officially retiring in 1923, Thomas continued his work. However, his wife died in mid-1928 and Oldfield Thomas terminated his life a year later. To this day, mammalogists owe him a debt, not only for his attempt to standardize skull measurements and tooth nomenclature, but for helping to frame the foundation that established the field of systematic mammalogy for the 20th Century.

## *Max Weber, 1928*

Born 5 December 1852 in Bonn, Germany; M.D., University of Bonn, 1877; died 7 December 1937 (*Journal of Mammalogy,* 18:389–390, 1937) (Fig. 1).

Max Weber studied biology and medicine at the University of Berlin and University of Bonn. In 1879, Weber accepted a position in Holland, first as Prosector of anatomy at the University of Amsterdam. After a year, he moved to the University of Utrecht as Lecturer in anatomy. He returned to Amsterdam as Professor of anatomy, a post he held until his retirement in 1922.

Weber became involved with various expeditions to the Dutch colonies. He was leader of the Netherlands Deep Sea Expedition of the ship *Siboga* to the East Indies. Weber studied the fishes from these expeditions and published on the zoogeography of the fauna. At the same time he became interested in cetaceans and, after several visits to whaling stations, completed a series of papers on the anatomy of whales. He established a program of salvage of stranded whales on the Dutch coast and utilized the carcasses for his anatomical studies. Because the university was near the Amsterdam zoo, Weber was able to salvage many unique zoo animals for his dissections. The synoptic coverage of his efforts continued to expand. Weber studied the hairs of mammals, correlations between brain weight and body weight, and squamation.

After making two trips to the East Indies, Weber went to South Africa in 1894. Numerous samples were brought back for his systematic and anatomical research. After a number of cooperative false starts on a compendium of the order Mammalia, Weber completed a volume which he published in 1904. His *Säugetiere* was a result of the accumulation of many years of data on anatomy, systematics, and paleontology, and it served as a single reference for many years. A more expanded second edition with two volumes was published in 1927. Although others collaborated with Weber on the second edition, it was still primarily his work. It was the first and most complete review of the field of mammalogy to date. This volume alone was sufficient to ensure Max Weber immortality in the field of mammalogy.

### *Henry Fairfield Osborn, 1929*

Born 8 August 1857 in Fairfield, Connecticut; B.A., Princeton University, 1877; died 6 November 1935 (*Journal of Mammalogy,* 17:84, 1936) (Fig. 1).

Osborn was the son of William Henry Osborn, President of the Illinois Railroad. He attended private schools and Princeton University. Upon graduation, he was sent to England for additional studies at the Royal College of Science, London, and Cambridge University.

After graduation from Princeton in 1877, Osborn began research in paleontology. In 1881, he was appointed to the faculty of Princeton as an Assistant Professor of natural science. Between 1883 and 1890, he was a Professor of paleontology at Princeton but, like most students of fossils, he divided his time equally with studies of anatomy. As a result of his anatomical research, he made significant contributions in the field of neurology. He received the De Costa chair of biology at Columbia University in 1890 and held this chair until 1910. At about the same time (1891), he was appointed Curator of Vertebrate Paleontology at the American Museum of Natural History. He subsequently served as President of the Museum from 1908 to 1932 and was directly responsible for the museum's emergence as a premier exhibit and research institution. He directed expeditions to various parts of North America, the Gobi Desert, Egypt, India, and Samos Island. Osborn also served as vertebrate paleontologist on the geological surveys of both the United States (1900–1924) and Canada (1900–1904).

Osborn received numerous honors and awards, including honorary degrees from Trinity College (1901), Princeton University (1902), Cambridge University (1904), Columbia University (1907), the University of Christiania (1911), Yale University (1923), Oxford University (1926), New York University (1927), Union College (1928), and the University of Paris (1931).

During his career Osborn published nearly 1,000 titles, many of which were lengthy memoirs in vertebrate paleontology. Among his best known works are: *From the Greeks to Darwin* (1894), *The Age of Mammals* (1910), *The Origin and Evolution of Life or the Theory of Action, Reaction, and Interaction* (1917), *Evolution and Religion* (1923), *The Titanotheres of Ancient Wyoming, Dakota, and Nebraska* (1929), and *Cope: Master Naturalist* (1931). At the time of his death at age 78, Osborn was actively completing a monograph on the Proboscidea. He exhibited the same enthusiasm and energy for all aspects of life and his work, but especially his studies on fossils, right up to his death.

### *Alfred Webster Anthony, 1936*

Born 25 December 1865 in Cayuga County, New York; Colorado School of Mines; died 14 May 1939 (Fig. 1).

From New York, Anthony moved to Colorado at age three. He followed in his father's profession as a mining engineer, moving to California and Baja California in search of gold. But, at the same time, he pursued his interest in birds and mammals. He made trips to islands off the Mexican coast where he studied seals, continued searching for gold in Alaska and Oregon, and even farmed for 10 years in Oregon.

In 1920, he became director of the San Diego Museum of Natural History. In 1924, he resigned to embark on a five-year collecting trip to Guatemala. Failing health caused him to return to San Diego. Except for a few short trips, he rarely strayed from San Diego for the remainder of his life. He did make a short visit to Ensenada, Mexico, to study the southern sea otter.

Anthony was not a prolific writer, preferring that others should study and report on his collections. His greatest contribution was the size and scope of the large collections, primarily birds and mammals, that he made during his life. Being a mining engineer, he also made very important collections of minerals while searching for gold.

It should be noted that Alfred Anthony fathered a son, Harold E. Anthony, who was to became an eminent mammalogist in his own right at the American Museum of Natural History, President of the American Society of Mammalogists, and an Honorary Member like his father. In addition to his son, Alfred Anthony had a reputation of starting many other young budding naturalists in pursuit of careers in natural history. He was a Charter Member of the ASM.

## *William Berryman Scott, 1936*

Born 12 February 1858 in Cincinnati, Ohio; A.B., Princeton University, 1877, Royal School of Mines, London, Cambridge University; Ph.D., Heidelberg University, 1880; died 29 March 1947 (Fig. 1).

The great-great-great-grandson of Benjamin Franklin through his mother, Scott was born into a family of clergy and theologians, professors, and authors. Upon receiving his doctorate in Germany, Scott returned to Princeton as an instructor in geology. He was awarded the Blair Chair in geology in 1884, and he held this position until his retirement in 1930. Although primarily interested in geology and paleontology, Scott also had conducted extensive research in embryology while at Cambridge and Heidelberg universities, publishing three monographs on newts and lampreys as a result of this work. His main research focus, however, was his studies of mammalian fossils of North and South America. Between 1877 and 1897, he led 11 major collecting and exploratory trips to South Dakota, Montana, and Wyoming. In addition to his numerous short publications in many journals, Scott published several books, including his well-known *History of Land Mammals of the Western Hemisphere* (1913), *The Theory of Evolution* (1917), and *Physiography* (1922). His textbook *An Introduction to Geology* (1897) had three editions, the last appearing in 1930. He was editor and author of fifteen quarto volumes on the results of the "Princeton University Expeditions to Patagonia."

Scott received numerous honors during his lifetime. The University of Pennsylvania conferred an LL.D. degree on him in 1906. He received Sc.D. degrees from Harvard University (1909), Oxford University (1912), and Princeton University (1930). He was awarded the E. K. Kane Gold Medal of the Geographic Society of Philadelphia (1905), the Wollaston Gold Medal of the Geological Society of London (1910), the F. V. Hayden Medal of the Academy of Natural Science, Philadelphia (1926), the Mary Clark Thompson Gold Medal of the National Academy of Sciences (1931), the Walker Grand Prize of the Boston Society of Natural History (1934), the Penrose Medal of the Geological Society of America (1936), and the Daniel Giraud Elliot Medal of the National Academy of Sciences (1940). He was a member of the National Academy of Sciences.

## *Leonhard Stejneger, 1937*

Born 30 October 1851 in Bergen, Norway; Frederic's University, Christiania, Norway; died 28 February 1943 (*Journal of Mammalogy*, 24:295, 1943) (Fig. 1).

Stejneger received his undergraduate and postgraduate education at Frederic's University in his native Norway. Upon completion of his education, he left Norway for the United States where, in 1881, he accepted a position in the U.S. National Museum, a part of the Smithsonian Institution. In 1884 he became Assistant Curator of Birds, a position he held until becoming Curator of Reptiles in 1889. In 1911 he became Head Curator of Biology, although continuing in his studies of reptiles and amphibians.

Stejneger was associated with an outstanding cadre of naturalists who were working in Washington, D.C. at this time. Field work associated with the new Biological Survey was widespread and very active, resulting in large quantities of vertebrates coming to the National Museum. Leonard took advantage of the many opportunities to study these collections of birds, mammals, reptiles, and amphibians. His first love was herpetology, so as often as possible he accompanied some of the early expeditions of the Biological Survey as herpetologist and studied the herpetological collections made by many of the others.

Stejneger's contribution to mammalogy results primarily from his activities as a member of the Fur Seal Commission. He first became involved with fur seals as a member of the team sent in 1895 to the Commander Islands by the U.S. Fish Commission. The report from this team has served as the primary program for managing fur seal resources of the North Pacific.

Stejneger's reputation as an all-round naturalist can be judged by his election to Honorary Membership in the ASM and to fellow of the American Ornithologists' Union.

## *Gerrit Smith Miller, Jr., 1941*

Born 6 December 1869 in Peterboro, New York; A.B., Harvard University, 1894; died 24 February 1956 (*Journal of Mammalogy,* 37:309, 1956) (Fig. 1).

Miller, a shy and sensitive boy, grew up on a large estate in central New York and attended private schools. He developed a great interest in the animals living in the forests and fields of the estate. His great uncle, Greene Smith, who lived on the estate, was interested in birds and probably also greatly influenced Miller.

After graduating from Harvard University, Miller joined an aunt for a summer tour of Europe to attend the Wagnerian festival at Beireuth. Music was always to be a very important part of Miller's life. Later, in 1894, he joined the Biological Survey in Washington, D.C., where he remained working for C. Hart Merriam until 1898. At that time, he took a position as Assistant Curator of Mammals at the United States National Museum. He became Curator in 1909 and remained in that position until he retired at age 70 in 1940. During the intervening years, Miller became one of the outstanding mammalogists of his time. Miller was a Fellow of the American Association for the Advancement of Science, and a member of the American Academy of Arts and Sciences, the American Philosophical Society, and the Academy of Natural Sciences.

Miller was married twice. Each of his wives was to influence his life greatly. His first wife, Elizabeth Page, was an older woman with three children when she married Miller in 1897. She was a quiet, reclusive woman. Rather than socialize, she and Miller found pleasure in scholarly activities. Miller spent his free time in his library. After a long illness, she died in 1920. During a trip to a meeting in Honolulu, Miller met Anne Chapin Gates. They were married in the summer of 1921. The Millers moved from Virginia to a hill overlooking the National Zoo. They socialized, and Miller came out of his private shell and interacted with people. He spent many hours observing primate behavior at the zoo and even published on his observations. He was well known in mammalogy as an author of more than 400 papers, including monographs and the following books: *The Families and Genera of Bats*; *Catalogue of the Land Mammals of Western Europe in the British Museum*; *List of North American Land Mammals in the United States National Museum, 1911*; *List of North American Recent Mammals, 1923.*

## *Ernest Evan Thompson Seton, 1941*

Born 14 August 1860 in South Shields, England; Royal Academy School of Painting and Sculpture, London; Julian Academy, Paris; died 23 October 1946.

Born in England of Scottish parents, Seton moved to Canada at age five when his father settled on a farm in rural Ontario. When he was nine, Seton moved to Toronto. However, four years of rural life had instilled in young Seton a love for nature that was to continue to grow throughout his life. Although his father was determined that Seton should be an artist, he was equally determined to become a naturalist. During a year of formal study at the Royal Academy in London in 1880, he was granted permission to use the Natural History Library at the British Museum, a singular waiver of an inflexible rule. He returned to rural Manitoba for further studies of wildlife. In late 1883 he moved to New York City for a brief time to write short stories, but he soon returned to Manitoba. While in New York, he made numerous contacts relating to his sketches and drawings. Back in Manitoba, his arthritis began to impede his travels by foot so, in 1890, Seton left for Paris to study at the Julian Academy. His studies were interrupted by a trip to New Mexico in 1892 to hunt wolves.

During a voyage to France in 1894, Seton met Grace Gallatin. They were married in 1896 and settled on an estate in New Jersey. At this time Seton was commissioned to illustrate Frank Chapman's *Bird Life.* Seton's career as an illustrator and writer flowered. He published his first collection of illustrated animal stories in 1898, *Wild Animals I Have Known.* The public clamored for his books. *The Trail of the Sandhill Stag* (1899), *Lives of the Hunted* (1901), *Woodmyth and Fable* (1905), *Animal Heroes* (1905), *Life-histories of Northern Animals* (2 vols.) (1909), *Wild Animals at Home* (1913), *Biography of a Grizzly* (1918), *Game Animals and the Lives They Live* (1924), and *Lives of Game Animals* (4 vols.) (1925–1928) followed. Seton was also an accomplished writer and illustrator of popular children's books. Among his best known are *Two Little Savages* (1903), *Rolf in the Woods* (1911), *Woodcraft and Indian Lore* (1912), *Wild Animal Ways* (1916), and *Woodland Tales* (1921). He was also a very successful lecturer, giving animated lectures that captured the attention of his audiences.

From New York he moved to an estate in Connecticut, where he practiced some of his ideas on attracting waterfowl and raising furbearers. In 1930 he moved to a ranch near Santa Fe, New Mexico, where he lived the remainder of his life. He established the Seton Institute to promote an appreciation of traditional Indian customs and life. With his second wife, Julia M. Battree Moss, a noted Indian expert, he fathered a daughter at age 78.

Seton was instrumental in establishing the Boy Scouts of America in 1910 and was honored as a Chief Scout. He received the John Burroughs Medal (1926) and the Daniel Girard Elliot Gold Medal (1928), the latter from the National Academy of Sciences, for his book *Game Animals and the Lives They Live.* Seton was endowed with an infectious personality which allowed him to carry his messages of conservation and nature to large audiences.

## *Rudolph Martin Anderson, 1947*

Born 30 June 1876 in rural Winneshiek County, Iowa; A.B. (1903) and Ph.D. (1906), University of Iowa; died 21 June 1961 (*Journal of Mammalogy,* 42:444, 1961).

Anderson had a passion for natural history from his early youth. Birds were his first love, and his first publication at age 17 was entitled *The Marsh Hawk.* His first book, *The Birds of Iowa,* was published in 1907. He spent as much time as possible studying the natural history of birds, especially nesting habits.

The physically large and strong young Anderson was attracted to athletics, especially track and field where he won numerous medals and awards at the university. At this same time he was a member of the Cadet Corps, was sent to the Spanish-American War in 1898, and served in the Iowa and Missouri national guards between 1900 and 1908.

Anderson's professional career began with a position as field agent and mammalogist on the American Museum of Natural History's expedition to Arctic Alaska and the Yukon and Northwest Territories from 1908–1912. Anderson had found his calling. He was selected second in command of the Stefanson-Canadian Arctic Expedition from 1913–1916 and was appointed mammalogist at the National Museum of Canada in 1913. He continued with the Museum and became Chief of the Biology Division in 1920, a position he held until his retirement in 1946.

During his career, Anderson conducted or supervised field work and research at sites in all provinces and territories of Canada, many of them in Arctic and mountainous areas under extremely difficult conditions. Over the years, administrative duties cut severely into the time he had available for field work. However, he persisted by helping his assistants and students carry on the field work he loved so much. By 1929, Anderson had spent seven winters and ten summers north of the Arctic Circle. He edited and partially wrote the 16 volumes and 64 papers resulting from the Canadian Arctic Expedition. Anderson published 134 papers and books. Noteworthy books are *Methods of Collecting and Preserving Vertebrate Animals* (1932), one of the first and most complete of its kind ever published, and *Catalogue of Canadian Recent Mammals* (1946).

Anderson was a member of 11 professional societies and associations and an honorary member or fellow of six more, including the American Association for the Advancement of Science and the Royal Society of Canada. He was a Charter Member of the ASM. Anderson served as a consultant or committee member of many governmental agencies from Mines and Resources, Parks and Forests, and Wildlife Protection, to Library.

Anderson was a gentle and quiet-spoken person with a keen sense of humor. As evidence, one need only read his account of *Homo sapiens* in the *Catalogue of Canadian Recent Mammals.*

## *Angel Cabrera Latorre, 1947*

Born 19 February 1879 in Madrid, Spain; Ph.D., University of Madrid, 1902; died 7 July 1960 (*Journal of Mammalogy,* 41:540, 1960) (Fig. 1).

Upon completion of his doctorate, Cabrera accepted an honorary position as Assistant Curator with the National Museum of Natural Sciences. He was to continue his association with this museum until 1925, when he moved to Argentina. Cabrera's first task was a review of the mammals of the Iberian Peninsula. He published this work as *Fauna Ibérica: Mamíferos* (1914). He next began a review of genera of mammals, which he published from 1919 through 1925 as *Genera Mammalium.* In 1922, he produced the first Spanish manual of mammalogy (*Manual de Mastozoología*). During this interval he began a study of the mammals of Morocco, part of which was a Spanish colony. This was published in 1932 as *Los Mamíferos de Marruecos.*

Cabrera accepted a position at the National University of La Plata, Argentina, in 1925. He was to focus the remainder of his career on neotropical mammalogy. From 1927 to 1947, he was Professor and Head of the Department of Paleontology in the La Plata Museum and held the Chair of Professor of Zoology at the School of Agriculture and Veterinary Medicine of the University of Buenos Aires. His research and field work centered on fossil and Recent mammals of Argentina. In 1940 Cabrera published the first of his momentous reviews of South American mammals. His

Theodore S. Palmer[a]
(1951)

Edward A. Preble[b]
(1952)

William K. Gregory[c]
(1954)

Albert R. Shadle[d]
(1956)

Magnus A. Degerbøl[e]
(1962)

Stanley P. Young
(1964)

Erna Mohr[f]
(1966)

Kazimierz Petrusewicz
(1972)

Charles S. Elton[g]
(1973)

FIG. 2.—Honorary members of the ASM, 1951–1973. Courtesy of: [a,b]The American Society of Mammalogists Records, Smithsonian Institution; [c]Department of Library Sciences, American Museum of Natural History; [d]Roswell Park Memorial Institute; [e]Zoological Museum, University of Copenhagen; [f]Zoologisches Institut und Zoologisches Museum, Hamburg, Germany; [g]Ken Marsland.

*Mamíferos Sudamericanos* was a collaborative effort with José Yepes. This was followed by the first volume of *Catálogo de los Mamíferos de la America del Sur* (1958). Although Cabrera died in 1960 before the completion of the second volume, it was sufficiently complete so as to be published that same year.

Cabrera was a prolific writer, authoring 218 papers on mammals, 27 books on mammals, and more than 400 popular articles. In addition he often illustrated his work, especially his popular articles, with his own watercolors and other forms of art. His talent and hard work were rewarded with numerous honors and distinctions. Most significant were his election as Corresponding Member (1907) and Honorary Foreign Member (1947) of the Zoological Society of London; Member of the International Commission on Zoological Nomenclature (1930–1960); and elected Member of the Royal Academy of Physical and Natural Sciences, Madrid (1931–1960). He was a Charter Member of the ASM.

## *Theodore Sherman Palmer, 1951*

Born 26 January 1868 in Oakland, California; B.A., University of California, Berkeley, 1888; M.D., Georgetown University, 1895; died 23 July 1955 (Fig. 2).

Although employed initially as a banker, Palmer was attracted to natural history and accepted a position as field agent in the Department of Agriculture in 1889. A year later he became the first assistant ornithologist and headed the Death Valley Expedition of 1891. He moved over to the new Biological Survey in 1896 and continued with the Survey in various positions until his retirement as a senior biologist in 1933. After retirement, Palmer worked for a time with the United States National Museum.

During his nearly 40 years with the Biological Survey, Palmer became an international expert on game protection and conservation, publishing five books on the subject and helping draft numerous international treaties and regulations covering migratory birds. He was one of the principal persons responsible for the first migratory bird treaty between the United States and Canada in 1916. In addition, he was deeply interested in nomenclature of birds and mammals. Using the vast library resources available to him in Washington, D.C., Palmer compiled his premier compendium of mammalian generic names, which was published as "Index Generum Mammalium" in *North American Fauna* number 23, 1904. At the same time, he was a prolific contributor to scientific journals.

Palmer was a Fellow of the American Ornithologists' Union, the American Association for the Advancement of Science, and the California Academy of Sciences. He was an active member of more than 27 other associations and societies, including four in Europe.

Few, including many of his contemporaries in ornithology and mammalogy, realize that Palmer had an equally distinguished record in his hobby of philately. He was a prolific contributor to journals and magazines of philately and was recognized as an expert in the field by his philatelic peers.

Like many of his colleagues who had trained as physicians, Palmer never practiced medicine. Rather he merely used the degree as a means to study his first love, which was natural history.

## *Edward Alexander Preble, 1952*

Born 11 June 1871 in Somerville, Massachusetts; no university degrees; died 4 October 1957 (*Journal of Mammalogy,* 38:546, 1957) (Fig. 2).

Preble could trace his ancestry in the United States to the early 17th Century of New England. Shortly after graduation from high school, in 1889, he took work as a plumber in Boston. After eight months of city life, he returned home to rural western

Massachusetts. A fellow birder who had moved to Washington, D.C., to take a position with C. Hart Merriam in the new Division of Ornithology and Mammalogy made arrangements for Preble to join Merriam's team. He began work on 1 April 1892 with a trip to Texas with Vernon Bailey. Numerous trips for the new Biological Survey followed to Maryland, Georgia, Oregon, Washington, and Utah.

In the summer of 1900, Preble made the first of many survey trips to northern Canada and Alaska, a region which was to be the focus of most of his remaining years with the Survey. The results of these biological surveys to northern regions were to be published as numerous numbers in *North American Fauna* during the next thirty years. In addition to Bailey, he worked with such Biological Survey notables as Merrit Cary, A. K. Fisher, E. T. Seton, Francis Harper, W. H. Osgood, W. L. McAtee, and J. A. Loring. Preble was a member, along with Osgood, of the famous Federal Commission to investigate the Pribilof Island fur seals in 1914.

Preble routinely was called upon by his colleagues to exercise his considerable editorial talents on their work. He had honed this talent by self study and considerable reading in a wide variety of fields in addition to nature.

Upon retirement from government service in 1935, Preble became an Associate Editor of *Nature Magazine.* This second professional career offered him a forum to speak out freely and forcefully on issues of conservation, a topic that had begun to consume his interest and time. He became a prolific writer on the topic. Because few of his pieces were signed, the exact number of contributions is unknown, but nearly every issue had numerous articles or reports written by him.

Preble was an unassuming individual who used the spoken word sparingly. Francis Harper reported that his ". . .outstanding traits were simplicity of character, forthrightness, extraordinary patience and forbearance, unswerving principles, and independence . . . ." In addition to his honors, including charter membership in the ASM (which he valued very highly), he was a Fellow of the American Ornithologists' Union. He is best known for his numerous scientific contributions published in *North American Fauna.*

## *William King Gregory, 1954*

Born 19 May 1876 in New York City, New York; A.B. (1900), A.M. (1905), and Ph.D. (1910), Columbia University; died 29 December 1970 (*Journal of Mammalogy,* 52:495, 1971) (Fig. 2).

Joining the American Museum of Natural History as research assistant to Henry Fairfield Osborn and Editor of the *American Museum Journal* in 1899, Gregory was to spend much of his career at that institution. He continued as editor until 1901 and as Osborn's assistant until 1913. His research interest was paleontology, and he was given a position as Assistant Curator in that department in 1911. In addition he was a curator in ichthyology and comparative anatomy. In 1916 he accepted an official position as a paleontologist at Columbia University and became Professor in 1925.

Gregory's research focused on the evolution of the vertebrates, evolution of humans and their dentition, and the relationship of humans and other anthropoids. With Osborn, he postulated that humans and higher anthropoids, especially the gorilla and chimpanzee, had a common, tailless ancestor during the Tertiary. Gregory's publications were mostly on fossil mammals, especially primates, but included such books on dentition as *The Origin and Evolution of the Human Dentition* (1922), *The Dentition of Dryopithecus and the Origin of Man* (1926), with Milo Hellman, and *Our Face from Fish to Man* (1929).

Gregory was a member of 17 professional societies and associations, including the National Academy of Science, Zoological Society of London, and the Anthropologische Gesellschaft, Vienna.

### *Lee R. Dice, 1956*

Born 15 July 1887, in Savannah, Georgia; B.A., Stanford University, 1911; M.A. (1914), and Ph.D. (1915), University of California, Berkeley; died 31 January 1977 (*Journal of Mammalogy,* 59:635–644, 1978).

Dice was raised on a farm in Prescott, Washington, and in his boyhood became deeply interested in natural history. He initially went to Washington State University (then an Agricultural College) in Pullman, but decided to transfer to the University of Chicago where he came under the influence of Professor V. E. Shelford, who introduced him to ecology. It was then that Dice decided to become an ecologist. He was, however, unable to continue at the University of Chicago for financial reasons, so went to Stanford University for his remaining undergraduate program. As a doctoral student, Dice worked under Joseph Grinnell at the Museum of Vertebrate Zoology, University of California, Berkeley. After several brief jobs and Army service, Dice became Curator of Mammals, Museum of Zoology, and Instructor of Zoology, University of Michigan, in 1919, and by 1942 had been made Professor. He remained at this institution throughout his career. Dice was the mentor and supervisor of many graduate students, several of whom later also became eminent mammalogists.

In 1922 Dice began to work with *Peromyscus* and kept several species in captivity. When geneticist Clarence C. Little became President of the University in 1925 and established the Laboratory of Mammalian Genetics (later renamed the Laboratory of Vertebrate Biology), he appointed Dice as an associate of the laboratory. From that time on Dice conducted his monumental studies of *Peromyscus* genetics, focusing especially on the genetic nature of subspecific boundaries. He also became interested in human heredity and helped to establish the Heredity Clinic at the University and, as his research focus intensified there, his work on *Peromyscus* lessened. The Laboratory and Clinic were merged as the Institute of Human Biology with Dice as its Director until retirement. Dice was the author of 138 publications, nearly half of which were about *Peromyscus.* Throughout his career, his research was supported by many granting agencies.

He was President of the Ecological Society of America, the Society for Systematic Zoology, the Ecological Union (now the Nature Conservancy) and the American Society of Human Genetics. Dice was a Charter Member of the ASM, and from 1947–1951 was Vice President. He died 20 years after retirement and is still remembered as the father of research on *Peromyscus.*

### *Albert R. Shadle, 1956*

Born 18 July 1885 in Lockbourne, Ohio; B.A. (1913) and M.A. (1915), Ohio State University; Ph.D., Cornell University, 1933; died 23 May 1963 (*Journal of Mammalogy,* 44:449, 1963) (Fig. 2).

After earning the M.A. degree, Albert Shadle went to Cornell as an Assistant in Zoology for a year, then became an Instructor for two years, and in 1918 was appointed Assistant Professor for one year. From there he moved to the Department of Experimental Biology, Roswell Park Memorial Institute in Buffalo, New York, where in 1920 he was appointed Professor. He held that position until his retirement in 1956. He was head of the Department for all but four years of his tenure there. In 1956, he was made Emeritus Professor and Research Associate at the Institute. In 1959, he also became Associate Director of the Institute's summer science program.

Shadle was a person of broad research interests, working on the insect fauna of the Allegheny State Park, respiration in fresh-water clams, prostate cancer, pelvic changes during pregnancy and parturition, and extensive growth and attrition of the incisors of rodents and lagomorphs. He was best known in the ASM for his deep commitment to the porcupine, and he studied its life history and reproductive biology extensively. He is remembered today as a cordial and outgoing man and one who could be counted on for a presentation on porcupines at almost every annual meeting of the ASM. He attracted a significant audience when he delivered lectures about their breeding activities, everyone hoping to find out just how porcupines did it!

Shadle was a member of a number of societies, including the New York Academy, Wildlife Society, Audubon Society, Society of Naturalists, and others. He was also supported by the National Science Foundation.

After his death, the ASM was informed that a fellowship in his name and that of his wife had been set up commencing in 1972 to foster the research of Ph.D. students from the United States. Although administered and ultimately approved by the Buffalo Foundation, the ASM is given the opportunity to select a finalist each year and to present the award. The Albert R. and Alma Shadle Fellowship provides several thousand dollars toward the support of the student's research. At the end of the year, the student presents the results of the work at the plenary session of the annual meeting of the ASM. Dr. Shadle's name and memory are carried on in this significant way.

## *Francis Harper, 1959*

Born 17 November 1886 in Southbridge, Massachusetts; B.A. (1914) and Ph.D. (1925), Cornell University; died 17 November 1972 (*Journal of Mammalogy*, 54:309, 1973).

Like many young biologists who were trained at the turn of the century, Francis Harper was interested in both birds and mammals. After receiving his first degree in 1914, he took his initial trip north to Lake Athabaska. Other noteworthy trips to the north included his lengthy visit to southern Keewatin in 1947 and to the interior Ungava Peninsula in 1953. During the intervening and later years, Francis managed to support himself with short periods of employment and meager grants. He was noted for his outstanding editorial skills and prodigious memory, as a writer of copious notes, and for his very strong opinions. During his lifetime, he had no long-term employment due to a self-professed inability to withstand close supervision. Rather, he chose to work mostly on projects funded by such groups as the Geological Society of Canada, the U. S. Biological Survey, the New York State Museum, the Boston Society of Natural History, the Penrose Fund, and the American Philosophical Society.

Francis Harper was a Guggenheim Fellow in 1950–1952 and was employed for a time by the Huyck Preserve in Rensselaerville, New York, after returning from Ungava Peninsula. In 1960 he moved to Chapel Hill, North Carolina, in order to resume his work on a favorite subject—the natural history and folklore of the Southeast, especially the Okeefenoke Swamp.

Francis Harper was a Charter Member of the ASM and was corresponding secretary from 1931–1932. He was Honorary Life Elective Member of the American Ornithologists' Union and member of Phi Beta Kappa.

During his lifetime Francis published about 135 titles on such subjects as mammals, birds, and other vertebrates, faunal zones, botany, conservation, Eskimos and Montagnais, folkore, and early naturalists. Particularly noteworthy are his lengthy papers on Keewatin (*The Barren Ground Caribou of Keewatin* and *The Mammals of Keewatin*) and Ungava Peninsula (*Land and Fresh-water Mammals of the Ungava Peninsula*), the two volume treatise on the Bartrams published in the *Transaction of the American Philosophical Society* in 1942 and 1943, and *The Travels of William Bartram*

(1958). His work on the Bartrams stands as a monument to his careful scholarship.

## *Nagamichi Kuroda, 1959*

Born 24 November 1889 in Tokyo, Japan; B.A. (1915) and Ph.D. (1924), Tokyo Imperial University; died 16 April 1978 (*Journal of Mammalogy,* 59:908, 1978).

After finishing his undergraduate studies in zoology in the College of Sciences, Kuroda was commissioned in 1916 by the Government-General of Taiwan to conduct research on animals in Taiwan. From there he received a similar commission the next year from the Government-General of Korea to do research on the birds of Korea. At the same time, he became involved in the preservation of natural areas as a member of the Society for Shimei. He became an examiner in 1919 in the society for the Ministry of Internal Affairs and held the post until 1924. This position allowed him to travel to many sites of these memorial natural areas. In 1921, he was appointed Chief of the Game Commission under the Department of the Imperial Household. He focused on matters of game law, a newly developing part of wildlife control in Japan, and gave numerous lectures on the subject throughout Japan. He held the post of Chief until 1940. From 1930 until 1937 he also served as Grand Master of Ceremonies and Commissioner of Game for the Imperial government. During the war years, Kuroda was commissioned to study various aspects of the natural resources of the Japanese Empire. Most of these studies were pursued through the auspices of the Ministry of Agriculture and Forestry.

From an early age Kuroda was interested in birds, following in the footsteps of his maternal grandfather with an interest in ducks. At age 19, he published his first paper on ducks, and in 1912 he published *Ducks of the World.* Although never holding a university position, Kuroda had a major influence on academia and scientific research in Japan. He was a founder of the Nippon Ornithological Society in 1911 and ultimately served as President. Kuroda is considered to be the father of Japanese ornithology, but he was also a charter member of the ASM and helped found the Nippon Mammalogical Society in 1923.

Because Kuroda was able to travel throughout the Empire, or to send others in his place, he acquired extensive collections of birds and mammals from parts of Manchuria, Korea, Taiwan, Philippines, Java, Celebes, Okinawa, and Japan. These collections formed the basis for numerous publications on mammals, including such books as *A Pictorial Book of Japanese Animals* (1927), *Outline of Vertebrate Animals—Mammals* (1937), *Catalogue of Japanese Mammals* (1938), *Colored Pictorial Book of Japanese Mammals* (1940), and *Classification System of Japanese Mammals with Diagrammatic Charts* (1953).

In addition to his extensive contributions to the taxonomy and biogeography of mammals of eastern Asia, Kuroda also published extensively on conservation, game laws and control of wildlife, and birds. He was equally prolific as a writer of popular articles on natural history, especially on conservation of the fauna. He was a man of enormous and intense energy who left a legacy of the founding of two scientific professional societies in Japan.

## *Magnus Anton Degerbøl, 1962*

Born 8 August 1895 in Sjorring, Thy, Jutland, Denmark; A.B. (1912), Ph.D. (1921), and D.Sc. (1933), University of Copenhagen; died 1977 (*Journal of Mammalogy,* 59: 894–897, 1978) (Fig. 2).

Magnus Degerbøl was born in rural Denmark of parents who directed a dairy cooperative. He showed an early interest in natural history. During his university studies he came under the influence of Professor Herluf Winge, who also held a position at the university zoological museum. Winge had been studying an enormous collection of bones from excavations in Denmark and Greenland. After Winge's death, Magnus became Curator of Mammals at the Museum and continued these studies of the Pleistocene distribution of vertebrates, especially mammals, in Scandinavia. He made detailed analyses of the morphology and distribution of various species. His benchmark study of prehistoric versus Recent predators was used for his D.Sc. degree.

In 1937, Magnus became Chief Curator of Vertebrates at the Zoological Museum. At the same time he started a program of exhibition growth, including new Arctic and African dioramas. Material for the African exhibits was obtained during Magnus' expeditions to Central Africa in 1947.

From 1927 to 1947, Degerbøl added ever increasing teaching responsibilities to those of his museum duties. He enjoyed teaching, relishing the opportunity that it gave him to present his research results to a wide audience. This desire was also reflected in the increasing number of contributions he made to popular scientific journals. He was sought after for lectures to societies and appearances on radio programs.

Magnus made four major international expeditions. The first was an expedition to his beloved Greenland in 1932. The next was the 1947 Danish Central African Expedition. In 1952, he participated in the Galathea Expedition to the Campbell Islands, which was followed by a 1954 trip to the Andes of South America.

Although small in physical stature, Degerbøl left a large mark in European Quaternary zoology and was a leading figure in Danish zoology. His impact on the Danish public through the zoological museum's exhibits, and his lectures, radio programs, and popular articles was profound.

## *Vladimir Georgievich Heptner, 1963*

Born 22 June 1901 in Moscow, Russia; D.Sc., Moscow State University, 1936; died 5 July 1975 (*Journal of Mammalogy*, 56: 728, 1975).

Heptner began his active career in mammalogy near the end of the illustrious career of S. I. Ognev at the Zoological Museum of Moscow State University. From the beginning of his career, Heptner participated in numerous expeditions to the far corners of the Union. He focused much of his field work on gerbils of Middle and Central Asia and Asia Minor.

Heptner published more than 300 titles during his career. He also served as an editor or on the editorial board of four Russian journals and three foreign ones. He instigated the translation from English to Russian of numerous books and edited the translations. At the same time, he was involved in academic activities and administrative duties with the university and Museum. Best known among his numerous early monographs and books are *Mammals of the Kopet Dagh and adjacent plains* (1929), *General Zoogeography* (1936), *Rodents of Middle Asia* (1936), *Vertebrate animals of Badkhyz* (1956), and *Harmful and useful mammals of the protective forest zones* (1950).

With the initiation in 1962 of an English translation of Ognev's multi-volume *Mammals of the USSR and Adjacent Countries*, an excellent work, although incomplete and now superseded, Heptner's plan for a new, more complete *Mammals of the Soviet Union* took on an added degree of urgency. The first volumes covered large mammals and partially filled the gap left by Ognev. This monumental work is a fitting tribute to the life of one of Russia's outstanding mammalogists, unequalled in the breadth and depth of his knowledge of the mammalian fauna of Eurasia.

Heptner was elected to honorary membership in the Gesellschaft Naturforschen der Freunde zu Berlin, the Deutschen Gesellschaft für Säugetierkunde, and the Zoological Society of Czechoslovakia. He was also a member of numerous Russian societies, including honorary membership in the

All-Russian Society of Wildlife Conservation.

## *Stanley Paul Young, 1964*

Born 30 October 1889 in Astoria, Oregon; B.A., University of Oregon, 1911, M.S. University of Michigan, 1915; died 15 May 1969 (*Journal of Mammalogy,* 51:131–141) (Fig. 2).

In his youth, he lived a free spirit life in Oregon, hunting, fishing and keeping small mammals captive to observe them. Although his undergraduate degree was in mining engineering, his interests changed in graduate school—first to geology and then to biology. Stanley Young's first job was as a ranger with the U.S. Forest Service in Arizona. Soon thereafter, he went to the Biological Survey as a U.S. Government Hunter in predator control. On one occasion, he inadvertently crossed into Mexico without credentials while tracking a wolf. He had to be rescued by the 25th U.S. Infantry, but not before being held captive for a week.

Following a brief stint as Assistant Inspector of predator control for Arizona and New Mexico, he was appointed Assistant Leader and then Leader in predatory animal control for the Colorado-Kansas district. He was based in Denver and remained there until 1927, when he became Assistant Head of the Division of Predatory Animal and Rodent Control in Washington, D.C. There he held a number of increasingly responsible positions, including Chief, Division of Game Management, and Chief, Division of Predator and Rodent Control. In 1939 he was appointed Senior Biologist, Branch of Wildlife Research, in the newly-merged Fish and Wildlife Service. Finally, in 1957 he became Director, Bird and Mammal Laboratories, U.S. National Museum, where he remained until his retirement in October, 1959. In his latter positions he published regularly, mainly about predator control measures and techniques, and about life histories of large mammalian predators. Even after retirement, Stanley Young remained active in publication, facilitated by a collaborative appointment at the U.S. National Museum. Volumes such as *The Wolf in North America, The Bobcat of North America,* and *The Clever Coyote* (with H.H.T. Jackson) are a few of his books that are now considered classics.

Young was a recipient of many honors, including Honorary Member of the Wildlife Society, Certificate of Appreciation from the Office of the Surgeon General of the U.S. Army, and the Distinguished Service Award from the Department of the Interior. Ten years after a retirement filled with writing, traveling, and tending to his rose garden, Young succumbed to a battle with cancer. His life came full circle when his ashes were returned to his birthplace in Oregon, where he had first savored the wilderness that became his lifelong interest.

## *Erna Mohr, 1966*

Born 11 July 1894 in Hamburg, Germany; Dr.H.c., University of Munich, 1950; died 10 September 1968 (*Journal of Mammalogy,* 50:232, 1969) (Fig. 2).

In the beginning of her career, Erna Mohr studied fish and invertebrates and established a reputation in those disciplines. In her later years, she became world famous for her prodigious volume of scientific work on mammals, especially large mammals. Her interests were ubiquitous, covering all aspects of mammalogy, including anatomy, taxonomy, behavior, ecology, general biology, and natural history. Her ability to synthesize the voluminous amounts of information available and her encyclopedic knowledge of international literature made the production of these works seem easy for her. But she was an indefatigable worker who continued at an incredible pace, even during months of illness near the end of her life. In all, she published more than 400 titles.

During most of her career, Mohr was Curator of Mammals at the Zoologisches Museum und Institut, Hamburg. The collections and library gave her an opportunity to complete the series of review monographs of such diverse groups of mammals as the rodents of Germany, European seals, European bison, wild boars, and porcupines. She initiated the studbooks for the European bison, Przewalski's horse, and onager.

During a life that spanned some of Germany's worst times, Mohr overcame this adversity to lead Germany's emergence as an international center of museum and zoo mammalogy. She is the only woman to be elected to Honorary Membership in the ASM.

## *Klaus Zimmerman, 1966*

Born 7 July 1894 in Berlin, Germany; Ph.D., University of Rostock, 1929; died 5 February 1967 (*Journal of Mammalogy,* 48: 357, 1976; 50:232, 1979).

After finishing his studies at the Bismarck Gymnasium in 1913, Zimmerman was faced with difficulties in finding employment because of the state of the economy in Germany. He did not serve in World War I but, following family wishes, went to work for the family business of selling lumber in Berlin. After a year of military duty in 1926, he went back to his studies of zoology. In 1929, he received his doctorate based on a dissertation on the systematics and geographic variation in the Palearctic vespid wasp *Polistes.* He continued studying Hymenoptera, Coleoptera, and Mollusca.

During the period leading up to and during World War II, Zimmerman, like most German biologists, was involved with exploration of the world and studies of the fauna and flora encountered. During this period, Zimmerman changed his research focus to small mammals. He began studies of Palearctic murids and the small mammals resulting from an expedition to Crete. He was also involved in a project attempting to show whether young dogs and mice could synthesize vitamins in their appendix.

In 1952 Zimmerman became Curator of Mammals at the Natural History Museum of the Humboldt Institut in Berlin and Professor at the University. He was to remain at this institution for the remainder of his career. From this position Zimmerman was able to continue his systematic studies of the Palearctic rodents, especially his analyses of geographic variation in *Apodemus sylvaticus, Microtus oeconomus,* and *Mus musculus.* In 1956, he participated in an expedition to northern China, and in 1963, at age 69, he went to the Tien-Shan region of Central Asia. His studies of the mammals from these expeditions contributed significantly to the knowledge of mammals of Central and Eastern Asia.

In the later years of his life, Zimmerman, along with H. W. Stein, was involved in translating from Russian to German the numerous volumes of the Mammals of the Soviet Union series begun by B. G. Heptner. This was an immense project to which Zimmerman gave all of his energies so that these important volumes would be available to the widest possible international audience.

## *George Gaylord Simpson, 1969*

Born 16 June 1902 in Chicago, Illinois; Ph.B. (1923) and Ph.D. (1926), Yale University; died 6 October 1984 (*Journal of Mammalogy,* 66:207, 1985).

George Gaylord Simpson was born in Chicago but moved to Colorado as a child and enrolled in the University of Colorado as an undergraduate before transferring to Yale. By 1926, with a newly obtained doctoral degree, he was already considered an international authority on Mesozoic mammals. This interest took him to the British Museum (Natural History) for a year as a National Research Council Fellow in Biological Sciences, and then to the American

Museum of Natural History for the next 32 years. There he advanced from Assistant Curator of Paleontology to Curator of Fossil Mammals and Birds and Chairman of the Department of Paleontology and Geology. It was immediately after World War II that he organized this department, having just spent several years in service within Army intelligence. Concurrent with his leadership of the department, he was also a Professor at Columbia University in Zoology, holding that position through 1959. In 1959, he moved to Harvard University as Agassiz Professor of Vertebrate Paleontology, a position he held until 1970.

His forte in communication was through writing. He was a prolific writer, his earlier works, some as monographs, emphasizing his interest in Mesozoic and early Tertiary mammals. For all concerned with the major groups of mammals, Simpson's monograph (1945) entitled *The Principles of Classification and a Classification of Mammals* became the primary reference worldwide. His expeditions to Patagonia, which he popularized in *Attending Marvels* and other books, and to various places in the United States resulted in extensive collections upon which this work was based. All this work reflected his rejection of plate tectonics as a mechanism of faunal dispersal. His Condon lectures, published in 1953, are a prime example of this. With his mathematician wife Anne Roe, he wrote the text *Quantitative Zoology* that identified his interest in applying methods of biostatistics to research on fossil mammals. To anyone teaching introductory biology in the late 1950s, the book *Life,* of which he was the senior author, was the most substantative and refreshingly different introductory text available. One of his works was classic in evolutionary biology: *Tempo and Mode in Evolution* (1944), which synthesized the entire field of evolutionary thought. Simpson was a leader in developing a synthetic theory of evolution in association with such other eminent scholars as J. Huxley, T. Dobzhansky, and E. Mayr.

The enormous impact of his prolific works on evolutionary theory, systematics, and vertebrate paleontology (numbering roughly 1,000 titles) made him not only one of the most respected scientists of his time, it also garnered him many honors. He was elected to the National Academy of Sciences, recipient of numerous honorary degrees and awards, and elected President of both the Society of Vertebrate Paleontology and the Society for the Study of Evolution.

From 1967 until the time of his death, Simpson and his wife lived in Tucson where he held the position of Professor of Geosciences at the University of Arizona. It was there that he became involved in fostering graduate students.

## *Kazimierz Petrusewicz, 1972*

Born 23 March 1906 in Minsk, Byelorussia; Maritime Academy, Tczew, 1928; M.S. (1933), Sc.D. (1936), Stephen Bathory University, Vilnius; died 26 March 1982 (*Journal of Mammalogy,* 63:543, 1982) (Fig. 2).

Originally trained in the merchant marines, Petrusewicz continued his studies in natural sciences between voyages. Both graduate degrees were based on studies of spiders. His career was interrupted by World War II, when he fought with the underground Army. After the war he held a number of significant posts in the new Polish government, helping to rebuild the ravaged countryside, economy, and educational system. In 1949, he was appointed Professor at the University of Warsaw. During the 20 years he held that post, he trained more than 50 doctoral students, as well as numerous master degree candidates.

Petrusewicz helped found the Polish Academy of Sciences and established a Department of Ecology within the Academy in 1952. This department was to become the Institute of Ecology in 1956. He headed that department and institute until 1973 and promoted it to world class status as a center of ecological research. He helped organize the International Biological Programme and chaired the Polish committee. The Polish Institute focused on studies of biological productivity. Petrusewicz was a leader in establishing the IBP Working Group on Small Mammals. He served as head of the group, editor of numerous reports and co-organizer of three international conferences.

Petrusewicz published more than 140 papers, including numerous books. He was elected to the Board of the International Association for Ecology, honorary member of the British Ecological Society (1977), and Full Member of the Polish Academy of Sciences (1965). Clearly, Petrusewicz was an international figure in the field of ecology. Even more significantly, he single-handedly influenced the development of ecology in Poland from its infancy to international importance.

## *Charles Sutherland Elton, 1973*

Born 29 March 1900 in Liverpool, England; A.B., Oxford University, 1922; died 1 May 1991 (Fig. 2).

While an undergraduate at Oxford, Elton was selected as an Ecological Assistant to Sir Julian Huxley on the University expedition to Spitzbergen in 1921. Elton's studies of the ecology of the region's animal life prompted him to return to the Arctic again in 1923, 1924, and 1930. Because he had extensive experience with Arctic animals, Elton was appointed as Biological Consultant to the Hudson's Bay Company. His initial duties were to investigate variation in the number of furbearing mammals.

In 1932, Elton helped establish the Bureau of Animal Population at Oxford University. In 1936, he was appointed Reader in animal ecology and a Senior Research Fellow at Oxford, positions he held until his retirement in 1967. His experiences with environmental factors and their effects on mammal populations, especially those of rodents, were used during the war effort of World War II. Elton conducted extensive research on how to control populations of mice and rats and, thus, to conserve food in storage.

Elton is best known for his numerous books, beginning with *Animal Ecology* (1927), followed by *Animal Ecology and Evolution* (1930), *Voles, Mice and Lemmings: Problems in Population Dynamics* (1942), *The Control of Rats and Mice* (1954), *The Ecology of Invasions by Animals and Plants* (1958), and *The Pattern of Animal Communities* (1966). During his career, Elton specialized in studies of food chains and cycles and the relationship of mammals to their environment and to other animals and plants. His early work on population cycles and numbers in the Arctic served as a basis for later research at the Bureau of Animal Population. It also won him the honor to be named the first editor of *Journal of Animal Ecology,* begun by the British Ecological Society in 1932.

Elton was awarded numerous medals and awards, the most noteworthy being the Gold Medal from the Linnean Society (1967), the Darwin Medal from the Royal Society (1970), the Tyler Ecology Award (1976), and the Edward W. Browning Award (Conservation) (1977). He was an honorary member of the American Academy of Arts and Sciences.

## *Vladimir E. Sokolov, 1976*

Born 1 February 1928 in Moscow, Russia; undergraduate degree (1950) and Doctor of Biological Sciences (1964), Moscow State University (Fig. 3).

After he received his undergraduate degree, Vladimir spent three years at the Moscow Fur Institute and four years as Lecturer at the Moscow Institute of Fishery. He then joined the Biological Department at Moscow State University as Senior Lecturer for ten years and later became Professor of that department, a position he still holds. Currently, he is also Head of the Department

Vladimir E. Sokolov
(1976)

Oliver P. Pearson[a]
(1979)

Victor B. Scheffer
(1981)

Z. Kazimierz Pucek
(1982)

Björn O. L. Kurten[b]
(1983)

John Edwards Hill[c]
(1985)

Bernardo Villa-Ramirez[d]
(1986)

Francis Petter
(1987)

Wuping Xia
(1988)

FIG. 3.—Honorary members of the ASM, 1976–1988. Courtesy of: [a,d]J. Mary Taylor; [b]Helsinki University, Photographic Service, Helsinki University Museum; [c]British Museum (Natural History).

of General Biology, Russian Academy of Sciences, and Director of the A.N. Severtzov Institute of Animal Evolutionary Morphology and Ecology.

Vladimir Sokolov has also held numerous other honorary positions, including membership on the Presidium and Russian Academy of Sciences and President of Theriological Congresses I, II, and III (1974–1982).

His research interests are mammalogy, ecological morphology, systematics, ecology, and nature conservation, and he teaches courses in vertebrate zoology, ecology, behavior, and the environment. Vladimir has more than 500 publications to his name, including several books. His service on editorial boards, such as *Reports of the U.S.S.R. Academy of Sciences, Advances in Modern Biology, Acta Zoologica,* and others, is extensive.

The Order of Lenin (1982, 1988), USSR State Prize, and Order of "The North Star," Mongolia, are but a few of the awards he has received.

## *Oliver Payne Pearson, 1979*

Born 21 October 1915 in Philadelphia, Pennsylvania; B.A., Swarthmore College, 1937; M.A. (1939) and Ph.D. (1947), Harvard University (Fig. 3).

Oliver Pearson, or Paynie as he is often called, credits his own training to such people as Robert K. Enders at Swarthmore and Francis Harper at the Academy of Natural Sciences.

From a Research Assistant of the Academy of Natural Sciences of Philadelphia for one year to Teaching Fellow at Harvard University for two, Paynie then became Instructor in Zoology at the University of California, Berkeley, in 1947, and Assistant Curator of Mammals the next year. He rose through the professorial ranks, became Director of the Museum of Vertebrate Zoology from 1967 to 1971, and briefly filled in as Acting Chairman of the Department of Zoology. Now he is Director Emeritus and Professor Emeritus.

Hardly a year has gone by in his scientific career when he has not made a field trip to South America—Peru, Colombia, Bolivia, and most recently to Argentina or Chile. Paynie spent a year as Visiting Professor of Ecology at the University of Buenos Aires, where he inspired a number of his students to become professional biologists. He has done extensive field research, primarily on rodents of South America, and his 100 or so publications include many landmark papers for South American mammalogy. Paynie and his co-worker wife, Anita, have done much to foster graduate student exchange between the Americas.

His earlier work dealt mainly with reproduction and physiology in birds as well as mammals. His emphasis has become increasingly ecological over the years. Paynie has been an inspiration and mentor for many students.

As a long-term Trustee of the ASM, he helped to guide the growth of the Society's endowment and also contributed the same expertise to the Cooper Ornithological Society. Paynie received the Jackson Award in 1982 and is also Honorary Member of the Comité Argentino de Conservación de la Naturaleza and Sociedad Argentina para el Estudio de los Mamíferos.

## *Victor B. Scheffer, 1981*

Born 27 November 1906 in Manhattan, Kansas; B.S. (1930) and Ph.D. (1936), University of Washington (Fig. 3).

In 1937, Victor Scheffer joined the U.S. Biological Survey, which became the U.S. Fish and Wildlife Service three years later. His entire career was in this organization, and he retired in 1969.

Initially, he was sent to the Aleutian Islands to conduct a wildlife survey. Next, he went to the Pribilof Islands where, from 1940 to 1974, he made a long-term study of Alaskan fur seals, with intervals at the

Rocky Mountain Forest and Range Experiment Station in Colorado. As a recipient of National Science Foundation support, he spent a year in Cambridge, England, to write the book, *Seals, Sea Lions and Walruses.* In 1964 he was a United States Observer on the first team to Antarctica under terms of the Antarctic Treaty of 1959.

Victor Scheffer was given the Distinguished Service Award by the U.S. Department of the Interior in 1965, and in 1977 he was made *Alumnus Summa Laude Dignatus* by the University of Washington. In 1986 he was elected Honorary Member, Society of Marine Mammalogy. For his book *The Year of the Whale* he received the Burroughs Medal of the John Burroughs Memorial Association in 1970, and for *A Voice for Wildlife* he received the Joseph Wood Krutch Award of the Humane Society of the United States in 1975. He is the author of eleven books.

Scheffer taught for a short time at the University of Washington and at the International College of the Cayman Islands. He was also a consultant for the National Oceanic and Atmospheric Administration for a year. From 1973 to 1976, he was the first Chairman of the Marine Mammal Commission. He currently is living in Bellevue, Washington, where he has retired.

## *Zdzislaw Kazimierz Pucek, 1982*

Born 2 April 1930 in Radzyń Podlaski, Lublin Palatinate, Poland; undergraduate studies, M. Curie-Sklodowska University, 1952; Master's degree, University of Warsaw, 1954; Ph.D., M. Curie-Sklodowska University, 1961; Docent degree, Jagiellonian University, 1966 (Fig. 3).

After his Master's degree, Pucek became a Junior Scientific Worker at the Mammal Research Institute, Polish Academy of Sciences, and was made Director in 1962. After being awarded the Docent degree, he became Senior Research Worker at the Institute, a position he still holds. Along with his research and administrative appointments, he teaches mammalogy at several Polish universities and has supervised 15 Masters' and 19 Ph.D. theses.

For 11 years Pucek was the Polish representative to the ITC, and he is currently the Chairman of the European Bison Specialist Group of the SSC/IUCN.

His research is primarily in biomorphology of shrews and rodents, small mammal ecology, and the fauna and protection of mammals in Poland. He is the author of five books and 140 papers and has been Editor-in-Chief of *Acta Theriologica* since 1963. In 1990, he was elected Honorary Member of the All-Union Theriological Society, Russia.

## *Björn Olof Lennartson Kurtén, 1983*

Born 19 November 1924 in Vasa, Finland; undergraduate degree (1952) and Ph.D. (1954), University of Helsinki; died 28 December 1988 (Fig. 3).

Whether fossil or living, the biology of the organism was always paramount in Björn Kurtén's work, in which he emphasized functional morphology and paleontology of mammals—actually, a paleoecological focus. This approach was evident as early as his doctoral dissertation, *On the variation and population dynamics of fossil and Recent mammal populations.*

After 17 years as a Lecturer at the University of Helsinki, Kurtén was Personal Professor of Paleontology from 1972 until his death. He was an inspiration to his students, some of whom came from England, the United States, Sweden, and Japan to study under his tutelage. Their claim is that he restricted them to minimal supervision to encourage their originality and independence. On occasion, he came to the United States for short periods as a Visiting Professor at the University of Florida and also at Harvard University.

He bridged with enormous success the road between scientific and lay audiences by writing popular paleontological books and novels, such as *The Cave Bear Story* (1976). His inspiring lectures captured students and public alike. He participated in a Finnish television serial on the Ice Age just before his death.

Throughout his life Kurtén received numerous awards, including UNESCO's Kalinga Award for the popularization of science. He also was elected Honorary Member of the Anthropological Association of Greece. Outstanding paleontologists, such as George G. Simpson and Stephen Jay Gould, consider Kurtén to be one of the finest paleontologists of all time. He was brilliant in his work and inspirational to all whose lives he touched.

## *John Edwards Hill, 1985*

Born 11 June 1928 in Ashdown House, Forest Row, near East Grinstead, Sussex, England; no university degrees (Fig. 3).

After receiving the Oxford Higher Schools Certificate in 1946, John joined the Royal Air Force as a Meteorological Observer. Two years later, he came to the British Museum (Natural History), Mammal Section, as Assistant Experimental Officer, where he was promoted through the ranks until he became Principal Scientific Officer in 1977. He retired in mid-1988 but continues his professional work and association with the Museum.

John's distinguished career in mammalogy was strongly shaped by R. W. Hayman, his tutor. He was also strongly influenced by the taxonomic work of Sir John Ellerman and Sir Terrence Morrisson-Scott and is, himself, a descriptive taxonomist. He has described 57 new taxa of mammals, including a new family of bats (Craseonycteridae), and is the author of more than 120 scientific publications and five books. Early in his career he was a generalist in mammalogy, later specializing in the systematics and classification of the Chiroptera. He is responsible for building the Museum's collection of bats to become one of the most oustanding in the world. His interest also lies in the history of mammal collections housed in London and their literature.

John Edwards Hill has several bats named after him, one of them named by Karl Koopman to honor both John Edwards Hill and another mammalogist of like name, John Eric Hill. John Edwards Hill collaborated with the American mammalogist James D. Smith on the book *Bats—A Natural History,* and with Gordon B. Corbett on *A World List of Mammalian Species* and *Mammals of the Indomalayan Region: A Systematic Review,* both invaluable references for systematic mammalogists.

## *Bernardo Villa-Ramirez, 1986*

Born 4 May 1911 in Teloloapan, Guerrero, Mexico; M.S., National University of Mexico, 1944; M.A., University of Kansas, 1947; Doctor of Biology, National University of Mexico, 1961 (Fig. 3).

While still at the University of Kansas, Bernardo held the post of Assistant Professor of Comparative Anatomy. He returned to Mexico after his Kansas degree and held the position of Assistant Professor of Zoology at the National University of Mexico for ten years. He was appointed Professor of Comparative Anatomy in 1960, was Head of the Section of Mammalogy from 1957–1967, and for three years was Head of the Department of Zoology.

In the years following his graduate studies at Kansas under E. Raymond Hall, Bernardo became a pioneer in guiding the development of mammalogy in Mexico and, through his teaching, has been the mentor of many students in this field. His own scope is broad, as befits his pioneering work. He is the author of more than 200 scientific papers (98 in mammalogy, with emphasis on bats), 94 technical papers, and 5 books. He established the first large scientific collection of mammals in Mexico and one of the country's first national game reserves, and he helped develop the laws and licensing protocol for game hunting in Mexico.

Bernardo endeared himself to the ASM decades ago for his faithful participation at annual meetings, often being the only person in attendance from outside the United States and Canada. He served on the ASM Board from 1956 to 1984 and was Vice President in 1965. His international perspective and travels are reflected also in his many publications coauthored with investigators outside of Mexico. He was the recipient of a John Simon Guggenheim fellowship in 1945–1947 and has received many other awards, including the Gerrit S. Miller Award in 1990 given by the 20th meeting of the North American Symposium on Bat Research. Bernardo was the first President of the Mexican Society for the Study of Marine Mammals, a founding member of the Marine Mammal Society, and honorary President of the Mexican Association of Mammalogists.

## *Francis Petter, 1987*

Born 28 July 1923 in Paris, France; D.V.M., University of Alfort, 1949; Sc.D., University of Paris, 1961 (Fig. 3).

After receiving a veterinarian degree in 1949, Francis Petter became Assistant in the Laboratory of Zoology (Mammalogy) at the Museum National d'Histoire Naturelle in Paris the same year. He specialized immediately on small rodents, their ecology, and epidemiology. He also began to investigate the history of the relationship of man and domesticated animals.

His earlier work took him to the Sahara, Iraq, and Madagascar, where he discovered and described several species of small mammals. Some of the parasites of these mammals were named for Petter.

Immediately after receiving his doctoral degree, he was appointed Director of the Museum. In addition, he taught mammalogy and supervised theses at the Institute of Tropical Veterinary Medicine for many years. He was Secretary General of *Mammalia,* founded in 1936.

Petter is probably best known for his systematic and ecological work on rodents of northern Africa. He is the author of close to 175 papers, also on Brazilian rodents and parasites, and on phylogeny based on electrophoretic analyses.

## *Wuping Xia, 1988*

Born 19 May 1918 in Baixing County, Hebei Province, China; university degree, Yenching University, 1945 (Fig. 3).

After his university training, Wuping Xia engaged in hydrobiological studies. However, the Sino-Japanese war took its toll on scientific studies in China, especially mammalogy. It was Xia, along with Professor T. H. Shaw and Professor H. S. Peng, who together put the field of Recent mammalogy on firm footing in China during the following decade. Particular emphasis was placed on ecological studies of small mammals. The rapid growth of mammalogy in the following decades led to the establishment of the Mammalogical Society of China in 1980. Wuping Xia was the first President of the society, a position he continues to hold. The journal *Acta Theriologica Sinica* was founded the following year, and Xia is its Managing Editor.

In 1980, Wuping became Director, Northwest Plateau Institute of Biology, Academia Sinica, then Honorary Director four years later, retiring in 1990. During his tenure, he established the Haibei Research Station of the Alpine Meadow Ecosystem, a field station located at 3,200 m in Quinhai Province. It is one of the highest research stations in the world for the study of grassland and plateau biology.

Wuping also has carried on an academic teaching career in the Academia Sinica, most recently as Professor. He is the author of seven books and more than 50 papers, mostly on rodent ecology and control.

Karl F. Koopman[a]
(1990)

Phillip Hershkovitz
(1991)

FIG. 4.—Honorary members of the ASM, 1990–1991. Courtesy of: [a]J. Mary Taylor.

## *Karl F. Koopman, 1990*

Born 1 April 1920 in Honolulu, Hawaii; B.A. (1943), M.A. (1945), and Ph.D. (1950), Columbia University (Fig. 4).

After graduate work, Karl became an Instructor in Biology at Queens College and, in 1958, moved to become Assistant Curator in Mammalogy, Academy of Natural Sciences of Philadelphia, for one year. He then went to the Chicago Natural History Museum at the same level of appointment for two years. His real home professionally became the American Museum of Natural History, commencing in 1961, where he rose through the curatorial ranks in the Department of Mammals, retiring officially in 1986 but still keenly active as Curator Emeritus.

Karl's chief interest is bats, especially Microchiroptera, but he has a wealth of knowledge about all mammalian groups. As a former student of Theodosius Dobzhansky, Karl carries forward a vast background in genetics and evolutionary biology.

His collecting trips, chiefly for mammals and reptiles, have been largely in the equatorial region and southern hemisphere, whereas his travels to professional meetings and museums have been worldwide. He is the author of many papers, particularly on bats, but also on primates and other vertebrates.

Karl serves the ASM in many capacities, including as a member of the Board of Directors for many years. His services on the Nomenclature and Checklist committees have been unbounding, and his incredible scholarly attention to the presentations delivered at the annual meetings of the ASM is unique. He has not only attended almost every meeting for more than 40 years, but is the guy in the front row of every session who asks such incisive questions! All this and more were recognized when he received the Jackson Award in 1988.

## *Philip Hershkovitz, 1991*

Born 12 October 1909 in Pittsburgh, Pennsylvania; B.S. (1938) and M.S. (1940), University of Michigan (Fig. 4).

Against all odds, Phil Hershkovitz sought training as a mammalogist in the depths of the Great Depression. As an undergraduate at the University of Michigan, he not only worked as a departmental assistant, he also took taxidermy jobs to support himself. In 1932, he was hired to collect blind cave salamanders. Eager to trap mammals there as well, he asked Lee R. Dice, then Curator of Mammals, for traps. Dice was unable to supply them. When hitchhiking en route to

Texas, he stopped in Chicago on a chance visit to the Field Museum of Natural History. Colin Sanborn, then Curator of Mammals there, loaned him the traps. In exchange, Phil sent the specimens to the Field Museum on this and subsequent field seasons. That stop at the Field Museum later shaped his future.

As the depression worsened, Phil went to Ecuador, where he remained for five years, collecting an impressive array of mammals for the University of Michigan, living off the land as he did so. This collection was the basis for his Master's degree work under William H. Burt, successor to Dice as Curator of Mammals. He interrupted his doctoral program to accept a prestigious traveling scholarship from the United States National Museum, and went to Colombia, where he collected mammals for that museum for two years.

After serving in World War II, he was offered a curatorial position at the Field Museum and accepted it, fully cognizant that the return to his doctoral program was the sacrifice. He has remained there throughout his career, traveling to the Neotropics whenever he could, sometimes for years at a time. It was there that he assembled invaluable collections of mammals upon which he has focused his research career.

His highly productive career is singular in the magnitude of his scholarly contributions, especially in evolution and biogeography of South American mammals, and in the fact that he is the sole author of 99% of his 300 or more articles. He has been more influential in the arena of neotropical mammalogy than has anyone else in this century. He has published major monographic revisions on every order of Recent mammals of South America. Although his work is often challenged, it serves as a great stimulus of ideas and of testing hypotheses.

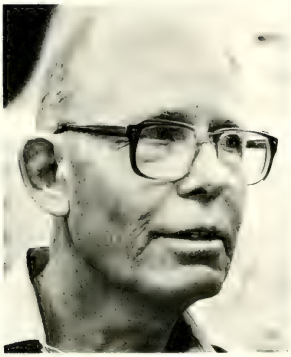
Hershkovitz became Research Curator at the Field Museum in 1961, formally retired in 1971, and continues today as Curator Emeritus.

## *C. Hart Merriam Awardees*

The C. Hart Merriam Award was established in 1974 to recognize outstanding contributions to the discipline of mammalogy by a member of the society in more than one of the following areas: scientific research, education of mammalogists, and service to the ASM (*Journal of Mammalogy,* 55:694, 1974). The recipient is given a statuette of a bison cow that is cast in fiberglass and painted in bronze. It is a copy of one made by John Paul Jonas of Jonas Brothers for an exhibit at the American Museum of Natural History on the mammals of New York State. According to Sydney Anderson, who oversees the reproductions of this statuette, the reason it is a bison cow is that the larger bull would not fit on a bookshelf!

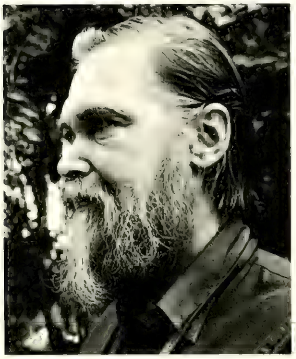
The Merriam Award requires unanimous approval of the nominee by the committee and two-thirds approval by the Board of Directors. In 1977, the board decided that, in addition to the two-thirds affirmative vote by the Board, the nominee must receive the approval of three elected officers plus five senior Directors, thus requiring close to unanimity within this group.

In 1981, the Board of Directors modified these criteria to reduce the emphasis on service, following the establishment of the Jackson Award, which is based on this intention. The Board revised the description of the Merriam Award to "The [Merriam] Award is to be made to a member of the Society, who, in his or her activities within the past ten years, has achieved a record of excellence in more than one of the following areas: scientific research, education of mammalogists, and service to the discipline of mammalogy" (unabridged minutes of the 1981 Board of Directors' Meeting). Furthermore, the policy established in 1979 of inviting the recipient of the Merriam Award to present a keynote address at the next annual meeting was reiterated. In 1989 the requirement of membership in the ASM was



Terry A. Vaughan[a]
(1979)

Robert J. Baker[b]
(1980)

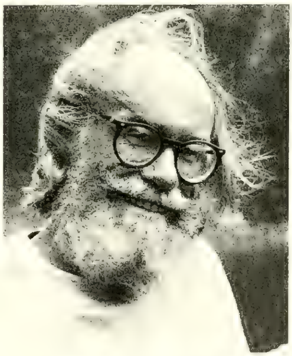


John F. Eisenberg[c]
(1981)

Michael H. Smith
(1985)

Jerry R. Choate[d]
(1988)

Timothy H. Clutton-Brock
(1991)



Guy G. Musser
(1992)

FIG. 5.—Merriam awardees of the ASM, 1979–1992. Courtesy of: [a]Department of Biological Sciences, Northern Arizona University; [b,c,d]J. Mary Taylor.

removed for nominees of this award. The criteria also were changed to "excellence in research and one or both of the other categories" (*Journal of Mammalogy,* 70:880, 1989).

The first recipient of the Merriam Award was James N. Layne. Until 1991, when Timothy Clutton-Brock received the award, all recipients were from the United States and were members of the society. Fourteen individuals have received the award. Of these, seven have served as President of the society, two have received Honorary Membership, and one received the H. H. T. Jackson Award. Their average age at the time the award was bestowed is 48, ranging from 38 to 56.

## *Terry A. Vaughan, 1979*

Born 5 May 1928 in Los Angeles, California; B.A., Pomona College, 1950; M.A., Claremont Graduate School, 1952; Ph.D., University of Kansas, 1958 (Fig. 5).

Terry, who spent two years in the U.S. Army before going on for his Ph.D., was appointed Research Biologist in the Department of Range Science at Colorado State University immediately after he completed his doctorate. He held that position until 1967, when he joined the Department of Biological Sciences, Northern Arizona University, first as Associate Professor and then Professor of Zoology. He retired there in late 1987.

His deep interest and extensive research on the biology of bats began early in his career, his first publication being on hoary bats (*Journal of Mammalogy,* 34:256, 1953). He has published about 50 scientific papers, largely in the field of chiropteran morphology, but also on the biology of pocket gophers and woodrats. Since its publication in 1972, Terry Vaughn's *Mammalogy* has gone through three editions and is still one of the most popular textbooks for the discipline.

His research support includes the National Science Foundation, National Geographical Society, U.S. Fish and Wildlife Service and International Biological Program. He is a member of the Ecological Society, the Paleontological Society, the Society for the Study of Evolution, and others.

Terry's formal service to the ASM has been as Editor for Feature Articles in the *Journal of Mammalogy,* 1966–1968, and as Second Vice President 1980–1982. He was a Visiting Professor of Zoology in Nairobi on two occasions, and most recently spent a year in Western Australia working on Megachiroptera.

Terry continues to live in Rimrock, Arizona, in his retirement, having descended several thousand feet to escape snowy Flagstaff.

## *Robert J. Baker, 1980*

Born 8 April 1942 in Warren, Arkansas; B.S., Arkansas A & M College, 1963; M.S., Oklahoma State University, 1965; Ph.D., University of Arizona, 1967 (Fig. 5).

Since receiving his Ph.D., Robert J. Baker has been a faculty member in the Department of Biological Sciences at Texas Tech University. He is now the distinguished Horn Professor, Director of the Natural Science Research Laboratory, and Curator of Mammals and Vital Tissues at Tech, and is also Research Associate at the Carnegie Museum of Natural History, and the University of New Mexico, Albuquerque.

Early in his career, he developed a deep interest in chromosomal evolution and is at the forefront of molecular genetics, in situ hybridization of chromosomal architecture, and the problems of contact zones between chromosomal races. His model is usually bats, although he uses murid rodents extensively as well. He teaches mammalogy, histology, cytology, general zoology, and various research courses, and is the recipient of several awards for both teaching and research.

Bob has received strong grant support from Texas Tech University and for 20 or more years from the National Science Foundation. The National Parks System and the Smithsonian Foreign Currency Program have also provided major support. His extensive field work is primarily in the neotropics, but also in Tunisia and England.

Since 1972, Bob has served long periods in editorial capacities for the *Journal of Mammalogy.* His society affiliations include Society of Systematic Biologists, Society for the Study of Evolution, and Texas Academy of Sciences. He has supervised more than 20 Master's degree students and 14 doctoral students. Bob is the author or coauthor of more than 175 papers, and he collaborates with a wide array of investigators.

## *John Frederick Eisenberg, 1981*

Born 20 June 1935 in Everett, Washington; B.S., Washington State University, 1957; M.A. (1959) and Ph.D. (1962), University of California, Berkeley (Fig. 5).

John Eisenberg became Assistant Professor of Zoology at the University of British Columbia in 1962, moved to the University of Maryland in 1964, and then in 1965 to the National Zoological Park (NZP) where he was Resident Scientist and then Head, Office of Zoological Research. Concurrently he was Associate, Department of Mental Hygiene at Johns Hopkins University, and Adjunct Professor of Zoology at the University of Maryland. In 1979, he became Assistant Director, Animal Programs at the NZP and, in 1982, moved to the University of Florida to become Ordway Professor, Curator, and Eminent Scholar, Ecosystem Conservation.

Early in his career, John began receiving significant recognition: Phi Beta Kappa, Phi Kappa Phi, President of the Animal Behavior Society in 1973, Fellow of the Animal Behavior Society and of the New York Zoological Society, and fellowships from the National Science Foundation and the National Academy of Sciences.

John is eminent worldwide in his field. His eclectic approach to mammalogy weaves together the fields of behavior, reproduction, ecology, systematics, and evolutionary adaptations in a truly integrated approach. His service in the ASM includes membership on the Board of Directors and committees. John is the author of more than 125 papers and is a recipient of grants from the Smithsonian Institution, National Science Foundation, U.S. Department of Interior, National Geographic Society, and others. His books, *Mammalian Radiations* and *Mammals of the Neotropics, Volumes I and II,* are landmark publications in the field of mammalogy, and he has used virtually the full spectrum of mammals of the world as subjects of his papers. His field work has taken him throughout the world, and he has been mentor and supervisor of more than 21 graduate students and 10 postdoctoral students.

## *Michael H. Smith, 1985*

Born 30 August 1938 in San Pedro, California; B.A. (1960) and M.A. (1962), San Diego State University; Ph.D., University of Florida, 1966 (Fig. 5).

After his doctoral work, Mike was a Research Associate and then went through the ranks to a full professorship, all at the University of Georgia. In 1973, he became Director of its Savannah River Ecology Laboratory. He teaches population biology, vertebrate ecology, and population genetics, and supervises many undergraduate research projects. He has also supervised over 15 graduate students. Mike has presented about 400 talks at universities, museums, and other institutions and professional meetings both here and in foreign countries.

His research is focussed on both short- and long-term responses of biological systems to natural and man-made environmental changes. He is interested in the genetics of natural populations and its importance to regulation, conservation, and management of populations of both aquatic and terrestrial vertebrates. His research cuts across many fields, and its approach is comprehensive.

Mike is the author or coauthor of more than 175 papers, several chapters, books, and other publications. He has been principal or co-principal investigator of major grants from the AEC, EPA, National Research Council, and National Science Foundation, and he has received over 16 million dollars of support.

Mike has served on the Board of Directors of the ASM for about a dozen years. He belongs to several ecological societies, the American Fisheries Society, the American Society of Ichthyologists and Herpetologists, the American Society of Naturalists, and is a member of Sigma Xi and Phi Sigma.

### *Jerry R. Choate, 1988*

Born 21 March 1943 in Bartlesville, Oklahoma; B.A., Kansas State College of Pittsburg, 1965; Ph.D., University of Kansas, 1969 (Fig. 5).

After completing the doctorate at the University of Kansas under the tutelage of J. Knox Jones, Jr., Jerry was Assistant Professor at the University of Connecticut for two years. In 1971, he returned to Kansas as Assistant Professor at Fort Hays State University. He is now Professor at that university. Additionally, in 1973 he became Curator of Mammals and Director at the university's Museum of the High Plains. In 1980, he assumed administrative responsibilities for all museums on campus, which have been merged as the Sternberg Museum of Natural History.

Jerry has received numerous honors, his most cherished (in addition to the Merriam Award) being the Southwestern Association of Naturalists' Robert L. Packard Excellence in Education Award. He has been recipient of numerous grants from the National Science Foundation and other state and federal agencies. He has served on several ASM standing committees and was Recording Secretary of ASM from 1974 through 1984. He presently serves as Chair of the ASM's Trustees (a position he also holds with the Southwestern Association of Naturalists) and a member of the Board of Directors.

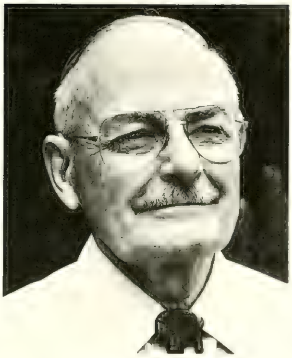
His research interests include systematics, biogeography, and natural history of mammals on the Great Plains. He is coauthor of one book (with another currently in press) and 140 scientific papers. In addition, he is coeditor of the present volume. His greatest professional achievement, however, has been in preparing undergraduate and masters-level students for Ph.D. studies in mammalogy.

### *Timothy Hugh Clutton-Brock, 1991*

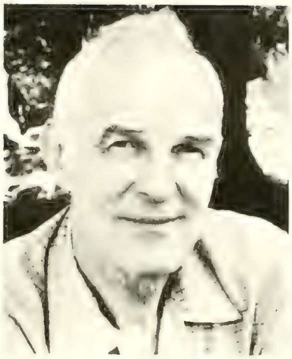
Born 13 August 1946 in London, England; M.A. (1968), Ph.D. (1972), and Sc.D. (1986), Cambridge University (Fig. 5).

Clutton-Brock's graduate work began with specialties in archaeology and anthropology, and his doctoral work focused on comparative social organization and ecology of colobus monkeys. This study took him to Tanzania and Uganda for field work. After one year as a postdoctoral fellow, he was appointed University Lecturer in Biology at the University of Sussex. He left in 1976 to become Senior Research Fellow in Behavioral Ecology at King's College, Cambridge, and in 1981 he was appointed Advance Research Fellow in the Department of Zoology there. Two years later he was made Royal Society Research Fellow in Biology, and it was during that time that he was awarded a Sc.D. from Cambridge. In 1987 he was appointed University Lecturer in the Department of Zoology at Cambridge, and in 1991 was promoted to Reader in Animal Ecology, an appointment he holds today.

Tim's research is focused primarily on the social organization, ecology, reproduction, and behavior of two mammalian groups: primates and red deer. Since 1986 he has been an author of 107 scientific papers and



Bryan P. Glass[a]
(1980)



Murray L. Johnson
(1986)

Marie A. Lawrence[b]
(1990)

John O. Whitaker, Jr.
(1991)

FIG. 6.—Hartley H. T. Jackson awardees of the ASM, 1980–1991. Courtesy of: [a]J. Mary Taylor; [b]Chacma Inc., New York.

three books, and he has served as editor of five other books. He has received major grant support, and has supervised research projects of 26 students, mainly at the doctoral level. In 1980 he started the Large Animal Research Group within the Department of Zoology at Cambridge. That same year he also became Chairman of the IUCN Deer Specialist Group.

In recognition of his prodigious scholarly work, Tim has received several major honors that include the Award for Best Book from the Wildlife Society of America in 1983, the Scientific Medal from the Zoological Society of London, and the Fellow of the Royal Society in 1993.

Tim is married to Dafila Kathleen Scott, daughter of the well-known ornithologist, the late Sir Peter Scott.

## *Guy G. Musser, 1992*

Born 10 August 1936 in Salt Lake City, Utah; B.S. (1959) and M.S. (1961), University of Utah; Ph.D., University of Michigan, 1967 (Fig. 5).

One year before receiving his Ph.D., Guy Musser was appointed Archbold Assistant Curator in the Department of Mammalogy at the American Museum of Natural History. He has remained at that institution to the present day. Guy became Chairman of the Department in 1981, five years after being promoted to Archbold Curator. Since 1983 he also has held the appointment of Research Associate in the Department of Vertebrate Zoology at the National Museum of Natural History.

Although born in the West and loving the wilderness country of the region, Guy moved to the crowded core of New York City because he was drawn to the resources of the mammal collections of the museum. He has made the large rodent collections his research tool in his lifelong commitment to the complexities of rodent systematics. As a graduate student, first of Stephen D. Durrant at Utah and later of Emmet T. Hooper at Michigan, Guy's training and background helped him become outstanding in this field. He has worked in Costa Rica, the United States, and particularly in southeast Asia, gathering field data and specimens for analysis. He has lived for years at camp sites in Sulawesi in an attempt to comprehend the subtleties of distributional limits of species in different altitudes and habitats. One only has to read his papers to realize the depth of his comprehension of environmental factors that relate to distributions and habits of species of rodents. He has described a number of species and genera of rodents and has proposed several changes at the higher taxonomic levels.

Guy's publications are generally long and comprehensive papers, many of monographic length. He is recognized internationally for his outstanding contributions to the systematics of muroid rodents.

## Hartley H.T. Jackson Awardees

The Hartley H. T. Jackson Award was established in 1977 and was first given to W. B. Davis in 1978. This award recognizes members of the society who have given long and outstanding service to the society (*Journal of Mammalogy,* 58:709, 1977). The recipient is given a certificate that includes a sketch of Jackson, and a plaque that has the ASM pronghorn logo on it. The Jackson Award Committee was established with the guidelines that the committee should remain small (5 members), it should be unanimous in its recommendation, and the Board of Directors should support the committee's nomination by a two-thirds majority if it is to be approved. The recipient is announced at the annual banquet.

In 1981 the Board of Directors further decided that there should be no more than one recipient of the Jackson Award and of the Merriam Award in any given year, and that the awards need not be given each year if, in the opinion of the selection committee, suitable candidates are not available (unabridged minutes of the 1981 Board of Directors' meeting).

Since the inception of the Jackson Award, 12 mammalogists have received it through 1992. Of these, four are past presidents, seven have been elected Honorary Members, and one is a recipient of the Merriam Award. One woman (Marie Lawrence) has received the Jackson Award. Recipients have, by the nature of the award, all been members of the society for a long time and to date all have been from the United States. The average age of the recipient at the time of receiving the award has been 66, ranging from 54 to 76.

### *Bryan P. Glass, 1980*

Born 21 August 1919 in Mandeville, Louisiana; A.B., Baylor University, 1940; M.S., Texas A & M University, 1946; Ph.D., Oklahoma State University, 1952 (Fig. 6).

Bryan spent his entire childhood in China, where he graduated from the China Inland Mission School, Chefoo, Shantung Province in 1953. He served in World War II, primarily as an intelligence officer in China with the 14th Air Force and OSS, and was awarded the Asiatic-Pacific Medal with two battle stars and a Presidential Unit Citation. Bryan has spent his professional life at Oklahoma State University from 1946–1985, progressing through all the professorial ranks; he became Director of the University Museum in 1966.

Bryan's research focus is primarily on mammals, particularly on microchiropteran bats. His publications reflect a special interest in distributional records, status, and in regional faunal surveys, primarily in Oklahoma, but he also made a survey of the mammals of Ethiopia and of a new national park in Brazil.

Throughout his professional career, Bryan Glass has given generously of his time and expertise to his university, his church, his city, and to the ASM. He is the recipient of Oklahoma State University's Outstanding Service Award (1965) and Outstanding Teacher Award (1966), and recently was elected 2nd Vice-President at the 20th Baptist General Convention, and is Past President of the Arts and Humanities Council in Stillwater.

Bryan was elected Corresponding Secretary of the ASM in 1956, and from 1957 to 1977 he served as Secretary-Treasurer. During those 20 years, membership grew from 1,500 to 3,900. He inaugurated the portrait file of Past Presidents and of group photographs at annual meetings. Assisted by his wife, Carolyn, Bryan maintained the mailing list of members and subscribers and oversaw the printing of the program for the annual meeting each year, all in pre-computerization years. During his tenure, he was the major writer of the Society's constitution.

Bryan's tangible contributions to the ASM have led to both strength and growth of the society, but so have his undocumented contributions. Bryan is often one of the first to welcome student mammalogists at annual meetings and make them feel at ease by introducing them to fellow scientists.

## *Murray L. Johnson, 1986*

Born 16 October 1914 in Tacoma, Washington; B.A. (1935) and M.D. (1939), University of Oregon School of Medicine (Fig. 6).

After postgraduate training in surgery at Union Memorial Hospital in Baltimore, Maryland, Murray joined the U.S. Naval Medical Corp and served for 3 years. He has been in the practice of medicine from 1946 through 1983, becoming a certified member of the American Board of Surgery in 1948.

Along with his medical practice, Murray has been a research biologist in mammalogy, spending almost 50% of his time in this field and, since his retirement, even more. From 1949 through 1983 he was Curator of Mammals at the Puget Sound Museum of Natural History, also chairing the Executive Board there for many years. He was principal investigator in the Marine Mammal Program Project Chariot (AEC) through the Arctic Health Reseearch Center in Anchorage from 1959 through 1964. From 1963 to 1983 he was Research Professor of Biology at the University of Puget Sound, held a number of National Science Foundation grants, and from 1984 to date has been an Affiliate in Mammalogy and Curator of Mammals at Burke Memorial Washington State Museum, University of Washington. From 1989 to 1992, he has been a member of the Scientific Advisors, U.S. Marine Mammal Commission, and 1984 to date the Secretary for the Foundation for Northwestern Natural History.

Murray has been the invited participant in many scientific meetings, international as well as within North America. He is a member of numerous scientific organizations, including a Fellow of the American Association for the Advancement of Science. In 1978, he was named Distinguished Citizen of the Year in Tacoma, Washington. He is the author of many papers on marine mammals and rodents, and some on reptiles and birds. He has special interest in blood protein electrophoretic studies in mammalian taxonomy. His investigations are largely centered around the Pacific Northwest. His wife and strong supporter, Sherry, accompanies Murray to every annual meeting of the ASM.

## *Marie A. Lawrence, 1989*

Born 20 October 1924 in Poughkeepsie, New York; B.A., Vassar College, 1945;

M.S.S., Smith College School for Social Work, 1952; M.A., New York University, 1970; died 21 September 1992 (Fig. 6).

Marie Lawrence began her career, not as a mammalogist or even as a biologist, but as a social worker in New York, a career she continued for almost 30 years. Her last position was Adjunct Associate Professor, New York University of Social Work, which she left in 1975. For the final two years, she was also Scientific Assistant, Department of Mammals, at the American Museum of Natural History. She held this position for nine years, during one of which she was also Assistant Professor of Zooarchaeology at Northwestern Archaeology Field School in Illinois. In 1982, she became Senior Scientific Assistant at the Museum, a position she held until her death.

Although driven by a keen interest in zooarchaeology, Marie concentrated her research on Old World arvicoline rodents, megachiropteran nectar feeders, Myospalacine rodents, and the assessment of Medieval knowledge of mammalian natural history.

Marie did yeoman's service to produce *Recent Literature in Mammalogy* for 16 years until the ASM discontinued it in 1985. She served on the Board of Directors and on several standing committees. She was the recipient of several prestigious awards, including a Ford Foundation Fellowship and the Margaret Mead/Kreiser Fellowship in Anthropology. She was not only the first woman to receive the Jackson Award, she was the first AfroAmerican to be honored by an award from the ASM.

## *John O. Whitaker, Jr., 1991*

Born 22 April 1935 in Oneonta, New York; B.S. (1957) and Ph.D. (1962), Cornell University (Fig. 6).

While still a graduate student, John worked as a field assistant during summers for the New York State Museum and the New York Conservation Department. Immediately following his doctoral work on *Zapus hudsonius,* under the direction of William J. Hamilton, Jr., John joined the Department of Life Sciences, Indiana State University, as Assistant Professor to teach vertebrate zoology, mammalogy, and other courses, including one on mammalian ectoparasites. He now holds the rank of Professor. To date, John has been the mentor for more than 50 graduate students in both M.A. and Ph.D. programs. The diversity of thesis titles, as well as his more than 230 publications, reflects his extraordinary diversity of interests and expertise within the breadth of vertebrate biology and mammalian parasites. He has written keys, analyzed diets, recorded new distributions, and studied herps and birds, as well as mammals, across a wide spectrum of research.

John is the recipient of numerous grants and contracts that have sustained portions of the studies made by him and his students. He was elected a Fellow in the American Association for the Advancement of Science in 1968, a Fellow in the Indiana Academy of Science in 1976, and was one of the first two people to be given an Indiana State University "Research and Creativity Award," in 1981.

Just as impressive as John's contributions to the field of mammalogy and students in that field are his staggering contributions to the discovery and description of over 130 new taxa of mammalian parasites, largely from North American mammals. His membership in professional societies also mirrors his breadth of interests and his extraordinary competence as an eclectic biologist.

## *B. J. Verts, 1992*

Born 19 April 1927 in Nelson, Missouri; B.S., University of Missouri, Columbia, 1954; M.S. (1956) and Ph.D. (1965), Southern Illinois University.

B. J.'s doctoral thesis on the biology of the striped skunk was the basis of his first book of that name published in 1967. Earlier, however, he was author of several papers in the *Journal of Mammalogy* and other major journals, having published 15 refereed scientific papers on a wide variety of mammals before receiving the Ph.D.

His first position after earning the M.S. degree was as District Biologist, North Carolina Wildlife Resources Commission, followed by that of Field Mammalogist and Project Leader, Illinois Natural History Survey, a position held during his tenure as a doctoral student. Upon receiving his doctoral degree, Verts was appointed Assistant Professor, Department of Fisheries and Wildlife, Oregon State University, where he has remained throughout his career, advancing to the rank of Professor. He spent one year as Visiting Professor at Pennsylvania State University. At Oregon State University he also curated the collection of mammals, developing it into the best collection of mammals from Oregon at any institution in the state. His endeavors are especially valuable because Oregon has no significant museum of natural history.

In 1979, B. J. married fellow mammalogist Leslie Carraway. They collaborate extensively, not only in revision of B. J.'s invaluable "Keys to the Mammals of Oregon," but on virtually half of B. J.'s publications since 1980. Currently, they are completing a book on the Mammals of Oregon, the first of its kind since Vernon Bailey's book written in 1936.

B. J.'s work focuses heavily on small mammals of Oregon, especially life histories and distributions. His interest in rabies and other diseases communicated by wild mammals is prevalent in his earlier publications. He has a long-term interest in devising techniques, such as those of ageing, baiting, and sexing. He is a major contributor to *Mammalian Species.*

The deep commitment that B. J. has to the ASM is reflected in the extent to which he contributes to the society. He has served as Managing Editor, Journal Editor, and Associate Editor of the *Journal of Mammalogy,* as Editor and Associate Editor of *Mammalian Species,* as Chairman of the Local Committee for the ASM's 59th Annual Meeting, as Chairman of both the Merriam Award Committee and the Grants-in-Aid Committee, and as a member of 5 other committees. He served two terms on the Board of Directors. In addition, B. J. has served in leadership capacities in other scientific societies related to wildlife.

B. J. has supervised 18 M.S. students and 2 Ph.D. students particularly on projects focusing on cottontail rabbits. Students under his guidance learn the art of scientific writing. B. J. is a rigorous master, having coauthored with D. E. Wilson and A. L. Gardner the ASM's 1989 *Guidelines for Manuscripts* and taught courses on science writing and on manuscript preparation at Oregon State University. He has guided many authors in the *Journal of Mammalogy* in his editorial capacities.

## *Conclusions*

Altogether, 76 mammalogists have been honored by the ASM between 1919 and 1992 (Tables 1, 2 and 3). Of these, 24 are Charter Members (no Jackson or Merriam awardees are in this group). The recipients come from 13 countries and represent nearly every discipline related to the biology and evolution of mammals. Edouard-Louis Trouessart, who was made an Honorary Member in 1921, was the first foreign recipient, and in 1966 Erna Mohr, also from Europe, became the first woman to be honored by the ASM. The only person to receive all three honors—the Merriam Award in 1977, the Jackson Award in 1983, and Honorary Membership in 1992—is the late J. Knox Jones, Jr., who also had been President of the society.

Of the 58 persons who have been given Honorary Membership, 14 are still alive; of the 12 people to receive Jackson Awards, 9 are living; of the 14 recipients of the Merriam Award, 13 are living.

Two of these three honors keep alive the names of two eminent founders of the ASM. C. Hart Merriam, first President of the society and one who not only began the *North American Fauna* series but also had a pro-

TABLE 1.—*Honorary Members of the American Society of Mammalogists. (P) Past President of ASM.*

| | |
|---|---|
| Joel Asaph Allen (1919) | V. G. Heptner (1963) |
| Edouard-Louis Trouessart (1921) | E. Raymond Hall (1964) (P) |
| Max Weber (1928) | Stanley P. Young (1964) |
| M. R. Oldfield Thomas (1928) | William J. Hamilton, Jr. (1965) (P) |
| Henry Fairfield Osborn (1929) | Erna Mohr (1966) |
| Edward W. Nelson (1930) (P) | Klaus Zimmerman (1966) |
| C. Hart Merriam (1930) (P) | William H. Burt (1968) (P) |
| William Berryman Scott (1936) | William B. Davis (1968) (P) |
| Alfred W. Anthony (1936) | George Gaylord Simpson (1969) |
| Leonhard Stejneger (1937) | Robert T. Orr (1970) (P) |
| Gerrit S. Miller, Jr. (1941) | Stephen D. Durrant (1971) (P) |
| Ernest E. Thompson Seton (1941) | Kazimierz Petrusewicz (1972) |
| Marcus Ward Lyon, Jr. (1942) (P) | Charles S. Elton (1973) |
| Rudolph M. Anderson (1947) | Emmet T. Hooper (1976) (P) |
| Angel Cabrere Latorre (1947) | Vladimir E. Sokolov (1976) |
| A. Brazier Howell (1951) (P) | Oliver P. Pearson (1979) |
| Theodore S. Palmer (1951) | Victor B. Scheffer (1981) |
| Edward A. Preble (1952) | Donald F. Hoffmeister (1982) (P) |
| Hartley H. T. Jackson (1952) (P) | Z. Kazimierz Pucek (1982) |
| William K. Gregory (1954) | Björn O. L. Kurtén (1983) |
| W. P. Taylor (1954) (P) | John Edwards Hill (1985) |
| Harold E. Anthony (1955) (P) | Bernardo Villa-Ramirez (1986) |
| Lee R. Dice (1956) | Randolph L. Peterson (1986) (P) |
| Albert R. Shadle (1956) | Francis Petter (1987) |
| Francis Harper (1959) | Wuping Xia (1988) |
| Nagmaichi Kuroda (1959) | Karl F. Koopman (1990) |
| Magnus A. Degerbøl (1962) | Philip Hershkovitz (1991) |
| Remington Kellogg (1963) (P) | J. Knox Jones, Jr. (1992) (P) |
| Tracy I. Storer (1963) (P) | Sydney Anderson (1992) (P) |

TABLE 2.—*Recipients of the Merriam Award. (P) = Past President of ASM; (Hon.) = Honorary Member of ASM; (Jack.) = recipient of the Jackson Award.*

| |
|---|
| James N. Layne (1976) (P) |
| J. Knox Jones, Jr. (1977) (P) (Hon., Jack.) |
| James S. Findley (1978) (P) |
| Terry A. Vaughan (1979) |
| Robert J. Baker (1980) |
| John F. Eisenberg (1981) |
| James L. Patton (1983) (P) |
| Michael H. Smith (1985) |
| William Z. Lidicker, Jr. (1986) (P) |
| Hugh H. Genoways (1987) (P) |
| Jerry R. Choate (1988) |
| James N. Brown (1989) (P) |
| Timothy H. Clutton-Brock (1991) |
| Guy G. Musser (1992) |

TABLE 3.—*Recipients of the Hartley H. T. Jackson Award. (P) = Past President of ASM; (Hon.) = Honorary Member of ASM; (Mer.) = recipient of Merriam Award.*

| |
|---|
| William B. Davis (1978) (P) (Hon.) |
| William H. Burt (1979) (P) (Hon.) |
| Bryan P. Glass (1980) |
| J. Knox Jones, Jr. (1983) (P) (Hon. Mer.) |
| Oliver P. Pearson (1984) (Hon.) |
| Sydney Anderson (1985) (P) (Hon.) |
| Murray L. Johnson (1986) |
| Donald F. Hoffmeister (1987) (P) (Hon.) |
| Karl F. Koopman (1988) (Hon.) |
| Marie A. Lawrence (1990) |
| John O. Whitaker, Jr. (1991) |
| B. J. Verts (1992) |

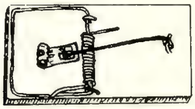
found effect on the development of the science of modern mammalogy; and Hartley H. T. Jackson, eleventh President of the society, who chaired the initial Organizing Committee of the society and served as its first Corresponding Secretary for six years.

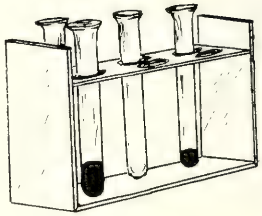
## *Acknowledgments*

Recognition of the invaluable assistance provided by several people at The Cleveland Museum of Natural History in the preparation of this chapter is due. First of all, the extensive work of B. Hallaran, Executive Secretary, is deeply appreciated. So is the help of librarians W. Wasman and D. Condon. We also are grateful to many members of the ASM, who helped to supply informational details. To all we owe a debt of gratitude in helping to bring this chapter together.

# *OTHER PROMINENT MEMBERS*

DAVID M. ARMSTRONG, MURRAY L. JOHNSON, AND
RANDOLPH L. PETERSON





## *Introduction*

This chapter is based on the observation that many of the mammalogists who have had enduring impacts on mammalogy in the past 75 years have not been honored formally by the ASM as Honorary Members or recipients of Merriam or Jackson awards; not all have served the society as senior officers. Given the organization of this volume, such individuals might have been overlooked.

This chapter has had a sadly difficult history because one of the original authors, Randolph L. Peterson, passed away as conceptualization of the chapter was in an early stage. It was Peterson who drafted the first list of noteworthy mammalogists who—having neither been honored previously by ASM nor served as a senior officer of the society—might go unmentioned in this volume. Peterson listed 76 names, and then more were added. The list quickly became unmanageable; difficult decisions eventually had to be made.

We understood at the outset that this chapter was unlikely to please everyone—and indeed might please no one—because space alone limited numbers of individuals included. Limits imply choice, and choice implies valuing, which no two mammalogists are likely to do in the same manner. There was early agreement that to be included an individual must be retired or deceased. Further, it was abundantly clear that treatment could not be comprehensive. Eventually, some organizational principles emerged: the chapter would be organized by decades, and biographies would be limited to no more than about five individuals who had left an indelible stamp on the mammalogical "character" of that decade. Finally, based on the premise that one cannot really recognize importance or a "classic" until its enduring impact can be gauged, we have not presumed to extend our subjective analysis beyond the 1970s. With standards and procedures so obviously judgmental, who could fault us for having omitted a favorite theriological character or a particularly inspirational academic "aunt" or "uncle," an esteemed mentor or field tutor?

We do not harbor any illusion that the history of the ASM is the history of American mammalogy. Mammalogy was well established as a branch of natural history and biology well before 1919. Many would date the origin of American mammalogy from

1858, with the publication of Spencer Fullerton Baird's monumental *Mammals,* Volume 8 of the Pacific Railroad Surveys. Others would dig deeper for roots, to Colonial naturalists like Mark Catesby and William Bartram, distinguished visitors like Sir John Richardson, or to the extraordinary zoological explorers and publicists of a new nation: Lewis and Clark, George Ord, James DeKay, John Godman, Thomas Say, or Audubon and Bachman. The late 19th and early 20th centuries were times of extraordinary productivity (see, for example, Hoffmeister and Sterling, 1994; Wilson and Eisenberg, 1990), and eminent mammalogists left marks that still inspire and influence our work, among them Harrison Allen, J. A. Allen, W. H. Osgood, G. S. Miller, Jr., C. Hart Merriam (who continues to sign the register annually at meetings of ASM a full half-century after his death).

## *The 1920s*

The roster of the organizational meeting of ASM in 1919 reads like a "Who's Who" of late 19th and early 20th century mammalogy. Many of the luminaries present went on to give distinguished service to mammalogy and ASM and are noted elsewhere in this volume. The decade in mammalogy was characterized by self-evaluation and definition, and dominated by the pioneers. Early numbers of the *Journal of Mammalogy* published earnest correspondence about taxonomic issues, the dubious value of common names for organisms neither commonly seen nor much discussed by common folk, still-useful lists of desiderata for life history studies, and the relative exchange value of specimens of mice and mink. Browsing through early volumes of the *Journal* and minutes of early meetings, one readily agrees that we continue to stand on the shoulders of those giants and continue to earn interest on the intellectual capital they invested. Of nine authors in the inaugural number of the *Journal* (28 November 1919), six served as President of the ASM, five eventually were named Honorary Members, and three received both of those recognitions. Here we note a few other individuals who left a mark during the first decade of ASM.

*Outram Bangs* (1863–1932) was born in Watertown, Massachusetts, and graduated from the Lawrence Scientific School of Harvard College in 1884. In the 1890s, Bangs published 50 papers on mammals. In a sense, Bangs represents a sizable class of individuals, largely unsung—the local naturalists. Like dozens of other noteworthy local mammalogists of his era, he began to collect mammals as a child. Eventually he built one of the finest private collections in the U.S., which was purchased by Harvard's Museum of Comparative Zoology in 1899, and Bangs was named Assistant in Mammalogy, although his research interests soon shifted to birds.

*Ned Hollister* (1876–1924) was the original editor of the *Journal of Mammalogy,* setting the high standards for editorial quality that are matched by few other scientific journals. Born in Delavan, Wisconsin, he collaborated with Ludwig Kumlien of Milton College on *Birds of Wisconsin* (1903), accompanied Vernon Bailey on a Biological Survey expedition to Texas (1902), and worked with W. H. Osgood in Alaska (1903). He formally joined the staff of the Bureau of Biological Survey in 1904. Reputed to have a genius for museum work (Osgood, 1925), he was appointed Assistant Curator of Mammals in the U.S. National Museum in 1909; in 1916 he became Superintendent of the National Zoological Park. In his brief career, Hollister collected 26 holotypes, named 162 taxa, and published 150 papers and monographs, including several works of enduring value, among them work on mammals of the Philippines (1913) and reviews of East African mammals in the U.S. National Museum (1918, 1919, 1924).

*A. H. Howell* (1872–1940) was the only author in the inaugural number of the *Journal of Mammalogy* who did not go on to the presidency of ASM or election to honorary membership. However, his impact on systematic mammalogy continues to be great, largely because he provided (mostly in *North American Fauna*) the first monographic treatments of a number of mammalian genera: striped skunks (1901), spotted skunks (1906), harvest mice (1914), marmots (1915), flying squirrels (1918), pikas (1924), chipmunks (1929), and ground squirrels (1938). His biological survey of Alabama (1921) was the only such product of the Bureau of Biological Survey outside the Mountain West. Mostly self-trained, Howell farmed and worked as a stock-clerk before being stimulated to a career in natural history through an association with the Linnaean Society of New York. He received a temporary appointment in 1895 as assistant to Vernon Bailey for field work in the Northern Rockies and Pacific Northwest. He continued with the Bureau of Biological Survey (and the Fish and Wildlife Service) until his death 44 years later.

*H. H. Lane* (1878–1965) was the original Recording Secretary of ASM, serving from 1919 until 1932. Born in Bainbridge, Indiana, and educated at DePauw, Indiana, Cornell, and Chicago, he received a Ph.D. from Princeton in 1915. Lane taught at Hiram College, the University of Oklahoma, and Phillips University before moving to the University of Kansas as Professor of Zoology and Paleontology in 1922. Mostly a paleontologist, he nonetheless influenced the classic generation of mammalogists at the University of Kansas, including William Henry Burt, E. Raymond Hall, Claude W. Hibbard, and Jean M. Linsdale.

## *The 1930s*

The 1930s saw progress in a number of areas of mammalogy, especially in mammalian ecology, and some of the most notable contributions remain classic autoecological studies.

*Robert T. Hatt* (1902–1989) served as Corresponding Secretary of ASM from 1932 to 1934. Born in Lafayette, Indiana, and educated at Michigan and Columbia, Hatt spent several years at the American Museum of Natural History and then directed the Cranbrook Institute of Science from 1935 to 1967, remaining as Senior Scientist until his retirement in 1971. Hatt's enduring contributions included fine autecological studies, especially of squirrels (e.g., Hatt, 1943), and work in anatomy (Hatt, 1932).

*Robert K. Enders* (1899–1989) pursued an extraordinarily diverse career, centered on academic work at Swarthmore College. He conducted field work on Panamanian mammals for more than 40 years, from 1929 to 1971. Although he served as Recording Secretary of ASM from 1933 to 1937, and in a variety of scientific organizations and agencies in leadership capacities, his most indelible mark on mammalogy may have been indirect, a consequence of his stewardship of the Rocky Mountain Biological Laboratory at Gothic, Colorado, as Director (1959–1968) and President (1969–1978). He also stimulated students, such as Oliver Pearson and Phil Myers, to pursue careers in mammalogy.

*Jean M. Linsdale* (1902–1973) was part of that legendary "bumper-crop" of mammalogists born in Kansas, and educated at the University of Kansas and the University of California, Berkeley, that included W. H. Burt and E. R. Hall. He may have described his most important legacy to vertebrate zoology best in the acknowledgments to his monumental work, *The California Ground Squirrel* (1946); among the list of students at the Hastings Natural History Reservation who contributed as observers were Lamont C. Cole, Carl Koford, Lloyd Tevis, P. Q. Tomich, G. A. Bartholemew, Jr., W. W. Dalquest, H. S. Fitch, W. V. Mayer, and C. G. Sibley. Linsdale spent his professional career with the Museum of Vertebrate Zoology, joining in 1922 the "fur book" project begun three years earlier by Grinnell and Dixon (Grinnell et al., 1937). His painstaking work on the dusky-footed woodrat

(Linsdale and Tevis, 1951) helped inspire the career of a younger great neotomologist, R. B. Finley, Jr.

*Olaus J. Murie* (1889–1963) was born in Moorhead, Minnesota, and served from 1920 to 1946 as a field biologist with the Bureau of Biological Survey, including work in the Canadian Arctic, Labrador, and the Aleutians. His work on the elk of Jackson Hole (begun in 1927) is an enduring classic, in part culminating in *Elk of North America* (O. J. Murie, 1951). *A Field Guide to Animal Tracks* (1954) remains an invaluable resource for naturalists who would read stories of mammals not in the library but in dust, mud, or snow. A confirmed conservationist, Murie retired from government service to help found The Wilderness Society, of which he was President from 1950 to 1957.

*Adolph Murie* (1899–1974) pursued his distinguished research career at the University of Michigan (where as recently as 1968 a pair of his boots occupied a place of honor in a specimen case), the U.S. Fish and Wildlife Service, and the National Park Service. After classic studies of moose on Isle Royale (A. Murie, 1934), he began research on gray wolf–Dall sheep interactions in Mount McKinley National Park in 1939. *The Wolves of Mount McKinley* (A. Murie, 1944) and *The Grizzlies of Mount McKinley* (reprinted, 1981) continue to inspire. Like his older brother Olaus, Adolph Murie was passionately committed to conservation and the ideal of national parks: "The national park idea is one of the bright spots in our culture. The idealism in the park concept has made every American visiting the national parks feel just a little more worthy" (A. Murie, 1981:241).

*Aldo Leopold* (1887–1948) continues to enrich our science and our philosophy nearly a half-century after his untimely death. It is difficult to know which decade deserves to be identified with his remarkable contributions. The publication of his seminal *Game Management* (1933) essentially redefined the field as applied ecology, nudging it hard from folk-art toward science. *A Sand County Almanac* appeared posthumously (1949), with sensitive, sensible insights into ecological ethics that continue to inspire students and their elders alike. In another dimension of his enduring legacy, several of Leopold's children went on to distinguished scientific careers, in wildlife biology (Starker), paleobotany (Estella), plant physiology (Carl), and earth sciences (Luna).

*Francis B. Sumner* (1874–1945) had an extraordinary career, documented in a remarkable autobiography (1945), *The Life History of an American Naturalist.* Educated at Minnesota and Columbia, he taught at the College of the City of New York, and worked on fish development as Director of the Biological Laboratory of the Bureau of Fisheries at Woods Hole. Remarks by David Starr Jordan about the importance of long-term studies of the effects of environment on evolution inspired his mammalogical work, which was made possible by an appointment at the Scripps Oceanographic Institute. Thus began a remarkable career in mammalogy, centered on painstaking laboratory studies of the genetics of geographic variation in species of *Peromyscus* (see Sumner, 1932).

## The 1940s

In the 1940s, many of a generation of mammalogists saw military service in World War II. An earlier generation of scholars continued to work despite limited academic and agency budgets and rationing of such theriological essentials as paper, gasoline, and tires, producing works that must still be consulted daily, such as G. G. Simpson's *Principles of Classification and a Classification of the Mammals.*

*Victor H. Cahalane* (1901–1993) was a Director of ASM at various times from the 1930s to the 1960s. Director of the Cranbrook Institute of Science from 1931–1934, his scientific career was spent mostly with the U.S. National Park Service, resulting in such studies as his survey of Katmai National Monument (1959). Chief of the Biology Branch from 1944–1955, he remained as a collaborator until 1970 while Assistant Director of the New York State Museum. Perhaps Cahalane's most enduring contributions were in the genre of popular natural history. *Mammals of North America* (1947), with its charming illustrations by Francis L. Jacques (1887–1969), remains an important landmark in mammalogical publishing, and *The Imperial Collection of Audubon Mammals* (Cahalane, 1967) made Audubon and Bachman's illustrations of mammals readily available to the 20th century.

*Paul Errington* (1902–1962) received his Ph.D. from the University of Wisconsin and spent his entire academic career at Iowa State University. He devoted much of his too-brief scientific career to a single species, the muskrat, a keystone in the glacial marshes of the Midwest, research that began ". . . with muddy feet on the family farm in east-central South Dakota" (Errington, 1967:xi). His central question was what determines numbers of free-living animal populations, a question pursued in remarkable depth, as "the study of predation is no field for snap judgments" (1967:xi). *Muskrat Populations* (1963) remains a standard reference, and Errington did not hesitate to apply lessons learned from muskrats to humankind, as he did in *Of Men and Marshes* (1957), and the posthumous works, *Of Predation and Life* (1967), and *The Red Gods Call* (1973).

*D. Dwight Davis* (1908–1965) was born in Rockford, Illinois, and joined the Field Museum in 1930, rising from Assistant in Osteology to Curator of Anatomy. His memoir on the functional morphology of the giant panda is a landmark in mammalogy (Davis, 1964), setting a new standard for morphological studies of species. Indeed, Gould (1980) called Davis's monograph ". . . probably the greatest work of modern evolutionary comparative anatomy."

*Ian McTaggart Cowan* was born in 1910 in Scotland and educated at the universities of British Columbia and California. His distinguished academic career at the University of British Columbia was marked by honorary degrees from Simon Fraser University and the universities of Alberta, Waterloo, British Columbia, and Victoria. Cowan's study of geographic variation in native American sheep (1940) was a painstaking example of the possibilities of deep insights from fragmentary material. With Charles Guiguet, the Curator of Birds and Mammals at the British Columbia provincial Museum, he authored *The Mammals of British Columbia* (Cowan and Guiguet, 1956), which has gone through three editions.

*Philip L. Wright* was born in 1914 and reared in New Hampshire, earning his doctorate from the University of Wisconsin in 1940. His entire professional career was spent at the University of Montana, where he retired in 1985. Wright's research was focused mostly on reproductive cycles of endotherms, and his enduring contributions to mammalogy include a number of pioneering papers on reproductive cycles of mustelids (e.g., Wright, 1942), as well as more recent work to maintain Boone and Crockett Club records on big game mammals.

## *The 1950s*

The 1950s were optimistic years typified not only by big projects—of which E. R. Hall and K. R. Kelson's *Mammals of North America* surely stands as the grandest—but also by big questions, on the nature of population regulation, for example. Through the decade governmental support of mammalogy increased in North America, resulting in patterns of funding and academic rewards that prevail today.

*A. W. F. Banfield* (born in Toronto in 1918) studied at the universities of Toronto and Michigan and served as a mammalogist in several Canadian governmental agencies, including the National Park Service, the

Wildlife Service, and the National Museum. He was Director of the Museum of Natural Science from 1964 to 1969 and later taught at Brock University. His contributions to mammalogy included definitive studies of the caribou over three decades (Banfield, 1951, 1961), a faunal survey of Banff National Park (1958), and his comprehensive *The Mammals of Canada* (1974).

*Donald R. Griffin* (born in 1915 in Southampton, New York) has had two distinguished careers in mammalogy, either of which would have earned him a prominent place in this chapter, in any of several decades. His academic career began at Cornell. While at Harvard, he published his classic *Listening in the Dark* (1958), which—along with *Echoes of Bats and Men* (1959)—continues to inspire chiropterologists. In 1965 he moved to Rockefeller University. *The Question of Animal Awareness* (1976) defined the new field of cognitive ethology and posed anew questions that had been dismissed as scientifically inaccessible a century earlier. A recent *Festschrift* for Griffin (Ristau, 1991) provided appropriate recognition for a distinguished mammalogist.

*John J. Christian* was born in Pennsylvania in 1917 and educated at Princeton and Johns Hopkins. In a research career in various commercial, federal, and academic laboratories, he pursued intensive experimental studies of the relationships among population density, reproduction, and the endocrine system, especially the adreno-pituitary axis (reviewed in Christian, 1963), stimulating renewed interest in field studies of fluctuations of numbers of small mammals. He received the Mercer Award from the Ecological Society of America in 1957 and was a professor at SUNY Binghampton from 1969 until his retirement.

*John B. Calhoun* was born in Elkton, Tennessee, in 1917, and educated at the University of Virginia and Northwestern. He taught at Emory, Ohio State, and Johns Hopkins. His research focused on principles of population dynamics, and he realized that "derivation of these principles requires more data than can be obtained by the efforts of a single individual" (Calhoun, 1956). In 1947 he organized and initiated the North American Census of Small Mammals (NACSM), sponsored first by the Rodent Ecology Project at Johns Hopkins, later by Jackson Laboratory at Bar Harbor, Maine, and finally by the National Institutes of Mental Health (where Calhoun moved in 1954). NACSM inspired volunteer fieldwork across the continent for a dozen years. By using consistent protocols, it not only developed a very large data set but underscored the importance and the difficulties of achieving a quantitative understanding of mammalian distributions in space and time. Calhoun's (1963) monograph on the ecology and sociology of the Norway rat was a landmark in considering in evolutionary and ecological terms the sociopathology of mammalian populations, both rats and people.

*Carl B. Koford* (1915–1980) was selected in 1939 by Joseph Grinnell and Alden H. Miller to study the California condor with the support of the National Audubon Society. Associated throughout his career mostly with the Museum of Vertebrate Zoology, Koford's work was characterized by extraordinary attention to detail and thorough pursuit of connections and relationships. Fortunately, he turned these skills to understanding the ecology of the black-tailed prairie dog, providing (Koford, 1958) a classic study of the species in the context of the dynamic and overused, but poorly known, ecosystem in which it is a kind of keystone. Fortunately, too, he invested his monograph with passionate concern for conservation that—in concert with the voices of such other committed mammalogists as Victor Cahalane, the brothers Murie, and E. R. Hall—finally is beginning to bear fruit.

## *The 1960s*

The 1960s saw the advent of new tools and concepts like digital computers, multivariate statistics, and the use of "biosystematic" characters in mammalogy. However, several of the landmarks of the decade were broad summaries in their fields, including J. A. King's edited *Biology of* Peromyscus, Anderson and Jones' edited *Recent Mammals of the World,* and Walker's *Mammals of the World.*

*Barbara Lawrence* (born in Boston in 1909) was educated at Vassar College and was associated with the Museum of Comparative Zoology at Harvard from 1931 until her retirement in 1976. In addition to important work on mammals of New England, the Caribbean, and Central America, Lawrence collaborated with William Bossert to produce a ground-breaking multivariate morphometric study of North American *Canis* (Lawrence and Bossert, 1967) that demonstrated the power of new kinds of statistics in gaining insights into complex evolutionary and ecological questions.

*E. Lendell Cockrum* (born in 1920 in Sesser, Illinois) published a comprehensive systematic work on the mammals of Kansas (1952) and went on to pursue a distinguished academic career at the University of Arizona. One of his most influential contributions to mammalogy was his textbook, *Introduction to Mammalogy* (1962), which served a generation of students. Cockrum also co-authored textbooks in general zoology and general biology and produced major studies of mammals of Organ Pipe National Monument (e.g., Cockrum, 1981).

*B. Elizabeth Horner* (born in 1917 in Merchantville, New Jersey) received her Ph.D. from the University of Michigan in 1948 and taught zoology at Smith College from 1940 until her retirement in 1982. In 1970, she was named Myra M. Sampson Professor of Biological Science. Her mammalogical contributions included classic studies of the biology of rodents, especially ecomorphology of *Peromyscus* (e.g., Horner, 1954) and marsupials.

*W. Frank Blair* (1912–1985) was born in Dayton, Texas, and educated at the universities of Tulsa and Florida, as well as the Laboratory of Vertebrate Biology at the University of Michigan. Perhaps best known for his work in herpetology at the University of Texas, he left an indelible stamp on the development of mammalogy in several ways, and over a period sufficiently long that it is difficult to ascribe his influence to a particular decade. His works on the biotic provinces of Oklahoma (Blair and Hubbell, 1938) and Texas (Blair, 1950) are still valuable, and *Vertebrates of the United States* (Blair et al., 1957) was consulted by generations of mammalogists. He was among the first ecologists to develop mark-recapture methods in studies of population ecology. Moreover, his leadership of the United States International Biological Program in the late 1960s and into the 1970s (see Blair, 1977; Mares and Cameron, 1994) allowed deep insights into the functional role of mammals in ecosystems, and facilitated international cooperation among mammalogists that continues to expand.

*Ernest P. Walker* (1891–1969) first made a mark on zoology with a 1913 book on birds of Wyoming. His monumental mammalogical project, *Mammals of the World,* began in 1930 while he was Assistant Director of the National Zoological Park, and continued for 30 years, resulting in the standard semi-technical reference on the extant genera of mammals, now in its fifth edition (Nowak, 1991). The work was painstakingly thorough and attempted to include a photograph of a representative species in each genus. The first edition (Walker et al., 1961) included a remarkable third volume, a classified bibliography of the literature of mammalogy, based in large part on the "Recent Literature" section of the *Journal of Mammalogy,* which remains an efficient entry to the literature of mammalogy to about 1960. Walker's original dedication was "To the MAMMALS, GREAT AND SMALL, who contribute so much to the welfare and happiness of man, another mammal, but receive so little in return, except blame, abuse, and extermination."

## *The 1970s*

The investigational and analytic tools of the 1960s bore rich fruit in the 1970s. It is too early to guess just which works will turn out to be classics, of course, but the decade had more than its share of classic workers, many of whom figure prominently in other chapters in this volume.

*Rollin H. Baker* (born in Cordova, Illinois, in 1916) was educated at the University of Texas, Texas A&M University, and the University of Kansas. He established a reputation as an ornithologist with his monograph on the avifauna of Micronesia (1951), but his professional efforts at the University of Kansas, and later at Michigan State University, soon focused on mammals of Mexico and Michigan. He and his students did pioneering work on the biosystematics of *Sigmodon,* and his monumental *Michigan Mammals* (1983) is a paragon of state mammal books. Baker retired in 1981.

*Karl Kenyon* (born in 1918 in La Jolla, California) was educated at Pomona and Cornell. After service in the U.S. Navy, he taught at Mills College. In 1947, he joined the U.S. Fish and Wildlife Service, under Victor B. Scheffer at the Fur Seal Laboratory (later the Marine Mammal Laboratory), pursuing a distinguished research career that made him the preeminent authority on the biology of the sea otter. His monograph on the biology of the species (Kenyon, 1969) will remain a classic of its genre.

*Ralph M. Wetzel* (1917–1984) received his Ph.D. from the University of Illinois in 1949. His professional career was spent mostly at the University of Connecticut, enriched by research appointments at the U.S. National Museum. He retired in 1982 and moved to a courtesy appointment at the University of Florida State Museum. Wetzel's well-known work in the Gran Chaco of Paraguay began in 1972. It was there that he discovered that the Chacoan peccary (*Catagonus wagneri*), previously known only from pre-Hispanic, subfossil deposits, remained alive (Wetzel, 1977), perhaps encouraging a younger generation of mammalogists to turn toward South America with the heightened sense that really remarkable discoveries remain to be made.

*Charles H. Southwick* was born in Wooster, Ohio, in 1928, graduated from the College of Wooster, and earned master's and doctoral degrees from the University of Wisconsin. After faculty appointments at Hamilton College, Ohio University, and Johns Hopkins (and research appointments at Oxford and Stanford), he moved to the University of Colorado in 1979 and retired there in 1993. Southwick's research career is focused on population and behavioral ecology. He continues to make fundamental contributions to our knowledge of mammalian species as diverse as grasshopper mice, pikas, and mule deer, but his enduring legacy surely will be in understanding the biology of species of *Macaca.* His longitudinal research effort on Indian populations of rhesus macaques (reviewed in Fa and Southwick, 1988), now over three decades long and continuing, may be unequalled for any species in the history of mammalogy. Further, he has shared his deep insights into the problems and prospects for global environmental conservation through texts such as *Ecology and the Quality of Our Environment* (Southwick, 1976) and *Global Ecology* (Southwick, 1988).

*William A. Wimsatt* (1917–1987) was educated at Cornell and spent most of his academic career there. His research career focused on the ecology and physiology of reproduction in eastern bats, especially *Myotis lucifugus,* and he pioneered techniques and insights (see Wimsatt and Kallen, 1957) that have since been applied to numerous other species. His edited series, *Biology of Bats* (1970*a,* 1970*b,* 1977), brought together a vast quantity of information and attendant literature and made it accessible to a new generation of chiropterologists.

*Robert L. Rausch* was born in 1921 in Marion, Ohio. From Ohio State University he received a bachelor's degree in 1942 and a D.V.M. in 1945. He then earned an M.S.

from Michigan State University in 1946 and a Ph.D. from the University of Wisconsin in 1949, in parasitology and wildlife management. He joined the Arctic Health Research Center of the U.S. Public Health Service, serving as Chief of the Zoonotic Disease Section from 1950 until its closure in 1974. Rausch was Adjunct Professor at the University of Alaska from 1967 to 1974 and Professor of Zoology from 1974 to 1975. He served as Professor of Parasitology at the University of Saskatchewan from 1975 to 1978 and then moved to the University of Washington, where he was Professor of Pathobiology in the School of Medicine and Adjunct Professor of Zoology until his retirement in 1992. As a mammalogist, Rausch established an international reputation for his systematic insights on Arctic mammals (e.g., Rausch, 1953) and received honorary degrees from the universities of Saskatchewan, Alaska, and Zürich. Rausch's wife, Virginia (Reggie), is a scientist in her own right and a frequent collaborator on joint projects (e.g., Rausch and Rausch, 1975).

*Claude W. Hibbard* (1905–1973) was born in Toronto, Kansas, and educated at the universities of Kansas and Michigan. He worked and taught at Kansas from 1928 to 1946 and then moved back to Ann Arbor, where he pursued a highly productive career as an energetic and insightful student of Pliocene and Pleistocene faunas of the Great Plains, with a strong emphasis on mammals. His most lasting scientific contributions were the development and use of a technique for collecting microfossils (described by Zakrzewski and Lillgraven, 1994).

*Walter W. Dalquest* (born 1917) is difficult to identify with any particular decade, for his career has been long and diversely productive. Educated at the University of Washington and Louisiana State, he published comprehensive faunal treatments of mammals of Washington (1948) and San Luis Potosi (1953) and went on to a distinguished academic career at Midwestern State University, Texas, making important contributions to the study of vertebrates (especially mammals and fishes) of south-central United States and Mexico. Over the years, his research focused increasingly on fossil vertebrates, especially those of Pliocene and Pleistocene localities. A well-deserved *Festschrift* (Horner, 1984) celebrated his contributions to students and science.

## A Final Word

Given the diversity and purview of mammalogy and mammalogists and the richness of research during the past three-quarters of a century, the foregoing survey can hardly hope to be definitive; indeed, it can be little more than suggestive. There was not even full agreement among the authors on whom to include. Peterson would have included more Canadians and chiropterologists, Johnson more northwesterners and theriologists from beyond North America, and—unrestrained by wiser colleagues—Armstrong would have been biased toward his own local heroes and mentors.

Whether one agrees with our commissions or omissions is hardly the point, however. Surely one cannot do science without understanding the process, and the process is a distinctly human enterprise, burdened with the full weight (and blessed with the full possibility) that "human" implies. If we see farther than our predecessors, it surely is because we stand on their shoulders.

## Literature Cited

Baker, R. H. 1951. The avifauna of Micronesia. University of Kansas Publications, Museum of Natural History, 3:1–359.

———. 1983. Michigan mammals. Michigan State University Press, East Lansing, xx + 642 pp.

Banfield, A. W. F. 1951. The barren-ground caribou. Department of Resources and Development, Ottawa, v + 52 pp.

———. 1958. The mammals of Banff National Park, Alberta, Canada. Bulletin, National Museum of Canada, 159:1–53.

———. 1961. A revision of the reindeer and caribou, genus *Rangifer*. Biological Series, National Museum of Canada, 66:vi + 1–137.

———. 1974. The mammals of Canada. University of Toronto Press, Toronto, xxv + 438 pp.

Blair, W. F. 1950. The biotic provinces of Texas. Texas Journal of Science, 2:93–117.

———. 1977. Big biology, the US/IBP. Dowden, Hutchison, and Ross, Stroudsburg, Pennsylvania, x + 261 pp.

Blair, W. F., A. P. Blair, P. Brodkorb, F. R. Cagle, and G. A. Moore. 1957. Vertebrates of the United States. McGraw–Hill Book Company, New York, 819 pp.

Blair, W. F., and T. H. Hubbell. 1938. Biotic districts of Oklahoma. The American Midland Naturalist, 20:425–454.

Cahalane, V. H. 1947. Mammals of North America. MacMillan, New York, x + 682 pp.

———. 1959. A biological survey of Katmai National Monument. Smithsonian Miscellaneous Collections, 138:1–246.

——— (ed.). 1967. The imperial collection of Audubon mammals. Hammond, Inc., Maplewood, New Jersey, xvi + 307 pp.

Calhoun, J. B. (ed.). 1956. 1951 annual report—North American Census of Small Mammals. Administrative Publication, U.S. Department of Health, Education, and Welfare, I + 164 pp.

Calhoun, J. B. 1963. The ecology and sociology of the Norway rat. Publications, U.S. Public Health Service, 1008:viii + 288 pp.

Christian, J. J. 1963. Endocrine adaptive mechanisms and the physiologic regulation of population growth. Pp. 189–353 *in* Physiological mammalogy (W. V. Mayer and R. G. Van Gelder, eds.). Academic Press, New York, 1:1–381.

Cockrum, E. L. 1952. Mammals of Kansas. University of Kansas Publications, Museum of Natural History, 7:1–303.

———. 1962. Introduction to mammalogy. Ronald Press Company, New York, 455 pp.

———. 1981. Bat populations and habitats at the Organ Pipe National Monument. University of Arizona Press, Tucson, 31 pp.

Cowan, I. McT. 1940. Distribution and variation in the native sheep of North America. The American Midland Naturalist, 24:505–580.

Cowan, I. McT., and C. J. Guiguet. 1956. The mammals of British Columbia. Handbook, British Columbia Provincial Museum, 11:1–413.

Dalquest, W. W. 1948. Mammals of Washington. University of Kansas Publications, Museum of Natural History, 2:1–444.

———. 1953. Mammals of the Mexican state of San Luis Potosi. Louisiana State University Press, 229 pp.

Davis, D. 1964. The giant panda: a morphological study of evolutionary mechanisms. Fieldiana: Zoology Memoirs, 3:1–339.

Errington, P. L. 1957. Of men and marshes. Iowa State University Press, Ames, 150 pp.

———. 1963. Muskrat populations. Iowa State University Press, Ames, x + 665 pp.

———. 1967. Of predation and life. Iowa State University Press, Ames, xii + 277 pp.

———. 1973. The red gods call (C. Errington, ed.) Iowa State University Press, Ames, ix + 171 pp.

Fa, J. E., and C. H. Southwick (eds.). 1988. Ecology and behavior of food-enhanced primate groups. Alan R. Liss Publishers, New York, 355 pp.

Gould, S. J. 1980. The panda's thumb, more reflections on natural history. W. W. Norton & Company, New York, 343 pp.

Griffin, D. R. 1958. Listening in the dark. Yale University Press, New Haven, 413 pp.

———. 1959. Echoes of bats and men. Anchor Books, Garden City, New York, 156 pp.

———. 1976. The question of animal awareness: evolutionary continuity of mental experience. Rockefeller University Press, New York, viii + 135 pp.

Grinnell, J., J. S. Dixon, and J. M. Linsdale. 1937. Fur-bearing mammals of California: their natural history, systematic status, and relations to man. University of California Press, Berkeley, 2 vols, 777 pp.

Hatt, R. T. 1932. The vertebral columns of ricochetal rodents. Bulletin of the American Museum of Natural History, 63:599–738.

———. 1943. The pine squirrel in Colorado. Journal of Mammalogy, 24:311–345.

Hoffmeister, D. F., and K. Sterling. 1994. Origin. Pp. 1–21, *in* Seventy-five years of mammalogy (1919–1994) (E. C. Birney and J. R. Choate, eds.). Special Publication, The American Society of Mammalogists, 11:1–433.

Hollister, N. 1913. A review of the land mammals of the Philippine Islands in the United States National Museum. Proceedings of the United States National Museum, 46:299–341.

———. 1918. East African mammals in the United States National Museum. Part I. Insectivora, Chiroptera, and Carnivora. Bulletin of the United States National Museum, 99:1–94.

———. 1919. East African mammals in the United States National Museum. Part II. Rodentia, Lagomorpha, and Tubulidentata. Bulletin of the United States National Museum, 99:1–175.

———. 1924. East African mammals in the United States National Museum. Part III. Primates, Artiodactyla, Perissodactyla, Proboscidea, and Hyracoidea. Bulletin of the United States National Museum, 99:1–151.

Horner, B. E. 1954. Arboreal adaptations of *Peromyscus* with special reference to use of the tail. Contributions from the Laboratory of Vertebrate Biology, University of Michigan, 61:1–84.

Horner, N. V. (ed.). 1984. *Festschrift* for Walter W. Dalquest in honor of his sixty–sixth birthday. Department of Biology, Midwestern State University, Wichita Falls, Texas, 163 pp.

Howell, A. H. 1901. Revision of the skunks of the genus Chincha. North American Fauna, 20:1–62.

———. 1906. Revision of the skunks of the genus Spilogale. North American Fauna, 26:1–55.

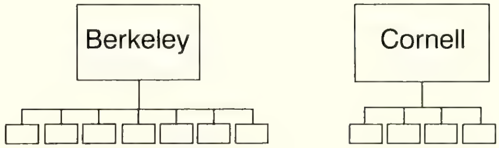
———. 1914. Revision of the American harvest mice (genus Reithrodontomys). North American Fauna, 36:1–97.

———. 1915. Revision of the American marmots. North American Fauna, 37:1–80.

———. 1918. Revision of the American flying squirrels. North American Fauna, 44:1–64.
———. 1921. A biological survey of Alabama. North American Fauna, 45:1–88.
———. 1924. Revision of the American pikas (genus Ochotona). North American Fauna, 47:1–57.
———. 1929. Revision of the American chipmunks (genera *Tamias* and *Eutamias*). North American Fauna, 52:1–157.
———. 1938. Revision of the North American ground squirrels with a classification of the North American Sciuridae. North American Fauna, 56:1–256.
Kenyon, K. W. 1969. The sea otter in the eastern Pacific Ocean. North American Fauna, 68:xiii + 1–352.
Koford, C. B. 1958. Prairie dogs, whitefaces, and blue grama. Wildlife Monographs, 3:1–78.
Lawrence, B., and W. H. Bossert. 1967. Multiple character analysis of *Canis lupus, latrans,* and *familiaris,* with a discussion of the relationships of *Canis niger.* American Zoologist, 7:223–232.
Leopold, A. S. 1933. Game management. C. Scribner's Sons, New York, xxi + 481 pp.
———. 1949. A Sand County almanac, and sketches here and there. Oxford University Press, New York, xiii + 226 pp.
Linsdale, J. M. 1946. The California ground squirrel. University of California Press, Berkeley, xi + 475 pp.
Linsdale, J. M., and L. B. Tevis, Jr. 1951. The dusky-footed woodrat. University of California Press, Berkeley, vii + 664 pp.
Mares, M. A., and G. N. Cameron. 1994. Community and Ecosystem Ecology. Pp. 348–376, *in* Seventy-five years of mammalogy (1919–1994) (E. C. Birney and J. R. Choate, eds.). Special Publication, The American Society of Mammalogists, 11: 1–433.
Murie, A. 1934. The moose of Isle Royale. Miscellaneous Publications, University of Michigan Museum of Zoology, 25:1–44.
———. 1944. The wolves of Mount McKinley. Fauna of the National Parks of the United States, 5:x + 1–238.
———. 1981. The grizzlies of Mount McKinley. Scientific Monograph Series, National Park Service, U.S. Department of the Interior, 14:xvi + 1–251.
Murie, O. J. 1951. The elk of North America. Stackpole Publishing Co., Harrisburg, Pennsylvania, 376 pp.
———. 1954. A field guide to animal tracks. Houghton Mifflin, Boston, xxii + 374 pp.
Nowak, R. M. (ed.). 1991. Walker's *Mammals of the World,* Fifth ed. Johns Hopkins University Press, Baltimore, 1:1–642, 2:643–1629.
Osgood, W. H. 1925. Ned Hollister. Journal of Mammalogy, 6:1–12.
Rausch, R. L. 1953. On the status of some Arctic mammals. Arctic, 6:91–148.
Rausch, R. L., and V. R. Rausch. 1975. Taxonomy and zoogeography of *Lemmus* spp., with notes on laboratory-reared lemmings. Zeitschrift für Säugetierkunde, 40:8–34.
Ristau, C. A. (ed.). 1991. Cognitive ethology: the minds of other animals, essays in honor of Donald R. Griffin. Erlbaum Associates, Hillsdale, New Jersey, xx + 332 pp.
Southwick, C. H. 1976. Ecology and the quality of our environment. Second ed. Van Nostrand Reinhold, New York, 426 pp.
——— (ed.). 1988. Global ecology. Sinauer Associates, Sunderland, Massachusetts, 323 pp.
Sumner, F. B. 1932. Genetic, distributional, and evolutionary studies of the subspecies of deermice (*Peromyscus*). Bibliographica Genetica, 9:1–106.
———. 1945. The life history of an American naturalist. Jaques Cattell Press, Lancaster, Pennsylvania, vii + 298 pp.
Walker, E. P., et al. 1961. Mammals of the world. Johns Hopkins University Press, Baltimore, 1:1–644, 2:647–1500, 3:1–769.
Wetzel, R. M. 1977. The Chacoan peccary *Catagonus wagneri* (Eusconi). Bulletin of Carnegie Museum of Natural History, 3:1–36.
Wilson, D. E., and J. F. Eisenberg. 1990. Origin and applications of mammalogy in North America. Current Mammalogy, 2:1–35.
Wimsatt, W. A. (ed.). 1970*a.* Biology of bats. Academic Press, New York, 1:1–406.
——— (ed.). 1970*b.* Biology of bats. Academic Press, New York, 2:1–477.
——— (ed.). 1977. Biology of bats. Academic Press, New York, 3:1–651.
Wimsatt, W. A., and F. C. Kallen. 1957. The unique maturation response of the Graafian follicles of hibernating vespertilionid bats and the question of its significance. Anatomical Record, 129:115–131.
Wright, P. L. 1942. Delayed implantation in the long-tailed weasel (*Mustela frenata*), the short-tailed weasel (*Mustela cigonanti*), and the marten (*Martes americana*). Anatomical Record, 83:341–349.
Zakrzewski, R. J., and J. A. Lillegraven. 1994. Paleomammalogy. Pp. 200–214, *in* Seventy-five years of mammalogy (1919–1994) (E. C. Birney and J. R. Choate, eds.). Special Publication, The American Society of Mammalogists, 11:1–433.

# *ACADEMIC PROPINQUITY*

JOHN O. WHITAKER, JR.




## *Introduction*

There have been at least three major papers on the history of North American mammalogy and the ASM (Hamilton, 1955; Hoffmeister, 1969; Storer, 1969). However, none of these papers presented information on the "roots" or "academic genealogy" of North American mammalogists. The 75th anniversary of the birth of the ASM is a good time to examine this topic. The idea arose from a paper given by J. Knox Jones, Jr., at the 1985 annual meeting of ASM at Orono, Maine. It was titled "Genealogy of Twentieth Century Systematic Mammalogists in North America: The Descendants of Joseph Grinnell," and was subsequently published (Jones, 1991). Jones indicated that the descendants of Joseph Grinnell at the University of California, Berkeley, along with a major subcenter founded by E. Raymond Hall at the University of Kansas, accounted for an academic dynasty that included perhaps 75% of North American systematic mammalogists. Elmer Birney, president of ASM in 1989, suggested this topic be examined in more detail and other "dynasties" be included as a chapter in a history of the society to be presented in conjunction with its 75th anniversary. This study is an attempt to trace the roots of mammalogy in North America during the first 75 years of the society.

The base data for this paper are given (Table 1) as a listing of many mammalogists who "have made their mark or are making their mark" on North American mammalogy. Most are or were associated with the ASM. I have drawn heavily from Jones (1991) for the material on the Grinnell dynasty but there is no other published set of data to which one can go for related information. It had to be obtained by word of mouth and through correspondence. Attempts were made to include as many of the more active North American mammalogists in this table as possible. However, not all could be included in the text, and little information could be obtained for some. I hope that omissions and oversights will not detract too greatly from the overall picture. The data accumulated should serve to indicate the source of our collective roots. The earliest group listed, the field mammalogists assembled for the United States Biological Survey by C. Hart Merriam, is not an academic group, but nevertheless made a major impact on North American mammalogy. Three major academic groups are included: the Harvard Group (Agassiz/Allen), the Berkeley/Kansas Group (Grinnell/Hall), and the Cornell Group (Hamilton). Besides those obtaining their training from members of these groups, there are some smaller groups (Florida, Purdue, Tulane, Wisconsin), and a number of mammalogists have received their degrees in related fields, such as ecology, ornithology, wildlife, and genetics.

## *I. The Merriam Group*

Before discussing the academically-oriented dynasties, it is important to mention the group formed in the latter part of the last century under Clinton Hart Merriam of the U.S. Biological Survey (Table 1, Section I). C. Hart Merriam was trained as an M.D. in New York and practiced medicine from 1879 to 1885 (Storer, 1969). However, Merriam was a field naturalist at heart and had written early natural history books on the birds of Connecticut (1877) and the mammals of the Adirondacks (1884). In 1885, he became chief of the federal bureau that later became the U.S. Biological Survey. He gathered under him a staff of outstanding mammalogists that published numerous papers and books and greatly influenced the development of mammalogy in this century. Members of his team included Vernon Bailey, Albert K. Fisher, Edward A. Goldman, Ned Hollister, Arthur H. Howell, Hartley H. T. Jackson, W. L. McAtee, Edward W. Nelson, Wilfred Osgood, Theodore S. Palmer, and Edward A. Preble. Merriam sent collectors into the field, stimulated numerous studies of distribution of mammals, and initiated the *North American Fauna* series, which included the first comprehensive taxonomic studies of North American mammals. Six individuals within this group became presidents of the ASM, including the first president, Merriam himself (Layne and Hoffmann, 1994). Some of C. H. Merriam's underlings said C. H. stood for "Christ Himself."

Merriam produced nearly 500 publications, and he and his colleagues in the U.S. Biological Survey published numerous papers and books that were largely responsible for the growth and development of systematic mammalogy in North America in the late 1800s and early 1900s. It must be remembered, however, that these men generally were not associated with academic institutions and therefore had no means to train students except by example and apprenticeship.

## *II. The Agassiz/Glover Allen Group (Harvard)*

The Harvard group also originated before the formation of the ASM (Table 1, Section II), and traces back to Louis Agassiz at the Museum of Comparative Zoology at Harvard College. J. A. Allen (1838–1921), ornithologist and mammalogist, studied under Agassiz before moving to the American Museum of Natural History in 1895, as did another of the early notable mammalogists, Gerrit Smith Miller, Jr., who graduated from Harvard in the class of 1894. Miller first worked for the U.S. Biological Survey, but in 1898 moved to the U.S. National Museum where he remained until retirement in 1940. Agassiz was at the base of this academic line, but one of his students, Glover M. Allen, was Curator of Mammals at Harvard's Museum of Comparative Zoology and sponsored most of the early mammalogists from Harvard. Allen earned three degrees from Harvard, including his Ph.D. in 1904. Glover Allen produced some of the giants of our time—George A. Bartholomew, Jr., David E. Davis, Donald R. Griffin, Charles Lyman, and Oliver P. Pearson.

George Bartholomew was one of the most eminent physiological ecologists in this

Table 1.—*Academic genealogy of selected 20th century North American mammalogists.*

- I. C. Hart Merriam Group (U.S. Biological Survey, Washington)
  - C. Hart Merriam
    - Vernon Bailey
    - Albert K. Fisher
    - Edward A. Goldman
    - Ned Hollister
    - Arthur H. Howell
    - Hartley H. T. Jackson
    - W. L. McAtee
    - Edward W. Nelson
    - Wilfred Osgood
    - Theodore S. Palmer
    - Edward A. Preble
    - Stanley P. Young
- II. Harvard University (The Agassiz/Allen Group)
  - Louis Agassiz
    - Bryan Patterson
      - Craig C. Black
        - J. Sutton
        - Lloyd E. Logan
        - L. Kristalka
        - I. Johnson
    - Glover M. Allen
      - George A. Bartholomew, Jr.
        - Mark A. Chappell
        - William R. Dawson
          - Richard W. Hill
        - Alan R. French
        - Jack W. Hudson, Jr.
        - James G. Kenagy
        - Richard E. MacMillen
        - Daniel K. Odell
        - Thomas Poulson
          - Barbara H. Blake
        - Bruce Wunder
      - David E. Davis
        - John J. Christian
        - Edward N. Francq
          - Ronald E. Barry
        - Frank B. Golley
        - Rexford D. Lord
        - Jan O. Murie
        - Steven H. Vessey
      - Donald R. Griffin
        - Jack Bradbury
        - Katherine Ralls
      - Charles Lyman (Allen/Hisaw)
        - Richard W. Thorington, Jr. (Ernst Mayr)
      - Oliver Pearson (Allen/Hisaw)
        - Daniel H. Brant
        - Donald R. Breakey
        - Gilbert S. Greenwald
        - Stuart O. Landry
        - Bert S. Pfeiffer

Table 1.—*Continued.*

        - Harold Reynolds
      - Barbara Lawrence Scheville
    - J. A. Allen
  - Herbert W. Rand
    - Harold B. Hitchcock
- III. The Joseph Grinnell/E. Raymond Hall Group (Berkeley and the University of Kansas)
  - Joseph Grinnell
    - Seth Benson
      - Robert L. Rudd
        - Guy N. Cameron
      - Peter Schramm
      - Charles S. Thaeler
        - Enrique P. Lessa
      - Alan C. Ziegler (technically with W. B. Quay)
    - W. H. Burt
      - A. W. Frank Banfield
      - Fred S. Barkalow
      - Harold E. Broadbooks
      - Robert K. Enders (Burt was mentor but not advisor)
      - Lowell L. Getz
        - Joyce Hoffman
        - Donald H. Miller
      - Harvey L. Gunderson
      - Evan B. Hazard
      - Timothy E. Lawlor
      - Richard H. Manville (final examination chaired by Hooper)
      - Illar Muul
      - William O. Pruitt
      - Dana P. Snyder
        - Wendell E. Dodge
      - Andrew Starrett
    - Ian McTaggart Cowan
      - Joseph F. Bendell
        - Fred C. Zwickel
      - Walter A. Sheppe
    - William B. Davis
      - Dilford C. Carter
        - Patricia Dolan
        - Richard K. Laval
        - Donald A. McFarlane
        - Ronald H. Pine
        - Raul Valdez
      - Paul W. Parmalee
      - Randolph L. Peterson (Ph.D. with J. R. Dymond)
        - Charles S. Churcher
        - Judith L. Eger
        - M. Brock Fenton
          - Robert M. R. Barclay
          - Gary P. Bell
          - R. Mark Brigham
          - Joe E. Cebek

Table 1.—*Continued.*

- - - James H. Fullard
    - Robert M. Herd
  - C. G. Van Zyll de Jong
- Lee R. Dice
  - W. Frank Blair
    - David L. Jameson
    - Michael A. Mares
      - Ruben M. Barquez
      - Thomas E. Lacher, Jr.
      - Ricardo Ojeda
      - Michael R. Willig
    - W. Howard McCarley
    - Paul G. Pearson
    - Richard D. Sage
    - James R. Tamsitt
  - Wallace D. Dawson
  - Van T. Harris
  - Don W. Hayne
    - Paul C. Connor
  - B. Elizabeth Horner
  - Walter E. Howard
    - Daniel B. Fagre
  - John A. King
    - Lee C. Drickamer
    - C. Richard Terman
  - Harley B. Sherman
    - B. A. Barrington
    - Joseph C. Moore
    - Dale W. Rice
  - Arthur Svihla
- E. Raymond Hall
  - Ticul Alvarez-S. (Masters)
  - Sydney Anderson
  - Rollin H. Baker
    - Donald P. Christian
    - Peter L. Dalby
    - James M. Dietz
    - Gary A. Heidt
    - Gordon L. Kirkland, Jr.
    - John O. Matson
    - Alan E. Muchlinski
    - Howard J. Stains
  - M. D. Bryant
  - E. Lendell Cockrum
    - Robert J. Baker
      - John W. Bickham
        - Luis Ruedas
      - William J. Bleier
      - J. Hoyt Bowers
      - Robert D. Bradley
      - Ira F. Greenbaum
        - David Hale
        - Philip Sudman
      - Mike Haiduk
      - Meredith Hamilton
      - Rodney L. Honeycutt

Table 1.—*Continued.*

- - - - Craig S. Hood
      - David C. Kerridge
      - Rick McDaniel
      - Margaret A. O'Connell
      - Calvin A. Porter
      - Mazin B. Qumsiyeh
      - Lynn W. Robbins (actual advisor was Francis Rose)
      - Fred B. Stangl, Jr.
      - Ron Van Den Bussche
      - Terry L. Yates
        - Joseph A. Cook
        - Scott L. Gardner
        - Sarah George
        - Gregory D. Hartman
        - Laura L. Janacek
        - Dwight W. Moore
        - David Reducker
        - Brett R. Riddle
        - Robert M. Sullivan
    - Glen Bradley
    - Russell P. Davis
    - Bruce J. Hayward
    - Keith Justice
      - Peter L. Meserve
    - James D. Layne
    - C. Brian Robbins
  - Robert G. Schwab
- Charles L. Douglas
- Stephan D. Durrant
    - Richard M. Hansen
      - Donald R. Johnson
    - Keith R. Kelson
    - M. Raymond Lee
      - Fred Elder
      - Mark L. McKnight
      - William S. Modi
      - Earl G. Zimmerman
        - C. William Kilpatrick
        - John V. Planz
- James S. Findley
  - Kenneth W. Anderson
  - Hal L. Black
  - Michael A. Bogan
  - William Caire
  - Eugene D. Fleharty
  - Patricia W. Freeman
  - Kenneth N. Geluso
  - Anthony L. Gennaro
  - David J. Hafner
  - Arthur H. Harris
  - Clyde Jones
    - John F. Pagels (co-chairs were Negus and Jones)
  - Karen E. Petersen
  - Daniel F. Williams

TABLE 1.—*Continued.*

  - Don E. Wilson
- Robert B. Finley
- Donald F. Hoffmeister
  - Wayne H. Davis
  - Luis de la Torre
  - Victor E. Diersing
  - L. Scott Ellis
  - John S. Hall
  - W. Z. Lidicker, Jr.
    - Blair A. Csuti
    - K. T. DeLong
    - Ayesha E. Gill
    - Edward J. Heske
    - David T. Krohne
    - William F. Laurance
    - Richard S. Ostfeld
    - David O. Ribble
    - Jeffy O. Wolff
  - Charles A. McLaughlin
  - Iyad A. Nader
  - David J. Schmidly
    - Paisley S. Cato (co-chaired with Clyde Jones)
    - James N. Derr (co-chaired with John Bickham)
    - Robert C. Dowler (co-chaired with John Bickham)
    - Mark D. Engstrom
    - James G. Owen
    - Stephen A. Smith (co-chaired with Ira Greenbaum)
  - William D. Severinghaus
  - H. Duane Smith
  - Richard G. Van Gelder
  - David B. Wright
  - Robert E. Wrigley
- J. Knox Jones, Jr.
  - David M. Armstrong
    - Kathleen A. Scott Fagerstone
    - James C. Halfpenny
    - Joseph F. Merritt (actual advisor was Olwen Williams)
  - Elmer C. Birney
    - Richard Lampe
    - Lynn L. Rogers
    - Robert M. Timm (actual advisor was Roger Price)
  - John B. Bowles
  - Alberto A. Cadena
  - Jerry R. Choate
  - Larry L. Choate
  - G. Lawrence Forman
  - Hugh H. Genoways
  - Robert R. Hollander
  - Thomas H. Kunz
    - Edythe L. P. Anthony

TABLE 1.—*Continued.*

      - Peter V. August
      - Martha S. Fugita
      - Allen Kurta
    - Richard W. Manning
    - Carleton J. Phillips
    - Ronald W. Turner
    - James Dale Smith
  - Philip L. Krutzsch
  - Charles A. Long
  - George H. Lowery, Jr.
    - Walter W. Dalquest
    - Alfred L. Gardner
  - Ronald M. Nowak
  - Robert L. Packard
    - Robert E. Martin
  - Robert J. Russell
  - Henry W. Setzer
    - Duane A. Schlitter (actual advisor was Richard Highton, a herpetologist)
  - Terry A. Vaughan
    - Cindy Rebar
    - O. J. Reichman
  - Bernardo Villa-R. (Masters with Hall, Ph.D. from Univ. Mexico)
    - Jose Ramirez Pulido
  - John A. White
- John Eric Hill
- Emmet T. Hooper
  - James H. Brown
    - Michael A. Bowers
    - Gerardo Ceballos
    - James C. Munger
    - Andrew T. Smith
  - Michael D. Carleton
  - Theodore H. Fleming
  - Charles O. Handley, Jr.
  - David G. Huckaby
  - David Klingener
  - James A. Lackey
  - Guy G. Musser
  - Albert Schwartz
- David H. Johnson
- A. Remington Kellogg (actual chair was William D. Mathew)
- Jean M. Linsdale
  - Quentin P. Tomich
- Alden H. Miller (ornithologist)
  - Richard F. Johnston (ornithologist)
    - Gary Schnell (ornithologist)
      - Troy L. Best
      - Janet K. Braun
      - Ronald K. Chesser
      - E. Gus Gothran
      - Michael L. Kennedy
        - George D. Baumgardner
        - Floyd W. Weckerly

Table 1.—*Continued.*

- Robert D. Owen
- Carl B. Koford
- A. Starker Leopold
  - Joseph G. Hall
  - William J. Hamilton III
  - Robert S. Hoffmann
    - Fernando A. Cervantes-Reza
    - Lawrence R. Heaney
    - Donald L. Pattie
    - Barbara R. Stein
    - Merlin D. Tuttle
    - John E. Warnock
    - W. Christopher Wozencraft
  - John H. Kaufmann
    - Frank J. Bonaccorso
  - Richard R. Lechleitner
- Frank A. Pitelka
  - George O. Batzli
    - Russell F. Cole
    - Elizabeth A. Desy
    - Richard Lindroth
  - Stephen D. West
- Charles A. Reed
  - Emily C. Oaks
- J. Mary Taylor
  - Barry Thomas
  - Marla L. Weston

Robert T. Orr

Tracy I. Storer (actual chair was Charles A. Kofoid)

Walter P. Taylor
- Bryan P. Glass
  - Stephen R. Humphrey
    - Hector T. Arita
    - Jacqueline Belwood
  - Ralph Kirkpatrick

Frederick H. Test

IV. The Hamilton Group (Cornell University)

William J. Hamilton, Jr.
- Roger W. Barbour
  - Michael J. Harvey
  - Marion Hassell
- Allen V. Benton
- Arthur H. Cook
- Robert A. Eadie
  - Kyle R. Barbehenn
  - Richard W. Dapson
  - Harold G. Klein
- Jack W. Gottschang
- Everett W. Jameson
  - Duncan Cameron, Jr.
  - John D. Phillips, Jr.
- James N. Layne
  - Harrison Ambrose
    - William Platt
  - Andrew A. Arata
    - Dan W. Walton
  - Dale E. Birkenholz
  - Llewellyn M. Ehrhart
  - James V. Griffo
  - John McManus
  - Elizabeth S. Wing
  - William O. Wirtz
  - James L. Wolfe
    - Robert J. Esher
- John G. New
- William G. Sheldon
- William Werner
- John O. Whitaker, Jr.
  - Wynn W. Cudmore
  - Thomas W. French
  - Gwilym S. Jones
    - Howard H. Thomas
  - David Pistole
  - Steven J. Ropski

From Professors in Related Fields

Ecology

- Marston Bates
  - John W. Twente
- Arthur D. Hasler
  - Kenneth B. Armitage
    - Orlando A. Schwartz
- Charles Elton
  - Dennis Chitty
    - Rudy Boonstra
    - Charles J. Krebs
      - Michael S. Gaines
        - Leroy R. McClenaghan
        - Robert K. Rose
      - Barry L. Keller
      - Robert H. Tamarin
        - Steven R. Pugh
  - Francis C. Evans
    - Lee H. Metzgar
    - Stanley C. Wecker
  - Richard R. Miller
- John T. Emlen
  - Garrett C. Clough
  - William A. Fuller
- Evelyn Hutchinson
  - Donald Livingston
    - Peter D. Weigl
  - Robert H. MacArthur
    - M. L. Rosenzweig
      - Joel S. Brown
      - Burt P. Kotler
      - Cliff Lemon
      - Gene D. Schroder
- John C. Neese
  - Tim W. Clark

Table 1.—*Continued.*

- Eugene Odum
  - W. Wilson Baker
  - Gary W. Barrett
    - Richard S. Mills
  - Reed Fantin
    - Clyde L. Pritchett
- William Prychodko
  - Mary Etta Hight
- William Reeder
  - Frank A. Iwen
- Victor Shelford
  - S. Charles Kendeigh
    - Robert M. Chew
    - John A. Sealander, Jr.
      - Donald W. Davis
      - Philip S. Gipson
    - Dana Snyder
    - Ralph Wetzel
      - Robert L. Martin

Genetics

- Peter Brussard (ecological genetics)
  - Gary F. McCracken
  - Robert Lacey
- Theodosius Dobzhansky
  - Karl F. Koopman
- W. B. Heed
  - James L. Patton
    - John C. Hafner
    - Mark Hafner
    - Philip Myers
      - G. K. Creighton
      - Robert Voss
    - Duke S. Rogers
    - Margaret F. Smith
    - Donald O. Straney
      - A. Christopher Carmichael

Ethology

- M. W. Fox
  - Marc Bekoff
    - Joel Berger
- Peter Marler
  - John F. Eisenberg
    - Cheri Jones
    - John G. Robinson
    - R. Rudran
    - Nicholas C. Smythe
    - C. Wenimer
- Franz Sauer
  - Michael H. Smith
    - Mark C. Belk
    - Donald W. Kaufman
    - Paul L. Leberg

Table 1.—*Continued.*

      - Susan McAlpine
      - Paul R. Ramsey
      - Kim T. Scribner

Wildlife/Conservation

- Aldo Leopold
  - James R. Beer
    - Charles F. MacLeod
  - Charles M. Kirkpatrick
    - Thomas W. Hoekstra
    - Russell E. Mumford
      - Virgil Brack, Jr.
      - David A. Easterla
    - Harmon P. Weeks
- William H. Marshall
  - John R. Tester
    - Donald B. Siniff
      - Douglas P. DeMaster
      - J. Ward Testa
      - Jeannette A. Thomas
- Robert A. McCabe
  - Lloyd B. Keith
- Thomas A. Scott/Edward Kozicky
  - Willard D. Klimstra
    - B. J. Verts
      - Leslie N. Carraway (actual advisor was Charles Warren)
      - Joseph A. Chapman
        - Kenneth L. Cramer
      - George A. Feldhamer

Entomology & Parasitology

- H. S. Fitch/Joseph Camin
  - Richard B. Loomis
- Cluff Hopla
  - Donald Gettinger (co-chaired with Michael A. Mares)
- Adrian Marshall
  - Donald W. Thomas

Anatomy/Physiology

- Howard Adelmann
  - William A. Wimsatt
  - Roy Horst
  - Alvar W. Gustafson
  - Gary G. Kwiecinski
- William J. McCauley
  - Henry Mitchell
  - G. Clay Mitchell
  - Eugene H. Studier
- Roland K. Meyer (endocrinologist)
  - William H. Elder
    - Richard F. Myers
  - Phillip L. Wright
    - Clinton H. Conaway

TABLE 1.—*Continued.*

- Larry N. Brown
- Milo E. Richmond
  - Frederick J. Jannet
  - John P. Hayes
- Rodney A. Mead

- Andrew V. Nalbandov (Univ. Ill., animal science)
  - Glen C. Sanderson
- Alfred C. Redfield (Harvard, physiology)
  - Peter R. Morrison
    - Brian K. McNab

Herpetology

- Robert Stebbins
  - Paul K. Anderson

Ornithology

- Arthur A. Allen
  - Ralph S. Palmer
- Eugene Dustman
  - Norman Negus
    - Pat Berger
    - Robert K. Chipman
    - Jack A. Cranford
      - Alicia T. Linzey
    - Edwin Gould
    - John F. Pagels (co-chaired with Clyde Jones)
    - Aelita S. Pinter
    - Carol N. Rowsemitt
    - Thomas E. Tomasi
- Miles Pirnie
  - Durwood L. Allen
    - Frederick F. Knowlton
      - Charles E. Harris
    - L. David Mech
      - Michael E. Nelson
    - Rolf O. Peterson
- Fred A. Ryser, Jr.
  - John R. Gustafson
- Herbert W. Rand
  - Harold W. Hitchcock

Miscellaneous

- William King Gregory (palaeontologist)
  - Albert E. Wood
- Bjorn Kurten (palaeontologist)
  - Phillip M. Youngman
- William F. Porter
  - Paul F. Steblein
- S. David Webb (palaeontologist)
  - Kenneth T. Wilkins

Training in Other Professions

Physicians

- H. Allen
- Elliot Coues
- Murray L. Johnson

TABLE 1.—*Continued.*

- Marcus Ward Lyon, Jr.
- Edgar A. Mearns
- C. Hart Merriam
- George Wislocki

Veterinarians

- Denny J. Constantine

Training in Museum or Field, No Ph.D.

- Rudolph M. Anderson
- Harold E. Anthony
- Benjamin P. Bole, Jr.
- Philip M. Blossom
- Victor Cahalane
- T. Donald Carter
- J. Kenneth Doutt
- Alfred J. Godin
- George F. Goodwin
- Arthur M. Greenhall
- Philip Hershkowitz
- A. Brazier Howell
- Laurence M. Huey
- Carl W. Kenyon
- Thomas J. McIntyre
- Gerrit S. Miller, Jr.
- John Paradiso
- Victor B. Scheffer
- Ernest Thompson Seton
- Albert R. Shadle
- Viola S. Shantz
- G. H. H. Tate
- Lloyd P. Tevis
- Hobart M. Van Deusen
- Ernest P. Walker

country and trained a number of students at UCLA. Davis and Lyman have been extremely influential in studies of hibernation: Davis at Penn State and North Carolina State; Lyman at Harvard. Griffin has had immense effect on studies of bat echolocation and behavior from positions at Harvard, Cornell, and Rockefeller University. Oliver Pearson of Berkeley is an ecological physiologist, well known for his work with poison glands of shrews, mammalian reproduction, and ecology and systematics of South American mammals. Pearson, like William J. Hamilton, Jr., was greatly influenced by Francis Harper. Harper had earlier been a high school teacher, but was editing for the American Philosophical Society and frequently used the library at the Philadelphia Academy of Science. Oliver Pearson used the library in conjunction with his work for Robert Enders and thereby came in contact with Harper, who had obtained his Ph.D. from Cornell in 1925 with the herpetologist, Albert Hazen Wright. All five of these Glover Allen-progeny have now produced academic offspring of their own. The influence of Harvard on the development of North American mammalogy cannot be overestimated.

### *III. The Joseph Grinnell/ E. R. Hall Group (Berkeley and Kansas)*

Early in this century, another intellectual dynasty was born on the West Coast, at Berkeley (Table 1, Section III). It was fostered by Annie Montague Alexander, who played an outstanding role in the development of mammalogy at Berkeley (H. Grinnell, 1958). She was the founder and a lifelong patron of the Museum of Vertebrate Zoology at Berkeley. She early developed a love for travel, hunting, and the natural sciences. Alexander also befriended C. Hart Merriam, and collected or purchased many of the bears that were studied by him; she supported and led three collecting expeditions to Alaska (1906, 1907, and 1908).

Alexander had thought for some time about establishing a museum at the University of California. When she returned from Alaska in the autumn of 1906 she began serious discussions with Merriam about this. She had come to realize how fast the native game birds and mammals of the west were disappearing and felt specimens (including skeletons) should be preserved, as was happening in the east. At this time she happened to meet Joseph Grinnell, and was impressed with his "energy and enthusiasm and the neat and scholarly way in which his records were kept." She mentally noted him as a possible coworker.

Upon returning from her 1907 Alaska expedition, Alexander presented her plan for the establishment of a museum of vertebrate zoology at The University of California to President Benjamin Wheeler. The regents accepted her plan and a contract establishing the museum was signed on 23 March 1908, with Joseph Grinnell appointed as its director for 1 year.

Many letters were exchanged between Alexander and Grinnell in order to ensure the greatest possible usefulness for the museum. Alexander preferred that young biologists be enlisted, "men with their accomplishments ahead of, rather than behind them," and that the time of staff members should be divided between curatorial, field, and research work. There was effort to obtain balance between specimens for research and for display in order to kindle popular interest in natural history. Alexander contributed monthly sums from 1908 to 1919, then she presented $200,000, plus another $225,000 in 1936, as perpetual endowments. However, she also gave many smaller amounts through the years until her death, and contributed hundreds of specimens collected by herself and her lifelong friend, Louise Kellogg.

The University of California wanted Grinnell to teach freshman Zoology, but Alexander objected. She wanted his time spent on research and development of the museum. However, Grinnell did become editor of the *Condor* in 1908 and continued in this position until his death in 1939. Headquartering the *Condor* at Berkeley provided practice in editing to numerous students.

Joseph Grinnell was born in 1877 in the Indian Territory, about 40 miles from Ft. Sill, in present-day Oklahoma. His family settled in California after his father's retirement. Grinnell earned the bachelor's degree from Throop Polytechnic Institute, which eventually became the California Institute of Technology, in 1897. He earned the M.A. and Ph.D. degrees from Leland Stanford, Jr., College in 1901 and 1913. This institution was named for its benefactor, Leland Stanford, Jr., and later became Stanford University. His major professor or at least one of them was Charles Henry Gilbert (Hall, 1939). Grinnell taught at Throop Polytechnic for a time before becoming Director of the Museum of Vertebrate Zoology in 1908. He held this post for 30 years, until shortly before his death at 62 in 1939. Grinnell had styled himself after C. Hart Merriam; thus the roots of the Grinnell Dynasty go back partly to Merriam. However, the roots also reached back to another giant in vertebrate zoology of the time, David Starr Jordan. Jordan was primarily an ichthyologist, but had broad interests in other vertebrates as well. Jordan did his undergraduate work at Cornell, where it is said that he camped out on campus. He earned an M.D. at Indiana Medical College in 1875, and a Ph.D. from Butler University (Indianapolis) in 1878. Jordan was President of Indiana University from 1885 to 1891, and in 1891 he became the first President of Leland Stanford, Jr., College.

Grinnell was an excellent mammalogist and ornithologist, and an expert on birds and mammals of the West Coast, especially California. He was very shy, but an energetic worker in the field. His shyness manifested itself, for example, in instinctively placing his own hand behind his back when a newcomer offered to shake it. He was an excellent scientist, editor, and museum curator. Emmet T. Hooper, one of Grinnell's students, said that Grinnell would drive on trips into the field and would point out interesting geological, vegetative, or faunal features. On the return trip, however, he would let a student drive while he sat in the back, in order to work up his field notes and even start work on the papers to be published from the specimens and data obtained.

During his tenure at Berkeley, Grinnell advised numerous graduate students in ornithology and mammalogy, and also some in herpetology, but not all were his students in the strict sense that he was their major advisor. Charles A. Kofoid also played a major role in the education of many Berkeley graduate students. Berkeley students fanned out over the land; they have played a major role in systematic mammalogy, and in vertebrate zoology as a whole throughout the world. Some of Grinnell's better known students, not all of whom he directed to the doctoral degree, were the following (Table 1, Section III).

Seth Benson and Alden H. Miller (Berkeley)
William H. Burt, Lee R. Dice, Emmet T. Hooper, and Fred R. Test (University of Michigan)
Ian McTaggart Cowan (University of British Columbia)
William B. Davis and Walter P. Taylor (Texas A&M University)
E. Raymond Hall (Berkeley and University of Kansas)
John Eric Hill (American Museum of Natural History)
David H. Johnson and Remington Kellogg (U.S. National Museum)
Jean M. Linsdale (Hastings Natural History Reservation)
Robert T. Orr (California Academy of Science)
Tracy I. Storer (University of California at Davis)

Burt, Davis, Hall, Hooper, Kellogg, Orr, Storer, and Taylor each served as President of the ASM. Cowan served as Vice President. Many members of this group established centers of learning of their own, from which additional students were trained, but others were in positions where having students was not an option. Some of the centers of learning and many of Grinnell's progeny are discussed below.

*Berkeley.*—Alden Miller was an ornithologist on the staff at Berkeley and became director of the Museum following Grinnell's death. He and Seth Benson, another Grinnell student, were much involved in the training of students in mammalogy at Berkeley. Today the fine tradition of mammalogy at Berkeley is continued by Oliver Pearson (a Harvard product), William Z. Lidicker, Jr. (a Grinnell "grandson"), and James L. Patton (the incumbent ASM president). Patton studied under W. B. Heed, a geneticist, at the University of Arizona.

*University of Michigan.*—Four of Grinnell's students, William H. Burt, Lee R. Dice, Emmet T. Hooper, and Fred H. Test, joined the staff at the University of Michigan, thus creating a major center for mammalogical training there. Burt sponsored a number of students, including A. W. Frank Banfield, Fred S. Barkalow, Lowell L. Getz, Timothy E. Lawlor, Richard H. Manville, and Illar Muhl. Students of Lee R. Dice included W. Frank Blair, Wallace Dawson, Don W. Hayne, B. Elizabeth Horner, and John A. King. Students of Emmet Hooper included James H. Brown, Michael D. Carleton, Theodore H. Fleming, Charles O. Handley, Jr., David Klingener, Guy G. Musser, and Albert Schwartz. Robert K. Enders deserves special note as he obtained his degree at Michigan, and then taught at Swarthmore where he was one of the great inspirational teachers. From Swarthmore he inspired David E. Davis, Philip Myers, and Oliver Pearson to enter the field.

*University of British Columbia.*—Ian McTaggart Cowan, born in Scotland, established his career at the University of British Columbia. Dennis Chitty, a student of Charles Elton (Oxford), and Cowan trained Charles Krebs, formerly of Indiana University and now also of UBC. Krebs students include Michael Gaines, Barry Keller, and Robert Tamarin. J. Mary Taylor was also at UBC for many years.

*Texas A&M University.*—At Texas A&M, a program developed under the leadership of William B. Davis and Walter P. Taylor, both Grinnell students. Some of Davis's most notable students were Dilford Carter, Bryan P. Glass (Oklahoma State University), and Randolph Peterson (Royal Ontario Museum at Toronto). Peterson's students included C. G. Van Zyll de Jong, Judith Eger, and Brock Fenton. Fenton has established an excellent program in chiropteran biology at York University, York, Ontario. Dilford Carter returned to curate the mammal collection at Texas A&M, then moved to Texas Tech University. David Schmidly, a student of Donald F. Hoffmeister at Illinois, now serves as Curator of Mammals at Texas A&M.

*University of Kansas.*—An outstanding program arising from the Grinnell dynasty was begun by E. Raymond Hall at the University of Kansas. The Grinnell contingent of mammalogists would not be nearly as spectacular if it were not for Hall; thus it appears best to title this the Grinnell/Hall dynasty rather than simply the Grinnell dynasty. Hall earlier spent 15 years at Berkeley, where he advised some students of Grinnell after Grinnell's death. Hall's first Ph.D. students were trained at Berkeley as well. Hall produced a large number of students, many of whom started programs at other institutions. To date, five of Hall's academic "sons" (Anderson, Durrant, Findley, Hoffmeister, and Jones) and six of his "grandsons" (Birney, Brown, Genoways, Lidicker, Van Gelder, and Wilson) have served as President of the ASM. Most of Hall's students are indicated in Table 1, but those who established major Ph.D. programs in their own right are:

Rollin H. Baker, first at Kansas and later at Michigan State
E. Lendell Cockrum at Arizona
Stephen D. Durrant at Utah
James S. Findley at New Mexico
Donald F. Hoffmeister at Illinois
J. Knox Jones, Jr., first at Kansas then at Texas Tech
George H. Lowery at Louisiana State
Terry A. Vaughan at Northern Arizona

Rollin Baker, a student of Hall's, and John King, a student of Dice's, thus both "grandsons" of Grinnell, trained a large number of students at Michigan State, including Donald P. Christian, Gary A. Heidt, and Gordon L. Kirkland, Jr. Mammalogy continues at Michigan State today under the leadership of Donald O. Straney and Richard W. Hill.

From Cockrum's program at Arizona came Robert J. Baker, who has established a major research program at Texas Tech, where he has trained a number of students, including John W. Bickham, Ira F. Greenbaum, Rodney L. Honeycutt, and Terry L. Yates.

At Utah, Stephen Durrant sponsored Richard M. Hansen, Keith R. Kelson, and M. Raymond Lee. Lee in turn sponsored Earl G. Zimmerman at the University of Illinois. An interesting sidelight related by Kelson is that Durrant, although a senior professor, had not yet finished his work on a doctorate at Kansas under Raymond Hall when he presided at Kelson's Ph.D. final. A year later, Durrant came to Kansas for his final oral defense of the Ph.D. thesis and was examined by Kelson.

Another major program arose under the tutelage of James S. Findley at the University of New Mexico. Some of Findley's outstanding students are Michael A. Bogan, William Caire, Eugene D. Fleharty, Patricia (Trish) Freeman, Arthur H. Harris, Clyde Jones, Daniel F. Williams, and Don E. Wilson. Findley was subsequently joined at New Mexico by J. Scott Altenbach, Terry L. Yates, and James H. Brown, all Grinnell descendants.

At least four faculty members associated directly or indirectly with Grinnell produced outstanding students at the University of Illinois. Faculty members were Donald H. Hoffmeister, M. Raymond Lee, George O. Batzli, and Lowell L. Getz along with ecologist S. Charles Kendeigh, a student of Victor Shelford. Some of the students of Hoffmeister are Wayne H. Davis (University of Kentucky), John S. Hall (Albright College), William Z. Lidicker, Jr. (Berkeley), David J. Schmidly (Texas A&M), H. Duane Smith (Brigham Young), and R. G. Van Gelder (American Museum). Mark L. McKnight (U.C. Davis) and Earl G. Zimmermann (North Texas State University) were students of Lee. Richard Lindroth (University of Wisconsin) was a student of Batzli, Joyce Hoffman (Illinois Natural History Survey) was a student of Getz, and Dana Snyder (University of Massachusetts) and Ralph Wetzel (University of Connecticut) were students of Kendeigh.

One of Hall's most productive students, J. Knox Jones, Jr., trained many fine students, first at Kansas, then at Texas Tech University, where he became Dean of the Graduate School and Vice President for Research. A team of six mammalogists on the faculty was assembled at Texas Tech, each with a Ph.D. from a different university—Arizona (Robert J. Baker), Texas A&M (Dilford C. Carter), Kansas (J. Knox Jones, Jr.), New Mexico (Clyde Jones), Oklahoma (first Ronald K. Chesser and currently Robert D. Owen), and Pittsburgh (Michael R. Willig). All are academic descendants of Joseph Grinnell.

Some of Jones' most accomplished students are David M. Armstrong (University of Colorado), Elmer C. Birney (University of Minnesota), Jerry R. Choate (Fort Hays State University, Hays, Kansas), Hugh H. Genoways (Carnegie Museum and University of Nebraska), Thomas H. Kunz (Boston University), Carleton J. Phillips (Hofstra University and Illinois State University), and James D. Smith (Fullerton State University, California). Some of Jones' notable academic grandsons are Joseph F. Merritt whose mentor was Armstrong (officially Olwen Williams), Robert M. Timm with Birney (officially Roger Price, an entomologist), and Edyth Anthony and Allen Kurta with Kunz. At Kansas, Hall was replaced by Robert S. Hoffmann, and subsequently Jones and Hoffmann were followed by Robert M. Timm and Norman R. Slade. Kenneth B. Armitage and Michael H. Gaines also have advised many students at Kansas as that center continues to train mammalogists.

The major centers of mammalogical instruction established by the first two generations of Grinnell students are indicated in Fig. 1. Four major centers of learning were established by Grinnell's first generation students at British Columbia, Kansas,

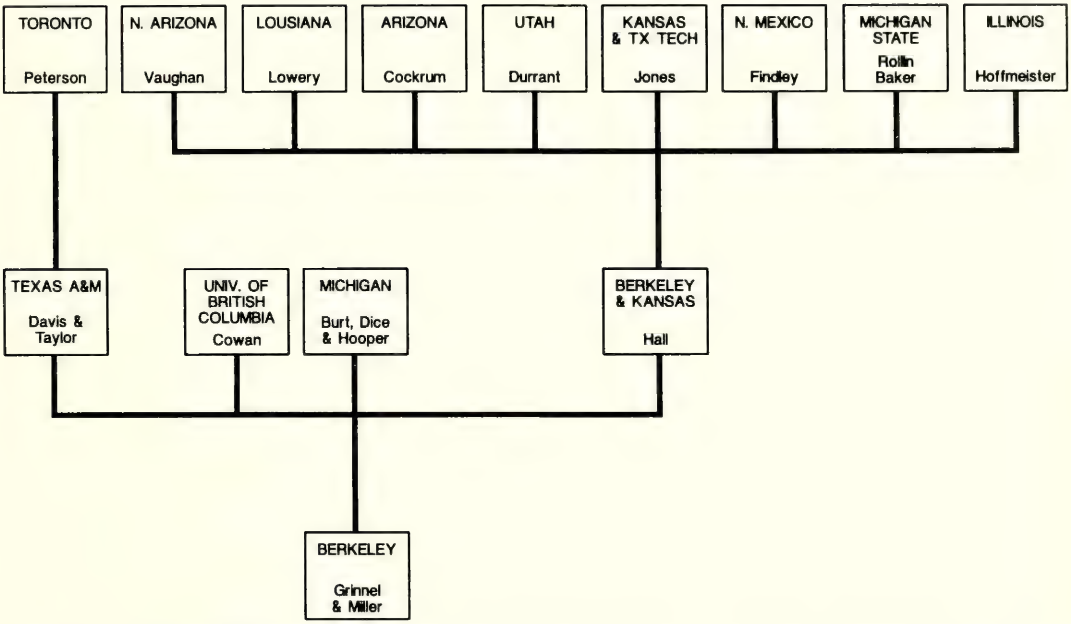



FIG. 1.—Outline of the main branches of the Grinnell Academic tree through the second generation students.

Michigan, and Texas A&M, whereas nine were established by the second generation, most through E. Raymond Hall at Kansas.

Other particularly successful students of Hall were Sydney Anderson at the American Museum of Natural History, R. M. Nowak with the U.S. Fish and Wildlife Service, Henry W. Setzer who retired from the Smithsonian, and Terry A. Vaughan who for many years was at the University of Northern Arizona. Ticul Alvarez and Bernardo Villa-R. obtained the Masters degree with Hall, but have provided the backbone of mammalogy in Mexico. Villa-R. eventually obtained the Ph.D. at the University of Mexico.

There are many other academic relatives whose Grinnellian attachments are not as obvious, but are nonetheless very real. For example, Robert S. Hoffmann, now at the Smithsonian Institution, is a "great-grandson." His major professor at Berkeley was A. S. Leopold, who started working with Grinnell but finished with Alden H. Miller after Grinnell's death. However, Miller's advisor was Grinnell! An academic program has developed at Oklahoma with Gary D. Schnell and has produced Ronald K. Chesser, Troy L. Best, Janet K. Braun, Michael L. Kennedy, and Robert D. Owen. Schnell's Ph.D. is from Kansas, with Richard F. Johnston, an ornithologist, serving as mentor. However, Johnston's Ph.D. is from Berkeley and his major professor was Grinnell's "son" Miller. Michael A. Mares at Oklahoma studied under W. F. Blair at Texas, whose doctorate was completed under L. R. Dice at Michigan. Grinnell was Dice's mentor, although not his major advisor, at Berkeley.

Several Grinnellites are currently at the U.S. National Museum of Natural History or with the Fish and Wildlife Service in Washington, D.C. They include Michael D. Carleton, Alfred L. Gardner, Charles O. Handley, Jr., Robert S. Hoffmann, Ronald M. Nowak, and Don E. Wilson.

In Mexico, the principals in the growth of systematic mammalogy were Ticul Alvarez and Bernardo Villa-R. Both earned their masters degrees at Kansas while studying with Hall. In Canada, Ian McTaggart Cowan and Donald L. Pattie in the west and, in the east, A. W. Frank Banfield, Randolph L. Peterson, M. Brock Fenton, and Robert E. Wrigley are all Grinnell descendants.

The Grinnell group has had tremendous impact on the ASM. Grinnell himself served as president in 1937–1938. Since 1940, when Walter P. Taylor was elected the 12th president, only three of the presidents in the succeeding 52 years—E. A. Goldman, W. J. Hamilton, Jr., and Hamilton's academic "son" James N. Layne—are academically unrelated to Joseph Grinnell.

Every recording secretary since 1938 has been a Grinnellite, as have all but three editors of the *Journal of Mammalogy* since 1941, including one unbroken string for the past 27 years.

## *IV. The William J. Hamilton, Jr., Group (Cornell)*

The other large and important North American dynasty in mammalogy is that of William J. Hamilton, Jr., at Cornell University (Table 1, Section IV). While the Grinnellian dynasty centered around systematic mammalogy, the Hamiltonian dynasty centered around mammalian ecology and natural history.

Hamilton received his B.S., M.S., and Ph.D. degrees in vertebrate zoology from Cornell University under A. H. Wright, apparently with much "unofficial" guidance from Francis Harper. Francis Harper was a teacher in a Long Island school class when Hamilton was reportedly "cutting up." Harper asked Hamilton what bird he was holding and Hamilton correctly identified it as an immature female rose-breasted grosbeak. That brought Hamilton and Harper into lifelong friendship. Hamilton's interests were in life history and ecology of vertebrates, with specialties in food habits, reproduction, and to some degree, parasites. He believed in obtaining as much information as possible from all animals sacrificed, and in working with the commonplace rather than always with the exotics. In that way one could better obtain adequate data to make generalizations. He passed these interests and philosophies on to his students.

James N. Layne, who taught at the University of Florida, and at Cornell, and is now at Archbold Biological Station, Lake Placid, Florida, was an academic "son" of Hamilton's. He has done much work on reproduction and development of mammals. This tradition has also been carried on by Harrison Ambrose and Andrew A. Arata, both academic "sons" of Layne. Also, Layne has had a longtime interest in parasites, especially fleas. Some other students of Layne who worked with ecology and behavior of mammals are James V. Griffo, Elizabeth Wing, Llewellyn Ehrhart, Dale Birkenholz, John McManus, and James Wolfe. Wolfe is now Dean of Graduate Studies, Emporia State University in Kansas, after several years as Executive Director of the Archbold Biological Station. Wolfe has produced "offspring" of his own, including Robert J. Esher, currently at Mississippi State University. James V. Griffo is at Fairleigh Dickinson University, and Birkenholz is at Illinois State University. Wing is presently Curator of Zooarcheology, Florida Museum of Natural History. William Platt started a Ph.D. with Layne at Cornell, but finished with Harrison Ambrose when Layne moved from Cornell to the Archbold Biological Station. Dan W. Walton, a student of Andrew Arata, is presently with the Australian Biological Resources Study, and is an editor of, and contributor to, the recently published mammal tome of the Fauna of Australia series. John McManus died a few years after he received his Ph.D., but was extremely productive while at Fairleigh Dickinson University.

Everett W. (Bill) Jameson, Jr., has carried on the tradition of parasite work far beyond his graduate student days with Hamilton where this interest began. Jameson is well known among parasitologists for his work on fleas and mites. Two of his "sons" are John Phillips, a Research Biologist at the San Diego Zoological Society; and Duncan Cameron, at York University near Toronto. Allen H. Benton, now retired from the New York State University at Fredonia, is another of the Hamilton students who became interested in parasites, greatly furthering our knowledge of fleas.

Roger Barbour carried on the tradition of studies in vertebrate natural history. For many years, Barbour was at the University of Kentucky, where he and Wayne Davis teamed up to teach, train students, and do research. Davis is a student of Donald Hoffmeister and therefore also a descendant of the Grinnellian dynasty. Michael J. Harvey, an academic "grandson" of Hamilton, is presently department head at Tennessee Tech University. Another is Marion D. Hassell, who taught at Murray State University until his recent death. Harrison Ambrose and Jim Griffo were undergraduate students inspired by Roger Barbour.

John O. Whitaker, Jr., was Hamilton's last student in mammalogy. He took a position at Indiana State University, which became a satellite for continuing studies of food habits of vertebrates and ectoparasites of mammals in the Hamiltonian tradition. He teamed up with a Grinnellian student trained by Burt, Russell E. Mumford, for long-term studies on the mammals of Indiana. Some of his students, the academic grandchildren of Hamilton, are now making their mark. Gwilym S. Jones (who took his master's degree with Mumford) has established a center for vertebrate studies at Northeastern University in Boston. Thomas W. French is Assistant Director of the Massachusetts Department of Fish and Game. David Pistole is on the staff at Indiana University, Indiana, Pennsylvania.

Robert W. Eadie, long associated with Hamilton at Cornell, had several students, including Kyle Barbehenn (EPA, Washington), Richard W. Dapson (now in private industry), and Harold Klein (Plattsburg, NY).

For many years, Jack W. Gottschang, a Ph.D. under Hamilton, has been at the University of Cincinnati, where he chaired the Department of Biology and taught many students in the Hamiltonian tradition.

And last, but not least, there is W. J. Hamilton III. "Young Bill" took his Ph.D. at Berkeley with Grinnell's "son" Alden Miller, and is now at the University of California, Davis. He has worked with behavior of primates, birds, and insects, and on growth and development of the red tree mouse. Early in his career, he worked on bird migration with Franz Sauer.

Hamilton did not restrict his work to mammals, and likewise, many of his academic descendants do not. Several have worked with parasites, notably Benton, Jameson, Layne, and Whitaker. Whitaker has also worked with herptiles and fish, and Layne with birds and herptiles. Ralph Yerger (Florida State University) and Margaret Stewart (State University of New York at Albany) are two of Hamilton's students who work primarily with fish and herps, respectively.

There are of course crossings of lines, and much inspiration at the undergraduate level. Recording this type of contribution would be endless, but a few notable examples follow. Bill Jameson was a student of Hall's at Kansas before going to Cornell. George Bartholomew got his M.A. with Alden Miller at Berkeley before going to Harvard. Robert K. Enders inspired David E. Davis, Oliver Pearson, and Philip Myers to pursue further studies. Jerry R. Choate at Fort Hays State University has inspired numerous students in mammalian systematics. Jerry has produced 32 master's students, at least 24 of whom have earned or are candidates for the Ph.D. These include Mark D. Engstrom, Sarah B. George, Cheri A. Jones, Nancy D. Moncrief, Philip D. Sudman, Michael P. Moulton, Lynn W. Robbins, Jerry W. Dragoo, and Brett R. Riddle. James B. Cope (Earlham College, Richmond, Indiana) is another of the outstanding undergraduate teachers. He was originally inspired as an undergraduate student by Bill Hamilton and went on to teach at Earlham college at Richmond, Indiana. Earlham has no graduate program, but the influence on bat biology exerted through Cope and his students is considerable. Some of Cope's undergraduate students at Earlham were Richard F. Myers (who influenced Thomas H. Kunz at the undergraduate level), Wilson Baker, Nixon Wilson, Anthony F. DeBlase, Steven R. Humphrey, Charles Thaeler, and Richard Mills.

Of course there has been continuous exchange between the Hamilton and Grinnell/Hall schools. Some outstanding workers that were influenced by Hamilton as undergraduates at Cornell, then went on to study under Grinnellian descendants are William Z. Lidicker, James H. Brown, Norman O. Negus, and Edwin Gould. E. W. Jameson started in the Grinnell school and did his Ph.D. with Hamilton. Earl G. Zimmerman, an eventual Grinnellite, began his productive career while working as an undergraduate student (and publishing his first paper) with Whitaker at Indiana State.

## *V. Other Groups*

There are a few other centers of learning that have produced students in the field of mammalogy. These tend to be smaller, but have made many excellent contributions to the field.

*Florida.*—A group of biologists has come together in recent years at the University of Florida, and Florida now can be thought of as a center for training mammalogists. Steven Humphrey (a student of Bryan Glass at Oklahoma State University), John H. Kaufmann (Grinnellite via A. S. Leopold), and John F. Eisenberg (student of behaviorist Peter Marler) are there. James N. Layne (Archbold Biological Station) has been influential in the development of this group. This group is supported by paleontologist S. David Webb, and ornithologists J. C. Dickinson and Franz Sauer. Jackie Belwood (student of Stephen Humphrey), Cheri Jones (student of John Eisenberg), Paul Pearson (student of Archie Carr), and Michael H. Smith obtained their training there. Mike Smith has headed the Savannah River Ecology Laboratory at Aiken, South Carolina, for many years.

*Purdue.*—Purdue University has had its influence on mammalogy, earlier under Durwood L. Allen and Charles M. Kirkpatrick, both essentially conservationists, and later under two of Kirkpatrick's students, Russell E. Mumford and Harmon P. Weeks. Some of the more notable students from this group are L. David Mech and Rolf O. Peterson, two wolf biologists, and Virgil Brack, Jr., a bat biologist.

*Tulane.*—Norman C. Negus and James S. Findley grew up together in suburban Cleveland, Ohio. Their "Bible" was Hamilton's *Mammals of the Eastern United States* (1943). Negus studied under Eugene Dustman, an ornithologist, at Ohio State. Findley ended up heading the Kansas subgroup at New Mexico, and Negus then established a mammal center at Tulane, with Jack A. Cranford, Edwin Gould, John F. Pagels (co-advised with Clyde Jones), Aelita J. Pinter, and Thomas E. Tomasi among his students. Negus now heads a research group at the University of Utah.

*Wisconsin.*—The University of Wisconsin has also served as a center, although neither of the two principals, John T. Emlen and Roland K. Meyer, is a mainstream mammalogist. Meyer is an endocrinologist and Emlen is a preeminent ecologist. Phillip L. Wright emerged from this program and established a program in mammalogy at the University of Montana. He was joined there for a time by Robert S. Hoffmann, who also had students at the University of Kansas and is now at the Smithsonian Institution. Garrett C. Clough and William A. Fuller were students of Emlen, and John E. Warnock, Rodney A. Mead, and Tim W. Clark are notable mammalogists from the Wisconsin and Montana programs.

*Other Sources.*—Many "mammalogists" have entered the field from other fields but are now working primarily with mammals.

Several physicians have made names for themselves in mammalogy, one being C. Hart Merriam. Others include Marcus Ward Lyon, Jr., who wrote *Mammals of Indiana* in 1936 and who is also a past president of the ASM; Murray L. Johnson, who received his M.D. from Oregon Medical School; and George Wislocki, an anatomist at Harvard Medical School. Denny G. Constantine, who has made many valuable contributions concerning bat rabies, is a veterinarian.

A number of individuals have received degrees in ecology, then have done concentrated work in mammalogy. For example, Dennis Chitty and Francis C. Evans worked with Charles Elton at Oxford, Michael Rosenzweig with Robert MacArthur at Pennsylvania, E. V. Komarek with W. C. Allee at the University of Chicago, and Wilson Baker and Gary Barrett with Eugene Odum at the University of Georgia. Charles Krebs, in turn, worked with Dennis Chitty.

Several individuals are associated with mammalogy from a wildlife biology background, including both the principles of the Purdue group, Durwood L. Allen and Charles M. Kirkpatrick, and also Willard D. Klimstra, B. J. Verts, Joseph A. Chapman, George A. Feldhamer, and Glen C. Sanderson.

Several have entered mammalogy from a genetics background, such as Gary F. McCracken, who worked with Peter Brussard; and James L. Patton, who worked with W. B. Heed at the University of Arizona, where he also was closely associated with E. Lendell Cockrum. Karl F. Koopman took his Ph.D. with T. H. Dobzhansky at Columbia. His doctoral dissertation, on natural selection and reproductive isolation between two closely related populations of *Drosophila,* was a classic of its day and frequently is cited in courses in evolution and genetics. Koopman has made numerous contributions on bats and is now an Honorary Member of ASM.

Other examples given in Table I include William A. Wimsatt and Roy Horst, who worked with a morphologist; Duane A. Schlitter, Paul K. Anderson, Paul Pearson, and Kenneth Wilkins, who worked with herpetologists; and Albert E. Wood, who worked in palaeontology.

There is another group of mammalogists who, similar to the Merriam group, did not have Ph.D.'s and thus did not have students, yet they have made major impacts on the field. These include individuals such as Rudolph M. Anderson, a long-time worker in Canada; G. H. H. Tate, who worked with mammals of eastern Asia and South America; Harold E. Anthony (mammals of North America); Hobart M. Van Deusen of the American Museum (mammals of New Guinea); and Phillip Hershkovitz of the Field Museum (South American mammals). Karl Kenyon (marine mammals) and Olaus Murie (large carnivores) are also high profile examples of this group.

Present day mammalogists of North America come from a few major lineages and several other sources and backgrounds. The few earlier stems stimulated the field but the great diversity present today allows for diverse methods and ideas to be applied to problems in mammalogy and should help us to continue to make major intellectual advances. Systematics and life history studies led the way and are still exceedingly important, but today many other areas, notably genetics, behavior, ecology, physiology, conservation biology, and many other fields make their contributions. Although our roots to this point are relatively few, diversity continues to increase as specialists continue to add to the field of mammalogy, and the genealogy of mammalogists becomes ever more complicated.

## Acknowledgments

This paper would not have been possible without the cooperation of many individuals too numerous to mention. However, special thanks are due to Elmer C. Birney, James H. Brown, Donald F. Hoffmeister, J. Knox Jones, Jr., William Z. Lidicker, Jr., Oliver P. Pearson, and Don E. Wilson, all of whom have read and greatly improved the manuscript.

## Literature Cited

Grinnell, H. W. 1958. Annie Montague Alexander. Grinnell Naturalists Society. Museum of Vertebrate Zoology, University of California, Berkeley, 27 pp.

Hall, E. R. 1939. Joseph Grinnell (1877 to 1939). Obituary. Journal of Mammalogy, 20:409–417.

Hamilton, W. J., Jr. 1943. Mammals of eastern United States. Comstock Publishing Co., Ithaca, New York, 432 pp.

———. 1955. Mammalogy in North America. Pp. 661–668, *in* A century of progress in the natural sciences 1853–1953. California Academy of Sciences, San Francisco, 807 pp.

Hoffmeister, D. F. 1969. The first fifty years of the American Society of Mammalogists. Journal of Mammalogy, 50:794–802.

Jones, J. K., Jr. 1991. Genealogy of twentieth-century systematic mammalogists in North America: the descendants of Joseph Grinnell. Pp. 48–55, *in* Latin American mammalogy: history, biodiversity, and conservation (M. A. Mares and D. J. Schmidly, eds). University of Oklahoma Press, Norman, 468 pp.

Layne, J. N., and R. S. Hoffmann. 1994. Presidents. Pp. 22–70, *in* Seventy-five years of mammalogy (1919–1994) (E. C. Birney and J. R. Choate, eds.). Special Publication, The American Society of Mammalogists, 11:1–433.

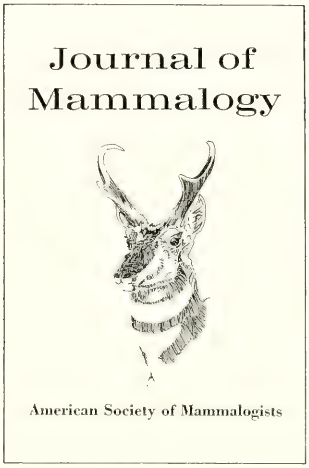
Storer, T. 1969. Mammalogy and the American Society of Mammalogists, 1919–1969. Journal of Mammalogy 50:785–793.

Merriam, C. H. 1877. A review of the birds of Connecticut, with remarks on their habits. Transactions Connecticut Academy of Arts and Sciences, 4:1–150.

Merriam, C. H. 1884. The vertebrates of the Adirondack region: the Mammalia. Transactions of the Linnean Society of New York, 1:1–124.

# *PUBLICATIONS*

B. J. VERTS AND ELMER C. BIRNEY




## *Introduction*

According to the Bylaws and Rules adopted by the American Society of Mammalogists on 3 April 1919, "The object of the Society shall be the promotion of the interests of mammalogy by holding meetings, issuing a serial or other publications, aiding research, and engaging in such other activities as may be deemed expedient" (Article I., Sec. 2.). Of the budget approved by the Board of Directors for 1992, $122,000 (74.1%) of the total $164,630 was allocated for expenses related directly to editorial activities of the society. Throughout the 75 years of the existence of the society, no single activity has been of higher priority, received a larger share of the budget, or, arguably, had a greater impact on the development of the discipline than has production of the society's publications, especially the *Journal of Mammalogy*. It is the purpose of this chapter to provide a brief summary of the 75-year history of the publications of the ASM, with special emphasis on trends observed in the content of the *Journal of Mammalogy* during this period.

## ***The* Journal of Mammalogy**

The *Journal of Mammalogy* has served the role of the serial publication authorized in the Bylaws and Rules since the ASM was founded. It also has functioned as an "official" publication of the society in that it includes announcements and minutes of meetings, lists of officers and committee members, and other announcements and communications. However, nowhere have we found that the *Journal of Mammalogy* ever was designated *the* official publication of the American Society of Mammalogists.

The *Journal of Mammalogy* commenced publication on 28 November 1919, <8 months after the society was founded. Volume 1 (259 pages) consisted of five numbers (issues); the four published in 1920 almost certainly were intended to establish the February, May, August, and November pattern of publication, but each actually was published in the following month. Authors of the articles published in the first volume included some of the most renowned and

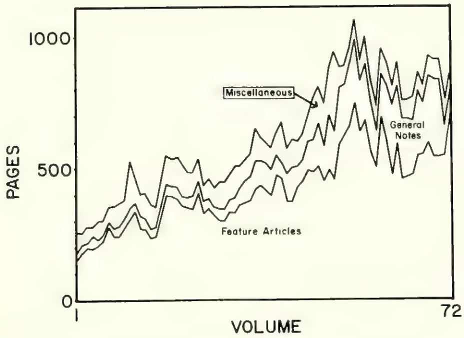



FIG. 1.—Strata-surface graph of the number of pages devoted to feature articles, general notes, and other components in volumes 1–72 (1919–1991) of the *Journal of Mammalogy.*

revered names in American mammalogy: Glover M. Allen, J. A. Allen, H. E. Anthony, Vernon Bailey, Lee R. Dice, James W. Gidley, Joseph Grinnell, G. Dallas Hanna, Francis Harper, Arthur H. Howell, A. Brazier Howell, Hartley H. T. Jackson, Stanley G. Jewett, C. Hart Merriam, Gerrit S. Miller, Jr., W. D. Matthew, Wilfred H. Osgood, John C. Phillips, Ernest Thompson Seton, Arthur de Carle Sowerby, H. L. Stoddard, Walter P. Taylor, P. A. Taverner, and Edward R. Warren. Interestingly, only a single article was coauthored (by G. S. Miller, Jr., and James W. Gidley), only one was by a researcher from other than North America (by A. de C. Sowerby of England), and only eight (10.8%) of the 74 articles published were about mammals other than those in North America (one each on African carnivores, cats, and monkeys; neotropical bats and cats; Asian bears; Japanese bats; and Brazilian tapirs).

The initial issue of the *Journal of Mammalogy* was a 51-page number consisting of 7 feature articles (37.3 pages), 4 general notes (4.6 pages), 3 reviews and 49 references in a recent-literature section, an editorial comment (1.6 pages), and the Bylaws and Rules adopted on 3 April 1919 (2.6 pages) when the society was founded. Both feature articles and general notes tended to be short; the former averaged 4.5 pages, the latter <1 page. The comments by Editor Ned Hollister consisted of a paragraph-long history of the organization of the society, a description of the scope of the *Journal,* solicitation of manuscripts for the *Journal,* a plea for members to recruit new members, an acknowledgment of Ernest Thompson Seton's contribution of the sketch of the pronghorn for the front of the *Journal,* a report of the election of J. A. Allen as an Honorary Member, and a comment on the paper by C. Hart Merriam titled "Criteria for the recognition of species and genera." Volume 1, number 4 contained a list of members, some of whom were listed subsequently as other than charter members (*Journal of Mammalogy,* 3: 203–218, 1922).

Although the basic composition of the *Journal of Mammalogy* was established at the onset, numerous changes have occurred in the proportion devoted to each of the sections. For example, during the first 3 decades of publication, general notes composed about 20–50 pages, irrespective of the total number of pages published in each volume (Fig. 1). However, after about 1950, more and more space was devoted to general notes; in both 1988 and 1989, >290 pages of general notes were published (Fig. 1). Editorial policy was altered in 1990 to limit the number of general notes published as a means of enticing bibliographic services to include references to more of the shorter papers published in the *Journal.* The general-note format was abandoned commencing with volume 73 (1992).

Over the years, some minor evolution has occurred in components of the *Journal of Mammalogy*: "Editorial Comment" in volume 1 (1919–1920) became "Correspondence" in volume 2 (1921) and remained so until volume 6 (1925) when it became "Comment and News," which in volume 35 (1954) became "Comments and News." The "Recent Literature" section was an integral part of the *Journal* from its inception through volume 50 (1969), published as a supplement to volumes 51–66 (1970–1985) of the *Journal,* then discontinued commencing with volume 67 (1986). Membership lists were published in volumes 1 (1919–1920), 3 (1922), 5 (1924), 11 (1930), 15 (1934), 18 (1937), 21 (1940), 29 (1948), 31 (1950), 35 (1954), 40 (1959), and 46 (1965), and as supplements accompanying volumes 54 (1973), 59 (1978), 65 (1984), and 70 (1989). Other supplements were published irregularly and include three editions of "*Guidelines for manuscripts,*" "*Roles of standing committees,*" "*Survey of North American collections of Recent mammals,*" and "*Acceptable field methods in mammalogy.*" The "Bylaws and Rules," or, when amended, parts thereof, were included in several issues.

Reviews of recent publications were included in the first issue and in most, but not all, subsequent issues of the *Journal of Mammalogy.* Until volume 17 (1936), reviews were included in the recent-literature section, but afterward were afforded a section of their own with the subheading "Reviews." Reviews occupied 4–11 ($\bar{X}$ = 4.7) pages in volumes 17–32 (1936–1951), 5–17 ($\bar{X}$ = 11.7) pages in volumes 33–50 (1952–1969), 20–31 ($\bar{X}$ = 23.6) pages in volumes 51–66 (1970–1985), and 12–19 ($\bar{X}$ = 15.7) pages in volumes 67–72 (1986–1991). Greater emphasis was placed on the publication of reviews commencing with volume 73 (1992); 26 pages were devoted to reviews in that volume.

An author-subject index is published in the last issue of each volume; however, the index to volume 52 (1971) was published as a supplement to the first number of volume 53 (1972). Commencing with that index and continuing to present, an alphabetical (by last name of author or editor) listing of books reviewed in the volume followed by the page number on which the review may be found concludes each index. Also, commencing with volume 67 (1986) author and subject indices were separated.

Announcements of the death of members of the American Society of Mammalogists were included in the *Journal of Mammalogy* for the first time in the fourth number of volume 1 (1919–1920). Like other components of the *Journal of Mammalogy,* death notices underwent considerable evolution. At the end of the first membership list, names of three deceased numbers were listed. The general-notes section of the same issue included a seven-line obituary for one of those listed (Thomas M. Owen) and a nearly page-long obituary for a Canadian naturalist and agency official (James M. Macoun) who apparently was never a member of the society. The second volume contained no death notices, but the third volume (1922) contained a list of nine deceased members, including the three listed in volume 1 (1919–1920); this appeared at the end of the new list of members. Seemingly, the intent initially was to include a list of all deceased members with each membership list, but the practice was abandoned after publication of the second such list. The first extensive obituary was the 7-page "appreciation" for one of the founders of North American mammalogy, Joel Asaph Allen, published in volume 3 (1922); a second obituary for Allen was published in volume 11 (1930) and, with a photograph, included >13 pages. However, no bibliography accompanied the text of either. For about 25 years, either lists of deceased members (usually in bold-face type) published in the comments and news section or short (from 6–10 lines to a page or so) obituaries for deceased members were common. Sometimes a deceased member's name appeared in one of the lists and an obituary for that member was published subsequently, but more often a deceased member was honored only once. Occasionally, obituaries for prominent members covered 3–5 pages or more and one that included a bibliography and correspondence (for President Edward A. Goldman) required 22 pages [volume 28 (1947)]. Since about 1950, names of deceased members were listed in the comments and news section under the subheading "Deaths Reported." Names were in boldface, but cities and states of residence and membership status (honorary, life, or emeritis), when included, were set in italic.

Also, since about 1950, obituaries have been limited to past presidents and prominent mammalogists. In a few instances, a death notice or obituary has been included in the *Journal of Mammalogy* for a mammalogist or naturalist (usually foreign) for which there is no published record of their having been a member of the society.

Miscellaneous items published in the *Journal of Mammalogy* from time to time include letters to the editor, letters from the president, publication policies and suggestions to authors, personal notices (mostly items for sale and items wanted), membership application forms, advertisements of society publications, and paid advertisements for equipment, supplies, and publications of interest to mammalogists. One issue, the third of volume 11 (1930), contained 64 pages of papers resulting from a symposium on predatory animal control. The fourth issue of each volume commences with a series of roman numbered pages (usually 8 pages, 2 of which are blank) that contain a list of editors, a reprinting of the verso of the front cover, and a reprinting of the contents of all four issues of the volume.

The artwork of Seton graced the cover of the *Journal of Mammalogy* for a decade, but commencing with the first issue of volume 11 (1931), a new cover designed by A. Brazier Howell and dominated by the head and cape of a pronghorn appeared. Howell's artwork appeared on the cover through volume 43 (1962). A new design depicting a standing pronghorn appeared on the cover of volumes 44–48 (1962–1967) and was followed by another head and cape view of the pronghorn in volumes 49–72 (1968–1991). Artwork for both cover designs was signed; "Hines" signed the former and the cryptographic signature on the latter is the initials of Frances L. Jacques. No "Hines" was listed as a member of the American Society of Mammalogists in membership lists published in 1959 or 1965, so likely the cover design used for volumes 44–48 (1962–1967) was drawn by a commercial artist. Jacques was an artist at the American Museum of Natural History and the James Ford Bell Museum of Natural History. A radical departure from the traditional green and black cover dominated by a pronghorn commenced with volume 73 (1992). The pronghorn, although still present and still the artwork used in volumes 49–72 (1969–1991), no longer dominates the cover, but is relegated to a small circle. The central figure, consisting to date of artwork depicting some mammal, is unique to each issue. Green, although a different shade, remains featured on the somewhat thicker and smoother cover, but on the front, the lettering, a square enclosing the central figure, and the small circle enclosing the drawing of the pronghorn are white. On the back cover, large lettering and a rectangle containing a list of officers and directors also are white. Also, the first color plate for a research article was published in volume 73 (1992); however, the first and only other color plate published in the *Journal* was that of *Rupicapra rupicapra* by F. Murr from Erna Mohr's *Säugetiere* included in the review by R. H. Manville of that book published in volume 40 (1959).

Through volume 57 (1976), the entire *Journal of Mammalogy* was printed in single-column format. Commencing with volume 58 (1977), literature-cited sections were printed in double-column format, but the text remained single column until volume 73 (1992) when the space-saving and the easier-to-read double-column format was adopted. The Williams and Wilkins Company, Baltimore, Maryland, printed the first 37 volumes of the *Journal of Mammalogy,* but commencing with volume 38 (1957) of the *Journal,* Allen Press, Lawrence, Kansas, has served as the printer for all publications of the American Society of Mammalogists.

Throughout the history of the *Journal of Mammalogy,* all editorial services have been provided by members who volunteered; for the first 37 volumes (1919–1956) all editorial services were provided by one person, designated the "editor." Subsequently, several systems of dividing the ever-growing editorial responsibilities were employed (Table 1). The present system, stable for the last 14 volumes (60–73) consists of a managing editor (the editor of record) responsible for production of the *Journal,* a journal editor responsible for matters of style and presentation, several associate editors responsible for conducting the review process and judging the scientific merit of manuscripts, an editor for reviews responsible for soliciting and editing reviews of books and assembling and publishing a "books received" list of books submitted but not reviewed, and an editor for advertising responsible for personal notices and commercial advertising. Since its inception, only 62 mammalogists have served the *Journal of Mammalogy* in one or more editorial capacities (Table 1); the length of service ranged from 1 to 16 years and averaged 4.6 years. The *Journal* has had only 17 editors of record; length of service averaged 4.5 years (range, 1–7 years).

From the onset, the *Journal of Mammalogy* was provided free to all members and was available to institutions by subscription. Just as there has been an increase in number of pages published (Fig. 1), there has been an increase in both membership dues and subscription rate (Fig. 2). Since 1953 (when publication of a summary of the annual budget in the *Journal* commenced), neither subscription rate nor membership dues has kept pace with funds budgeted for publication of the *Journal of Mammalogy* (Fig. 2). Income from the J. A. Allen Memorial Fund and other investments managed by the society's trustees (Kirkland and Smith, 1994) make it possible to continue to provide members and subscribers with a quality publication at a modest cost.

In his initial solicitation of papers, the first editor, Ned Hollister, emphasized the need to make the *Journal of Mammalogy* an essential tool for workers in all phases of mammalogy. To ascertain the effectiveness of this and similar pleas by subsequent editors, we analyzed trends related to length,

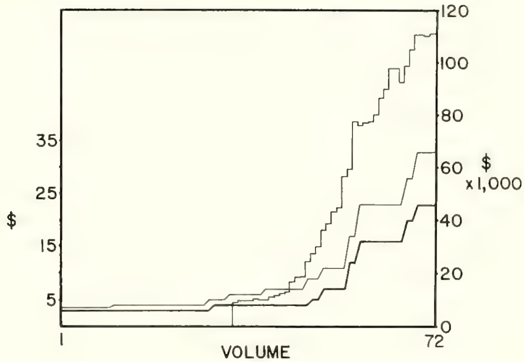



FIG. 2.—Line graphs of membership dues (heavy line) and subscription rates (light line) for volumes 1–72 (1919–1991) on left ordinate and histogram of funds budgeted by the Board of Directors (as published in the *Journal of Mammalogy*) for production and distribution of volumes 34–72 (1953–1991) of the *Journal of Mammalogy* on right ordinate.

subject matter, and authorship of papers published in the *Journal of Mammalogy* by sampling alternate volumes from volume 1 (1919–1920) to volume 71 (1990). Length measured to the nearest 0.1 page, the continent of origin for species reported on, number and residence of authors, number of references cited, and major topic covered were recorded for each article published in volumes sampled.

Editors and authors have maintained a diversity of topics among articles published in the *Journal of Mammalogy*; after an initial paucity of papers on morphology, reproduction, and behavior they have maintained a more even balance among topics. Articles published as feature articles (Fig. 3a) cover more diverse topics than general notes (Fig. 3b) as >20% were on topics other than the six classifications that we used to present results of our analysis. Overall, approximately one-fourth of all articles published as feature articles were devoted to ecology and life history, and, among general notes, the same proportion was devoted to articles describing distributions and new locality records (Fig. 3). Since about 1964, the number of general notes devoted to distri-

TABLE 1.—*The editorial staff and editors of the* Journal of Mammalogy, *1919–1993.*

| Year(s) | Volume(s) | Editor |
|---|---|---|
| 1919–1924 | 1–5 | N. Hollister |
| 1925–1929 | 6–10 | H. H. T. Jackson |
| 1930–1935 | 11–16 | E. A. Preble |
| 1936–1937 | 17–18 | A. B. Howell |
| 1938–1940 | 19–21 | A. H. Howell |
| 1941–1947 | 22–28 | W. B. Davis |
| 1948–1952 | 29–33 | W. H. Burt |
| 1953–1956 | 34–37 | W. R. Eadie |

| Year | Volume | Editor | Associate editors |
|---|---|---|---|
| 1957 | 38 | R. H. Manville | R. H. Baker, K. L. Duke, P. L. Wright |
| 1958 | 39 | R. H. Manville | R. H. Baker, K. L. Duke, P. L. Wright |
| 1959 | 40 | R. H. Manville | R. H. Baker, K. L. Duke, P. L. Wright, R. S. Miller |
| 1960 | 41 | R. H. Manville | R. H. Baker, K. L. Duke, P. L. Wright, R. S. Miller |
| 1961 | 42 | R. H. Manville | R. H. Baker, K. L. Duke, P. L. Wright, R. S. Miller |
| 1962 | 43 | R. H. Manville | R. H. Baker, K. L. Duke, P. L. Wright, R. S. Miller |
| 1963 | 44 | J. R. Beer | R. H, Baker, W. H. Davis, P. L. Wright, W. B. Quay |
| 1964 | 45 | J. R. Beer | R. H. Baker, W. H. Davis, P. L. Wright, W. B. Quay |
| 1965 | 46 | M. R. Lee | L. L. Getz, J. N. Layne, W. Z. Lidicker, Jr., R. S. Miller, W. B. Quay |
| 1966 | 47 | M. R. Lee | L. L. Getz, F. B. Golley, D. J. Klingener, J. N. Layne, W. Z. Lidicker, Jr., W. B. Quay |

| Year | Volume | Managing editor | Editor for feature articles | Editor for general notes and reviews |
|---|---|---|---|---|
| 1967 | 48 | J. K. Jones, Jr. | T. A. Vaughan | P. L. Wright |
| 1968 | 49 | J. K. Jones, Jr. | T. A. Vaughan | P. L. Wright |

| Year | Volume | Managing editor | Editor for feature articles | Editor for general notes | Editor for reviews |
|---|---|---|---|---|---|
| 1969 | 50 | J. K. Jones, Jr. | D. C. Carter | J. R. Tamsitt | R. S. Hoffmann |
| 1970 | 51 | J. K. Jones, Jr. | D. C. Carter | J. R. Tamsitt | R. S. Hoffmann |
| 1971 | 52 | J. K. Jones, Jr. | D. C. Carter | G. G. Musser | R. S. Hoffmann |
| 1972 | 53 | J. K. Jones, Jr. | G. G. Musser | R. J. Baker | R. S. Hoffmann |
| 1973 | 54 | J. K. Jones, Jr. | G. G. Musser | R. J. Baker | C. Jones |

TABLE 1.—*Continued.*

| Year | Volume | Managing editor | Associate managing editor | Editor for feature articles | Editor for general notes | Editor for reviews | Advertising editor |
|---|---|---|---|---|---|---|---|
| 1974 | 55 | H. H. Genoways | R. S. Hoffmann | R. J. Baker | D. J. Klingener | C. Jones | |
| 1975 | 56 | H. H. Genoways | R. S. Hoffmann | R. J. Baker | D. J. Klingener | C. Jones | |
| 1976 | 57 | H. H. Genoways | R. S. Hoffmann | D. J. Klingener | D. J. Schmidly | C. Jones | R. G. Van Gelder |
| 1977 | 58 | H. H. Genoways | R. S. Hoffmann | D. J. Schmidly | D. E. Wilson | J. L. Patton | R. G. Van Gelder |
| 1978 | 59 | H. H. Genoways | R. S. Hoffmann | D. J. Schmidly (D. E. Wilson, assoc. editor) | A. L. Gardner | J. L. Patton | R. G. Van Gelder |
| **Year** | **Volume** | **Managing editor** | **Associate managing editor** | **Journal editor** | **Associate editors** | **Editor for reviews** | **Advertising editor** |
| 1979 | 60 | E. C. Birney | T. E. Lawlor | D. E. Wilson | A. L. Gardner<br>R. E. McMillen<br>B. J. Verts | J. L. Patton | J. S. Mellett |
| 1980 | 61 | E. C. Birney | T. E. Lawlor | D. E. Wilson | M. A. Bogan<br>R. E. McMillen<br>B. J. Verts | J. L. Patton | J. S. Mellett |
| 1981 | 62 | E. C. Birney | T. E. Lawlor | D. E. Wilson | M. A. Bogan<br>G. N. Cameron<br>B. J. Verts | J. L. Patton | J. S. Mellett |
| 1982 | 63 | R. J. Baker | | E. C. Birney | M. A. Bogan<br>G. N. Cameron<br>J. M. Taylor | J. L. Patton | J. S. Mellett |
| 1983 | 64 | R. J. Baker | | E. C. Birney | D. M. Armstrong<br>G. N. Cameron<br>C. J. Phillips | J. K. Jones, Jr. | J. S. Mellett |
| 1984 | 65 | R. J. Baker | | E. C. Birney | D. M. Armstrong<br>G. N. Cameron<br>G. R. Michener<br>C. J. Phillips | J. K. Jones, Jr. | J. S. Mellett |
| 1985 | 66 | C. Jones | | R. J. Baker | D. M. Armstrong<br>M. A. Mares<br>G. R. Michener<br>C. J. Phillips | J. K. Jones, Jr. | J. S. Mellett |

TABLE 1.—*Continued.*

| Year | Volume | Managing editor | Journal editor | Associate editors | Editor for reviews | Advertising editor |
|---|---|---|---|---|---|---|
| 1986 | 67 | C. Jones | R. J. Baker | D. M. Armstrong<br>D. P. Christian<br>M. A. Mares<br>G. R. Michener | J. K. Jones, Jr. | M. A. Bogan |
| 1987 | 68 | C. Jones | R. J. Baker | D. M. Armstrong<br>D. P. Christian<br>M. A. Mares<br>G. R. Michener | J. K. Jones, Jr. | M. A. Bogan |
| 1988 | 69 | C. Jones | B. J. Verts | D. P. Christian<br>M. S. Hafner<br>M. A. Mares<br>R. H. Tamarin | J. K. Jones, Jr. | M. A. Bogan |
| 1989 | 70 | C. Jones | B. J. Verts | D. P. Christian<br>M. S. Hafner<br>R. H. Tamarin<br>K. T. Wilkins | J. K. Jones, Jr. | M. A. Bogan |
| 1990 | 71 | C. Jones | B. J. Verts | J. W. Bickham<br>J. F. Merritt<br>R. H. Tamarin<br>K. T. Wilkins | J. K. Jones, Jr. | M. A. Bogan |
| 1991 | 72 | B. J. Verts | T. L. Best | J. W. Bickham<br>J. F. Merritt<br>R. H. Tamarin<br>K. T. Wilkins | J. K. Jones, Jr. | M. A. Bogan |
| 1992 | 73 | R. J. Baker | T. L. Best | J. W. Bickham<br>R. T. Bowyer<br>J. F. Merritt<br>S. H. Vessey<br>K. T. Wilkins<br>M. R. Willig | B. D. Patterson | R. K. Rose |

TABLE 1.—*Continued.*

| Year | Volume | Managing editor | Publications editor | Journal editor | Associate editors | Editor for reviews | Advertising editor |
|---|---|---|---|---|---|---|---|
| 1993 | 74 | R. J. Baker | R. M. Timm | T. L. Best | R. T. Bowyer<br>P. W. Freeman<br>K. McBee<br>J. F. Merritt<br>S. H. Vessey<br>M. R. Willig | B. D. Patterson | R. K. Rose |

butions and new locality records has declined steadily (Fig. 3b); manuscripts composed largely of descriptions of extensions of geographic ranges of taxa based on single locality records were specifically excluded from the *Journal* by publication policy commencing in 1988. No other major trends in the diversity of topics of articles published in the *Journal* are discernable.

Authorship has remained largely North American; of 1,691 feature articles and 2,613 general notes published in alternate volumes from volume 1 (1919–1920) to volume 71 (1990), 1,555 (91.9%) and 2,456 (94.0%), respectively, were written exclusively by North American authors. Nevertheless, a trend toward more articles authored by researchers outside of North America seems to be becoming established. In volume 71 (1990), 23.8% of the 63 feature articles and 30.8% of the 39 general notes were authored by one or more researchers from other continents. Although 84.8% of the 2,613 general notes and 81.8% of the 1,691 feature articles were about North American taxa, a trend established after World War II toward publication of more articles on mammals from other continents continues. In volume 71 (1990), 34.9% of 63 feature articles and 38.5% of 39 general notes were about mammals from other than North America. Coauthorship became an increasing trend for feature articles and general notes; however, three or more authors were rare before volume 27 (1946) for feature articles, and volume 39 (1958) for general notes (Fig. 4). In volume 71 (1990), the last for which we separated papers by type, 84.6% of general notes and 55.6% of feature articles were written by more than one author (Fig. 4). Thus, not only is the number of authors increasing, but both the scope and the clientele of the *Journal of Mammalogy* are becoming more international.

After the initial volume, average length of feature articles (Fig. 5a) was 6–9 pages during most years until volume 45 (1964) when the average length began a steady climb

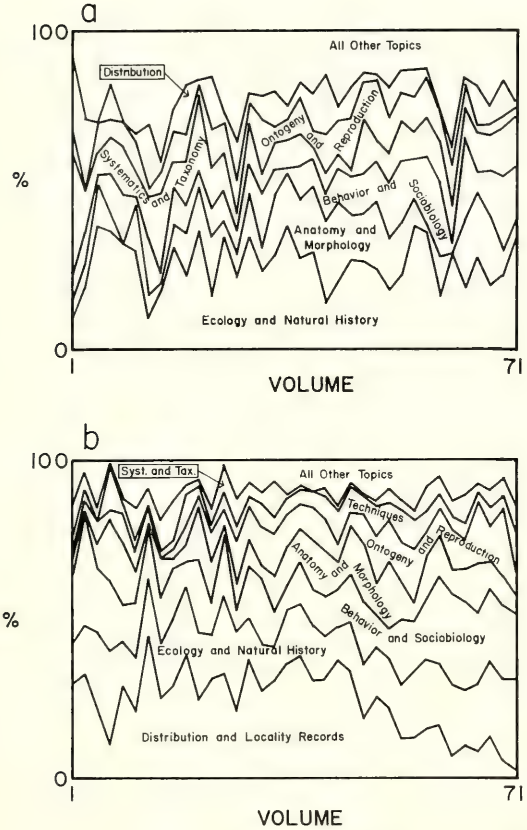



FIG. 3.—Surface graph of proportions of the total number of articles on each of several topics in alternate volumes for volumes 1–71 (1919–1990) of the *Journal of Mammalogy*: a, feature articles; b, general notes.

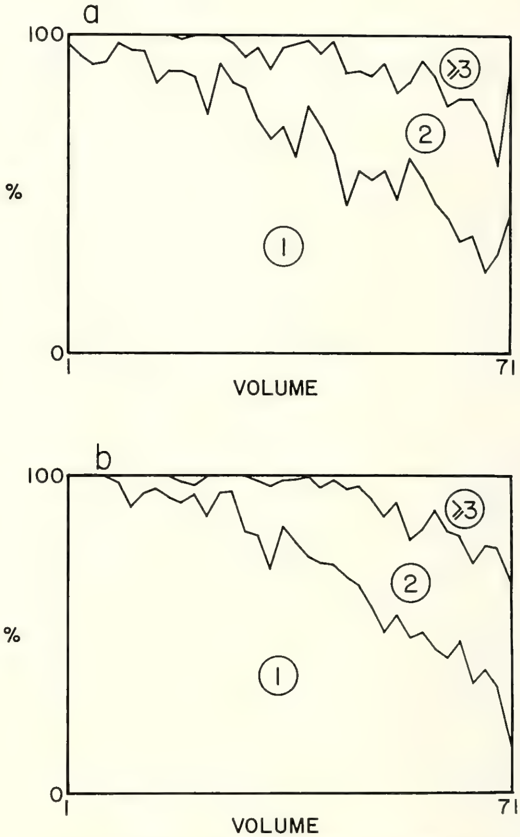



FIG. 4.—Surface graph of proportions of the total number of articles authored by one, two, and three or more authors in alternate volumes for volumes 1–71 (1919–1990) of the *Journal of Mammalogy*: a, feature articles; b, general notes.

that reached a peak of >14 pages in volume 56 (1975). The peak was followed by a somewhat precipitous decline to a plateau of <10 pages. During only 1 year before volume 45 (1964) did the average length of general notes exceed 1 page (Fig. 5b), but after volume 45 (1964), average page length increased gradually to >4 pages in volume 69 (1988), but declined to 3.0 in volume 71 (1990) in response to efforts by editors to emphasize feature articles.

The number of references cited per paper averaged ≤10 for feature articles and less than two for general notes in most volumes before volume 45 (1964; Fig. 6). However, commencing about 1945, the average number of references proliferated greatly, attaining an apex of >35 for feature articles and >15 for general notes published in most recent volumes. No doubt, the almost logarithmic increase in number of references cited per paper in both feature articles and general notes was a response to both the greater need to document previous findings and the greater availability of information on all aspects of mammalogy (Anderson and Van Gelder, 1970).

In the first volume, new taxa were described in 12 (36.4%) and new names were applied to named taxa in three (9.1%) of the 33 feature articles. Describing and naming new taxa remained a common topic of ar-

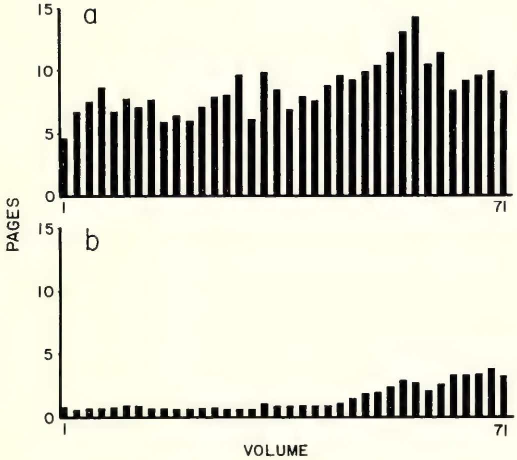



FIG. 5.—Bar graphs of the average number of pages per article published as: in alternate volumes for volumes 1–71 (1919–1990) of the *Journal of Mammalogy*: a, feature articles; b, general notes.

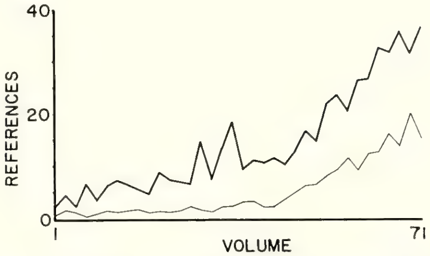



FIG. 6.—Line graph of the average number of references cited per feature article (heavy line) and general note (light line) published in alternate volumes for volumes 1–71 (1919–1990) of the *Journal of Mammalogy*.

ticles published in the *Journal of Mammalogy* in the first 20 volumes; subsequently, alpha taxonomy was the topic of <10% of the articles published. Overall, only 3.6% of 4,304 articles published in alternate volumes of the *Journal of Mammalogy* contained descriptions of new taxa.

Rodents, bats, and carnivores, in that order, were the most popular topics of articles published as general notes in the *Journal of Mammalogy* (Fig. 7a). Fewer general notes on insectivores or on more than one order were published in the last 15 years that papers were segregated by type. Among feature articles, however, trends toward publication of more and more articles on rodents and fewer and fewer articles on taxa representing more than one order of Mammalia were evident almost from the beginning of publication of the *Journal* (Fig. 7b). A similar trend was noted in oral presentations at annual meetings (Gill and Wozencraft, 1994). Obviously, manuscripts containing information on more than one order of mammals were not converted to general notes as the proportion of general notes on multiordinal topics also has declined in recently published volumes (Fig. 6a). Likely, the ordinal topic chosen reflects the abundance, diversity, and ease of catching and handling rodents and bats.

From this brief analysis, we conclude that the *Journal of Mammalogy* has filled and

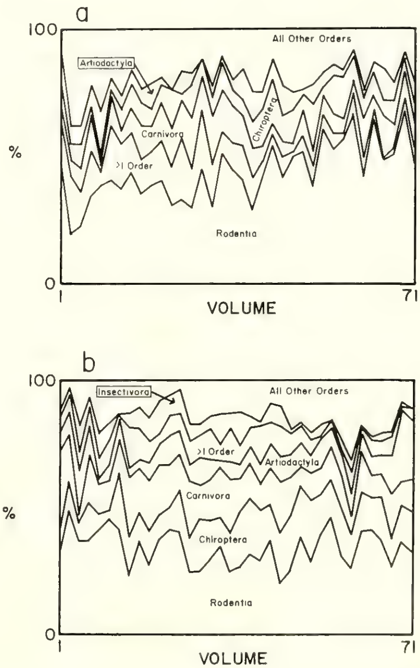



FIG. 7.—Surface graph of proportions of the total number of articles devoted primarily to each of several orders of mammals (and to more than one order of mammals) published in alternate volumes from volumes 1–71 of the *Journal of Mammalogy*: a, feature articles; b, general notes.

continues to fill the role and scope that the founders of the American Society of Mammalogists envisioned for it. The diversity of subjects and orders of mammals treated, and the diversity in length and depth of treatments remains its greatest strength. Likely, this strength is one of the major binding forces of the American Society of Mammalogists.

## Mammalian Species

*Mammalian Species* is the most recently established serial publication of the American Society of Mammalogists. The objective of *Mammalian Species* "is to provide a critically compiled, accurate, and concise summary of the present state of our biological knowledge (and ignorance) of a species of mammal in a standard format . . ." (Instructions for contributors to *Mammalian Species,* 1987). Each account includes a complete synonymy and sections in which context and content, diagnosis, distribution, general characters, fossil record, form and function, ontogeny and reproduction, ecology, behavior, and genetics are considered. A remarks section, commonly containing an explanation of complex nomenclature, and an extensive literature cited section completes each account. One account in each genus must contain a generic synonymy and context and content sections. Most accounts contain a photograph or artist's depiction of a representative of the species, photographs or line drawings of dorsal, ventral, and lateral views of the skull, and a map depicting the geographic distribution of the species. Some accounts contain photographs or line drawings of certain diagnostic features such as the baculum, phallus, specific teeth or parts of toothrows, and karyotype. The intention was to limit the length of accounts to 8 pages (printed double-column), but several accounts, especially those on well-researched species, exceed that length.

The concept of *Mammalian Species* was presented to the Board of Directors at the 1968 meeting (*Journal of Mammalogy,* 49: 844, 1968) and was approved by the board at the 1969 meeting as a publication "to be sold by subscription" (*Journal of Mammalogy,* 50:908, 1969). At the latter meeting, the board budgeted $2,000 for initial publication of the series. An announcement in the same issue of the *Journal* (p. 913) indicated that the first account (on *Macrotus waterhousii*) would be mailed to all members with a price list and subscription form. The following year an announcement (*Journal of Mammalogy,* 51:842, 1970) indicated that the cost of a subscription to *Mammalian Species* would be $9.60 to members and $12.00 to nonmembers; the first fascicle of six accounts was published 16 June 1971. Although timing of publication and number of accounts per fascicle were variable during the first 10–12 years, during recent years, two fascicles consisting of 8–20 accounts each were published annually. The present cost of subscriptions for members and nonmembers is $10 per year; individual accounts may be purchased (accounts in same order: $2 each for five or fewer, $1.50 each for six–10, and $1 each for ≥11) and special packages of accounts (grouped by region, taxa, or other classification) are available at 25% discount.

Initially, authors for *Mammalian Species* accounts were solicited from among those especially knowledgeable of a taxon, but, more recently, prospective authors have requested assignment of exclusive privileges to produce accounts on specific species. Currently, assignments are made by the managing editor for a period of 3 years with authors retaining the option of requesting an extension of 1 year to complete accounts in progress. On the matter of timely completion of assignments, editors have been flexible, to a point.

As of 23 April 1993, 443 accounts including 452 species had been published (nine accounts each covered two closely related species). Through the first 443 accounts, numbers of accounts by order of mammal was strongly correlated ($r^2 = 95.04$, $n = 20$)

with numbers of species classified by order (Anderson and Jones, 1984:5–8). Orders that deviate most within this relationship are Primates with accounts published for only 3 (1.7%) of 180 species and Carnivora and Artiodactyla for which accounts have been published for 54 (20.1%) of 269 species and 27 (14.6%) of 185 species, respectively. As 215 (48.5%) of the 443 published accounts are on North American mammals north of Mexico (comprising 50.6% of the species native to the region—Jones et al., 1992), the series is particularly valuable for North American researchers.

Not only was *Mammalian Species* the brainchild of Sydney Anderson, but he sought and obtained approval for the new publication, demonstrated the concept by writing the first account, and nurtured the publication by serving in an editorial capacity for 312 of the accounts published. During the first year of publication he even sold the subscriptions to *Mammalian Species.*

Others who served *Mammalian Species* in a regular editorial capacity for the first 443 accounts were D. F. Williams, T. E. Lawlor, B. J. Verts, J. K. Jones, Jr., A. L. Gardner, C. J. Phillips, T. L. Best, K. F. Koopman, G. N. Cameron, C. S. Hood, J. A. Lackey, and D. E. Wilson. Several others served as guest editors of single accounts when authorship constituted a potential conflict of interest.

## *Monographs and Special Publications*

Three *Monographs of the American Society of Mammalogists* were published, one each in 1926, 1927, and 1928. These were: number 1, *Anatomy of the Wood Rat* by A. Brazier Howell; number 2, *The Beaver* by Edward R. Warren; and number 3, *Animal Life of the Carlsbad Cavern* by Vernon Bailey. Hartley H. T. Jackson served as editor for all three, but was assisted by Edward A. Preble, Ethel M. Johnson, and Emma M. Charters on the last volume. All volumes were published by the Williams and Wilkins Company, Baltimore, Maryland. Number 1 was priced at $5.00, numbers 2 and 3 at $3.00 each; members of the American Society of Mammalogists were afforded an 8% discount.

*Anatomy of the wood rat* consists of nine chapters in 225 pages that include 4 tables, 37 line drawings (seven overprinted with red and blue), 3 plates (photographs), a 3-page bibliography, and a 5-page index. *The beaver* consists of an introduction, acknowledgments, and 13 chapters in 177 pages that include 78 illustrations (70 photographs), a 5-page bibliography, and a 3-page index. *Animal life of the Carlsbad Cavern* consists of eight chapters in 195 pages that include 67 figures (62 photographs, 2 maps, and 3 drawings by L. A. Fuertes), and a 9-page index; no bibliography was included. In addition to chapters on mammals, the volume contained chapters on birds, reptiles, and invertebrates.

Strangely, minutes of the meetings of the Board of Directors or of the members at large published in the *Journal of Mammalogy* in the years before publication of the monographs contain no mention of official sanction or other involvement of the society. However, the minutes of the eighth annual meeting contain a statement announcing the forthcoming publication of the first monograph (*Journal of Mammalogy,* 7:241, 1926). Advertisements of the availability of the monographs appeared on the inside of the back cover of the *Journal of Mammalogy* for several years.

The minutes of the meeting of the Board of Directors at the 44th annual meeting held at Ciudad Universitaria, Mexico City, D.F., Mexico, include the statement, "The revival of a monograph series was approved" (*Journal of Mammalogy,* 45:668, 1964). However, no mention was made in those minutes or those of subsequent meetings regarding the decision not to continue the monographs series per se, but to initiate an entirely new series. According to J. K. Jones, Jr. (pers. comm., 8 August 1990), a member of the committee involved in reestablishing a monograph series, the 25-year period between publication of the third monograph and consideration of reestablishment of the series, and the desire to change the focus of the monograph series, were paramount in the decision. At a special meeting of the Directors at the 45th annual meeting, "A maximum of $8,000 was authorized for the publication of an acceptable manuscript for the first Special Publication of the Society" (*Journal of Mammalogy,* 46:731, 1965).

The first Special Publication, *The natural history and behavior of the California sea lion,* by Richard S. Peterson and George A. Bartholomew, was published 5 December 1967. On page ii of this number the series was described as follows: "This series, published by the American Society of Mammalogists, has been established for papers of monographic scope concerned with some aspect of the biology of mammals." William H. Burt was editor of the initial number, and J. Knox Jones, Jr., James N. Layne, and M. Raymond Lee were listed as additional members of the Committee on Special Publications. The original price of the 91-page clothbound book was $3.50.

Eleven numbers in this series have appeared, the most recent being the present volume in 1994. Published numbers, authors or editors, and dates of publication of Special Publications, in addition to the first, are as follows: number 2, *Biology of* Peromyscus (*Rodentia*), edited by John A. King, 20 December 1968; number 3, *The life history and ecology of the gray whale* (Eschrichtius robustus), by Dale W. Rice and Allen A. Wolman, 30 April 1971; number 4, *Population ecology of the little brown bat,* Myotis lucifugus, *in Indiana and north-central Kentucky,* by Stephen R. Humphrey and James B. Cope, 30 January 1976; number 5, *Ecology and behavior of the manatee* (Trichechus manatus) *in Florida,* by Daniel S. Hartman, 27 June 1979; number 6, *Locomotor morphology of the vampire bat,* Desmodus rotundus, by J. Scott Altenbach, 22 August 1979; number 7, *Advances in the study of mammalian behavior,* edited by John F. Eisenberg and Devra G. Kleiman, 11 March 1983; number 8, *Biology of New World* Microtus, edited by Robert H. Tamarin, 12 September 1985; number 9, *Dispersal in rodents: a resident fitness hypothesis,* by Paul K. Anderson, 30 March 1989; number 10, *Biology of the Heteromyidae,* edited by Hugh H. Genoways and James H. Brown, 20 August 1993; and number 11, *Seventy-five years of mammalogy* (*1919–1994*) edited by Elmer C. Birney and Jerry R. Choate, 1994.

Although all monographic in scope, these 11 Special Publications can be categorized by scientific content and organization. Numbers 1, 3, 4, 5, and 6 each concentrate on one mammalian species, contain 79–153 ($\bar{X}$ = 118) numbered pages, and typically concern natural history and related topics. Of these, number 6 focuses exclusively on locomotor morphology, thus is the most specialized in terms of topics covered. Numbers 2, 7, 8, and 10 (which has a double-column format) contain 593–893 ($\bar{X}$ = 740) numbered pages and consist of several (14–22) contributed manuscripts on a topic selected by an organizing editor. Numbers 2 and 8 focus on a particular genus of mammals and number 10 pertains to a family of mammals, whereas number 7 covers a general topic (animal behavior). Number 9 fits neither of these categories, thus is unique within the series in that it presents and advocates a new hypothesis (on dispersal in rodents) and compares and contrasts it with competing hypotheses. Number 11 also is unique, reviewing 75 years of mammalogy, as influenced by the ASM.

Several members of the American Society of Mammalogists have served as editor or managing editor of the books in the Special Publications series. In addition to editing the first number, William H. Burt also edited number 2. Beginning with number 3, each number had both an editor and a managing editor; the former was responsible for selection, content, and quality control, the latter for matters related to production. James N. Layne served as editor and J. Knox Jones, Jr. as managing editor for numbers 3–6; Hugh H. Genoways (editor) and Timothy E. Lawlor (managing editor) edited numbers 7 and 8; and Elmer C. Birney and Carleton J. Phillips served in these two capacities, respectively, for number 9. Additionally, Jerry R. Choate served as editor and Don E. Wilson as managing editor for a brief period, and Michael A. Mares (editor) Craig S. Hood (managing editor) edited volume number 10. Mares (editor) and Joseph F. Merritt (managing editor) were responsible for number 11.

## *Cumulative Indices and Miscellaneous Publications*

Four cumulative indices to the *Journal of Mammalogy* have been published to date, and a fifth is scheduled for publication. The first was a 20-year index to volumes 1–20 (1919–1939) edited by Viola S. Schantz and Emma M. Charters; it consists of 219 pages and sold for $2.50 in paperback, $3.50 clothbound, when published on 1 August 1945. Each of the next three published indices covered a 10-year span: volumes 21–30 (1940–1949), 31–40 (1950–1959), and 41–50 (1960–1969). The second index also was edited by Schantz and Charters, the third by Schantz and a committee of four others, and the fourth was prepared by James S. Findley and six additional members of the Index Committee. The fifth index is to cover a 20-year period (volumes 51–70) and is being prepared by Michael Carleton and the four or five other members of the 1983–1990 Index Committees. The cumulative index for the decade of the 1940s consists of 146 numbered pages, appeared on 27 October 1952, and sold originally for $3.25 in paperback, $3.75 in clothbound. That for the 1950s has 150 pages, a publication date of 18 May 1961, and sold for $5.00 in clothbound only. The fourth cumulative index consists of 109 numbered pages, is dated only as 1974, and sold for $5.00 in clothbound only. Each of these indices contains a few (4–10) pages of introduction and explanation in addition to the numbered pages.

Six indices to *Mammalian Species* have been published; these are to species accounts numbered 1–100, 1–200, 1–300, 1–400, 101–200, and 201–306. Except for the indices to accounts numbered 1–300 and 1–400, which lack author indices, each index contains systematic, generic, and author lists. These accounts were distributed to subscribers with fascicles containing appropriately numbered accounts.

In April 1981, the American Society of Mammalogists published a limited edition of a pamphlet titled "*Career trends and graduate education in mammalogy,*" by Gary W. Barrett and Guy N. Cameron. An announcement of the availability of publication and a notice of publication of a quarterly newsletter for graduate students appeared in the comments and news section of the *Journal of Mammalogy* (62:875, 1981).

In June–July 1985, the American Society of Mammalogists cosponsored with the Australian Mammal Society publication of a special issue (volume 8, numbers 3 and 4) of *Australian Mammalogy* containing papers presented at symposia at the 1984 joint meeting of the two societies in Sydney, New South Wales, Australia. Number 3 contained six papers from a symposium titled "Niche spaces and small mammal communities"; number 4 contained papers from two symposia: "A" titled "Form-function analyses: the teeth and skulls of carnivores" with five papers, and "B" titled "Studies in the biology of bats" with nine papers. Each of the three sections was edited by a different pair of editors: the first by Barry Fox and Roger A. Powell, the second by Roger A. Powell and Michael Archer, and the third by Leslie S. Hall and Suzanne J. Hand. Each section also included a preface in which one of the editors summarized and synthesized material presented by the participants. Lastly, an envelope attached inside the back cover contains a microfiche with appendices to a paper in the niche–space symposium and contains abstracts of other papers presented at the joint meeting. The issue of *Australian Mammalogy* (volume 8, numbers 3 and 4, 1985) was available from the secretary-treasurer of the American Society of Mammalogists for $10 for those attending the joint meeting and $15 for others.

For several years, the secretary-treasurer has published brochures that contain lists and descriptions of Special Publications and *Mammalian Species* accounts with appropriate order forms. Another brochure titled "*The science of mammalogy*" includes a description and a brief history of mammalogy in North America and of the American Society of Mammalogists. Lastly, a brochure titled "*Careers in mammalogy*" contains brief descriptions of the types of work that mammalogists do and of career opportunities in mammalogy. The latter two brochures were produced by the Committee on Education and Graduate Students. All of the brochures are revised or updated from time to time.

## Acknowledgments

Thanks are due L. N. Carraway and L. F. Alexander for assistance with the analyses. This is Technical Paper No. 10,041, Oregon Agricultural Experiment Station.

## Literature Cited

Anderson, S., and J. K. Jones, Jr. 1984. Introduction. Pp. 1–10, *in* Orders and families of Recent mammals of the world (S. Anderson and J. K. Jones, Jr., eds.). John Wiley & Sons, New York, 686 pp.

Anderson, S., and R. G. Van Gelder. 1970. The history and status of the literature of mammalogy. BioScience, 20:949–957.

Gill, A. E., and W. C. Wozencraft. 1994. Committees and annual meetings. Pp. 155–170, *in* Seventy-five years of mammalogy (1919–1994) (E. C. Birney and J. R. Choate, eds.). Special Publication, The American Society of Mammalogists, 11:1–433.

Jones, J. K., Jr., R. S. Hoffmann, D. W. Rice, C. Jones, R. J. Baker, and M. D. Engstrom. 1992. Revised checklist of North American mammals north of Mexico, 1991. Occasional Papers, The Museum, Texas Tech University, 146:1–23.

Kirkland, G. L., Jr., and H. D. Smith. 1994. Membership and finance. Pp. 170–178, *in* Seventy-five years of mammalogy (1919–1994) (E. C. Birney and J. R. Choate, eds.). Special Publication, The American Society of Mammalogists, 11:1–433.

# COMMITTEES AND ANNUAL MEETINGS

AYESHA E. GILL AND W. CHRIS WOZENCRAFT

*Publications*
*Life Histories*
*Study of Game Mammals*
*Anatomy and Phylogeny*
*Bibliography*

## Introduction

The first meeting of the ASM was held 3–4 April 1919 in Washington, D.C., 2 years after the end of World War I. This was the year that Prohibition, the 18th Amendment to the United States Constitution, was ratified and that the great Mexican leader, Emiliano Zapata, was killed. This organizational meeting was attended by 60 members of a charter membership of over 250. After discussion and approval of by-laws and a constitution, six officers and 10 councilors (now called the Board of Directors) were elected. An editor was selected for the society's *Journal of Mammalogy* that was to start publication that year. Five standing committees were formed: Publications, Life Histories of Mammals, Study of Game Mammals, Anatomy and Phylogeny, and Bibliography. The policy of the society set forth at its organizational meeting was "to devote its attention to the study of mammals in a broad way, including life histories, habits, evolution, palaeontology, relations to plants and animals, anatomy, and other phases." The annual dues were $3 (Kirkland and Smith, 1994).

ASM currently (1993) has nearly 4,000 members residing in 60 countries. The society has held a general membership meeting every year since 1919 except for 2 years during World War II (1943 and 1944), when only the directors met. General membership meetings have been held in Washington, D.C., Canada, Mexico, and 30 states of the U.S. ASM has had 38 presidents between 1919 and 1993 (Layne and Hoffmann, 1994). During this period, 74 volumes of the *Journal of Mammalogy,* 10 *Special Publications* and close to 450 *Mammalian Species* accounts have been published (Verts and Birney, 1994). New standing and ad hoc committees were formed and old ones phased out; the current number of standing committees is 23.

Hartley H. T. Jackson, a young staff member of the U.S. Biological Survey, played a prominent role in planning for the establishment of the ASM (ASM 50th Anniversary Program, 1969; Hoffmeister, 1969; Hoffmeister and Sterling, 1994).

## History of the Committees of ASM

Many members have served the ASM by actively participating in the work of the society's committees and thus have contributed to its development and vigor. Standing committees have functioned since the inception of ASM to promote the goals of the society through ongoing activities between annual meetings. These committees and their chairpersons are appointed by the president. The committees have a two-fold purpose—to conduct affairs of the society and to accord members the responsibilities and rewards of active participation in it. An ad hoc committee was appointed in 1982 under the presidency of J. Mary Taylor to evaluate the standing committees and explore all facets of their roles in the society. Past and present members of standing committees and other members of the society were contacted with questions pertaining to the committees. Through their responses, the ad hoc committee compiled detailed reports on standing committees, including their history, function, effectiveness, and recommendations of committee members on the continued need and role of each committee. These reports are sent to members of the committees so that they can have a better understanding of the committee's purpose and how to serve on it effectively. Shorter descriptions of the functions of the current standing committees were first published as a supplement to Vol. 68, No. 1 (1987) of the *Journal of Mammalogy* ("Roles of Standing Committees of the American Society of Mammalogists"). We have updated the list of Standing Committees of the ASM from its inception to extend it to the present (1993) (Table 1). In addition to the 40 standing committees formed during the society's history, ad hoc committees have been established frequently to perform specific tasks. They cease to exist when their charge is completed. Often, however, a standing committee develops from an ad hoc committee, if a more lasting need for its function is perceived by the Board of Directors. Current standing committees and their members are listed on the inside of the back cover of each issue of the *Journal.*

The standing committees created during the history of ASM can be divided into categories concerned with the promotion of mammalogy, the development of the society itself, or the interactions of ASM with non-mammalogists. Committees have dealt with publications and particular topics in mammalogy (such as physiology and anatomy, ecology, and conservation); some have dealt with taxonomy in general and others with specific taxa. Committees have been created to encourage young mammalogists and to build the society, to honor and reward its outstanding members and other mammalogists, and to record its history. Committees exist to promote the interaction of the society's members with other mammalogists and to present the society's views on critical national and international issues affecting mammalogy. Brief descriptions of the committees involved in each of these areas of activity follow.

*Promotion of mammalogy.*—The original Publications Committee formed in 1919 evolved in 1930 into the Editorial Committee, which remains active. It oversees production of the *Journal of Mammalogy, Mammalian Species,* Special Publications, and miscellaneous publications such as membership lists. It sets editorial policy for the ASM, nominates new editors for approval by the Board of Directors, and manages the publication budget. The committee is composed almost entirely of current editors, who can be divided into two groups: those involved in the review process and judging the scientific merit of papers and those involved in the technical production of the publications. As the *Journal of Mammalogy* grew over the years, the need developed for a committee to prepare the index for each volume. The Index of *Journal of Mammalogy* Committee was formed in 1947, chaired by Viola S. Schantz, who also served the society for 23 years (1930 to 1952) as Treasurer. The name of this committee was abbreviated to Index Committee in 1972. Besides preparing the index for each volume of the *Journal,* it prepares summary indices. The Bibliography Committee, which existed for 67 years, compiled the list of *Recent Literature in Mammalogy* for many years before it ceased to exist. This information is now available through other

TABLE 1.—*Standing committees of the ASM from its inception in 1919 to 1993.*

| Year formed ASM President | Committee | Original chairperson/members | Year ended |
|---|---|---|---|
| 1919 C. H. Merriam | Publications | G. S. Miller, Jr./E. A. Preble, W. P. Taylor, H. H. T. Jackson | 1930 |
| | Life Histories of Mammals | C. C. Adams/R. M. Anderson, V. Bailey, H. C. Bryant | 1927 |
| | Study of Game Mammals | C. Sheldon/G. B. Grinnell | 1922 |
| | Anatomy and Phylogeny | W. K. Gregory/J. C. Merriam, H. H. Donaldson, A. Wetmore, H. von W. Schulte, J. W. Gidley | 1948 |
| | Bibliography | T. S. Palmer/W. H. Osgood, H. H. T. Jackson | 1985 |
| 1920 C. H. Merriam | Conservation | W. H. Osgood/E. W. Nelson, J. Dwight | 1922 |
| 1921 E. W. Nelson | Marine Mammals | E. W. Nelson/G. S. Miller, Jr., T. S. Palmer, B. W. Evermann, R. C. Murphy, G. M. Allen | active |
| | Economic Mammalogy | A. K. Fisher/W. B. Bell, H. C. Bryant | 1953 |
| 1922 E. W. Nelson | J. A. Allen Memorial | M. Grant/H. F. Osborn, C. Frick, G. B. Grinnell, H. E. Anthony | 1929 |
| 1927 G. M. Allen | Life Histories and Ecology | W. P. Taylor/C. S. Adams, V. Bailey | 1947 |
| | Conservation of Land Mammals | E. A. Preble/J. C. Phillips, T. S. Palmer | active |
| 1928 G. M. Allen | Nomenclature | W. H. Osgood/G. M. Allen, A. H. Howell, G. S. Miller, Jr., T. S. Palmer | active |
| 1930 W. Stone | Editorial | E. A. Preble/G. M. Allen, A. H. Howell, R. Kellogg, G. S. Miller, Jr., G. B. Wislocki | active |
| | Membership | W. P. Harris, Jr./T. Gregory, V. Bailey, R. M. Anderson, M. R. Thorpe, J. Dixon, W. P. Taylor | active |
| 1945 R. Hall | Special Committee on Trapping Methods | W. E. Sanderson/C. C. Adams, E. A. Preble, W. A. Young | 1947 |
| 1947 R. Kellogg | Ecology (including life histories and populations) | D. L. Allen/F. S. Barkalow, Jr., C. D. H. Clarke, W. J. Hamilton, Jr., J. M. Linsdale | 1948 |
| | Economic Mammalogy and Conservation | E. R. Kalmbach/D. L. Allen, R. M. Anderson, A. E. Borell, H. J. Coolidge, T. I. Storer, C. T. Vorhies | 1948 |
| | Index of Journal of Mammalogy | V. S. Schantz/H. H. T. Jackson, D. H. Johnson, R. Kellogg | 1972 |
| 1950 T. I. Storer | Means for Encouraging Young Mammalogists | D. E. Davis/F. S. Barlow, Jr., P. D. Dalke | 1951 |
| | Dues Status of Retired Members | A. R. Shadle/J. K. Doutt, R. I. Peterson | 1951 |
| 1953 W. H. Burt | Honoraria for Graduate Students | W. R. Eadie/F. S. Barkalow, Jr., S. D. Durrant, R. T. Orr | active |
| 1956 W. B. Davis | Resolutions | K. R. Kelson/E. T. Hooper, W. V. Mayer, S. D. Durrant, G. C. Rinker | active |

TABLE 1.—*Continued.*

| Year formed ASM President | Committee | Original chairperson/members | Year ended |
|---|---|---|---|
| 1957 W. B. Davis | Honorary Membership | W. H. Burt/E. R. Hall, W. J. Hamilton, Jr. | active |
| 1960 S. D. Durrant | International Relations | A. De Vos/W. O. Pruitt, Jr., H. M. Van Deusen | active |
| 1962 E. T. Hooper | Anatomy and Physiology | L. C. Dearden/K. L. Duke, M. Hildebrand, P. H. Kurtzsch, P. R. Morrison, W. B. Quay | 1983 |
| 1966 R. G. Van Gelder | Historian | D. F. Hoffmeister | 1986 |
| 1971 J. N. Layne | Grants In Aid | J. S. Findley/R. Horst, H. M. Van Duesen, J. L. Wolfe | active |
| 1971 J. N. Layne | Program | B. E. Horner/L. N. Brown, O. P. Pearson, M. H. Smith, H. M. Van Duesen | active |
| 1972 J. K. Jones, Jr. | Information Retrieval | S. Anderson/L. de la Torre, H. H. Genoways, R. S. Hoffmann, C. Jones, D. R. Patten, J. L. Patton, H. W. Setzer | active |
| | Index | D. E. Wilson/R. D. Fisher, C. Jones, J. L. Paradiso, R. H. Pine, H. W. Setzer, R. W. Thorington, Jr. | active |
| | Systematic Collections | J. R. Choate/J. H. Brown, E. T. Hooper, M. L. Johnson, C. Jones, J. L. Patton, T. A. Vaughan | active |
| 1974 S. Anderson | Merriam Award | J. K. Jones, Jr./C. C. Black, W. H. Burt, J. F. Eisenberg, M. E. Hight, T. A. Vaughan, J. Whittaker | active |
| 1976 W. Z. Lidicker, Jr. | Legislation and Regulations | H. H. Genoways/M. M. Alexander, S. Anderson, M. A. Bogan, J. R. Choate, R. C. Dowler, C. A. Hill, A. M. Johnson, C. Jones, T. J. McIntyre, J. L. Paradiso, R. L. Peterson | active |
| 1977 W. Z. Lidicker, Jr. | Jackson Award | R. L. Peterson/W. H. Burt, J. S. Findley, D. F. Hoffmeister, C. Jones | active |
| | Mammal Slide Library | J. A. Lackey/P. V. August, S. J. Bleiweiss, P. L. Dalby, D. C. Gordon, H. L. Gunderson, J. G. Hall, G. C. Hickman, L. L. Master, J. S. McCusker, G. L. Tweist | active |
| 1978 R. S. Hoffmann | Education and Graduate Students | G. W. Barrett/A. E. Baker, G. N. Cameron, A. F. DeBlase, S. R. Humphrey, K. A. Shump, Jr. | active |
| 1982 J. M. Taylor | Checklist | K. Koopman/J. H. Calaby, F. Dieterlen, R. S. Hoffmann, J. H. Honacki, J. G. Mead, G. G. Musser, P. Myers, R. W. Thorington, Jr. | active |
| 1986 D. E. Wilson | Archives | D. F. Hoffmeister, Historian; W. C. Wozencraft, Archivist | active |
| 1989 E. C. Birney | Development | S. R. Humphrey/S. Anderson, J. R. Choate, H. H. Genoways, W. Z. Lidicker, Jr., R. L. Peterson, D. J. Schmidly, J. M. Taylor, R. G. Van Gelder, M. R. Willig, D. E. Wilson | active |

TABLE 1.—*Continued.*

| Year formed ASM President | Committee | Original chairperson/members | Year ended |
|---|---|---|---|
| 1990 E. C. Birney | Animal Care and Use | T. H. Kunz/R. J. Baker, T. Carter, J. R. Choate, J. A. Cranford, G. Glass, I. F. Greenbaum, L. R. Heaney, G. R. Michener, T. H. McIntyre, D. K. Odell, R. S. Ostfeld, A. Pinter, V. Scheffer, S. D. Thompson, R. A. Van Den Bussche | active |

Source: *Journal of Mammalogy,* Volumes 1–73, Supplement to Vol. 68, No. 1 (1987).
Summary: In 1993, 23 active ASM committees, 17 extinct.
See Layne and Hoffmann (1994) for additional information on presidents.

means, such as computerized literature searches.

The Mammal Slide Library Committee was established in 1977 to provide low-cost slides of mammals, often in natural habitats, principally for educational purposes. It now also stresses use of its slides for worldwide conservation efforts. The committee solicits, selects, and catalogs slides, and advertises their availability to potential users world-wide. By 1993 over 1,000 different slides depicting 756 species in 19 orders were available. Over 100,000 duplicate slides were sold between 1978 and 1993.

Many of the ASM committees that dealt with specific topics in mammalogy no longer exist. These include the Life Histories of Mammals Committee (1919–1927), which evolved into the Life Histories and Ecology Committee (1927–1947) and finally into the Ecology Committee (including life histories and populations) (1947–1948). One committee focused on morphology, the Anatomy and Phylogeny Committee (1919–1948), and again in 1962–1983 (Anatomy and Physiology) but, although lasting for much of the society's history, is no longer in existence. One special topics committee has proved remarkably resilient. The Marine Mammals Committee, established in 1921 when the society was just 2 years old, is still functioning. It provides the society membership with information about marine mammalogy, including conservation and legislative issues, spearheads resolutions and legislation involving marine mammals, and serves as a liaison between ASM and the Society for Marine Mammalogy (SMM). Committee members frequently are active in both ASM and SMM. The committee is particularly active on legislative issues regarding marine mammals.

Several of the society's committees have been concerned with economic mammalogy and conservation, of which one still exists. The earliest of these committees, the Study of Game Mammals, was initiated in 1919 and lasted only 4 years; the Conservation Committee (1920–1922) also was short-lived. The successor to these committees, however, lasted much longer. The Committee on Economic Mammalogy lasted 33 years (1921–1953). The Committee on Economic Mammalogy and Conservation had a brief life (1947–1948), but the Committee on Conservation of Land Mammals, established in 1927, is one of the oldest active committees of the society. It monitors state, national, and international governmental activities and other activities that relate to conservation of land mammals, and it advises officers and members of the society on issues of concern. The committee responds to these issues via formal resolutions to the membership, letters to responsible individuals or agencies, and other appropriate means. It serves as a clearinghouse for information, leads or facilitates collective or individual responses to conservation issues, and, in a related function, establishes and maintains liaison with other conservation groups. Conservation always has been a concern of the society and, today, with the increasing loss of genetic variability in the world, remains a major concern.

The society has four active committees concerned with taxonomy and systematic collections. The earliest, the Nomenclature Committee, was formed in 1928 to give advice to members of ASM on problems pertaining to nomenclature and to answer any taxonomic questions that members might pose. About 1977 the committee also assumed an advisory relationship with the International Commission of Zoological Nomenclature. It screens applications involving North American mammals to ascertain whether the facts as presented are both correct and complete and provides an opinion on what the general effect of the requested ruling will be on taxonomic and nomenclatural practice.

The Systematic Collections and the Information Retrieval Committees both were formed in 1972. The former was an outgrowth of an ad hoc committee established at the request of the National Science Foundation to evaluate mammal collections for support by the NSF Biological Research Resources Program. The original charge included advising the society on matters pertaining to systematics and systematic collections and reviewing criteria for appraising collections. It also reviewed proposals submitted to granting agencies for monetary support of systematic collections. The present role of the committee focuses on the general objective of promoting proper maintenance of systematic collections. The committee has established minimal standards for proper maintenance of collections, and it serves, on behalf of the society, as an informal inspecting and accrediting agency for the curatorial status of collections. It also is responsible for surveys of collections of Recent mammals published periodically in the *Journal of Mammalogy.*

The birth of the Information Retrieval Committee is indicative of the revolution that has occurred in information-retrieval systems and computers. Its original charge was to examine the feasibility of developing a national data-retrieval system for Recent mammal collections and, if possible, to develop funding for such a system. The committee's activities have involved developing standardized documentation and retrieval methods, producing a publication on automatic data processing, and providing information on computerization of mammal collection data. The evolving interests of the committee include, but expand beyond, collection-based information to bibliographic data and other natural-history data bases in mammalogy.

The Checklist Committee was established in 1980 to provide advice on *Mammal Species of the World,* edited by J. H. Honacki et al. (1982) and published by Allen Press and the Association for Systematics Collections. The first edition was prepared by 189 professional mammalogists from 23 countries and was coordinated by the Checklist Committee, with R. S. Hoffmann as the Project Coordinator. During the last 10 years it has become the international standard for mammalian taxonomy. The dynamics of mammalian taxonomy demand periodic updates of this vast amount of information. ASM and the Checklist Committee assumed responsibility for the maintenance of this data base and its periodic revisions. The committee serves as both scientific consultant to editors and final arbitrator of nomenclatural, or other, decisions on content. The material has been transferred from a text-based manuscript to an information retrieval data base to facilitate future updates and to enhance the ability of the user to interactively access this information. The second edition of *Mammal Species of the World* (Wilson and Reeder, 1993) was published in cooperation with the Smithsonian Institution Press.

*Development of the society.*—The society has established five committees to encourage young mammalogists, and four of these are still extant. The Committee on Honoraria (originally Honoraria for Graduate Students), formed in 1953, selects graduate students to be honored for their research in mammalogy. At present, three awards are given: the Anna M. Jackson, the A. Brazier Howell, and the American Society of Mammalogists awards. Recipients are awarded an honorarium to attend the annual meeting, where they present results of their research at a plenary session. The Grants-in-Aid Committee was created in 1971 to solicit applications and select recipients for grants-in-aid of research and a nominee for the Albert R. and Alma Shadle Fellowship in Mammalogy. The grants are presently given to 11 students, with a monetary limit of $1,000 per student. The highest ranking student is honored with the B. Elizabeth Horner Award and gets a bonus of $100. The Shadle Fellowship, usually about $3,000, is awarded annually by the Buffalo Foundation and is intended to promote a professional career for a mammalogy student showing great promise. The ASM Grants-in-Aid Committee nominates the student and an alternate. Nominees for this award do not have to be members of the ASM but must be citizens of the United States. The recipient of the Shadle Fellowship is invited to speak on his or her research at an annual ASM meeting.

The Committee on Education and Graduate Students was formed in 1978, with the purpose of assisting students of mammalogy to make more informed choices of career, to improve their scientific expertise, and to find employment in the discipline. These aims are achieved through preparation of brochures and reports and through sponsoring of workshops related to education of mammalogists, career opportunities, research support, and other topics of interest to students. The Development Committee began as an ad hoc committee in 1989. It has raised monies for the Future Mammalogists Fund, established by R. L. Peterson in 1985, through a variety of means, including contributions to patron membership ($1,000), the Seventy-five Year Club ($75), and other individual contributions. The initial goal of raising $100,000 for the Fund was achieved in 1991. In 1993, at the recommendation of this committee, the Board of Directors initiated a major program of planned giving, including living trusts, pooled income funds, and wills and bequests.

The Membership Committee and the Program Committee are instrumental in maintaining the society. The Membership Committee was established in 1930 to encourage persons with an interest in mammals to become members of the society. In recent years an emphasis has been placed on making new members feel "at home" in the society and encouraging retention of members through writing welcoming letters to new members, pursuing any problems in the mailing of journals, and writing to 2-year delinquents to determine their reasons for dropping membership. In 1990–1991 the committee wrote to non-member authors who submitted manuscripts to the *Journal* (171 persons), inviting them to join the society; 14% of them did, accounting for 6% of the new members at that time.

The Program Committee was established in 1971 in response to the need for a more effective method of selecting sites for and improving the organization of the annual meeting. It promotes the annual meeting and assists in its organization and conduct. This committee selects the basic format of the meeting, solicits, reviews, and selects symposia and workshops, and develops guidelines to increase the effectiveness of presentation of papers and posters. It also explores possibilities for special meetings, such as joint meetings with other mammal societies, and participates in planning the content and format of such meetings. It advises local committees and provides liaison between successive local committees. The Program Committee constantly re-evaluates the organization of annual meetings, based on the accumulated experiences of local host committees.

The society takes pride in honoring individuals who have made outstanding contributions to mammalogy and has set up a number of committees to evaluate and select these outstanding mammalogists.

The Honorary Membership Committee was formed in 1957 to recommend candidates for honorary membership in ASM in recognition of distinguished service to the science of mammalogy, but honorary members have been chosen since the first meeting of the society, when Joel A. Allen was selected (Hoffmeister, 1969). The committee is comprised of the five most recent past presidents with the chair held for a 2-year period by the second-most senior member. The C. Hart Merriam Award was established in 1974 to provide recognition for outstanding contributions to mammalogy by a member of the society. It was named in honor of one of the foremost early North American mammalogists, who also was first president of the society. The award is now given in recognition of excellent scientific research and either education of mammalogists or service to mammalogy (Anonymous, 1992). Nominations for the Merriam Award are open to all mammalogists, regardless of country or membership in ASM. The Jackson Award Committee was established in 1977 to provide recognition of persons who have rendered long and outstanding service to the society. The committee evaluates nominations received and, based on supporting documentation, makes its recommendation of a recipient to the Board of Directors. These awards need not be made each year, as they are reserved for truly worthy candidates.

The position of Historian was created in 1966 when it was realized that important historical material of value to the society was not being preserved. Donald F. Hoffmeister has served as the society's historian since the inception of this committee. The material originally was preserved in the Museum of Natural History, University of Illinois, but in 1986 the decision was made to move all materials to the care of the Archives of the Smithsonian Institution. At that time the Archives Committee was formed, consisting of Hoffmeister, who continued as Historian, and W. Chris Wozencraft as Archivist. The archives include information on annual meetings; minutes of board meetings and business meetings; photographs of past presidents, honorary members, and some other award recipients; an official set of the *Journal of Mammalogy* and other society publications; and a variety of miscellaneous materials, including correspondence of many past presidents.

*Interactions of ASM with the broader society.* —Throughout its history, ASM has assumed a responsible role in expressing its views on issues relating to mammals and mammalogists, partly by means of resolutions passed by the membership of ASM. A Resolutions Committee was established in 1956 primarily to avoid the problem of hastily submitted and poorly drafted last-minute resolutions on subject matter of direct concern to the society. The purpose of this committee is to provide a mechanism for the society to express its views and to try, collectively, to influence local, national, and world issues relating to mammals. These views are expressed in the form of resolutions proposed by ASM committees or members, or, sometimes, initiated by the Resolutions Committee itself, which reviews proposed resolutions with the proposers and other knowledgeable persons to ensure their accuracy and appropriateness. The committee decides through which agencies or channels to send resolutions that have been approved by a majority vote of the membership. Reports of this committee are available in the abridged minutes of ASM meetings in issue number 4 of each volume of the *Journal of Mammalogy.*

A partial listing of resolutions passed by ASM is available from the archivist. Conservation issues have been and remain an overriding concern of ASM and this is reflected in its resolutions. Conservation and protection of large mammals especially, such as cetaceans, carnivores, and artiodactyls, have been the subject of many resolutions.

The society consistently has urged the protection of national parks, threatened habitats, and endangered species and populations, including recent resolutions on the conservation of biological diversity and support for the National Institute for the Environment. It has opposed the use of inhumane methods of predator control and those that poison the environment. The society has advocated forcefully the humane treatment of mammals in the wild and in captivity, with resolutions ranging from opposition to den hunting to destroy wolves in Minnesota and Wisconsin to support for humane and professional maintenance of mammals in captivity. An ad hoc committee on Animal Care and Welfare updated acceptable field methods and proper laboratory care in the collection and use of wild mammals in research and teaching. This committee became the standing committee on Animal Care and Use in 1992. The society has taken a stand against scientific creationism, supported biological surveys and studies of threatened populations and of the effects of animal introductions, and has hailed the establishment of new societies such as the Mexican Society of Mammalogists (1984) and the Society for Marine Mammalogy (1984).

ASM also acts through its Legislation and Regulations Committee, established in 1976, to bring its expertise to bear on this area. The committee was established in response to the need for monitoring and providing input into the rapidly burgeoning state and federal legislation and regulations in such areas as endangered species, steel-trapping regulations, and use of animals for experimental purposes of direct concern to mammalogy. The committee also interacts with the legislative monitoring group of AIBS. Members of the committee are familiar with federal and state agencies and operations and they attend agency hearings when necessary.

The International Relations Committee was formed in 1960 to maintain and enhance communication between ASM and mammalogists outside North America. It is truly an international committee with many of its members living outside North America. It maintains liaisons with counterpart societies overseas, participates in the International Theriological Congresses (ITC), which it helped initiate, and organizes joint meetings with other societies. ITC has held meetings in Russia, Czechoslovakia, Finland, Canada, Italy, and Australia. Joint meetings have been held with mammal societies in Australia, Argentina, and China. The International Relations Committee maintains names and addresses of mammal societies and mammalogists throughout the world. It facilitates exchange of material on mammalogy, encourages foreign colleagues to attend annual ASM meetings, and fosters good relations between mammalogists internationally. Members outside North America provide a link for international activities and serve as representatives of ASM in their own countries.

## *The History of ASM Annual Meetings*

*Population dynamics.*—The membership of the ASM quickly grew from its initial 252 members, breaking the 1,000 mark in 1930, but throughout the 1930s and most of the 1940s the number of members returned to a range between 800 and 900 (Hoffmeister, 1969). In 1948 the membership again exceeded 1,000, passed 2,000 in 1963, and topped 3,000 in 1968; in recent years the membership figures have hovered around 3,700 (Secretary-Treasurer's annual report, 1993). There presently are five categories of membership in ASM: annual (at $30 one of the best bargains in any professional society), life (currently $750), patron (currently $1,000), honorary, and emeritus. Emeritus membership was established in 1951 for persons who had regular membership in the society for 25 years or more, were in good standing, and requested such membership (Hoffmeister, 1969). In 1993, ASM had 636

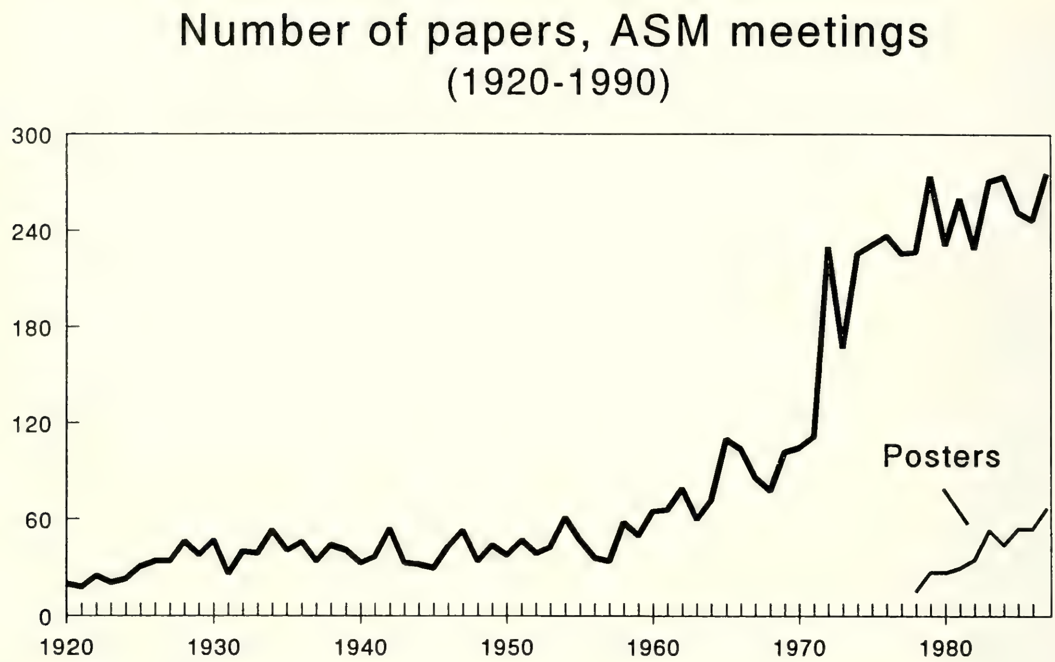



FIG. 1.—The number of papers and posters presented at ASM meetings, 1920–1990.

life, 16 patron, 13 honorary, 147 emeritus, and 2,938 annual, for a total of 3,750 members.

The number of papers and, more recently posters, presented by persons attending annual meetings has remained relatively constant over the years at 42–55% of the total number of registered participants. Although the general trend has been an increase in the number of papers presented, mirroring the increase in membership, this increase was gradual during the first four decades, increased more rapidly in the fifth decade, and increased dramatically in the mid-1970s (Fig. 1). There was a doubling of the number of papers in the first half of the 1970s, a high that was maintained from that time on, with active participation of graduate students becoming a major factor in oral and, later, poster presentations and greatly affecting the atmosphere and emphasis of the meetings.

The membership of ASM always has been skewed toward males. It is difficult to obtain a reliable estimate of the sex ratio of biologists at annual meetings, so two approximate methods were employed here. The number of females in annual meeting photographs was counted, although this method has the bias of including some non-members. This was especially a factor for some of the earlier meetings, where non-members frequently appeared with their spouses for the photographs. This estimate was compared to the number of papers presented at annual meetings for which the first author was female (Fig. 2). Although women have increased significantly in a society that was essentially male (with active support from wives) at the beginning, in 1991 they still constituted only 20–30% of the membership and were first authors on about the same percentage of papers. This increase in the number of women has occurred principally since the early 1970s and largely as a result of an influx of female graduate students, corresponding to the dramatic increase in the number of graduate students, in general, participating in meetings. Only one of the 38 presidents of the ASM (through 1993) has been a woman, J. Mary Taylor, who was elected in 1982 (Layne and Hoffmann, 1994). Four of the chairpersons of

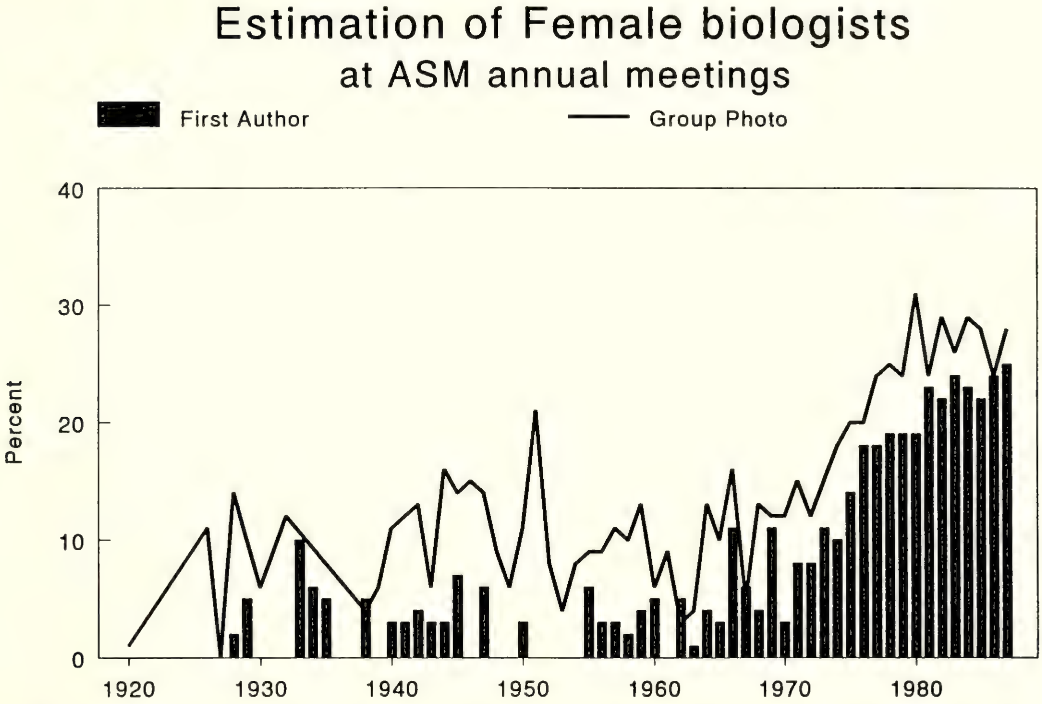



FIG. 2.—Estimation of the number of female biologists at ASM annual meetings, based on the first author of papers presented (bar graph) and the group photo (line drawing).

the 23 current standing committees of the society are women, lower than the percentage of women in the society.

An ad hoc committee on Women and Minority Issues is currently functioning and it is hoped that its activities will facilitate greater involvement of women and minorities in leadership positions in the society in the future. Even more stark than the skewed sex ratio of ASM members is the obvious lack of visible minority members in ASM. We do not have figures on minority membership in ASM, but it is minimal as judged by those attending annual meetings, where the participants are predominantly white. Minority membership in ASM may reflect low numbers of minorities in mammalogy in the U.S. This immediately suggests the urgency of outreach by ASM to attract minority students to the study of biology.

*Geographic distribution.*—Throughout its history, ASM has attracted mammalogists from all states of the U.S. as well as from Canada and Mexico. Nearly all states typically are represented at each annual meeting. Representation of each state and Canada and Mexico was determined by noting the home region of the first author of each paper at annual meetings (Fig. 3, Table 2). Canadians have participated in notable numbers since the founding of the society. During its 70-year history, 10 states, listed in decreasing order, have accounted for half of the participants at annual meetings: California, New York, Texas, Michigan, District of Columbia, Kansas, Massachusetts, Illinois, Florida, and New Mexico. This reflects the strong foundation of the society in mammalian systematics collections, as these 10 states also contain the 10 largest collections in North America. It was not until the 21st meeting in 1939 that an annual meeting was held at an institution not dominated by a large museum, and, during the first 50 meetings, more than two-thirds

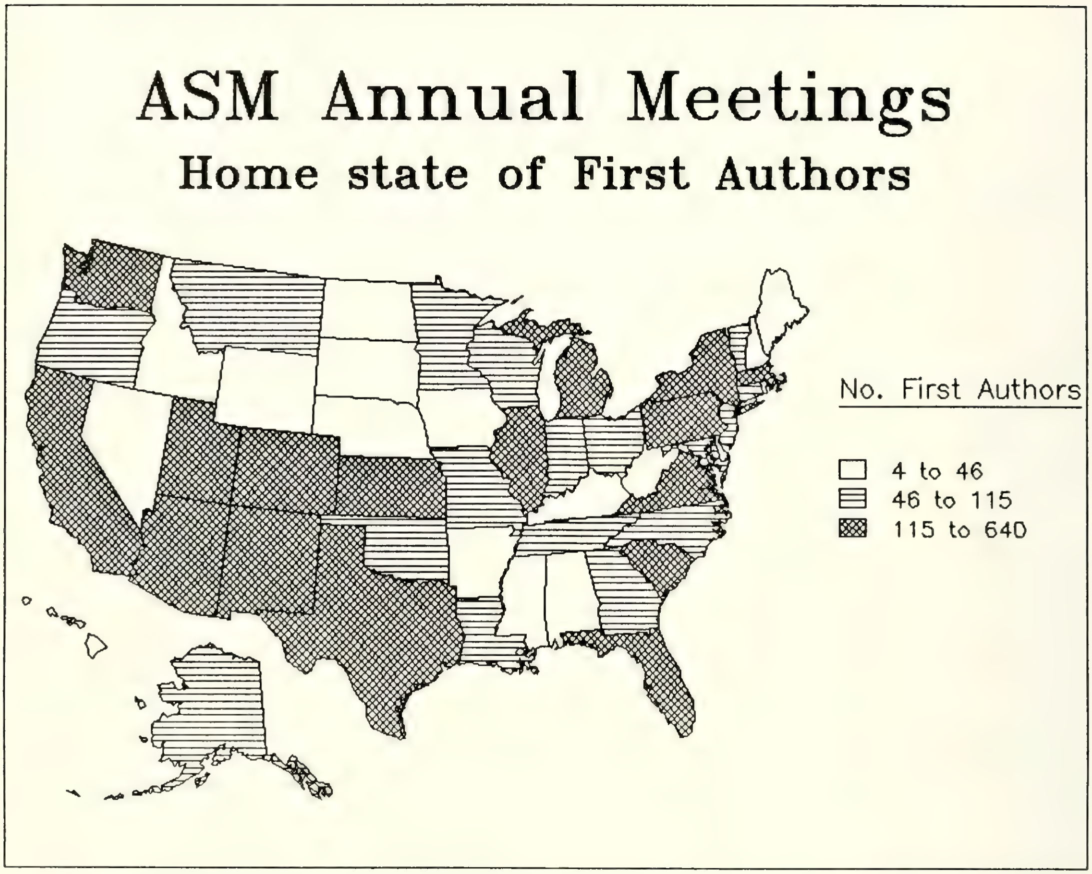



FIG. 3.—Map of the distribution in the U.S. of first authors of papers given at ASM annual meetings, 1920–1990.

of the meetings were held in association with large systematics collections. Since the mid-1960s this trend is less noticeable, with a gradual shift away from "museum" institutions to more general academic settings. When started, the society was principally an East Coast organization, with only one of the first 20 meetings held west of the Appalachians. By the third decade, states from the Far West and Midwest were having a much greater influence at society meetings. The states with the fewest representatives at annual meetings are Alabama, Arkansas, Delaware, Idaho, New Hampshire, Rhode Island, West Virginia, Nevada, Hawaii, and Maine. Meetings have been rotated throughout the United States for many years, with only two areas, the Northern Great Plains states (no meetings) and the southern U.S. (seven states have not hosted meetings) being under-represented. A map of the states that have hosted annual meetings closely resembles the map of the home state of first authors (Fig. 3), with the states heavily represented there all having hosted meetings. Geographic rotation of the meetings contributes significantly to participation by graduate students, who may find it difficult to attend distant meetings.

*Topical and taxonomic emphasis of papers at annual meetings.*—The 51st annual meeting of the society at the University of British Columbia in 1971 established the format for annual meetings that has been used since: organized around topics, with a plenary session and concurrent sessions

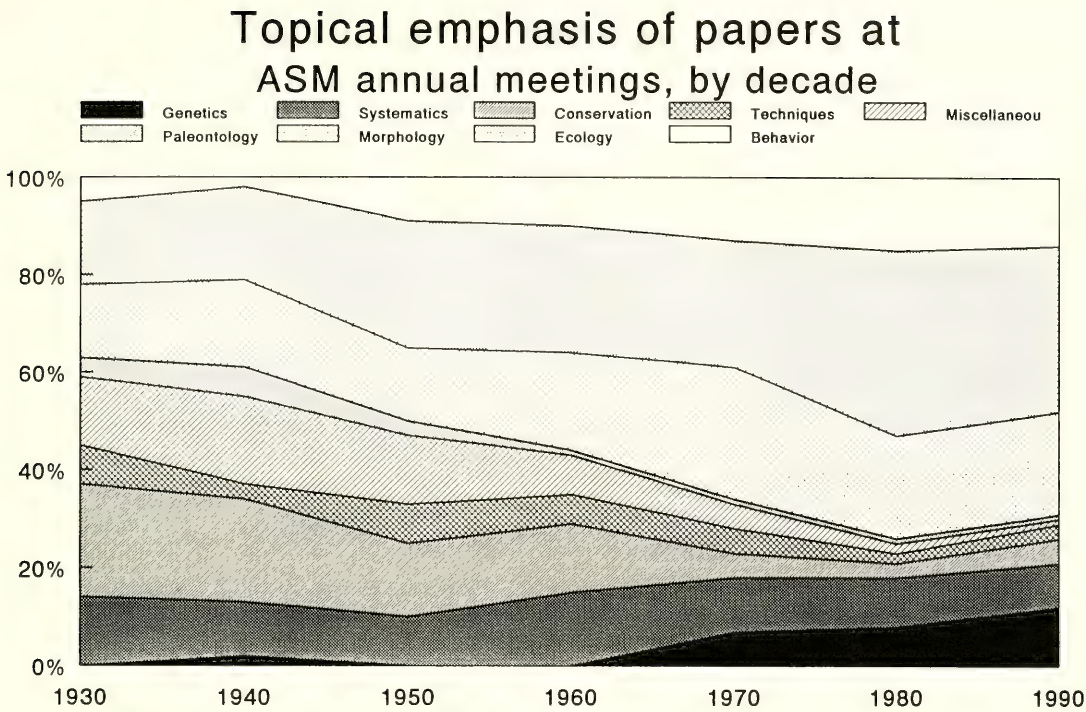



FIG. 4.—Topical emphasis of papers given at ASM annual meetings, by decade, 1920–1990 (key: 1930 represents papers from 1920–1929, etc.).

throughout the meeting. The topical emphasis of papers at ASM annual meetings was examined, based on the titles of papers in the program of the annual meetings. Papers were placed in one of nine categories: genetics (including all types of biochemical analysis); systematics (including evolution and geographic variation); conservation (only those papers specifically identified as dealing with conservation); techniques; paleontology (papers dealing with fossil taxa); morphology (including reproductive biology, physiology, and anatomy); ecology (including community and population); behavior; and a catch-all field, miscellaneous, for all papers that could not be assigned clearly to one of the above categories or that cut across several topics.

Several trends can be seen from changes in the relative representation of these categories during the last 70 years (Fig. 4). Early in our society's history, broadly based papers that covered a variety of topics were

TABLE 2.—*Ranked sequences by largest numbers of presentations of the 10 political units listed as address of first authors on papers and posters listed in the program at ASM annual meetings 1920–1990. Political units included were U.S. states and the District of Columbia (U.S. postal zip code abberviations), Canada (CD), Central America, and Mexico (the latter two not yet in top 10).*

| | Meeting numbers (number of political units represented by first authors) | | | | | | |
|---|---|---|---|---|---|---|---|
| Rank | 1–10 (11) | 11–20 (26) | 21–30 (35) | 31–40 (39) | 41–50 (49) | 51–60 (50) | 61–70 (54) |
| 1 | DC | NY | NY | CA | CA | CA | CA |
| 2 | NY | DC | MI | MI | NY | MI | TX |
| 3 | PA | MI | CA | NY | MI | NY | KS |
| 4 | CT | CA | DC | IL | IL | CD | NY |
| 5 | MA | MA | TX | CD | CD | KS | FL |
| 6 | MD | PA | CD | UT | TX | FL | MN |
| 7 | CD | MD | PA | CO | CO | IL | CD |
| 8 | MI | CD | IL | AZ | LA | SC | MA |
| 9 | KS | IN | KS | DC | SC | MN | MI |
| 10 | VT | WA | MD | WI | NM | WA | PA |

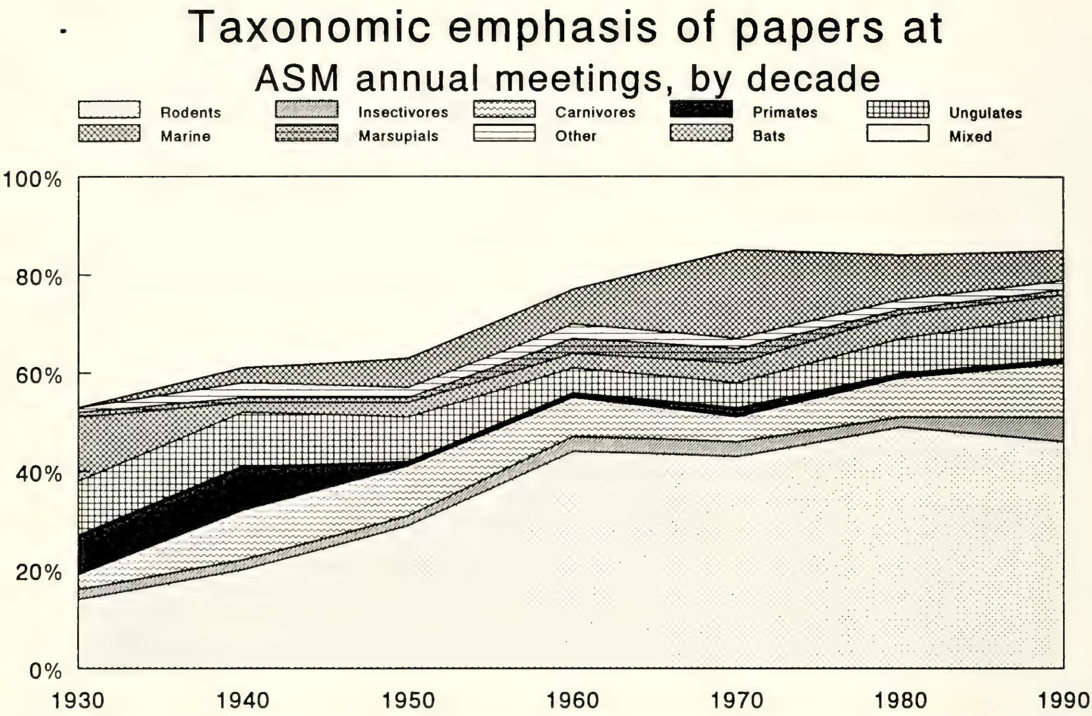



FIG. 5.—Taxonomic emphasis of papers given at ASM annual meetings, decade, 1920–1990 (key: 1930 represents papers from 1920–29, etc.).

a significant component of the meetings (miscellaneous category). As the field has become more specialized, broadly based papers have decreased and are now only a small part of the papers presented at annual meetings. This situation is typical of the increased specialization in society, in general, and of teaching and research in academic institutions, in particular.

One of the dominant foci for the establishment of ASM, which was reflected in titles of papers, was concern for the conservation of mammals. The trend, as illustrated here, reflects a decrease in titles specifically identifiable as conservation issues; however, many of the papers in other categories have implications to the field of conservation biology and could appropriately be presented at conservation meetings. Morphology and physiology have always been a major component of annual meetings; within this category there is a general trend of a decreasing number of anatomy and an increasing number of physiology papers. It appears that most papers on anatomy are now presented within the broader framework of evolutionary or systematic theory. Genetics, a topic present since the earliest days of the society, did not become a significant part of the meetings until the 1970s, increasing with the proliferation of biochemical and molecular techniques in mammalian research. The actual number of papers in this category may be much greater, as many authors may not have used keywords in their titles that would lead to inclusion of their papers in this category; therefore, they were not counted in this survey. Perhaps the most noticeable trend among papers at the meetings is the dominance of ecology and behavior, which started about 1970. Roughly half the papers presented in the last 20 years fall into these two categories. There are other professional societies that overlap with the ASM in covering these two topics, but they have had no noticeable effect on the topical makeup of papers at the mammal meetings.

The taxonomic emphasis of papers at ASM annual meetings also was examined based on titles from annual meeting programs. Papers were placed in one of 10 categories: Rodentia, Insectivora, Marsupialia (sensu lato), Carnivora (excluding pinnipeds), Primates, ungulates (Artiodactyla, Perissodactyla, Proboscidea), Chiroptera, marine mammals (pinnipeds, Cetacea, Sirenia), other (groups not mentioned), and mixed (papers not identifiable with a particular taxonomic group or those that deal with multiple groups). Papers were tallied by decade (Fig. 5).

Several trends can be seen from changes in the representation of these categories during the last 70 meetings. Studies of Rodentia have increased from less than 20% of the total papers to nearly half in the last decade. This category probably would be inflated more if those papers that deal with small mammal ecology in their titles (included here in mixed) were counted. The representation of most other taxonomic groups remained rather consistent over the years, with the notable exception of the Chiroptera and the Primates. Chiroptera were poorly represented in the early meetings, but now are a much larger portion, the number of papers on bats peaking in the 1960s. The Primates were well represented in early meetings but are nearly absent from the later half of the 70-year span. Most poorly represented in terms of taxonomic diversity are Insectivora, generally only included here in the mixed category. Another marked difference between the first and last decade is in the number of papers that cut across taxonomic boundaries or are on topics that are not restricted to specific taxa (e.g., animal welfare, trapping, remote sensing, and the like), which were close to 50% in the 1920s and are less than 20% in the 1980s. We believe that this change is a direct reflection of the increasing specialization of mammalogists throughout this time period, an effect also apparent in the increasing specialization of topics at annual meetings.

During the 70-year period that ASM has had annual meetings, several more specialized societies have developed in which some ASM members have joint membership. Primatologists and physical anthropologists have a professional history as long, if not longer, than ASM and some of the early founders of ASM were drawn from this group. After the first decade, however, perhaps with the initial retirement or withdrawal of the founding primate biologists, the society has failed to attract this subject matter at annual meetings. Three new societies have developed in the last two decades. When bat biologists began to meet on an annual basis, there was a marked decrease in the number of papers on the Chiroptera at the annual meetings. Effects of the newly formed Society for the Study of Mammalian Evolution may have a similar effect on papers in systematics and evolution. When the Society for Marine Mammalogy was formed, however, it did not produce a corresponding drop in the number of papers on marine mammals at ASM meetings.

Many profound changes that affect the lives and work of mammalogists have occurred in the world during the first 75 years of the ASM. In 1927, Charles Lindbergh's historic flight ushered in the age of commercial aviation. Now mammalogists fly all over the globe to conduct research and to interact with colleagues at ITC and other international meetings. The U.S. urban population exceeded the rural in 1920 and another major shift occurred in the 1940s, during World War II. Economic changes that accompanied these and later population shifts, such as new agricultural methods with intensive use of fertilizers, irrigation, pesticides, and herbicides, have had a dramatic impact on the habitats and well being of mammalian populations. The society continues its struggle for the conservation of mammals, meeting these new challenges through the research of its members, education, and activities to influence legislation.

World War II deeply affected the membership of ASM and was the only period during which meetings were not held each year. Major growth in the membership of ASM occurred in the 1950s and 1960s, with an increase in graduate students in the 1970s. The interests, as well as numbers, of ASM members have changed over the decades. There has been increased specialization in teaching and research, and in papers at annual meetings, no doubt mirroring the situation in society at large. The revolution in biotechnology and information systems, although facilitating research and exchange of information, has contributed to this increased specialization. Some events, however, appear cyclic: the teaching of evolution was banned in Tennessee and the "monkey trial" was held in 1925. Now there is a renewed onslaught against the teaching of evolution, to which the society has responded.

Over the past seven and a half decades the society has continued to grow and change. An enduring curiosity about and concern for mammals, a determination to conserve natural habitats, and the plants and animals that live there, and a continuing enjoyment of the work itself, of field biology, and of the fascinating mammals we work with, sustains the fundamental spirit and camaraderie of the ASM.

## *Literature Cited*


Anonymous. 1992. Nominations for the Merriam Award. Journal of Mammalogy, 73:951–952.

Hoffmeister, D. N. 1969. The first fifty years of the American Society of Mammalogists. Journal of Mammalogy, 50:794–802.

Hoffmeister, D. N., and K. Sterling. 1994. Origin. Pp. 1–21, *in* Seventy-five years of mammalogy (1919–1994) (E. C. Birney and J. R. Choate, eds.). Special Publication, The American Society of Mammalogists, 11:1–433.

Honacki, J. H., K. E. Kinman, and J. W. Koeppl (eds.). 1982. Mammal species of the world: a taxonomic and geographic reference. Allen Press, Incorporated and The Association of Systematics Collections, Lawrence, Kansas, 694 pp.

Kirkland, G. L., Jr., and H. D. Smith. 1994. Membership and finance. Pp. 171–178, *in* Seventy-five years of mammalogy (1919–1994) (E. C. Birney and J. R. Choate, eds.). Special Publication, The American Society of Mammalogists, 11:1–433.

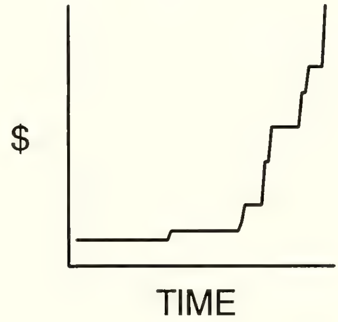
Layne, J. N., and R. S. Hoffmann. 1994. Presidents. Pp. 22–70, *in* Seventy-five years of mammalogy (1919–1994) (E. C. Birney and J. R. Choate, eds.). Special Publication, The American Society of Mammalogists, 11:1–433.

Verts, B. J., and E. C. Birney. 1994. Publications. Pp. 139–154, *in* Seventy-five years of mammalogy (1919–1994) (E. C. Birney and J. R. Choate, eds.). Special Publication, The American Society of Mammalogists, 11:1–433.

Wilson, D. E., and D. M. Reeder. 1993. Mammal species of the world: a taxonomic and geographic reference. 2nd ed. Smithsonian Institution Press, Blue Ridge Summit, Pennsylvania, 1,206 pp.

# *MEMBERSHIP AND FINANCE*

GORDON L. KIRKLAND, JR. AND H. DUANE SMITH




## *Introduction*

The American Society of Mammalogists has a deserved reputation as one of the most fiscally conservative and financially successful scientific societies in North America. The society's current dues of $30 are among the lowest of major professional societies in biology. This reflects in large measure the substantial contribution made each year to the general operating fund by the society's Reserve Fund, which is managed by the society's three trustees. Approximately one-fifth to one-quarter of each year's general operating budget comes from income earned by the Reserve Fund, which had a net value in excess of $1,000,000 on 1 June 1992. Funds transferred to the general operating account represent income derived principally from the investment of life membership payments and special bequests. As we review the membership and financial history of the American Society of Mammalogists during its first 75 years, we will document and salute the foresight of the founding members in terms of establishing the firm financial base upon which the society continues to operate.

## *Membership Classes*

The American Society of Mammalogists has five classes of membership: active, life, patron, emeritus, and honorary. Active members pay annual dues and receive the *Journal of Mammalogy* and other correspondence, such as the "Call for Papers" and program of the annual meeting, from the society.

An individual may become a life member by making a payment equal to 25 times the current annual dues. This may be a single payment or may be made in four equal annual installments. The dues structure for life memberships has remained unchanged since the founding of the society in 1919, at which time annual dues were $3.00 and life memberships were $75.00. Life members receive the *Journal of Mammalogy* for life or until they no longer wish to do so. Life members currently comprise 17% of total ASM membership. By contrast, in 1920 only 2.5% of ASM members were life members. During the succeeding four decades, the percentage of life members fluctuated slightly but had

TABLE 1.—*Pattern of growth in life memberships.*

| Year | Total membership | Life members | % life members |
|---|---|---|---|
| 1920 | 443 | 11 | 2.5 |
| 1930 | 1,005 | 62 | 6.2 |
| 1940 | 898 | 51 | 5.7 |
| 1950 | 1,232 | 49 | 4.0 |
| 1960 | 1,765 | 115 | 6.5 |
| 1970 | 3,315 | 342 | 10.3 |
| 1980 | 3,862 | 530 | 13.7 |
| 1990 | 3,661 | 611 | 16.7 |

TABLE 2.—*Annual dues and subscription rate changes for American Society of Mammalogists.*

| Year | Dues | Subscriptions |
|---|---|---|
| 1919 | $ 3.00 | $ 3.00 |
| 1947 | 4.00 | 4.00 |
| 1952 | 4.00 | 6.00 |
| 1959 | 4.00 | 7.00 |
| 1967 | 4.00 | 9.00 |
| 1968 | 5.00 | 9.00 |
| 1969 | 7.00 | 9.00 |
| 1971 | 7.00 | 11.00 |
| 1974 | 7.00 | 15.00 |
| 1975 | 12.00 | 17.00 |
| 1977 | 16.00 | 17.00 |
| 1978 | 16.00 | 23.00 |
| 1986 | 20.00 | 28.00 |
| 1988 | 23.00 | 33.00 |
| 1993 | 30.00 | 45.00 |

risen only to 6.5% in 1960. Since then, the proportion of life members has increased by about 3% per decade (Table 1). This increase may reflect the desire of many members to save money by becoming life members just before dues increases, which have been more frequent during the past three decades (Table 2).

Patron members are individuals who make a $1,000 payment to the society within a one-year period. Such individuals are entitled to receive the *Journal* and all other ASM publications for life. Although this membership category has existed throughout the history of the society, the first patron membership was not purchased until 1990. Today, patron memberships represent the society's best financial bargain if viewed from the perspective that today's patron memberships can be obtained for the same payment of $1,000 as in 1919. If the cost of patron memberships had kept pace with increases in dues over the past 75 years, patron memberships would cost $10,000.

The emeritus membership category was established in 1951. Individuals who have been active members for at least 25 years may request emeritus membership status. These individuals pay no dues and do not receive the *Journal of Mammalogy,* but they do continue to receive other ASM correspondence. Emeritus members also do not have voting rights at annual meetings.

The highest honor bestowed by the society is honorary membership, which is conferred in recognition of distinguished service to mammalogy. Fifty-eight individuals have been thus honored. These individuals are chronicled in this volume by Taylor and Schlitter (1994).

The American Society of Mammalogists has always had one of the highest benefits to dues ratios among professional societies. Annual dues were $3 in 1919 and have increased to only $30 today. Historically, the society has been reluctant to raise dues, and it has been able to maintain its modest dues because many of the services that other societies pay for are provided to the ASM on a volunteer basis by its members. Thus, ASM dues largely go to pay the costs of publishing the *Journal of Mammalogy.* As a consequence, increases in dues over the years (Table 2) have largely mirrored increases in the costs of publishing the *Journal* (Table 3).

The philosophy that has supported retention of lower dues also has been applied to subscription rates. During the society's first 33 years subscription rates were the same as member dues, but in 1952 the subscription rate was increased to $6 per year while dues remained at $4 (Table 2). There has been a differential between dues and subscription rates since that time. With proceeds from the Reserve Fund subsidizing society services to members, the subscription rate is still comparable in value to the subsidized membership dues. Subscription rates have increased since 1967, when they were $9 per year, to the current $45 per year (Table 2).

## *Membership History*

The American Society of Mammalogists had 252 charter members—i.e., individuals who joined the society in 1919. The first member, based on payment of dues, was Dwight D. Stone (3 April 1919). Ernest Thompson Seton was the first life member and seventh member overall. The first woman member was Viola S. Schantz, who served as the society's treasurer from 1930 to 1953. Annie M. Alexander was the society's first woman life member. The last surviving charter member was Vasco M. Tanner, who died in 1989, 70 years after joining the society.

The society grew rapidly during its early years. Membership more than doubled within the first three years to 527 in 1921 (Fig. 1). The society reached the 1,000-member level (1,005) in 1930. Membership exceeded 1,000 members (1,017) the following year, but the Depression had a significant negative impact on the society's membership, which dropped to 931 in 1932 and reached a low of 770 in 1935 (a decrease of 24% in four years). Membership remained below 1,000 throughout the remainder of the Depression and during the war years (Fig. 1). Numerous ASM members who served on active duty in World War II were carried on the society's books as inactive members during the war years. All such members were required to reactivate their memberships by 31 January 1948 or be dropped from membership. It was not until 1948 that membership again exceeded 1,000 (1,071). Membership grew steadily during the next 15 years, finally surpassing 2,000 in 1963, but it took only five more years to reach 3,000 (3,194 in 1968). This rapid increase in membership corresponded

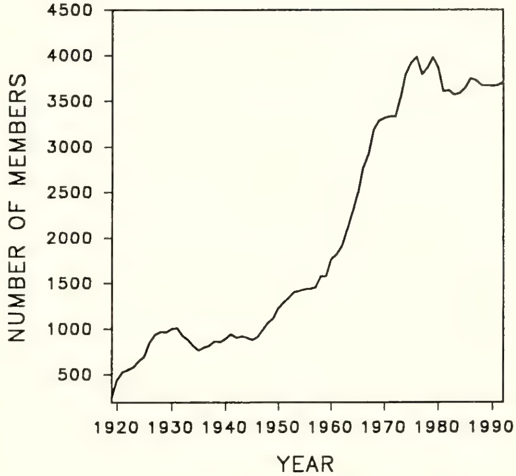



FIG. 1.—Growth in the membership of the American Society of Mammalogists from 1919 to 1992.

to the dramatic expansion of graduate training in the 1960s and the establishment of many new programs in mammalogy by ASM members who received their Ph.D.s during the 1950s and 1960s. Although membership exceeded 3,900 in 1975, 1976, and 1979, it has yet to reach 4,000. During the past decade, membership has stabilized at 3,600–3,700 (Fig. 1).

## *International Membership*

Despite its name, the American Society of Mammalogists is an international scientific organization with a strong contingent of members who reside outside the United States. The international nature of the society's membership dates from its earliest years. For example, the first List of Members published in the *Journal of Mammalogy* (1922, vol. 3, number 3) contained the names of 50 members who resided in 19 countries outside the United States and its territories. These individuals represented 9% of the society's 555 members in 1922. As of October 1992 the society's 718 non-U.S. members comprised 19% of total membership. These non-U.S. members resided in

70 countries. The society's strong international focus is also reflected in the individuals elected to honorary membership in the ASM during its first 75 years. Of 58 individuals thus honored, 17 (29.3%) were non-U.S. mammalogists, including Prof. E. L. Trouessart, Museum d'Histoire Naturelle in Paris, who was the second individual elected to honorary membership in 1921.

The society's International Relations Committee, which was established in 1960, has endeavored during the past decade to coordinate activities with mammal societies in other countries. These efforts have resulted in four joint meetings between the ASM and mammal societies in Australia (1985), Mexico (1987), China (1988), and Argentina (1990). These meetings have provided opportunities for many ASM members in those countries to participate in an ASM activity for the first time.

## *Corresponding Secretary, Treasurer, and Secretary-Treasurer*

From 1919 to 1957 the membership of the society was served by the separate offices of Corresponding Secretary and Treasurer. Eleven individuals held the office of Corresponding Secretary: H. H. T. Jackson (1919–1925), A. Brazier Howell (1925–1931), Francis Harper (1931–1932), Robert T. Hatt (1932–1935), William H. Burt (1935–1938), William B. Davis (1938–1941), Emmet T. Hooper (1941–1947), Donald F. Hoffmeister (1947–1952), Keith R. Kelson (1952–1954), George C. Rinker (1954–1956), and Bryan P. Glass (1956–1957). Six of these individuals (Jackson, Howell, Burt, Davis, Hooper, and Hoffmeister) subsequently served as presidents of ASM. The tenures of treasurers were longer and only five individuals held this position: Walter P. Taylor (1919–1920), J.W. Gidley (1920–1921), Arthur J. Poole (1921–1930), Viola S. Schantz (1930–1953), and Caroline A. Heppenstall (1953–1957). Walter P. Taylor subsequently served the society as its president.

In 1957 the offices of Corresponding Secretary and Treasurer were combined into a single office of Secretary-Treasurer in order to conduct the business affairs of the expanding society more efficiently. To date, four individuals have held this office: Bryan P. Glass (1957–1977), Duane A. Schlitter (1977–1980), Gordon L. Kirkland, Jr. (1980–1986), and H. Duane Smith (1986–present).

The Secretary-Treasurer is the chief administrative officer of the ASM and is responsible for the society's day-to-day operations. Duties include managing the society's general operating account and the accounts for *Mammalian Species* and Special Publications, maintaining membership records, corresponding with ASM members and others seeking information or assistance, printing and mailing the "Call for Papers" and the program for the annual meeting, assisting with preparation of the annual budget, arranging for the annual audit for the society's financial records, sending mailing labels for the *Journal of Mammalogy* and *Mammalian Species* to the printer, processing orders for Special Publications, and distributing copies of the resolutions passed at the annual meetings.

## *Reserve Fund*

The founders of the society showed exceptional foresight in establishing a mechanism to invest life and patron membership dues and gifts to the society in a permanent fund, some of the income from which was to be used to subsidize various functions of the society. This provision was incorporated in the society's first By-laws and Rules adopted in April 1919. The year 1922 marked the first major initiative to develop the permanent fund, namely the J. A. Allen Memorial Fund. The initial goal of that fund was $10,000. The campaign to achieve that goal was supervised by the J. A. Allen Me-

TABLE 3.—*Growth of the Reserve Fund and contributions to the general operating budget (values rounded to nearest whole dollar).*

| Year | Value of Reserve Fund | Reserve Fund contribution to annual budget | Reserve Fund contribution as % of Reserve Fund |
|---|---|---|---|
| 1930 | $ 11,070 | $ 500 | 4.5% |
| 1940 | $ 23,235 | $ 500 | 2.2% |
| 1950 | $ 53,517 | $ 1,500 | 2.8% |
| 1960 | $124,747 | $ 3,751 | 3.0% |
| 1970 | $208,603 | $11,506 | 5.5% |
| 1980 | $475,370 | $20,234 | 4.3% |
| 1990 | $809,376 | $39,000 | 4.8% |

TABLE 4.—*Relationship between funds transferred by the Reserve Fund to support the general operating account and funds transferred to the Reserve Fund for investment.*

| Decade | Mean annual transfer to general operating account (A) | Mean annual transfer to Reserve Fund (B) | Ratio of A to B |
|---|---|---|---|
| 1930s | $ 470.00 | $ 549.10 | 0.86 |
| 1940s | $ 670.00 | $ 747.10 | 0.90 |
| 1950s | $ 2,300.60 | $1,720.90 | 1.34 |
| 1960s | $ 6,489.10 | $2,278.20 | 2.85 |
| 1970s | $16,865.90 | $5,386.00 | 3.13 |
| 1980s | $27,553.50 | $4,790.60 | 5.75 |

morial Committee. The first contributions to the fund, by W. D. Matthew, T. G. Pearson, J. T. Nichols, B. S. Bowdish, and C. W. Richmond, totalled $105.00. The Allen Fund grew rapidly. The value of the fund was $6,335.42 in 1924, $7,606.12 in 1925, $8,525.24 in 1926, and $9,156.01 in 1927. With the fund at $9,975 in 1928, a special collection was taken among members attending the annual meeting to raise $25, with the following contributing: A. Brazier Howell, H. H. Lane, Carl Hartman, C. C. Adams, Lee R. Dice, M. W. Lyon, Jr., R. T. Hatt, H. C. Raven, and A. W. Leighton. The fund officially reached its goal on 9 April 1929 when the fund totalled $10,465.27. Two hundred and seventy-three contributors had given $8,428.78, with the difference of $1,848.90 representing interest and bond coupons. Upon achieving its goal, the Allen Memorial Committee was dissolved and the funds subsequently were managed by the society's trustees.

In 1923, the by-laws were amended to provide for three trustees to administer the permanent fund. Trustees are elected by the Board of Directors and serve three-year, rotating terms. The first three trustees were Henry Bannon, Childs Frick, and Charles Sheldon. Thanks to the efforts of these and subsequent trustees, the Reserve Fund has experienced sustained growth during the past 70 years. In general, the value of the Reserve Fund has doubled each decade (Table 3). As the value of the Reserve Fund has grown, the amount of money transferred to the general operating account has increased; however, when figured as a percentage of the net value of the Reserve Fund, the amount transferred annually has remained relatively constant, fluctuating between 2.2 and 5.5% (Table 3).

Each year, funds are transferred between the Reserve Fund and the society's general operating account. Money transferred to the fund accrues principally from life membership payments. The average amount transferred annually to the Reserve Fund increased from the 1930s through the 1970s but decreased slightly in the 1980s (Table 4). During the 1930s and 1940s the amount transferred annually to the Reserve Fund exceeded the amount received annually from the fund to support operations of the society, specifically publication of the *Journal of Mammalogy*; however, since then the amount transferred to the general operating account has exceeded the amount annually transferred to the Reserve Fund (Table 4). Throughout the past 60 years, the ratio of funds received from the Reserve Fund compared to money transferred from the general operating account to the Reserve Fund has increased steadily, so that in the 1980s more than five times as much was received from the Reserve Fund as was transferred to it (Table 4).

TABLE 5.—*Growth of the Future Mammalogists Fund, 1985–1992.*

| Year | Balance | Year | Balance |
|---|---|---|---|
| 1985 | $ 4,938 | 1989 | $ 69,090 |
| 1986 | 34,720 | 1990 | 71,644 |
| 1987 | 51,468 | 1991 | 92,204 |
| 1988 | 60,637 | 1992 | 128,000 |

Davis (1969) prepared a comprehensive history of the Reserve Fund on the occasion of the society's 50th anniversary. He examined the growth of the "Permanent Fund" on a decade by decade basis and provided a more detailed analysis of the finances of the fund, including the composition of the fund's portfolio by decade and strategies for investing the society's funds in light of the prevailing economic climate.

The American Society of Mammalogists has always been concerned about the science of mammalogy and about providing opportunities for its members. In 1985, this concern led the society to establish the Future Mammalogists Fund with the goal to raise a minimum of $100,000 for investment. Interest from this investment will support young mammalogists who are just getting started professionally. The fund-raising efforts of the members and wise investments by the trustees have been very successful. Reference to Table 5 shows that the fund began slowly with a balance of $4,938 in 1985, but has grown rapidly in recent years, surpassing the original goal between 1991 and 1992. The 1992 balance, $128,000, constituted 13% of the society's Reserve Fund. The proceeds are now being used to support young mammalogists from around the world.

## *ASM Budgets*

Traditionally, the bulk of the society's annual operating budget has been devoted to publishing the *Journal of Mammalogy*. The budgeted cost of publishing the *Journal* (including production costs, editorial expenses

TABLE 6.—*Comparison of the annual budgets of the American Society of Mammalogists and the costs of publishing the* Journal of Mammalogy *by decade.*

| Decade | Mean annual budget | Mean annual cost of producing *Journal** | Cost of *Journal* as % of budget |
|---|---|---|---|
| 1920s | $ 2,741.50 | $ 2,440.00 | 89.0% |
| 1930s | 3,080.56 | 2,755.56 | 89.4% |
| 1940s | 3,600.00 | 3,240.00 | 90.0% |
| 1950s | 11,817.86 | 9,800.00 | 83.0% |
| 1960s | 23,108.70 | 18,765.70 | 81.2% |
| 1970s | 76,306.80 | 65,222.40 | 85.5% |
| 1980s | 150,957.30 | 116,443.90 | 77.1% |
| 1990s | 161,693.33 | 119,133.33 | 73.7% |

* Includes costs of printing, distribution, editorial expenses, editorial honoraria, preparation of the index and Recent Literature in Mammalogy.

and honoraria, and costs incurred by the bibliography and index committees) has risen from $1,600 in 1920 to $122,000 in 1992 (a 7,525% increase). During that period, dues increased from $3.00 to $23.00 (a 667% increase). The cost of publishing the *Journal* averaged about 90% of the society's annual budgets during its first three decades (Table 6). In the 1950s annual budgets increased substantially (228%) compared to the preceding decade, whereas the cost of publishing the *Journal* increased 202% (Table 6). This difference reflected increased costs of running the society's executive office and a broader scope of society expenditures, including funds for graduate student honoraria and dues to affiliate societies (e.g., membership in AIBS). As a consequence, in the 1950s expenditures for publishing the *Journal* averaged 83% of the annual budget. This percentage remained about the same in the 1960s (Table 6); however, the society's budgets in the 1960s averaged about twice those of the preceding decade, as did costs of publishing the *Journal of Mammalogy* (Table 6). In the 1970s, both average annual budgets (230% increase) and costs of publishing the *Journal* (248% increase) more than doubled. As a consequence, the percentage of the annual budget devoted to publishing the *Journal* during the 1970s increased to 85.5%.

The first budget in excess of $100,000 was approved for 1977. There was less than a two-fold increase in budgets and costs of publishing the *Journal* in the 1980s with the percentage contribution of publishing the *Journal* declining to 77% (Table 6). During the first three years of the 1990s, budgets have increased little over those for the 1980s (Table 6).

## Summary

Members of the American Society of Mammalogists can take singular pride in the financial history of their society. Today's members benefit from the financial acumen and foresight of the society's founding members. In terms of its finances, the ASM is a model for other scientific and professional societies, who in the past have contacted the society's executive office for advice on financial matters. Members of the ASM not only belong to the oldest and largest scientific society devoted to the study of mammals, they are members of a society whose astute and prudent financial management over the years has made it one of the "best buys" among professional societies.

## Acknowledgments

We thank staff members of the Smithsonian Archives, especially W. Cox, for facilitating access to the society's historical files. We also thank W. C. Wozencraft for his assistance in locating ASM archival materials.

## Literature Cited

Davis, W. D. 1969. The American Society of Mammalogists permanent fund: a special report of the trustees. Pp. 33–40, *in* The American Society of Mammalogists 50th anniversary celebration. Processed by the American Museum of Natural History, New York, New York. 44 pp.

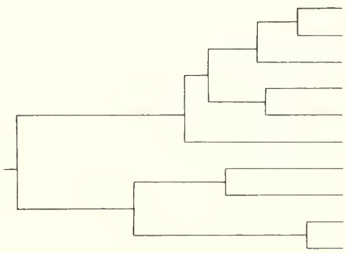
Taylor, J. M., and D. A. Schlitter. 1994. Awardees. Pp. 71–109 *in* Seventy-five years of Mammalogy (1919–1994) (E. C. Birney and J. R. Choate, eds.). Special Publication, The American Society of Mammalogists, 11: 1–433.

# PART II

## INTELLECTUAL DEVELOPMENT OF THE SCIENCE OF MAMMALOGY

# *TAXONOMY*

MARK D. ENGSTROM, JERRY R. CHOATE, AND HUGH H. GENOWAYS



## *Introduction*

Taxonomy has been termed the "theory and practice of classifying organisms" (Mayr and Ashlock, 1991:2), whereas systematics is the broader study of the history and diversity of life. In practice, in distinction between these disciplines is often blurred. In this review, we focus on the role of taxonomy and taxonomists in the development of the discipline of mammalogy in North America over the past 75 years, although we occasionally will slip into broader discussions of systematics where it has influenced the philosophical underpinnings of taxonomy. For purposes of discussion and in practice, taxonomy also can be divided conveniently into two levels: *microtaxonomy*—the methods and principles by which species are recognized and delimited; and *macrotaxonomy*—the methods and principles by which recognized kinds of organisms are classified (Mayr, 1982).

## *Historical Perspective*

Development of mammalian taxonomy in North American was a natural consequence of exploration of the continent. Many of the early descriptions of new mammals from the East were made by Linnaeus and his contemporaries based on specimens returned to Europe from the American colonies. Some of the most important taxonomic contributions by American authors were taxonomic catalogues (reviewed by Hoffmeister and Sterling, 1994). However, American naturalists were largely responsible for taxonomic investigations resulting from exploration of the West, beginning with the Lewis and Clark expedition and culminating with the expeditions of Major Stephen Long, Zebulon Pike, Thomas Say, Maximilian Prince of Wied-Neuweid, John C. Fremont, and numerous others. The taxonomic products of those expeditions included such monumental catalogues as Baird's (1857) report on the mammals of North America, Coues and Allen's (1877) review of North American rodents, Elliot's (1904) checklist of mammals of North America and the West Indies, and Mearns' (1907) Mammals of the Mexican boundary of the United States.

Most of the taxonomic collections made by naturalists of the 19th Century were returned to museums in the East, notably the Charleston Museum, Peale's Museum in Philadelphia, Museum of Comparative Zoology at Harvard College, American Museum of Natural History in New York, United States National Museum, Chicago Academy of Sciences, and Field Museum of Natural History in Chicago. Taxonomists associated with those museums were among the leaders in development of the science of mammalogy, as were naturalists associated with the most influential universities of the day: Harvard, Yale, Michigan, Cornell, California, and others. California was especially important because it was there that Joseph Grinnell had begun a dynasty of mammalogists that persists even today (Jones, 1991; Whitaker, 1994).

However, the most productive group of North American mammalogists of the day by far were those associated with the Bureau of the Biological Survey, the progenitor of the U.S. Fish and Wildlife Service (described by Hoffmeister and Sterling, 1994). Authors of monographic revisions published by bureau employees in its *North American Fauna* series read like a who's who of North American mammalogy in the years preceding the origin of the ASM: Vernon Bailey; Edward A. Goldman; Ned Hollister; A. Brazier Howell; Arthur H. Howell; Hartley H. T. Jackson; C. Hart Merriam; E. W. Nelson; Wilfred H. Osgood; Edward A. Prebel. Of the monographs published before 1919, Osgood's (1909) revision of the genus *Peromyscus* arguably has stood the test of time better, and has stimulated more taxonomic studies, than any other.

The ASM came into being at a time when much of the work of North American mammalogists was directed at understanding the diversity of mammals on the continent. Most of the founding fathers of ASM were thus taxonomists, and taxonomists subsequently have had a greater influence on the society than have mammalogists of any other subdiscipline.

For North American taxonomists from the mid-1800s until about the turn of the century, the predominant species concept was typological—species were held to be nearly fixed entities that varied about a finite number of types. By this concept, rooted in the classical philosophy of European systematics, species were delimited subjectively based on relative degree of morphological difference and consisted of aggregations of individuals that agreed with the author's diagnosis. There was little appreciation of the distinction between variation due to gender, age, or individual and geographic differentiation. During this period, most new forms were described as species despite the fact that the category of subspecies was already in common use in ornithology. Designation of morphologically distinct forms as species was understandable in that most early collections consisted of specimens from widely separated localities and the concept of geographic variation was poorly understood. The extensive collections amassed under the auspices of the Bureau of the Biological Survey (among others), however, eventually demonstrated the pervasiveness of geographic variation and intergradation among many nominal "species." Gradually, the practice of sorting apparently distinctive specimens into species was replaced by a broader view of species as interrelated groups of populations united by reproductive ties. Taxonomists shifted from describing and classifying objects (specimens) to attempting to describe the living diversity of populations that those specimens represented. Perhaps the most notable early example of this shift was Osgood's (1909) revision of *Peromyscus*. Osgood reduced the number of recognized species of deer mice from 130 to 43 (see review by Carleton, 1989) and, in one instance, combined 28 nominal species into the taxon he recognized as *Peromyscus maniculatus*. Many of the former species names were retained as formal subspecies, and the practice of recognizing polytypic species (consisting of two or more subspecies), in use since the late 1800s, thus became entrenched.

Change from a typological or strict morphological concept of species to recognition of polytypic species composed of morphologically distinct, intergrading subspecies was gradual and was not universally accepted by the time of formation of the ASM in 1919. For example, the first issue of the

*Journal of Mammalogy* contains a staunch defense of a morphological species concept by Merriam (1919). He stated (p. 7) that "the *criterion of intergradation* is one of the most pernicious that has ever been introduced into the systematic study of animals and plants . . ." and, quoting a previous article in *Science* (p. 9), "forms which differ only slightly should rank as subspecies even if known not to intergrade, while forms which differ in definite, constant and easily recognized characters should rank as species even if known to intergrade." This philosophy, coupled with samples inadequate to demonstrate the full range of intra- and interpopulational variation, led him (Merriam, 1918) to recognize two genera and 78 species of brown bears, all now considered to represent a single species (Hall, 1984). Interestingly, a rejoinder by Taverner (1920: 126) in the first volume of the *Journal of Mammalogy* advocated the essentials of what later would become known as the biological species concept: "the species is a definite entity and its essential quality is its genetic isolation."

Many of the taxonomy publications of the 1920s were by employees of the Bureau of the Biological Survey; however, the most important taxonomic catalogue of the period was by Gerrit S. Miller, Jr. (1924), Curator of Mammals at the U.S. National Museum, who updated his earlier (Miller, 1912) list of North American mammals. Several taxonomic revisions were published during this decade, most notably those by A. B. Howell (1926, 1927), Jackson (1928), Miller and Allen (1928), and A. H. Howell (1929). Most of the taxonomic publications of the period were monographic in extent.

Taxonomic work in the 1930s was dominated less than that of the previous decade by employees of the Bureau of the Biological Survey. An increasing number of mammalogists at academic institutions and at museums other than the United States National Museum began to have an impact. One of the most important taxonomic revisions of the period was the monograph on squirrels by A. H. Howell (1938). Other revisionary studies emanated from the Field and American museums of Natural History and dealt largely with Latin American mammals (e.g., Sanborn, 1937; Tate, 1933). During this decade, there was an increasing tendency for taxonomic work to be less than monographic in extent and to focus on individual species rather than genera or higher categories (e.g., Nelson and Goldman, 1933).

Most North American mammalogists would agree that the taxonomic highlight of the 1940s was Simpson's (1945) *The Principles of Classification and a Classification of Mammals.* Few generic revisions were published during the decade, as an increasing number of taxonomic studies focused on geographic variation within species (e.g., Hooper, 1943).

The 1950s was a watershed decade for mammalian taxonomy in North America. An important taxonomic catalogue (*North American Recent Mammals,* by Miller and Kellogg, 1955) was published early in the decade only to be overshadowed by another (*The Mammals of North America,* by Hall and Kelson, 1959). Hall and Kelson's monumental two-volume work quickly became a veritable landmark in mammalogy in that it summarized everything then known about the distribution and taxonomy of native mammals in North America. Much of the explosion of taxonomic research (especially on relationships within genera and geographic variation within species—see discussion of subspecies, beyond) was a direct result of studies leading to or stimulated by publication of this epic monograph. In place of faunal studies, numerous taxonomic revisions were published during the 1950s. Some of the best known of those revisions were by Goldman (1950), Hall (1951), Hoffmeister (1951), Hooper (1952), Handley (1959), Moore (1959), and Van Gelder (1959). The number of studies of variation within species continued to climb, that by Findley (1955) serving as an example.

The explosion of taxonomic literature on North American mammals that began in the 1950s continued in the 1960s. Taxonomic catalogues published during the decade included those of Hershkovitz (1966) on living whales, and Anderson and Jones (1967) on mammals of the world. Taxonomic revisions continued to be numerous, a few examples being those of Lidicker (1960), Packard (1960), Russell (1968*a*, 1968*b*), Davis (1968, 1969, 1970), Musser (1968), and Lawlor (1969). Increasingly, these revisions were of small genera and were less than monographic in length—a phenomenon possibly resulting in part from the increasing difficulty in finding outlets for lengthy, monographic manuscripts.

The 1970s witnessed publication of few taxonomic catalogues (one example being Varona's 1974 catalogue of Antillean mammals), but a large number of both "Mammals of . . ." books and taxonomic revisions. A sample of the many taxonomic revisions of the period includes those by Choate (1970), Findley and Traut (1970), Zimmerman (1970), Genoways and Jones (1971), Hooper (1972), Pine (1972), Smith (1972), Thaeler (1972), Birney (1973), Gardner (1973), Genoways (1973), Carleton (1977), Eger (1977), Hennings and Hoffmann (1977), Yates and Schmidly (1977), Hoffmeister and Diersing (1978), Williams (1978), Carleton and Eshelman (1979), Hafner et al. (1979), Silva-Taboada (1979), and Williams and Genoways (1979). By the end of the decade, new techniques for taxonomic analysis (Baker and Hafner, 1994; Honeycutt and Yates, 1994) and changing priorities at academic institutions and funding agencies were beginning to take a toll on faunal studies and taxonomic revisions, often relegating both to the category of long-term, low priority projects.

The 1980s began with publication of Hall's (1981) long-awaited update of *The Mammals of North America.* As noted by Jones (1982:718) in his review of this monumental taxonomic catalogue, "It is unlikely that any other American mammalogist would have undertaken, or will undertake again, such a gigantic task." Another useful catalogue published during the decade was Anderson and Jones' (1984) revised synopsis of mammals of the world. During the previous decade, an enthusiastic cadre of young mammalian taxonomists had begun developing in Mexico, and the 1980s were marked by the beginnings of taxonomic products from this group (e.g., Arita and Humphrey, 1988; Ceballos and Galindo, 1984; Ramírez-Pulido et al., 1986). It seems likely that a substantially greater percentage of the taxonomic papers on Latin American mammals will be authored by Latin American mammalogists in decades to come. Finally, the decade was marked by Koopman's (1984) classification of bats and a multitude of taxonomic reviews, many of the latter employing genetic techniques or focusing on species or species groups. A few examples were the studies by Carleton (1980), Huckaby (1980), Engstrom and Wilson (1981), George et al. (1981), Patton and Smith (1981), Patton et al. (1981), Honeycutt and Williams (1982), George et al. (1982), Griffiths (1982), Hafner (1982), Rogers and Schmidly (1982), Heaney and Timm (1983), Baker (1984), van Zyll de Jong (1984), Sullivan (1985), Sullivan et al. (1986), Webster and Handley (1986), Baker et al. (1988), George (1988), Robbins and Sarich (1988), Voss (1988), Baker et al. (1989), Carleton and Musser (1989), van Zyll de Jong and Kirkland (1989), and Wozencraft (1989*a*, 1989*b*).

The 1990s show promise of a continuation of the existing emphasis on microtaxonomic studies employing modern genetic methods plus development of a much greater emphasis than in the past on macrotaxonomy. Early examples of the research that will characterize the decade include the studies by Patton and Smith (1990), Hafner (1991), Johnson and George (1991), Rogers and Engstrom (1992), and Wall et al. (1992).

## *Biological Species Concept*

The empirical demonstration of species as natural aggregates of populations delineated from related species by reproductive

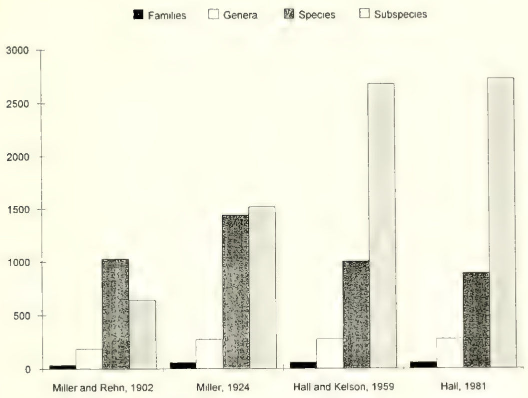



FIG. 1.—Total number of families, genera, species, and subspecies of North American mammals recognized as valid in major taxonomic summaries of the 20th Century.

gaps led to formulation of a biological species concept: "Species are groups of interbreeding natural populations that are reproductively isolated from other such groups" (Mayr, 1969:26). Viewing species as natural, objective entities rather than classes of objects had its genesis in the late 1700s and was accepted by ornithologists and ichthyologists by the turn of the century. Mammalogists were more conservative, but the concept (with its common recognition of polytypic species) had taken hold by the 1920s. Coupled with this philosophical shift was the ascendancy of the neo-Darwinian school of "new systematics" (Huxley, 1940), led by R. A. Fisher, J. B. S. Haldane, S. Wright, T. Dobzhansky, E. Mayr, G. G. Simpson, V. Grant, and others from the 1930s through the 1960s. This philosophy reasserted the fundamental importance of taxonomy and systematics. With its concern for microevolutionary processes underlying intraspecific genetic variation and the generation of diversity, this school focused on issues of population genetics, geographic variation, and speciation. Several classic generic revisions of mammals were written during this period, with an emphasis on discerning patterns of geographic variation and taxonomic limits of species rather than on primary descriptions.

Abandonment of a typological or strict morphological concept and recognition of geographically variable, polytypic species, led to a clarification and simplification of the classification of North American mammals at the species level. In the 35-year period between 1924 and 1959, the 1,441 species of North American mammals admitted by Miller (1924) were reduced to 1,003 (Hall and Kelson, 1959), despite the description of numerous new, valid species (Figs. 1 and 2). This led Hall and Kelson (1959:vi) to remark that "The decrease in number of species results from many of the named kinds having been reduced from specific to subspecific status in the past thirty years. Certainly the number of species listed in the present work is still too large, many geographically adjacent pairs of nominal species will prove to be only subspecies of one and the same species when adequate specimens are studied from geographic areas between the known areas of occurrence of the two kinds." Unfortunately, the descriptive efforts of some mammalian taxonomists soon were directed to the formal recognition of taxa below the level of species, and an explosion of new subspecies ensued (see following section on subspecies). Conversely, from 1902 to 1924 the number of recognized genera and families increased by a factor of about one-half, due mostly to a less inclusive view of higher taxa; this number has remained relatively stable since that time (Fig. 1).

In the enthusiasm for polytypic species as a taxonomic device to address the problem wrought by the proclivity of some early taxonomists to name every local variant as a species, application of the biological species concept sometimes was overly conservative. In the never-ending search for real or inferred intergrades, several subtle but distinct species were subsumed under the headings of single species. Thus, Merriam's (1919:7) admonition rings true: "it [the criterion of intergradation to delimit species] has often resulted in bringing together forms between which intergradation has not only *not* been demonstrated, but which in many cases never existed . . ." Moreover, some authors came to view any evidence of hybridization as proof of intergradation and conspecificity (see discussion of Hall, 1981, in Patton and Smith, 1990). That the number of distinct species of North American mammals currently is underestimated has become increasingly evident with the application of modern genetic and morphological techniques to studies of geographic variation and speciation. Recent systematic studies often have revealed that many purportedly intergrading taxa actually represent protected, reproductively isolated gene pools (Baker, 1984; Baker et al., 1985; Birney, 1976; Carleton, 1989; Genoways and Choate, 1972; Patton and Smith, 1990; Schmidly et al., 1988; Zimmerman, 1970). The number of recognized species of North American mammals declined from 1,003 to 887 between 1959 and 1981 (Fig. 1), as previously predicted by Hall and Kelson (1959). Between 1981 and 1993 the number decreased again to 866 (Wilson and Reeder, 1993). Included in that total, however, is the long-awaited systematic review of brown bears (Hall, 1984), wherein the number of species was reduced from 78 to 1. Discounting the 77 species names belatedly placed in synonymy by Hall, the number of admitted species actually rose by 56 during this period despite the fact that discovery of hitherto unknown species of mammals slowed to a trickle (Fig. 2). We anticipate that the number of recognized species will continue to rise as our view of species is refined, as more specimens become available, as geographic coverage improves, and especially as multidisciplinary techniques are applied to studies of geographic variation in a wider variety of taxa (see also Carleton, 1989). To the casual observer, these changes probably will appear to result from a frictionless pendulum perpetually swinging between "lumpers" and "splitters." Instead, we would argue that these oscillations represent significant progress in our understanding of the composition and distribution of North American mammals during the past 75 years.

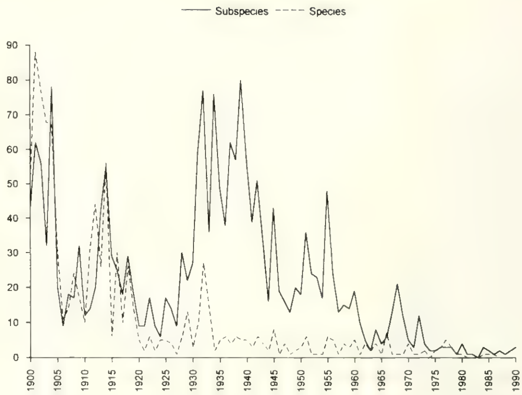



FIG. 2.—Number of species and subspecies of North American mammals described between 1900 and 1990. Data for 1900 to 1977 were compiled from Hall (1981), and those for 1977 to 1990 were taken from *The Zoological Record.*

Although the biological species concept was, and continues to be, the dominant concept applied by North American mammalogists, it is by no means universally accepted. Space precludes a full review of this ongoing debate, but a few comments may be pertinent. For operational reasons, pheneticists dispute the idea that species are objective units bound by reproductive continuity. Instead, they reiterate the nominalist claim that the only objective unit in nature is the individual, and that all collective higher categories (including species) are human constructs (Sokal and Crovello, 1970). This claim appears intuitively false when applied to sympatric species of sexually reproducing taxa, such as mammals or birds (Mayr, 1969). It does, however, highlight the difficulty of applying the biological species concept to allopatric and allochronic populations where the potential for interbreeding and intergradation must be inferred, or in geographically contiguous populations among which gene flow is minimal (Ehrlich and Raven, 1969). In these cases, biological species indeed are subjective constructs, and the erection of polytypic species as a taxonomic device runs the risk of underestimating or misrepresenting the number of independent evolutionary units. More recently, Wiley (1978, 1981) restated Simpson's (1961) concept of evolutionary species. "An evolutionary species as a single lineage of ancestor-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate" (Wiley, 1981:25). This concept stresses that species are bound by unique common ancestry, whether or not reproductive continuity is evident, and adds the missing element of common evolutionary history to the biological species concept (Brooks and McLennan, 1991). This broader definition provides a conceptual means of delineating natural species, although operationally it sometimes is no less subjective than the biological species concept. For example, faced with a monophyletic set of allopatric populations, the taxonomist must now decide if these populations represent a single evolutionary lineage, instead of deciding whether or not they potentially could interbreed. Nonetheless, in our view, this theoretical concept more closely approximates real species-level units (i.e., actual evolutionary units as manifested by the organisms themselves). Its application in mammalogy portends a more realistic view of species-level taxonomy and the process of speciation (but see alternative view in Mayr and Ashlock, 1991). Operational variations on this theme, such as the phylogenetic species concept (Cracraft, 1983; Donoghue, 1985; McKitrick and Zink, 1988) also may prove useful but, strictly applied, run the risk of recognizing all apparently distinctive populations as species and a return to a typological concept (for a recent application, see Engstrom et al., 1992).

## *Subspecies Concept*

The history of the category of subspecies is closely tied to that of species. Subspecies came into regular use in North American mammalogy near the turn of the century, although the formal trinomen had been used by ornithologists since the mid-1800s. Originally conceived as a substitute for the ambiguous term variety (which had been used as a catch-all for a plethora of intra- and interpopulational miscreants), subspecies had the general connotation of geographic race (e.g., Osgood, 1909). As with species, they initially were viewed typologically and were defined on a morphological basis: a subspecies was a set of specimens that differed from another set but not to the same degree as species. The general acceptance of polytypic species, and the potential for intergradation as a means of discerning species-limits, spurred use of the category as a means of characterizing morphologically distinct but intergrading sets of populations.

Application of the trinomen initially was conservative and, until about 1920, about as many subspecies were named as new species (Fig. 2). With the onset of the "new systematics" in the 1930s and its focus on microevolutionary processes, considerable effort was expended by mammalogists in studying patterns of geographic variation, which were formally recognized using the trinomen. Unfortunately, rather than examining the role of geographic differentiation in the generation of diversity, discovery of statistically distinct subspecies soon became a primary goal of some mammalian taxonomists and the "wild-goose chase" (Mayr, 1963:347) to find new subspecies was on. As a consequence, the rate of description of subspecies relative to species rose dramatically during the period from 1930 to 1960 (Fig. 2). The number of recognized subspecies of North American mammals nearly doubled during this time, whereas the number of species decreased by about a third (Fig. 1). These changes reflected both increased acceptance of the utility of subspecies as a taxonomic device and conservative application of a biological species concept.

During this period, different authors had different concepts of subspecies, ranging from subjective geographic divisions of taxonomic convenience to incipient species. For example, Mayr (1969) regarded subspecies as an arbitrary device to facilitate intraspecific classification and not as evolutionary entities, whereas Lidicker (1960) believed that the category should be reserved for phylogenetically delimited subunits of species. Given that subspecies are subjective and at a point in a gradient between local populations and species, the lower-limit of divergence at which they were recognized also varied greatly among authors. As noted by Lidicker (1960:161) "it is axiomatic that populations which consist of different individuals are different. The ability to prove this difference statistically depends only on the size of the samples used and the perceptual ability of the investigator." Nonetheless, some authors (Mayr et al., 1953; Simpson, 1961) advocated a 75% rule—if 75% of the individuals in one population could be distinguished from all individuals of an adjacent population, ensuring a statistically significant difference, the two could be formally recognized as subspecies (presumably based on even a single character). In some species, where localized patterns of geographic differentiation were pronounced, numerous microgeographic races were described. Hence, Setzer (1949) recognized 35 subspecies of Ord's kangaroo rat, *Dipodomys ordii,* many occupying small geographic areas. In perhaps the most infamous example, 213 subspecies of the pocket gopher, *Thomomys umbrinus,* were admitted in Hall and Kelson (1959). This latter case prompted Simpson (1961:173) to remark critically "those who enjoy this game may go on until every little colony of these gophers sports its own Linnaean name." As a mere device for cataloguing geographic variants based on a few or single characters, recognition of subspecies often has little biological meaning and results in formal recognition of rankless groups, with no predictive value relative to additional characters (Barrowclough, 1982). In our view, the largest abuses of the category were made by authors who described subspecies based on small samples from limited geographic areas without a thorough analysis of variation within the entire species.

By 1950, subspecies of North American mammals had become an amalgam of old names not relegated to full synonymy, localized variants, arbitrarily partitioned sections of geographic clines, polytopic and microgeographic races, discrete evolutionary units and, in some instances, subtle but distinct species. Not surprisingly, infraspecific taxonomy of vertebrates came under heavy criticism during a debate on the utility of the category that raged largely in the pages of *Systematic Zoology* for 10 years, sparked by Wilson and Brown (1953). They noted (p. 100), "the subspecies concept is the most critical and disorderly area of modern systematic theory" and advocated that the category be abandoned. For North American mammalogists, among the most influential contributions to this debate were those of Lidicker (1960, 1962), who defined subspecies as (1962:169) "a relatively homogeneous and genetically distinct portion of a species which represents a separately evolving, or recently evolved, lineage with its own evolutionary tendencies, inhabits a definite geographic area, is usually at least partially isolated, and may intergrade gradually, although over a fairly narrow zone, with adjacent subspecies." This restrictive definition has been widely cited although it probably is no coincidence that its most successful applications have been with geomyoid rodents (Genoways, 1973; Lidicker, 1960; Smith and Patton, 1988) in which gene flow among local populations often is restricted, pronounced local microgeographic differentiation is commonplace, and geographic variation is partitioned hierarchically. In other groups for which rates of gene flow are higher and geographic differentiation is less abrupt, taxa fitting the above definition most often would be regarded as distinct evolutionary species.

After this debate, application of the subspecies category in mammalian taxonomy became much more conservative and the rate of description of new subspecies approximated that of species, as it had prior to 1920 (Fig. 1). Thus, between 1959 and 1981, the number of recognized subspecies of North American mammals remained relatively stable (Fig. 2) owing to nearly equal rates of additions (new descriptions) and deletions (relegation to synonymy of existing subspecies). Since 1981, the rate of description of new subspecies of North American mammals has decreased to less than five per year, and there has been a tendency to attach less significance to the category (e.g., Wilson and Reeder, 1993). As an aside, critics of the subspecies category often have branded museum curators as the culprits who use subspecies as a convenient device to aid them in arranging and subdividing groups of specimens in drawers. As curators who have spent many unproductive hours attempting to assign specimens to poorly defined, undiagnosable subspecies, which seem inevitably to be from geographically intermediate areas, we can assure the reader that arbitrarily defined infraspecific taxa are no boon to curatorial efficiency or order.

The current state of the subspecies category in vertebrate taxonomy (and concomitantly of recognized taxa at this level) is muddled. Some authors would abandon the category entirely (Cracraft, 1983; McKitrick and Zink, 1988), whereas several mammalian systematists find a restricted concept useful in formally depicting discrete patterns of geographic variation (e.g., Patton and Smith, 1990). In our view, the real purpose of the trinomen is to describe formally patterns of geographic variation by calling attention to geographic discontinuities among distinctive, evolutionarily discrete subsets of populations. We anticipate that, as detailed multidisciplinary studies of geographic variation are completed for more species, and as a conservative concept of subspecies is consistently employed, the number of recognized subspecies of North American mammals will decline substantially over the coming decades.

## Higher Level Taxonomy

*Schools of systematics and classification.*—After the exploratory phase of taxonomy of North American mammals in the late 19th and early 20th centuries, the focus of studies shifted more towards discerning systematic relationships among species. The new systematics emphasized studies at lower taxonomic levels and down-played phylogenetic research. Thus, during the period from 1930 to 1960 many comprehensive taxonomic studies of North American mammals focused on species and generic level revisions rather than on higher classification. The guiding philosophical basis of this research was the somewhat intuitive school of evolutionary taxonomy championed by E. Mayr, G. G. Simpson, and others. The goal was to discern genealogical relationships among taxa and then to represent both genealogy and extent of phyletic divergence in the final classification. How these factors were to be weighed was up to the discretion of the investigator, and the process was said to be part art and part science (Simpson, 1961). Examples of this approach include Simpson (1945) and Koopman (1984). These classifications were meant to be inherently stable, utilitarian devices, consistent with what was known about evolutionary relationships and magnitude of evolutionary change.

The seeming lack of objectivity of the evolutionary school triggered a change in systematic philosophy through development of the opposed phenetic and phylogenetic schools of systematics in the 1950s and 1960s. These schools were largely responsible for the revival of interest in macrotaxonomy that continues today. Early proponents of phenetics (or numerical taxonomy) suggested that, because genealogies were difficult to reconstruct and phylogenies largely unknown, "natural" higher taxa were most objectively discerned by overall similarity (Sneath and Sokal, 1973; Sokal and Sneath, 1963). This operationalist (theory-free) school is concerned primarily with multivariate, numerical methodologies for representing empirical phenetic relationships, typically weighting all characters equally. The method has its genetic extension in DNA hybridization, where overall similarity between species is calculated from average melting temperatures of hybrid DNA molecules. Exemplary studies in North American mammalogy that employed these techniques (but did not necessarily adhere to a strict view of the philosophy) include those by Findley (1972), Schnell et al. (1978), Freeman (1981), Brownell (1983), Owen (1988), and Kirsch et al. (1993). Criticisms of the use of phenetics in classification include: that overall similarity often gives a distorted view of phylogenetic relationships, especially when shared primitive, convergent, or uniquely derived character states predominate; and that the method, although repeatable using the same characters, produces inherently unstable classifications likely to be altered when new attributes are examined. Although phenetic philosophy for construction of classifications has not been widely accepted in mammalogy, numerical methodology for analyzing patterns of variation, particularly at the microtaxonomic level, has become an integral part of the repertoire of techniques used by mammalian taxonomists.

At about the same time as the development of phenetics, the school of phylogenetic systematics (or cladistics) arose and has produced a revolution in macrotaxonomy. Stimulated by the writings of Hennig (1950, 1966), phylogenetics aims to fulfill the goal set by Darwin to base classifications directly on genealogy. Phylogenetic relationships are based on propinquity of descent determined from special similarity of homologous characters (shared derived character states) rather than unweighted, overall similarity. Reconstructed phylogenies subsequently are translated directly into classifications. Space precludes a review of the development of this school, but much of the debate concerning its methodology and philosophy (which is far from uniform) appears in the pages of *Systematic Zoology* from the 1970s to the present and is summarized in the texts by Wiley (1981) and Eldredge and Cracraft (1980) (see also the primer by Wiley et al., 1991). North American mammalogists have been bit players in the development of phylogenetics, although arguably the most important recent advances in higher classifications of mammals have employed this method (at least to reconstruct cladistic branching sequences). In particular, molecular systematists working on North American mammals who initially used phenetic methods almost exclusively now routinely apply cladistic parsimony to discern relationships. One only need peruse the pages of the *Journal of Mammalogy* or *Systematic Biology* (formerly *Systematic Zoology*) for the past 10 years to see the predominant influence of this school on vertebrate taxonomy and systematics. Publications on North American mammals employing this methodology are too numerous to cite, but a few exemplary studies include: Greenbaum and Baker (1978); Carleton (1980); Smith and Madkour (1980); Griffiths (1982); Hood and Smith (1982); Rogers et al. (1984); Owen (1987); Voss (1988); Baker et al. (1989); Miyamoto et al. (1989); Wozencraft (1989*a*); Wyss (1989); Hafner (1991); Pacheco and Patterson (1991); Lim (1993).

Continued dialogue (often acrimonious) among these three schools of systematics has resulted in considerable refinement of taxonomic methodology. By partitioning historical evolution (descent with modification) into the separate components of phenetic divergence and genealogy, classifications no longer need rest on intuition and authority; instead, they are based on empirical evidence of change in character states. Thus, as Hooper (1968:33) noted: "A classification is a tentative thing; it is not sacred." This change has resulted in a rekindled interest in macrotaxonomy in general, and in the higher classification of mammals, in particular. It also has sparked a new interest in using classifications to test hypotheses about historical processes in biological disciplines outside the field of systematics (Brooks and McLennan, 1991).

*Higher classification.* —The history of mammalian classification was reviewed by Gregory (1910), Simpson (1945), Szalay (1977), and Novacek (1982, 1990), and only a few highlights will be mentioned here. Since the turn of the century, much of the outstanding work by North Americans on classification of mammals has emanated from the Department of Vertebrate Paleontology of the American Museum of Natural History. Before the formation of the ASM in 1919, the most comprehensive and influential mammalian classification was that of Gregory (1910: Table 1). Phylogenetic in approach, Gregory was concerned with distinguishing between primitive and derived traits and with eliminating convergence (although these tenets were not always consistently followed in defining groups). Gregory's classification was relatively highly resolved; an optimistic solution not shared by several later workers (including Simpson, 1945), who more often regarded relationships among most eutherian orders as an unresolved phylogenetic "bush." Among several other groups, Gregory (1910) defined and defended the Archonta (including elephant shrews, tree shrews, bats, gliding lemurs, and primates), over which there has been much recent debate. Included in this synthesis (Gregory, 1910) is a fascinating historical review of mammalian classification that merits careful reading by anyone interested in the development of systematics.

Simpson (1945) later published what has been widely regarded as the standard classification of mammals (Table 1). This work was more detailed than that of Gregory, in that all mammals were classified to genus. Until the last decade, the pervasive influence of this monograph could be seen by touring the large museum and university collections of mammals in the United States, most of which were "arranged according to Simpson (1945)." Part of that influence stemmed from Simpson's position as a leading evolutionary theorist and his strong advocation of intuitive, evolutionary taxonomy. Many of his groups were based on his perception of phylogeny (e.g., recognition of the Ferungulata, including carnivores, ungulates, and related orders to the exclusion of other mammals), although these groups were not justified by shared derived features and have not been well accepted. In fact, despite its comprehensiveness, there was little explicit discussion of characters on which the classification was based. For example, Simpson (1945:173) dismissed Gregory's Archonta, without reference to characters or literature citations: "it is incredible to me . . . that the primates are more closely related to bats than to the insectivores, and all recent research . . . opposes that opinion."

Thirty years later, changes in systematic philosophy and discovery of new Mesozoic fossils led to a radical departure from Simpson (McKenna, 1975; Table 1). This was the first major classification of mammals that used cladistic methodology to reconstruct phylogeny and it included explicit discussion of character state transformations (especially dental homologies). Initially, McKenna (1975) was criticized because his classification was complex and because he erected a large number of new superordinal categories to reflect relative recency of common ancestry directly (Szalay, 1977). However, as noted by Novacek (1982), his departure from "traditional" systematics by providing explicit considerations of alternative phylogenetic hypotheses has not received due credit. Some of McKenna's (1975) more important departures from Simpson include (Table 1): early branching of the Edentata from the rest of the eutherian mammals; resurrection of Gregory's Archonta (sans the elephant shrews—Macroscelidea); phylogenetic association of Macroscelidea and lagomorphs; arrangement of whales (Cetacea) within a superordinal group including ungulates and their relatives but excluding carnivores. Al-

TABLE 1.—*Selected 20th century, higher-level classifications of extant mammals.*

**Gregory, 1910**

Class Mammalia
  Subclass Prototheria
      Order Monotremata
  Subclass Theria
    Infraclass Metatheria
      Order Marsupialia
        Suborder Diprotodontia
        Suborder Paucituberculata
        Suborder Polyprotodontia
    Infraclass Eutheria
      Superorder Therictoidea
        Order Insectivora
          Suborder Lipotyphla
        Order Ferae
          Suborder Fissipedia
          Suborder Pinnipedia
      Superorder Archonta
        Order Menotyphla [includes Tupaidae, Macroscelidae]
        Order Dermoptera
        Order Chiroptera
        Order Primates
      Superorder Rodentia
        Order Glires
          Suborder Duplicidentata [Lagomorpha]
          Suborder Simplicidentata [Rodentia]
      Superorder Edentata
        Order Tubulidentata
        Order Pholidota
        Order Xenarthra
      Superorder Paraxonia
        Order Artiodactyla
      Superorder Ungulata
        Order Sirenia
        Order Hyraces
        Order Mesaxonia [includes Perissodactyla]
      Superorder Cetacea
        Order Odontoceti
        Order Mystacoceti

**Simpson, 1945**

Class Mammalia
  Subclass Prototheria
        Order Monotremata
  Subclass Theria
    Infraclass Metatheria
        Order Marsupialia
    Infraclass Eutheria
      Cohort Unguiculata
        Order Insectivora [includes Lipotyphla, Macroscelidae]
        Order Dermoptera
        Order Chiroptera
        Order Primates

TABLE 1.—*Continued.*

        Order Edentata
        Order Pholidota
      Cohort Glires
        Order Lagomorpha
        Order Rodentia
      Cohort Mutica
        Order Cetacea
      Cohort Ferungulata
        Superorder Ferae
          Order Carnivora
            Suborder Fissipedia
            Suborder Pinnipedia
        Superorder Protungulata
          Order Tubulidentata
        Superorder Paenungulata
          Order Proboscidea
          Order Hyracoidea
          Order Sirenia
        Superorder Mesaxonia
          Order Perissodactyla
        Superorder Paraxonia
          Order Artiodactyla

**McKenna, 1975**

Class Mammalia
  Subclass Prototheria
    Infraclass Ornithodelphia
              Order Monotremata
  Subclass Theria
    Infraclass Tribosphenida
      Supercohort Marsupialia
      Supercohort Eutheria
        Cohort Edentata
              Order Cingulata
              Order Pilosa
        Cohort Epitheria
          Magnorder Ernotheria
              Order Macroscelidea
              Order Lagomorpha
          Magnorder Preptotheria
            Grandorder Ferae
              Order Carnivora
            Grandorder Insectivora
              Order Erinaceomorpha
              Order Soricomorpha
            Grandorder Archonta
              Order Scandentia
              Order Dermoptera
              Order Chiroptera
              Order Primates
            Grandorder Ungulata
              Mirorder Eparctocyona
              Order Tubulidentata
              Order Artiodactyla
              Mirorder Cete
              Order Cetacea

TABLE 1.—*Continued.*

| |
|---|
| Suborder Odontoceti |
| Suborder Mysticeti |
| Mirorder Phenacodonta |
| Order Perissodactyla |
| Order Hyracoidea |
| Mirorder Tethytheria |
| Order Proboscidea |
| Order Sirenia |
| Magnorder Preptotheria, *incertae sedis* |
| Order Pholidota |
| Cohort Epitheria, *incertae sedis* |
| Order Rodentia |
| Eutherian Mammals (**Novacek, 1986**) |
| Subclass Theria |
| Infraclass Eutheria |
| Cohort Edentata |
| Order Xenarthra |
| Order Pholidota |
| Cohort Epitheria |
| Superorder Insectivora |
| Order Lipotyphla |
| Superorder Volitantia |
| Order Dermoptera |
| Order Chiroptera |
| Superorder Anagalida |
| Order Macroscelidea |
| Grandorder Glires |
| Order Rodentia |
| Order Lagomorpha |
| Superorder Ungulata |
| Order Artiodactyla |
| Order Cetacea |
| Order Perissodactyla |
| Grandorder Paenungulata |
| Order Hyracoidea |
| Mirorder Tethytheria |
| Order Proboscidea |
| Order Sirenia |
| Cohort Epitheria *incertae sedis* |
| Order Tubulidentata |
| Order Carnivora |
| Order Primates |
| Order Scandentia |
| Metatherian Mammals (**Marshall et al., 1990**) |
| Subclass Theria |
| Infraclass Metatheria |
| Supercohort Marsupialia |
| Cohort Ameridelphia |
| Order Didelphimorphia |
| Order Paucituberculata |
| Cohort Australidelphia |
| Order Microbiotheria |
| Order Dasyuromorphia |
| Order Peramelina |
| Order Notoryctemorphia |
| Order Diprotodontia |

though subsequent authors (e.g., Szalay, 1977) have disagreed with some of McKenna's (1975) interpretations of characters and methodology, this paper set the stage for a dynamic reinvestigation of higher-level relationships in mammals.

Szalay (1977) examined phylogeny of eutherian mammals based on largely on tarsal morphology. His resulting classification was derived both from the proposed genealogy and his view of "adaptational history." He supported some of the same groups as McKenna (1975), such as the Archonta, the association of the Macroscelidea and Lagomorpha, and the existence of an ungulate supergroup, but was not convinced of the early derivation of edentates.

A more recent phylogeny and classification of eutherian mammals was proposed by Novacek (1986; Table 1), reconstructed using a large suite of skeletal and soft anatomical characters (although his cladograms were based on characters of the skull). Although far from fully resolved, this is the most explicit statement and defense of eutherian superordinal relationships to date. Therein (Table 1), he supported McKenna's (1975) early derivation of edentates (including pangolins—Pholidota) from other eutherians, an ungulate superorder, and the association of Macroscelidea with lagomorphs and rodents. He was, however, unable to find support for Gregory's (1910) Archonta (tentative justification for this group based on penial morphology and structure of the tarsus is given in Novacek and Wyss, 1986; Novacek et al., 1988, but see comments in Novacek, 1993).

Perhaps the most radical recent change in the higher classification of mammals is the subdivision of marsupials into several orders (Aplin and Archer 1987; Marshall et al., 1990; Ride, 1964; Szalay, 1982; Table 1). In particular, the recognition of the South American Microbiotheridae as a member of the Australidelphia clade (Aplin and Archer, 1987; Kirsch et al., 1991; Marshall et al., 1990; Szalay, 1982) is novel.

The past 20 years have witnessed a remarkable improvement in the state of our knowledge concerning higher classification of mammals, aided immeasurably by the formulation of explicit, falsifiable hypotheses of monophyly and evolution of character states. Thus, the statement by Ammerman and Hillis (1992:230) that, "Mammalogists today have less confidence in the branching order of the 18 orders of mammals than they did 100 years ago" is overly pessimistic. Analyses of molecular data hold considerable promise in the resolution of several of the seemingly intractable problems of mammalian phylogeny and interordinal relationships (Czelusniak et al., 1990; Honeycutt and Yates, 1994; Miyamoto and Goodman, 1986). Examination of congruence (or the lack thereof) among molecular and morphological data sets, however, suggests that this promise has yet to be fully realized (Novacek, 1989, 1990; Novacek et al., 1988; Wyss et al., 1987). We cautiously agree with McKenna (1987:82), referring to the congruence of amino acid sequences and morphology: "As with all information, there is a mixture of signal and noise, . . . , but the situation *seems* to be getting quieter [italics ours]."

## *Faunal Surveys*

One of the natural outgrowths of taxonomic work on mammals has been production of catalogues of mammals occurring in circumscribed geographic areas. The best of these catalogues have been written by practicing taxonomists. For the most part, these catalogues were not compiled within a "biodiversity" framework; however, they form the basis of our knowledge of mammalian diversity and geographic distribution. Mammalian faunal surveys have deep roots reaching back to the 19th Century to such classics as Harlan's (1825) *Fauna Americana,* Richardson's (1829) *Fauna Boreali-Americana,* DeKay's (1842) *Zoology of New-York,* and Audubon and Bachman's (1846 to 1854) *The Viviparous Quadrupeds of North America.* The monumental classic of the era was Baird's (1857) review of mammals of North America. This publication preceded by 100 years the classic of the next century, *The Mammals of North America,* by Hall and Kelson (1959). Both monographs stimulated considerable additional taxonomic studies and faunal surveys.

Faunal studies in the 10 years following the establishment of the ASM included those of Goldman (1920) for Panama, Howell (1921) for Alabama, and Bailey (1926) for North Dakota. The number of "Mammals of . . ." monographs showed a marked increase during the 1930s, the most notable by Bailey (1932, 1936) for New Mexico and Oregon, Grinnell (1933) for California, and Goodwin (1935) for Connecticut. However, a sign of things to come was the publication of the first faunal studies by two of Grinnell's professional progeny (Burt, 1938, Sonora; Davis, 1939, Idaho). The 1940s, like the 1930s, were characterized by publication of an increasing number of faunal studies, a few of the best known being those of Bole and Moulthrop (1942) for Ohio, Hamilton (1943) for the eastern U.S., Anderson (1947) for Canada, Burt (1948) for Michigan, and Dalquest (1948) for Washington. Also published during this period was Hall's (1946) *Mammals of Nevada,* which set the standard for subsequent mammalian surveys.

Relatively few faunal studies were published in the 1950s, the most important being the classic *Biological Investigations in Mexico,* by Goldman (1951). Additional examples were the state faunas and regional surveys by Cockrum (1952) for Kansas, Durrant (1952) for Utah, Dalquest (1953) for San Luis Potosí, Baker (1956) for Coahuila, and Bee and Hall (1956) for northern Alaska. Noteworthy faunal studies during the 1960s were those of Jackson (1961) for Wisconsin, Baker and Greer (1962) for Durango, Alvarez (1963) for Tamaulipas, Hall and Dalquest (1963) for Veracruz, Jones (1964) for Nebraska, Long (1965) for Wyoming, Peterson (1966) for eastern Canada, Villa-R. (1967) for Mexico, and Goodwin (1969) for Oaxaca. Some of the more important of the large number of "Mammals of . . ." books produced during the 1970s were those of Armstrong (1972) for Colorado, Anderson (1972) for Chihuahua, Banfield (1974) for Canada, Lowery (1974) for Louisiana, Findley et al. (1975) for New Mexico, Youngman (1975) for the Yukon Territory, and Schmidly (1977) for Trans-Pecos Texas. Faunal studies published during the 1980s included those of Mumford and Whitaker (1982) for Indiana, Baker (1983) for Michigan, Jones et al. (1983) for the Great Plains, Schmidly (1983) for eastern Texas, Hoffmeister (1986, 1989) for Arizona and Illinois, Caire et al. (1989) for Oklahoma, and Merritt (1987) for Pennsylvania.

Coincident with the formation of the Mexican Society of Mammalogy (AMMAC), there has been an increasing trend for locally produced faunal surveys and identification guides in Mexico over the last decade, a few examples of which include Ceballos and Galindo (1984) for the valley of México, Ceballos and Miranda (1986) for Chamela, Jalisco, Ramírez-Pulido et al. (1986) for Mexico, Aranda and March (1987) for Chiapas, Coates-Estrada and Estrada (1986) for Los Tuxtlas, Veracruz, and Alvarez-Castañeda and Alvarez (1991) for Chiapas. These studies herald the burgeoning local interest and expertise in the region of highest diversity of mammals in North America, and we anticipate an increasing number of faunal surveys in Mexico over the coming decades.

## Acknowledgments

We thank B. K. Lim for his assistance in compiling historical data and producing the figures.

## Literature Cited

Alvarez, T. 1963. The Recent mammals of Tamaulipas. University of Kansas Publications, Museum of Natural History, 14:363–473.

Alvarez-Castañeda, S. T., and T. Alvarez. 1991. Los murciélagos de Chiapas. Instituto Politecnico Nacional, México, D. F., 211 pp.

Ammerman, L. K., and D. M. Hillis. 1992. A molecular test of bat relationships: monophyly or diphyly? Systematic Biology, 41:222–232.

Anderson, R. M. 1947. Catalogue of Canadian Recent mammals. National Museum of Canada Bulletin, Biological Series, 102:1–238.

Anderson, S. 1972. Mammals of Chihuahua: taxonomy and distribution. Bulletin of the American Museum of Natural History, 148:149–410.

Anderson, S., and J. K. Jones, Jr. 1967. Recent mammals of the world: a synopsis of families. Ronald Press Company, New York, 453 pp.

———. 1984. Orders and families of Recent mammals of the world. John Wiley and Sons, New York, 686 pp.

Aplin, K. P., and M. Archer. 1987. Recent advances in marsupial systematics with a new syncretic classification. Pp. xv–xxii, *in* Possums and opossums: studies in evolution (M. Archer, ed.). Surrey Beatty and Sons Pty. Ltd., and Royal Zoological Society of New South Wales, Sydney, 1:1–400.

Aranda, M., and I. March. 1987. Guia de los mamíferos silvestres de Chiapas. Instituto Nacional de Investigaciones sobre recursos bioticos, Xalapa, Veracruz, 149 pp.

Arita, H. T., and S. R. Humphrey. 1988. Revisión taxonómica de los murciélagos del género *Leptonycteris* (Chiroptera: Phyllostomidae). Acta Zoologica Mexicana, n. ser., 29:1–60.

Armstrong, D. M. 1972. Distribution of mammals in Colorado. Monograph of the Museum of Natural History, The University of Kansas, 3:1–415.

Audubon, J. J., and J. Bachman. 1846–1854. The viviparous quadrupeds of North America. V. G. Audubon, New York, 3 volumes (1:1–389; 2:1–334; 3:1–348).

Bailey, V. 1926. A biological survey of North Dakota. North American Fauna, 49:1–226.

———. 1932. Mammals of New Mexico. North American Fauna, 53:1–402.

———. 1936. The mammals and life zones of Oregon. North American Fauna, 55:1–416.

Baird, S. F. 1857. General report upon the zoology of the several Pacific railroad routes: mammals. Vol. 8, pt. 1, *in* Reports of explorations and surveys to ascertain the most practicable and economical route for a railroad from the Mississippi River to the Pacific Ocean. Senate executive document no. 78, Washington, D.C., 757 pp.

Baker, R. H. 1956. Mammals of Coahuila, México. University of Kansas Publications, Museum of Natural History, 9:125–335.

———. 1983. Michigan mammals. Michigan State University Press, East Lansing, 642 pp.

Baker, R. H., and J. K. Greer. 1962. Mammals of the Mexican state of Durango. Publications of the Museum, Michigan State University, 2:1–154.

Baker, R. J. 1984. A sympatric cryptic species of mammal: a new species of *Rhogeessa* (Chiroptera Vespertilionidae). Systematic Zoology, 33:178–183.

Baker, R. J., and M. S. Hafner. 1994. Cytogenetics. Pp. 310–321, *in* Seventy-five years of mammalogy (1919–1994) (E. C. Birney and J. R. Choate, eds.).

Special Publication, The American Society of Mammalogists, 11:1–433.

Baker, R. J., J. W. Bickham, and M. L. Arnold. 1985. Chromosomal evolution in *Rhogeessa* (Chiroptera: Vespertilionidae): possible speciation by centric fusions. Evolution, 39:233–243.

Baker, R. J., C. S. Hood, and R. L. Honeycutt. 1989. Phylogenetic relationships and classification of the higher categories of the New World bat family Phyllostomidae. Systematic Zoology, 38:228–238.

Baker, R. J., J. C. Patton, H. H. Genoways, and J. W. Bickham. 1988. Genic studies of *Lasiurus* (Chiroptera: Vespertilionidae). Occasional Papers, The Museum, Texas Tech University, 117:1–15.

Banfield, A. W. F. 1974. The mammals of Canada. The University of Toronto Press, Toronto, 438 pp.

Barrowclough, G. F. 1982. Geographic variation, predictiveness, and subspecies. Auk, 99:601–603.

Bee, J. W., and E. R. Hall. 1956. Mammals of northern Alaska on the Arctic Slope. Miscellaneous Publications, Museum of Natural History, University of Kansas, 8:1–309.

Birney, E. C. 1973. Systematics of three species of woodrats (genus Neotoma) in central North America. Miscellaneous Publications, University of Kansas, Museum of Natural History, 58:1–173.

———. 1976. An assessment of relationships and effects of interbreeding among woodrats of the *Neotoma floridana* species-group. Journal of Mammalogy, 57:103–132.

Bole, B. J., Jr., and P. N. Moulthrop. 1942. The Ohio Recent mammal collection in the Cleveland Museum of Natural History. Scientific Publication of the Cleveland Museum of Natural History, 5:83–181.

Brooks, D. R., and D. A. McLennan. 1991. Phylogeny, ecology, and behavior: a research program in comparative biology. The University of Chicago Press, Chicago, 434 pp.

Brownell, E. 1983. DNA/DNA hybridization studies of muroid rodents: symmetry and rates of molecular evolution. Evolution, 37:1034–1051.

Burt, W. H. 1938. Faunal relationships and geographic distribution of mammals in Sonora, Mexico. Miscellaneous Publications of the Museum of Zoology, University of Michigan, 39:1–77.

———. 1948. The mammals of Michigan. The University of Michigan Press, Ann Arbor, 288 pp.

Caire, W., J. D. Tyler, B. P. Glass, and M. A. Mares. 1989. Mammals of Oklahoma. University of Oklahoma Press, Norman, 567 pp.

Carleton, M. D. 1977. Interrelationships of populations of the *Peromyscus boylii* species group (Rodentia, Muridae) in western Mexico. Occasional Papers of the Museum of Zoology, University of Michigan, 675:1–47.

———. 1980. Phylogenetic relationships in neotomine-peromyscine rodents (Muroidea) and a reappraisal of the dichotomy within New World Cricetinae. Miscellaneous Publications, Museum of Zoology, University of Michigan, 157:1–146.

———. 1989. Systematics and evolution. Pp. 7–141, *in* Advances in the study of *Peromyscus* (Rodentia) (G. L. Kirkland, Jr., and J. N. Layne, eds.). Texas Tech University Press, Lubbock, 366 pp.

Carleton, M. D., and R. E. Eshelman. 1979. A synopsis of fossil grasshopper mice, genus *Onychomys,* and their relationships to Recent species. University of Michigan, Museum of Paleontology, Papers on Paleontology, 21:1–63.

Carleton, M. D., and G. G. Musser. 1989. Systematic studies of oryzomyine rodents (Muridae, Sigmodontinae): a synopsis of *Microryzomys.* Bulletin of the American Museum of Natural History, 191: 1–83.

Ceballos, G., and C. Galindo. 1984. Mamíferos silvestres de la Cuenca de México. Instituto de Ecología y Museo de Historia Natural de la Ciudad de México, México, D. F., 299 pp.

Ceballos, G., and A. Miranda. 1986. Los mamíferos de Chamela, Jalisco. Instituto de Biología, Universidad Nacional Autónoma de México, México, D. F., 436 pp.

Choate, J. R. 1970. Systematics and zoogeography of Middle American shrews of the genus *Cryptotis.* University of Kansas Publications, Museum of Natural History, 19:195–317.

Coates-Estrada, R., and A. Estrada. 1986. Manual de identificación de campo de los mamíferos de la estación de biología "Los Tuxtlas." Instituto de Biología, Universidad Nacional Autónoma de México, México, D. F., 151 pp.

Cockrum, E. L. 1952. Mammals of Kansas. University of Kansas Publications, Museum of Natural History, 7:1–306.

Coues, E., and J. A. Allen. 1877. Monographs of North American Rodentia. Report of the U.S. Geological Survey of the Territories (F. V. Hayden, U.S. Geologist-in-Charge), Washington, D.C., Volume 11, 1,091 pp.

Cracraft, J. 1983. Species concepts and speciation analysis. Current Ornithology, 1:159–187.

Czelusniak, J., et al. 1990. Perspectives from amino acid and nucleotide sequences on cladistic relationships among higher taxa of Eutheria. Pp. 545–577, *in* Current mammalogy (H. H. Genoways, ed.). Plenum Press, New York, 2:1–577.

Dalquest, W. W. 1948. Mammals of Washington. University of Kansas Publications, Museum of Natural History, 2:1–444.

———. 1953. Mammals of the Mexican state of San Luis Potosí. Louisiana State Universities Studies, Biological Science Series, 1:1–229.

Davis, W. B. 1939. The Recent mammals of Idaho. Caxton Printers, Ltd., Caldwell, Idaho, 400 pp.

———. 1968. A review of the genus *Uroderma* (Chiroptera). Journal of Mammalogy, 49:676–698.

———. 1969. A review of the small fruit bats (genus *Artibeus*) of Middle America. The Southwestern Naturalist, 14:15–29.

———. 1970. A review of the small fruit bats (genus *Artibeus*) of Middle America. Part II. The Southwestern Naturalist, 14:389–402.

DeKay, J. E. 1842. Zoology of New-York, or the New-York fauna; comprising detailed descriptions of all the animals hitherto observed within the state of New-York, with brief notices of those occasionally found near its borders and accompanied by appropriate illustrations. Part 1. Mammalia. Printed by W. A. White and J. Visscher, Albany, 146 pp.

Donoghue, M. J. 1985. A critique of the biological species concept, and recommendation for a phylogenetic alternative. Bryologist, 88:172–181.

Durrant, S. D. 1952. Mammals of Utah: taxonomy and distribution. University of Kansas Publications, Museum of Natural History, 6:1–549.

Eger, J. L. 1977. Systematics of the genus *Eumops* (Chiroptera: Molossidae). Life Sciences Contributions, Royal Ontario Museum, 110:1–69.

Ehrlich, P. R., and P. H. Raven. 1969. Differentiation of populations. Science, 165:1228–1232.

Eldridge, N., and J. Cracraft. 1980. Phylogenetic patterns and the evolutionary process. Columbia University Press, New York, 349 pp.

Elliot, D. G. 1904. A checklist of mammals of the North American continent, the West Indies, and the neighboring seas. Field Columbian Museum, Publication 105, Zoological Series, 6:1–761.

Engstrom, M. D., and D. E. Wilson. 1981. Systematics of *Antrozous dubiaquercus* (Chiroptera: Vespertilionidae), with comments on the status of *Bauerus* Van Gelder. Annals of Carnegie Museum, 50: 371–383.

Engstrom, M. D., O. Sanchez-Herrera, and G. Urbano-Vidales. 1992. Distribution, geographic variation, and systematic relationships within *Nelsonia* (Rodentia: Sigmodontinae). Proceedings of the Biological Society of Washington, 105:867–881.

Findley, J. S. 1955. Speciation of the wandering shrew. University of Kansas Publications, Museum of Natural History, 9:1–68.

Findley J. S. 1972. Phenetic relationships among bats of the genus *Myotis*. Systematic Zoology, 21: 31–52.

Findley, J. S., and G. L. Traut. 1970. Geographic variation in *Pipistrellus hesperus*. Journal of Mammalogy, 51:741–765.

Findley, J. S., A. H. Harris, D. E. Wilson, and C. Jones. 1975. Mammals of New Mexico. University of New Mexico Press, Albuquerque, 360 pp.

Freeman, P. W. 1981. A multivariate study of the family Molossidae (Mammalia: Chiroptera): morphology, ecology, evolution. Fieldiana, Zoology, New Series, 7:1–173.

Gardner, A. L. 1973. The systematics of the genus *Didelphis* (Marsupialia: Didelphidae) in North and Middle America. Special Publications, The Museum, Texas Tech University, 4:1–81.

Genoways, H. H. 1973. Systematics and evolutionary relationships of spiny pocket mice, genus *Liomys*. Special Publications, The Museum, Texas Tech University, 5:1–368.

Genoways, H. H., and J. R. Choate. 1972. A multivariate analysis of systematic relationships among populations of the short-tailed shrew (genus *Blarina*) in Nebraska. Systematic Zoology, 21:106–116.

Genoways, H. H., and J. K. Jones, Jr. 1971. Systematics of southern banner-tailed kangaroo rats of the *Dipodomys phillipsii* group. Journal of Mammalogy, 52:265–287.

George, S. B. 1988. Systematics, historical biogeography, and evolution of the genus *Sorex*. Journal of Mammalogy, 69:443–461.

George, S. B., J. R. Choate, and H. H. Genoways. 1981. Distribution and taxonomic status of *Blarina hylophaga* Elliot (Insectivora: Soricidae). Annals of Carnegie Museum, 50:493–513.

George, S. B., H. H. Genoways, J. R. Choate, and R. J. Baker. 1982. Karyotypic relationships within the short-tailed shrews, genus *Blarina*. Journal of Mammalogy, 63:639–645.

Goldman, E. A. 1920. Mammals of Panama. Smithsonian Miscellaneous Collections, 69:1–309.

———. 1950. Raccoons of North and Middle America. North American Fauna, 60:1–153.

———. 1951. Biological investigations in Mexico. Smithsonian Miscellaneous Collections, 115:1–476.

Goodwin, G. G. 1935. The mammals of Connecticut. State of Connecticut, State Geological and Natural History Survey, Bulletin, 53:1–221.

———. 1969. Mammals from the state of Oaxaca, Mexico, in the American Museum of Natural History. Bulletin of the American Museum of Natural History, 141:1–269.

Greenbaum, I. F., and R. J. Baker. 1978. Determination of the primitive karyotype of *Peromyscus*. Journal of Mammalogy, 59:820–834.

Gregory, W. K. 1910. The orders of mammals. Bulletin of the American Museum of Natural History, 27:1–524.

Griffiths, T. A. 1982. Systematics of the New World nectar-feeding bats (Mammalia, Phyllostomidae) based on features of the morphology of the hyoid and lingual regions. American Museum Novitates, 2742:1–45.

Grinnell, J. 1933. Review of the Recent mammal fauna of California. University of California Publications in Zoology, 40:71–234.

Hafner, D. J., J. C. Hafner, and M. S. Hafner. 1979. Systematic status of kangaroo rats, genus *Microdipodops*: morphometric, chromosomal, and protein analyses. Journal of Mammalogy, 60:1–10.

Hafner, M S. 1982. A biochemical investigation of geomyoid systematics (Mammalia: Rodentia). Zeitschrift fur Zoologische Systematik und Evolutionsforschung, 20:118–130.

———. 1991. Evolutionary genetics and zoogeography of Middle American pocket gophers, genus *Orthogeomys*. Journal of Mammalogy, 72:1–10.

Hall, E. R. 1946. Mammals of Nevada. University of California Press, Berkeley, 710 pp.

———. 1951. American weasels. University of Kansas Publications, Museum of Natural History, 4:1–466.

———. 1981. The mammals of North America. Second ed. John Wiley and Sons, New York, 1:1–600 + *90*, 2:601–1181 + *90*.

———. 1984. Geographic variation among brown and grizzly bears (*Ursus arctos*) in North America. Special Publication, Museum of Natural History, University of Kansas, 13:1–16.

Hall, E. R., and W. W. Dalquest. 1963. The mammals of Veracruz. University of Kansas Publications, Museum of Natural History, 14:165–362.

Hall, E. R., and K. R. Kelson. 1959. The mammals of North America. Ronald Press Co., New York, 1:1–546 + *79*, 2:547–1083 + *79*.

Hamilton, W. J., Jr. 1943. The mammals of eastern United States: an account of Recent land mammals occurring east of the Mississippi. Comstock Publishing Co., Inc., Ithaca, New York, 432 pp.

Handley, C. O., Jr. 1959. Revision of American bats of the genera *Euderma* and *Plecotus.* Proceedings of the United States National Museum, 110:95–246.

Harlan, R. 1825. Fauna Americana, being a description of the mammiferous animals inhabiting North America. Anthony Finley (publisher), Philadelphia, 320 pp.

Heaney, L. R., and R. M. Timm. 1983. Relationships of pocket gophers of the genus *Geomys* from the central and northern Great Plains. Miscellaneous Publications, Museum of Natural History, University of Kansas, 73:1–59.

Hennig, W. 1950. Grundzuge einer Theorie der phylogenetischen Systematik. Deutscher Zentralverlag, Berlin, 370 pp.

———. 1966. Phylogenetic systematics. University of Illinois Press, Urbana, 263 pp.

Hennings, D., and R. S. Hoffmann. 1977. A review of the taxonomy of the *Sorex vagrans* species complex from western North America. Occasional Papers of the Museum of Natural History, University of Kansas, 68:1–35.

Hershkovitz, P. 1966. Catalog of living whales. Bulletin of the United States National Museum, 246:1–259.

Hoffmeister, D. F. 1951. A taxonomic and evolutionary study of the pinion mouse, *Peromyscus truei.* Illinois Biological Monographs, 21:1–104.

———. 1986. Mammals of Arizona. The University of Arizona Press, Tucson, 602 pp.

———. 1989. Mammals of Illinois. University of Illinois Press, Urbana, 348 pp.

Hoffmeister, D. F., and V. E. Diersing. 1978. Review of the tassel-eared squirrels of the subgenus *Otosciurus.* Journal of Mammalogy, 59:402–413.

Hoffmeister, D. F., and K. B. Sterling. 1994. Origin. Pp. 1–21, *in* Seventy-five years of mammalogy (1919–1994) (E. C. Birney and J. R. Choate, eds.). Special Publication, The American Society of Mammalogists, 11:1–433.

Honeycutt, R. L., and S. L. Williams. 1982. Genic differentiation in pocket gophers of the genus *Pappogeomys,* with comments on intergeneric relationships in the subfamily Geomyinae. Journal of Mammalogy, 63:208–217.

Honeycutt, R. L., and T. L. Yates. 1994. Molecular systematics. Pp. 288–309, *in* Seventy-five years of mammalogy (1919–1994) (E. C. Birney and J. R. Choate, eds.). Special Publication, The American Society of Mammalogists, 11:1–433.

Hood, C. S., and J. D. Smith. 1982. Cladistical analysis of female reproductive histomorphology in phyllostomatoid bats. Systematic Zoology, 31:241–251.

Hooper, E. T. 1943. Geographic variation in harvest mice of the species *Reithrodontomys humulis.* Occasional Papers of the Museum of Zoology, University of Michigan, 477:1–19.

———. 1952. A systematic review of harvest mice (genus *Reithrodontomys*) of Latin America. Miscellaneous Publications of the Museum of Zoology, University of Michigan, 77:1–255.

———. 1968. Classification. Pp. 27–74, *in* Biology of *Peromyscus* (Rodentia) (J. A. King, ed.). Special Publication, The American Society of Mammalogists, 2:1–593.

———. 1972. A synopsis of the rodent genus *Scotinomys.* Occasional Papers of the Museum of Zoology, University of Michigan, 665:1–32.

Howell, A. B. 1926. Voles of the genus Phenacomys. North American Fauna, 48:1–66.

———. 1927. Revision of the American lemming mice (genus Synaptomys). North American Fauna, 50:1–37.

Howell, A. H. 1921. A biological survey of Alabama. North American Fauna, 45:1–88.

———. 1929. Revision of the American chipmunks. North American Fauna, 52:1–157.

———. 1938. Revision of the North American ground squirrels, with a classification of the North American Sciuridae. North American Fauna, 56:1–256.

Huckaby, D. G. 1980. Species limits in the *Peromyscus mexicanus* group (Mammalia: Rodentia: Muroidea). Contributions in Science, Natural History Museum of Los Angeles County, 326:1–24.

Huxley, J. S. (ed.). 1940. The new systematics. Clarendon Press, Oxford, 583 pp.

Jackson, H. H. T. 1928. A taxonomic review of the American long-tailed shrews. North American Fauna, 51:1–238.

———. 1961. Mammals of Wisconsin. University of Wisconsin Press, Madison, 504 pp.

Johnson, M. L., and S. B. George. 1991. Species limits within the *Aborimus longicaudus* species–complex (Mammalia: Rodentia) with a description of a new species from California. Contributions in Science, Natural History Museum of Los Angeles County, 429:1–16.

Jones, J. K., Jr. 1964. Distribution and taxonomy of mammals of Nebraska. University of Kansas Publications, Museum of Natural History, 16:1–356.

———. 1982. [Review of] The mammals of North America, Second ed., by E. R. Hall. Journal of Mammalogy, 63:717–718.

———. 1991. Genealogy of Twentieth-century systematic mammalogists in North America: the descendants of Joseph Grinnell. Pp. 48–56, *in* Latin American mammalogy: history, biodiversity, and conservation (M. A. Mares and D. J. Schmidly, eds.). University of Oklahoma Press, Norman, 468 pp.

Jones, J. K., Jr., D. M. Armstrong, R. S. Hoffmann, and C. Jones. 1983. Mammals of the northern Great Plains. University of Nebraska Press, Lincoln, 379 pp.

Kirsch, J. A. W., R. E. Bleiweiss, A. W. Dickerman, and O. A. Reig. 1993. DNA/DNA hybridization studies of carnivorous marsupials. III. Relationships among species of *Didelphis* (Didelphidae). Journal of Mammalian Evolution, 1:75–97.

Kirsch, J. A. W., A. W. Dickerman, O. A. Reig, and M. S. Springer. 1991. DNA hybridization evidence for the affinity of the American marsupial *Dromiciops australis.* Proceedings of the National Academy of Sciences, USA, 88:10465–10469.

Koopman, K. F. 1984. A synopsis of the families of bats—part VII. Bat Research News, 25:25–27.

Lawlor, T. E. 1969. A systematic study of the rodent genus *Ototylomys.* Journal of Mammalogy, 50:28–42.

Lidicker, W. Z., Jr. 1960. An analysis of intraspecific variation in the kangaroo rat *Dipodomys merriami.* University of California Publications in Zoology, 67: 125–218.

———. 1962. The nature of subspecific boundaries in a desert rodent and its implications for subspecific taxonomy. Systematic Zoology, 11:160–171.

Lim, B. K. 1993. Cladistic reappraisal of Neotropical stenodermatine bat phylogeny. Cladistics, 9:147–165.

Long, C. A. 1965. The mammals of Wyoming. University of Kansas Publications, Museum of Natural History, 14:493–758.

Lowery, G. H., Jr. 1974. The mammals of Louisiana and its adjacent waters. Louisiana State University Press, Baton Rouge, 565 pp.

Marshall, L. G., J. A. Case, and M. O. Woodburne. 1990. Phylogenetic relationships of the families of marsupials. Pp. 433–505, *in* Current Mammalogy (H. H. Genoways, ed.). Plenum Press, New York, 2:1–577.

Mayr, E. 1963. Animal species and evolution. The Belknap Press of Harvard University Press, Cambridge, Massachusetts, 797 pp.

———. 1969. Principles of systematic zoology. McGraw-Hill Book Co., New York, 428 pp.

———. 1982. The growth of biological thought: diversity, evolution, and inheritance. The Belknap Press of Harvard University Press, Cambridge, 974 pp.

Mayr, E., and P. D. Ashlock. 1991. Principles of systematic zoology. Second ed. McGraw-Hill Inc., New York, 475 pp.

Mayr, E., E. G. Linsley, and R. L. Usinger. 1953. Methods and principles of systematic zoology. McGraw-Hill Book Co., New York, 336 pp.

McKenna, M. C. 1975. Toward a phylogenetic classification of the Mammalia. Pp. 21–46, *in* Phylogeny of the primates: a multidisciplinary approach (W. P. Luckett and F. S. Szalay, eds.). Plenum Publishing Co., New York, 483 pp.

———. 1987. Molecular and morphological analysis of high-level mammalian interrelationships. Pp. 55–93, *in* Molecules and morphology in evolution: conflict or compromise? (C. Patterson, ed.). Cambridge University Press, Cambridge, Great Britain, 229 pp.

McKitrick, M. C., and R. M. Zink. 1988. Species concepts in ornithology. Condor, 90:1–14.

Mearns, E. A. 1907. Mammals of the Mexican boundary of the United States . . . Pt. 1, Families Didelphidae to Muridae. Bulletin of the United States National Museum, 56:1–530.

Merriam, C. H. 1918. Review of the grizzly and big brown bears of North America (genus *Ursus*) with description of a new genus, *Vetularctos.* North American Fauna, 41:1–36.

———. 1919. Criteria for the recognition of species and genera. Journal of Mammalogy, 1:6–9.

Merritt, J. F. 1987. Guide to the mammals of Pennsylvania, University of Pittsburgh Press, Pittsburgh, Pennsylvania, 408 pp.

Miller, G. S., Jr. 1912. List of North American land mammals in the United States National Museum, 1911. Bulletin of the United States National Museum, 79:1–455.

———. 1924. List of North American Recent mammals. Bulletin of the United States National Museum, 128:1–673.

Miller, G. S., Jr., and G. M. Allen. 1928. The American bats of the genera *Myotis* and *Pizonyx.* Bulletin of the United States National Museum, 144: 1–218.

Miller, G. S., Jr., and R. Kellogg. 1955. List of North American Recent mammals. Bulletin of the United States National Museum, 205:1–954.

Miller, G. S., Jr., and J. A. G. Rehn. 1902. Systematic results of the study of North American land mammals to the close of the year 1900. Proceedings of the Boston Society of Natural History, 30:1–352.

Miyamoto, M. M., and M. Goodman. 1986. Biomolecular systematics of eutherian mammals: phylogenetic patterns and classification. Systematic Zoology, 35:230–240.

Miyamoto, M. M., S. M. Tanhauser, and P. J. Laipis. 1989. Systematic relationships in the artiodactyl tribe Bovini (Family Bovidae), as determined from mitochondrial DNA sequences. Systematic Zoology, 38: 342–349.

Moore, J. C. 1959. Relationships among the living squirrels of the Sciurinae. Bulletin of the American Museum of Natural History, 118:157–206.

Mumford, R. E., and J. O. Whitaker, Jr. 1982. Mammals of Indiana. Indiana University Press, Bloomington, 537 pp.

Musser, G. G. 1968. A systematic study of the Mexican and Guatemalan gray squirrel, *Sciurus aureogaster* F. Cuvier (Rodentia: Sciuridae). Miscellaneous Publications, Museum of Zoology, University of Michigan, 137:1–112.

Nelson, E. W., and E. A. Goldman. 1933. Revision of the jaguars. Journal of Mammalogy, 14:221–240.

Novacek, M. J. 1982. Information for molecular studies from anatomical and fossil evidence on higher eutherian phylogeny. Pp. 3–41, *in* Macromolecular sequences in systematic and evolutionary biology (M. Goodman, ed.). Plenum Press, New York, 418 pp.

———. 1986. The skull of leptictid insectivorans and the higher-level classification of eutherian mammals. Bulletin of the American Museum of Natural History, 183:1–112.

———. 1989. Higher mammal phylogeny: the morphological-molecular synthesis. Pp. 421–435, *in* The hierarchy of life (B. Fernholm, K. Bremer, and H. Jornvall, eds.). Elsevier Science Publishers B.V. (Biomedical Division), 499 pp.

———. 1990. Morphology, paleontology, and the higher clades of mammals. Pp. 507–543, *in* Current Mammalogy (H. H. Genoways, ed.). Plenum Press, New York, 2:1–577.

———. 1993. Reflections on higher mammalian phylogenetics. Journal of Mammalian Evolution, 1:3–30.

Novacek, M. J., and A. R. Wyss. 1986. Higher-level relationships of the Recent eutherian orders: morphological evidence. Cladistics, 2:257–287.

Novacek, M. J., A. R. Wyss, and M. C. McKenna. 1988. The major groups of eutherian mammals. Pp. 31–71, *in* The phylogeny and classification of the tetrapods, volume 2: mammals (M. J. Benton, ed.). Clarendon Press, Oxford, 329 pp.

Osgood, W. H. 1909. Revision of the mice of the American genus Peromyscus. North American Fauna, 28:1–285.

Owen, R. D. 1987. Phylogenetic analyses of the bat subfamily Stenodermatinae (Mammalia: Chiroptera). Special Publication, The Museum, Texas Tech University, 26:1–65.

———. 1988. Phenetic analyses of the bat subfamily Stenodermatinae (Chiroptera: Phyllostomidae). Journal of Mammalogy, 69:795–810.

Pacheco, V., and B. D. Patterson. 1991. Phylogenetic relationships of the New World genus *Sturnira* (Chiroptera: Phyllostomidae). Bulletin of the American Museum of Natural History, 206:101–121.

Packard, R. L. 1960. Speciation and evolution of the pygmy mice, genus *Baiomys*. University of Kansas Publications, Museum of Natural History, 9:579–670.

Patton, J. L., and M. F. Smith. 1981. Molecular evolution in *Thomomys*: phyletic systematics, paraphyly, and rates of evolution. Journal of Mammalogy, 62:493–500.

———. 1990. The evolutionary dynamics of the pocket gopher, *Thomomys bottae*, with emphasis on California populations. University of California Publications in Zoology, 123:1–161.

Patton, J. L., S. W. Sherwood, and S. Y. Yang. 1981. Biochemical systematics of chaetodipine pocket mice, genus *Perognathus*. Journal of Mammalogy, 62:477–492.

Peterson, R. L. 1966. The mammals of eastern Canada. Oxford University Press, Toronto, 465 pp.

Pine, R. H. 1972. The bats of the genus *Carollia*. Technical Monograph, Texas Agricultural Experiment Station, Texas A&M University, 8:1–125.

Ramírez-Pulido, J., and M. C. Britton. 1981. An historical synthesis of the Mexican mammalian taxonomy. Proceedings of the Biological Society of Washington, 91:1–17.

Ramírez-Pulido, J., M. C. Britton, A. Perdomo, and A. Castro. 1986. Guia de los mamíferos de México, referencias hasta 1983. Universidad Autónoma Metropolitana, Unidad Iztapalapa, México, D. F., 720 pp.

Richardson, J. 1829. Fauna boreali-Americana; or the zoology of the northern parts of British America: containing descriptions of the objects of natural history collected on the northern land expedition under the command of Captain Sir John Franklin, R. N. Part first, containing the quadrupeds. John Murray (publishers), Ltd., London, 300 pp.

Ride, W. D. L. 1964. A review of the Australian fossil marsupials. Journal Proceedings of the Royal Society of Western Australia, 47:97–131.

Robbins, L. W., and V. M. Sarich. 1988. Evolutionary relationships in the family Emballonuridae (Chiroptera). Journal of Mammalogy, 69:1–13.

Rogers, D. S., and M. D. Engstrom. 1992. Evolutionary implications of allozymic variation in tropical *Peromyscus* of the *mexicanus* species group. Journal of Mammalogy, 73:55–69.

Rogers, D. S., and D. J. Schmidly. 1982. Systematics of spiny pocket mice (genus *Heteromys*) of the *desmarestianus* species group from Mexico and northern Central America. Journal of Mammalogy, 63:375–386.

Rogers, D. S., I. F. Greenbaum, S. J. Gunn, and M. D. Engstrom. 1984. Cytosystematic value of chromosomal inversion data in the genus *Peromyscus*. Journal of Mammalogy, 65:457–465.

Russell, R. J. 1968*a*. Evolution and classification of the pocket gophers of the subfamily Geomyinae. University of Kansas Publications, Museum of Natural History, 16:473–579.

———. 1968*b*. Revision of pocket gophers of the genus *Pappogeomys*. University of Kansas Publications, Museum of Natural History, 16:581–776.

Sanborn, C. C. 1937. American bats of the subfamily Emballonurinae. Field Museum of Natural History, Zoological Series, 20:321–354.

Schmidly, D. J. 1977. The mammals of Trans-Pecos Texas. Texas A&M University Press, College Station, 225 pp.

———. 1983. Texas mammals east of the Balcones Fault Zone. Texas A&M University Press, College Station, 400 pp.

Schmidly, D. J., R. D. Bradley, and P. S. Cato. 1988. Morphometric differentiation and taxonomy of three chromosomally characterized groups of *Peromyscus boylii* from east-central Mexico. Journal of Mammalogy, 69:462–480.

Schnell, G. D., T. L. Best, and M. L. Kennedy. 1978. Interspecific morphologic variation in kangaroo rats (*Dipodomys*): degree of concordance with genic variation. Systematic Zoology, 27:34–48.

Setzer, H. W. 1949. Subspeciation in the kangaroo rat, *Dipodomys ordii*. University of Kansas Publications, Museum of Natural History, 1:473–573.

Silva-Taboada, G. 1979. Los murciélagos de Cuba. Editorial Academia, 423 pp.

Simpson, G. G. 1945. The principles of classification and a classification of mammals. Bulletin of the American Museum of Natural History, 85:1–350.

———. 1961. Principles of animal taxonomy. Columbia University Press, New York, 247 pp.

Smith, J. D. 1972. Systematics of the chiropteran family Mormoopidae. Miscellaneous Publications, Museum of Natural History, University of Kansas, 56:1–132.

Smith, J. D., and G. Madkour. 1980. Penial morphology and the question of chiropteran phylogeny. Pp. 347–365, *in* Proceedings of the fifth international bat research conference (D. E. Wilson and A. L. Gardner, eds.). Texas Tech University Press, Lubbock, 434 pp.

Smith, M. F., and J. L. Patton. 1988. Subspecies of pocket gophers: causal bases for geographic differentiation in *Thomomys bottae*. Systematic Zoology, 37:163–178.

Sneath, P. H. A., and R. R. Sokal. 1973. Numerical taxonomy: the principles and practice of numerical classification. W. H. Freeman and Co., San Francisco, 573 pp.

Sokal, R. R., and T. J. Crovello. 1970. The biological species concept: a critical explanation. The American Naturalist, 104:127–153.

Sokal, R. R., and P. H. A. Sneath. 1963. Principles of numerical taxonomy. W. H. Freeman and Co., San Francisco, 359 pp.

Sullivan, R. M. 1985. Phyletic, biogeographic and ecological relationships among montane populations of least chipmunks (*Eutamias minimus*) in the Southwest. Systematic Zoology, 34:419–448.

SULLIVAN, R. M., D. J. HAFNER, AND T. L. YATES. 1986. Genetics of a contact zone between three chromosomal forms of the grasshopper mouse (genus *Onychomys*): a reassessment. Journal of Mammalogy, 67:640–659.

SZALAY, F. S. 1977. Phylogenetic relationships and a classification of the eutherian Mammalia. Pp. 315–374, *in* Major patterns in vertebrate evolution (M. K. Hecht, P. C. Goody, and B. M. Hecht, eds.). Plenum Press, New York, 908 pp.

———. 1982. A new appraisal of marsupial phylogeny and classification. Pp. 621–640, *in* Carnivorous marsupials (M. Archer, ed.). Royal Zoological Society of New South Wales, Mosman, 2:397–804.

TATE, G. H. H. 1933. A systematic revision of the marsupial genus *Marmosa*. Bulletin of the American Museum of Natural History, 66:1–250.

TAVERNER, P. A. 1920. The test of the subspecies. Journal of Mammalogy, 1:124–127.

THAELER, C. S., JR. 1972. Taxonomic status of the pocket gophers, *Thomomys idahoensis* and *Thomomys pygmaeus* (Rodentia: Geomyidae). Journal of Mammalogy, 53:417–428.

VAN GELDER, R. G. 1959. A taxonomic revision of the spotted skunks (genus *Spilogale*). Bulletin of the American Museum of Natural History, 117:229–392.

VAN ZYLL DE JONG, C. G. 1984. Taxonomic relationships of Nearctic small-footed bats of the *Myotis leibii* group (Chiroptera: Vespertilionidae). Canadian Journal of Zoology, 62:2519–2526.

VAN ZYLL DE JONG, C. G., AND G. L. KIRKLAND, JR. 1989. A morphometric analysis of the *Sorex cinereus* group in central and eastern North America. Journal of Mammalogy, 70:110–122.

VARONA, L. S. 1974. Catalogo de los mamíferos vivientes y extinguidos de las Antillas. Instituto de Zoología, Academia de Ciencias de Cuba (Havana), 139 pp.

VILLA-R., B. 1967. Los murciélagos de México. Anales de Instituto de Biología, Universidad Nacional Autónoma de México, México, D.F., 491 pp.

VOSS, R. S. 1988. Systematics and ecology of ichthyomyine rodents (Muroidea): patterns of morphological evolution in a small adaptive radiation. Bulletin of the American Museum of Natural History, 188: 259–493.

WALL, D. A., S. K. DAVIS, AND B. M. READ. 1992. Phylogenetic relationships in the subfamily Bovinae (Mammalia: Artiodactyla) based on ribosomal DNA. Journal of Mammalogy, 73:262–275.

WEBSTER, W. D., AND C. O. HANDLEY, JR. 1986. Systematics of Miller's long-tongued bat *Glossophaga longirostris*, with description of two new subspecies. Occasional Papers, The Museum, Texas Tech University, 100:1–22.

WHITAKER, J. O., JR. 1994. Academic Propinquity. Pp. 121–138, *in* Seventy-five years of mammalogy (1919–1994) (E. C. Birney and J. R. Choate, eds.). Special Publication, The American Society of Mammalogists, 11:1–433.

WILEY, E. O. 1978. The evolutionary species concept reconsidered. Systematic Zoology, 28:88–92.

———. 1981. Phylogenetics: the theory and practice of phylogenetic systematics. John Wiley and Sons, New York, 439 pp.

WILEY, E. O., D. SIEGEL-CAUSEY, D. R. BROOKS, AND V. A. FUNK. 1991. The compleat cladist: a primer of phylogenetic procedures. Special Publication, The University of Kansas, Museum of Natural History, 19:1–158.

WILLIAMS, D. F. 1978. Systematics and ecogeographic variation of the Apache pocket mouse (Rodentia: Heteromyidae). Bulletin of Carnegie Museum of Natural History, 10:1–57.

WILLIAMS, D. F., AND H. H. GENOWAYS. 1979. A systematic review of the olive-backed pocket mouse, *Perognathus fasciatus* (Rodentia: Heteromyidae). Annals of Carnegie Museum, 48:1–36.

WILSON, D. E., AND D. M. REEDER. 1993. Mammal species of the world: a taxonomic and geographic reference. Second ed. Smithsonian Institution Press, Washington, D.C., 1,206 pp.

WILSON, E. O., AND W. L. BROWN, JR. 1953. The subspecies concept and its taxonomic application. Systematic Zoology, 2:97–111.

WOZENCRAFT, W. C. 1989*a*. The phylogeny of Recent Carnivora. Pp. 495–535, *in* Carnivore behavior, ecology, and evolution (J. L. Gittleman, ed.). Cornell University Press, Ithaca, New York, 620 pp.

WOZENCRAFT, W. C. 1989*b*. Classification of the Recent Carnivora. Pp. 569–593, *in* Carnivore behavior, ecology, and evolution (J. L. Gittleman, ed.). Cornell University Press, Ithaca, New York, 620 pp.

WYSS, A. R. 1989. Flippers and pinniped phylogeny: has the problem of convergence been overrated? Marine Mammal Science, 5:343–360.

WYSS, A. R., M. J. NOVACEK, AND M. C. MCKENNA. 1987. Amino acid sequence versus morphological data and the interordinal relationships of mammals. Molecular Biology and Evolution, 4:99–116.

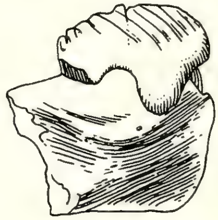
YATES, T. L., AND D. J. SCHMIDLY. 1977. Systematics of *Scalopus aquaticus* in Texas and adjacent states. Occasional Papers, The Museum, Texas Tech University, 45:1–36.

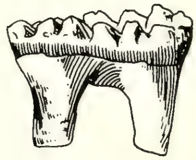
YOUNGMAN, P. M. 1975. Mammals of the Yukon Territory. National Museum of Natural Sciences (Ottawa), Publications in Zoology, 10:1–192.

ZIMMERMAN, E. G. 1970. Karyology, systematics and chromosomal evolution in the rodent genus *Sigmodon*. Publications of The Museum, Michigan State University Biological Series, 4:385–454.

# PALEOMAMMALOGY

Richard J. Zakrzewski and Jason A. Lillegraven





## Introduction

Major differences between neo- and paleomammalogy already existed as early as 1919, primarily because of the nature of the materials researched and the technologies that could be utilized. Even so, paleomammalogists have made major advances toward a better understanding of mammalogy since the founding of the society. These contributions can be considered under four areas: general, geological, biological, and a blending of the latter two. General advances include a significant increase in the number of individuals and institutions working in paleomammalogy; a tremendous increase in the size of collections, especially of smaller taxa, due to the development and modification of screen washing techniques; a better understanding of the fossilization process through taphonomic studies; and development of a comprehensive bibliography. Geologically oriented advances include the use of improved biostratigraphic techniques, together with radiometric dating and magnetostratigraphy, to increase our understanding of the sequential occurrence of mammalian faunas and decipher the complex geology of the highly deformed ranges and intermontane basins in the American West; and use of the plate tectonics model to explain biogeographic distributions and patterns. Biologically oriented advances include major improvements in our understanding of the reptile–mammal transition and the definition of "mammal"; important systematic studies of many mammalian taxa, using various taxonomic philosophies; and multitudinous studies of form, function, and phylogenetic relationships of particular groups of Cenozoic mammals. These have all been blended into important studies considering the issues of tempo and mode in evolution and the cause of extinctions.

## Compartmentalization of Mammalogy

By 1919, the discipline of mammalogy already had become compartmentalized into neo- and paleomammalogy. Osborn (1921), in the first article of Volume 2 of the *Journal of Mammalogy,* pointed out that paleomammalogists were constrained to dealing only with hard parts and, therefore, the types of studies that were undertaken usually were different from those of neomammalogists.

However, he further suggested that there should be more standardization of terms and approaches to research problems in mammalogy, as well as cooperative studies between neo- and paleomammalogists for their mutual benefit. He cited, as an example, the work on rodents by Miller and Gidley (1918). Unfortunately, such collaborations have been infrequent (e.g., Carleton and Eshelman, 1979; White and Keller, 1984). A classic exception is the work of the late John E. Guilday who, perhaps as well as anyone in this century, fused mammalogy and paleomammalogy (e.g., Guilday, 1971). The less-than-expected level of interchange between paleo- and neomammalogists probably relates to a perception that the former still are constrained to studying only hard parts in a geological context, whereas the latter have even more avenues and methods of study available to them now than existed 75 years ago. Also, geophysical advances of the 20th Century that are critically important to geologically oriented paleomammalogists often have appeared scientifically irrelevant to neomammalogists. Perhaps advances in specialized technology themselves have led to wider gulfs between subdisciplines of mammalogy. Be that as it may, paleomammalogists have made major contributions to the general field of mammalogy, and a small sampling of these is considered below.

Analogous to the dichotomy between neo- and paleomammalogists, there exists significant compartmentalization among paleomammalogists. The splits result, in part, from interest and training, but also stem from the use of fossils in approaching geological versus biological problems. Some paleontologists (who might prefer to be called mammalian biostratigraphers) study fossil mammals principally to determine the age of enclosing sediments to solve stratigraphic or structural problems; paleomammalogists sensu stricto, like neomammalogists, typically are more interested in anatomical and functional problems and evolutionary implications associated with fossils. Many paleontologists, however, have attempted to work in both areas.

Before considering contributions made in these two areas, we briefly examine important developments of a general nature that have led to enormous benefit both within geologically and biologically oriented paleomammalogy. These include an increase in the number of paleomammalogists, techniques in collecting fossils, understanding how particular associations of fossils come to be, and the development of a comprehensive bibliography.

## General Advancements

### *A Slow Start for American Paleomammalogy*

When the ASM was founded in New York on 3 April 1919, there were only two major centers of mammalian paleontology in the United States. One at the American Museum of Natural History, led by Henry Fairfield Osborn, William Diller Matthew, and Childs Frick, the other at the University of California, Berkeley, where John C. Merriam had built a program. About the time the ASM was founded, Merriam became president of the Carnegie Institution of Washington. He was among the charter members of the society, together with colleagues from New York and the Smithsonian Institution. Merriam and Matthew were two of the first council members of the society. Merriam also served on the first Anatomy and Physiology Committee, together with William King Gregory of Columbia University and Alexander Wetmore and James W. Gidley of the Smithsonian Institution. Matthew served as President of the society in 1926, the only paleomammalogist to have done so.

Why there were so few centers of mammalian paleontology as late as 1919 is not clear. Perhaps it was, in part, a legacy from the days of Cope and Marsh, when the impetus was for the collection of large reptiles from Mesozoic deposits of the American West. This tendency extended into early parts of the 20th Century with collections made by Earl Douglass for the Carnegie Museum in Pittsburgh and the Sternbergs for various Canadian institutions. Many of the paleontologists in the first quarter of the 20th Century were interested principally in lower vertebrates rather than mammals. In marked contrast, there exist today in North America about 120 institutions in which individuals perform research on fossil mammals; estimating conservatively, at least 20 of these research centers must be considered major. Such increase in interest since 1919 must, in itself, be considered a huge advance in American paleomammalogy.

### *Finding the Tiny*

Philip D. Gingerich (1986), in lamenting the demise of the paleontology program at his alma mater, aptly showed that theoretically oriented paleontology depends upon extensive personal experience based, in turn, upon a solid data base. For all paleontological endeavors, the fundamental objective elements of data are the fossils themselves, set within geological contexts. Early collectors of fossil mammals, perhaps influenced by their predecessors' searches for dinosaurs, selectively looked for sites with accumulations of large mammals. Although small mammals certainly were not intentionally ignored, quarrying techniques employed by many early collectors were not conducive to discovery of minuscule fossils. A "fossil" to many of these individuals had to be at least six inches long, preferably bearing teeth.

A change in attitude began about a decade after the founding of the ASM. In 1928, Claude W. Hibbard (a future director of the ASM) was hired as cook and camp caretaker for a field party from the University of Kansas led by Handel Tong Martin. The crew was returning to Edson Quarry (late Miocene, Sherman County, Kansas) for another summer of collecting. During the previous summer, Martin had found some fossil salamander bones and was asked to collect additional remains by an anatomist who was interested in studying the group. When Hibbard went to the quarry, after finishing camp chores, Martin greeted him with a pair of tweezers and told him to collect all the small bone he could find on the spoil pile. Hibbard soon decided to expedite matters. Obtaining some window screen from the local rancher, he attached the screen to a wooden frame to produce a little box. Loose sediment from the spoil pile passed easily through the screen and the fossil bone was trapped by it and picked out. Hibbard thought he might hurry the process even more by the use of water. Thus, he took the sediment and his box to a nearby buffalo wallow and proceeded to agitate the box in the water. Within a few days, he had enough small material to fill a large matchbox. When Hibbard showed the material to Martin, the latter stated that there were enough small specimens in the box to keep paleontologists occupied for years. Despite the innovation, Hibbard spent the remainder of the summer in the quarry, helping Martin collect "real" (i.e., large) fossils.

Subsequently, Hibbard (1949) expanded on the washing technique and used it to accumulate tens of thousands of specimens from southwestern Kansas and northwestern Oklahoma. Thereby, he was able to document a sequence of faunas that reflected both phylogenetic and climatic change (Bayne, 1976; Zakrzewski, 1975). Subsequent workers (e.g., McKenna, 1962) have modified the technique for massive collection of fossils from other areas and ages. An example of the importance of widespread use of screen-washing techniques is the increase in our knowledge of Mesozoic mammals. When George Gaylord Simpson (1928, 1929) published his comprehensive summary of known Mesozoic mammals (based, in part, on his Ph.D. thesis), he worked with fewer than a thousand specimens, collected by standard quarrying from around the world. When William A. Clemens, Jr. (1963, 1966, 1973) and Jason A. Lillegraven (1969) published their Ph.D. theses on latest Cretaceous mammals, their specimens from only two local faunas numbered well into the thousands. Mammalian paleontology in North America, especially dealing with the Mesozoic, was never quite the same again. As Simpson (1971) stated, it "would not be possible now, as it was in 1871, 1888, and 1928–1929 for one person to treat all available material on Mesozoic mammals. . . ."

### *Grasping the "How" of Fossil Accumulations*

Most workers are painfully aware of important biases in the fossil record. Before useful scientific inferences can be drawn from paleontological data, one needs to know how the fossils themselves accumulated. Although inadequacies and biases in the fossil record have been appreciated for many years (e.g., Darwin, 1859), it has been only relatively recently that formal study of the process of fossilization (i.e., taphonomy) has been undertaken on a large scale. The majority of early taphonomic work was by the Russians, applied to faunas of lower vertebrates (Olson, 1980). Perhaps the seminal work in North America for explaining the occurrences of accumulations of large mammals is that of Michael R. Voorhies (1969) on the Verdigre Quarry in northeastern Nebraska. Subsequent work by Anna K. Behrensmeyer and her colleagues (e.g., Behrensmeyer and Hill, 1980) have added much to the understanding of how deposits of fossil mammals might accumulate. James S. Mellett (1974) demonstrated that many micromammal accumulations result from owl predation, a mechanism suggested earlier by Hibbard (1941). Subsequently, problems of origin of microvertebrate fossils have been addressed by various workers, such as Dodson and Wexlar (1979) and Korth (1979). The subdiscipline of taphonomy is only in its infancy relative to understanding associations of fossil mammals.

### *Unique Research Tool*

The development of a unique bibliographic research tool cannot be omitted from discussion of 20th Century progress in paleomammalogy; we refer to the *Bibliography of Fossil Vertebrates* (BFV) (Gregory et al., 1989, plus predecessor volumes involving various editors, including Charles L. Camp). The BFV is published by the Society of Vertebrate Paleontology (which shares a large membership with the ASM), and provides unparalleled, annual access to the breadth of world literature on fossil mammals.

## Geologically Directed Paleomammalogy

### *Toward a More Useful Time Scale*

Original versions of the geologic time scale were developed using the law of superposition in combination with the stage of evolution of marine invertebrates, mostly involving European rock sequences. Some of the sequences could be correlated with those in North America using marine invertebrates. Where American continental and marine deposits interfingered, there was little problem in placing the terrestrial units into a scheme of relative chronology. However, as workers moved on to the High Plains and into the structurally isolated intermontane basins of the American West, many mammal-bearing nonmarine stratigraphic units could not be placed easily into context within the standard time scale. As mammals often were the most abundant fossils in these strata, early workers sometimes named deposits after the most common kinds. Names such as the *Equus* beds of Kansas and the *Titanotherium* and *Oreodon* beds of South Dakota were established. These ill-defined units were assigned to European-based Tertiary epochs through comparative estimation of the stage of evolution of contained mammals. This procedure often involved little more than guesswork, however, and it ultimately led to widespread misconceptions in correlation. All but one of the standard Tertiary epochs were based on marine fossils, and few North American continental deposits could be superpositionally related to marine strata. Clearly, a new method for dating and correlating the North American mammal-bearing continental units had to be developed, independent of the standard European marine sequence.

Eventually, a committee was established to devise such a time scale independent of the marine standard. Work of the "Wood Committee" led to the development of the North American Land-Mammal Ages (NALMAs; Wood et al., 1941), as reviewed by Hesse (1941). NALMAs were defined principally on the first occurrence of certain genera and the unique occurrences or consistent associations of others. Although last occurrences also were considered, these usually were given less weight because of potential complications to correlation resulting from relictual taxa. The original NALMAs applied only to Tertiary time. Subsequent to work by the Wood Committee, Savage (1951) established the Irvingtonian and Rancholabrean NALMAs for the Pleistocene. Although all NALMAs originally were intended to be independent of the Lyellian, European-based Tertiary epochs, NALMAs inevitably became almost synonymized with Lyellian epochs in the minds of geologists and paleontologists alike. Such mental linkages (e.g., Bridgerian = middle Eocene; Chadronian = early Oligocene; etc.) have proven highly unfortunate in the history of North American geological research, being a source of much confusion in temporal correlation between vertebrate paleontologists and traditional geologists. Gradually, however, expanded use and reliability of radioisotopic dating techniques (starting most importantly with the pioneering work of Evernden et al., 1964), in conjunction with data from fossil mammals has increased markedly the reliability of temporal correlation between North American nonmarine sequences and other parts of the world (see Savage and Russell, 1983).

In 1973, a symposium on Vertebrate Paleontology and Geochronology was held in Dallas at the annual meeting of the Geological Society of America. One outcome of the symposium was re-establishment of committees to refine the various NALMAs. After much trial, tribulation, and delay, their work resulted in publication of *Cenozoic Mammals of North America, Geochronology and Biostratigraphy* (edited by Woodburne, 1987).

The use of mammals for biostratigraphic purposes reached its acme in the deciphering of the complex Cenozoic history of mountain ranges and intermontane basins in western North America. Beginning late in the Cretaceous and continuing to the present time, most of this area has been subjected to major tectonism. Large segments of the continental crust experienced important displacement, both horizontally and vertically. Erosion of zones of deformation provided sediments that accumulated to prodigious thicknesses in the intermontane basins. Mammalian assemblages, involving all Cenozoic NALMAs, have proven to be of outstanding utility in the relative dating of structural and depositional histories of western North America. Perhaps there exist no better examples of the marriage between paleomammalogy and historical geology than the various works of Galusha and Blick (1971), Dorr et al. (1977), Skinner et al. (1977), and Wilson (1978).

### *Mobile Continents and Oceanic Basins*

The advent of plate tectonics in the late 1960s had a profound effect upon American paleomammalogy of the 20th Century. As imaginatively summarized by McKenna (1973, 1983), general recognition that major plates across the surface of the earth were mobile (and, by way of seafloor spreading, subduction, and collision, could change in shape and size through geologic time) revolutionized the discipline of historical biogeography. The geological impact of plate tectonics upon historical biogeography can, without exaggeration, be compared to the importance of Darwinism within the biological sciences.

It is certainly true that the two editions (1915, 1939) of Matthew's *Climate and Evolution* established the foundations of modern historical biogeography. Significant additional refinements in principles were provided by Simpson (e.g., 1952, 1953*a*). Further, influences on evolutionary thought of continental stabilist biogeographic viewpoints issuing from these two eminent American paleomammalogists were profound. Both workers had developed convincing biogeographical interpretations (principally involving fossil mammals) that seemingly did not require mobilized continents, especially for geologic intervals as young as the Cenozoic.

In essence, it took independent development and observational application of new techniques in geophysics (especially paleomagnetism) to shake the American community of geoscientists into accepting the reality of highly mobile continents (and actively evolving oceanic basins). Interestingly, much of the European community of paleontologists had accepted various forms of continental drift far in advance of most Americans, even though all proposed physical mechanisms seemed inadequate for purposes of explanation. Once geophysically established, however, American paleomammalogists jumped solidly onto the plate-tectonic bandwagon, and continental mobilism has been a fundamental component of their training and research ever since. Further, it has been accepted that plate tectonics is highly relevant in explaining distributional patterns of particular groups of Cenozoic mammals, such as marsupials (e.g., Tedford, 1974; Woodburne and Zinsmeister, 1984), and even of wholesale continental exchanges (e.g., Dawson, 1980; Webb, 1985).

Along with acceptance of a continental mobilistic perspective came appreciation of a whole series of new possible mechanisms (in supplement of Simpsonian corridors, filter bridges, and sweepstakes routes) for explanation of geographic distributions of suites of fossils. Some processes involved passive transport of already-fossilized assemblages (e.g., the "grounded Viking funeral ships" of McKenna, 1983), but most were pertinent to ancient groups of organisms at times during which they were still alive (e.g., continental "Noah's arks" of McKenna, 1973; "escalator counterflow," "hopscotch on the escalator," and "voyages to nowhere and return" of McKenna, 1983). As occurs all too often in the case of real progress in scientific understanding, recognition of the possibility of several of these cited mechanisms also has served to complicate interpretations of historical biogeography, especially in situations involving archipelagos.

## *Biologically Directed Paleomammalogy*

### *So What Is a Mammal?*

If one studies only modern-day elements of earth's biota, mammals can be differentiated easily from all other vertebrate groups. As one traces the paleontological history of Mammalia back into the middle Mesozoic, however, one-by-one the usual features used to define what a mammal *is* appear in more and more primitive stages, becoming blurred to generally non-mammalian in therapsid ancestors. As a result, paleomammalogists, much more than neomammalogists, have given attention to definition of the Mammalia, and to questions of phylogenetic relationships within the class. One result of such effort is an interesting paradox. On the one hand, the reptile–mammal (or perhaps better, the therapsid–mammal or cynodont–mammal) transformation is better understood anatomically than any other interclass transition within the Vertebrata. But, in contrast, and in large part because of the deadly combination of great Triassic diversity, extensive parallel evolution in many features, and a generally spotty Mesozoic fossil record, the phylogenetic path(s) from therapsids toward mammals is (are) exceedingly uncertain (compare results, for example, among Crompton and Sun, 1985; Hopson and Barghusen, 1986; Miao, 1991; Rowe, 1988).

### *Paleomammalogy and Systematics*

Most of the early paleomammalogists were typologists. Each morphological variant seemed to demand at least a new specific (if not generic) name. Likewise, it seemed that scientific reputation and prestige for some workers was directly proportional to the number of taxa described and named. A classic example of this situation was provided by E. D. Cope when he named the arvicoline genera *Anaptogonia* and *Sycium*. *Anaptogonia,* originally considered a subgenus of *Arvicola* (Cope, 1871), was based primarily upon m1s of the taxon, whereas *Sycium* was based on upper teeth (Cope, 1899). Subsequently, Hibbard (1947) demonstrated that these two taxa were junior synonyms for the modern muskrat, *Ondatra.* Fortunately, a major advance within paleomammalogy during the 20th Century has been to step away from typological approaches to science.

As the flood of newly discovered fossils accumulated in museums, and as masses of data became available from new and diverse fields of biological science (e.g., population genetics), workers in the 1930s and 1940s tried to integrate all aspects of the study of life, as dubbed the "new synthesis." Particularly important parts of this integration were publication by Simpson of *Tempo and Mode in Evolution* (1944) and *The Major Features of Evolution* (1953*b*). The seminal paper on mammalian interrelationships is *The Principles of Classification and a Classification of Mammals* by Simpson (1945). Compiled before WW II, Simpson's classification dealt with every mammalian genus known to him, taxonomically utilizing the philosophy of the new synthesis. A rationale of his approach to the classification of mammals was presented at the 24th annual meeting of ASM at the American Museum of National History, and the work was reviewed in the *Journal of Mammalogy* by E. Raymond Hall (1946). Although in many places outdated, Simpson's work remains an invaluable taxonomic reference; a more detailed compendium has yet to be published.

Toward that end, however, McKenna (1975) has updated information for a comprehensive revision of mammalian taxonomy, with development of elaborately annotated computer files. McKenna (1975) provided a first approximation of this monumental work, using cladistic philosophy as developed by Willi Hennig (1966). McKenna's tentative classification remained above the level of family, and involved many new taxonomic terms that have not been readily accepted by the professional community.

Cladistics as a taxonomic philosophy is being used increasingly by paleomammalogists as seen in a recent special volume by the Systematics Association edited by Benton (1988). A more detailed discussion of the cladistic method can be found in Engstrom et al. (1994). Additional synthesis by attempting to combine morphological and molecular studies in the phylogeny of mammals can be found in the volumes edited by Szalay et al. (1993).

### *Knowledge of the First Two-thirds of Mammalian History*

Tremendous strides have been made during the 20th Century in documentation of Mesozoic mammals. Because few Mesozoic mammals have yet proven their potential worth as biostratigraphic tools, most research on them has been taxonomic or of generally biologic nature. Published research on systematic paleontology of Mesozoic taxa is expanding at an astounding rate (e.g., Cifelli, 1990; Clemens, 1973; Fox, 1989), to the point that necessity for taxonomic and stratigraphic specialization in study of Mesozoic mammals has become a reality, as has long been the case for Cenozoic forms. Additionally, major features in the origin of tribosphenic molars have been worked out (e.g., Crompton, 1971); serious attempts have been made at determining origins of mammalian metabolic pathways (e.g., McNab, 1978); and even study of major steps in Mesozoic mammalian reproduction (e.g., Blackburn et al., 1988) have been approached. Cladistic methodology has figured importantly within comparative studies of detailed anatomy of Mesozoic mammals (e.g., Wible and Hopson, 1993), largely in pursuit of phylogenetic analysis. Diverse forms of research (biological and geological) on Mesozoic Mammalia hold promise for an unusually bright future.

### *Unparalleled Expansion of New Biological Information on Cenozoic Mammals*

The extent of increased knowledge made available since 1919 on comparative anatomy, biological function, paleogeographical distribution, and evolutionary relationships among Cenozoic mammals is no less than astounding. Whole new disciplines of paleobiological research, such as paleoneurology (e.g., Edinger, 1948; Jerison, 1973; Radinsky, 1981), have come into existence. Major paleogeographic surprises, such as the discovery of North American pangolins (Emry, 1970), have occurred. Documentation of highly specialized adaptive realms for mammalian life, such as origin of powered flight (e.g., Jepsen, 1970; Novacek, 1987) or entry into the sea (e.g., Barnes et al., 1985; Domning et al., 1986; Kellogg, 1936; Repenning et al., 1979) has become available.

Functional studies, varying from mechanisms of mastication (e.g., Krause, 1982) to origins of arborealism (e.g., Jenkins, 1974) to recognition of the importance of body size in ancient mammals (e.g., Damuth and MacFadden, 1990), have burgeoned. Finally, at least rough phylogenetic frameworks have been established for most mammalian orders (e.g., Gazin, 1953; Novacek, 1990; Prothero and Schoch, 1989; Schoch, 1986; Simons and Kay, 1983; Wilson, 1986; Wood, 1955). Unquestionably, the greatest diversity and absolute volume of research in 20th Century paleomammalogy has been in the documentation of form, function, and phylogenetic relationships of particular Cenozoic taxa.

## *The Blending of Geologically and Biologically Directed Paleomammalogy*

### *Tempo and Mode in Evolution*

Paleomammalogy can provide unique information that is of key importance to the research of neomammalogists. Obvious examples include paleobiogeographic histories and minimum dates of evolutionary divergence of particular taxa. Potential for such useful applications has been recognized since the origin of paleontology as a science. More recently, however, new kinds of evolutionary inquiry have resulted from the blending of procedural advances derived jointly from the geological and biological sciences. A few examples follow.

Rates and mechanisms of evolutionary change involve questions that have intrigued scientists since the appearance of Charles Darwin's (1859) *The Origin of Species.* For nearly a century after its publication, however, most questions remained vaguely posed, with little real progress being made toward understanding the detailed nature of evolutionary modification. Principal underlying reasons involved an inadequately documented fossil record combined with infancy of the science of genetics. Both areas were strengthened during the first 40 years of the 20th Century, setting the stage for the "new synthesis." It was in large part the greatly improved fossil record of mammals, developed through literally centuries of man-years of field and laboratory effort, and exploited by Simpson (1944, 1953*b*), that allowed integration of paleontological knowledge with paradigms derived from advances in population genetics. Better documentation of morphological change through geologic time, as based on detailed studies of fossil mammals, allowed greater scientific focus on tempos of evolution. Simpson demonstrated, for example, that rates of mammalian evolution varied within and among taxa. He also noticed that paleontologically recognizable change occurred in spurts and starts, separated by what appeared to be extensive intervals of morphological stability. Simpson was a firm believer, however, in the essential gradualness of evolutionary change, and attributed much of the apparent irregularity in rates to stratigraphic and geographic imperfections and biases within the fossil record.

More recently, questions of tempo and mode in evolution have been reconsidered by Eldredge and Gould (1972), using a more literal interpretation of the fossil record. They suggested that the apparent stasis within species, and the paucity of transitional forms between species, are real, and represent ways in which the allopatric model of speciation would be expected to be reflected in the fossil record. Because of the apparent sudden appearance of new species in local stratigraphic columns above long sections of morphological stasis, they coined the term "punctuated equilibrium" for their concept. Although their suggestion originally attempted to reconcile the fossil record with the concept of allopatric speciation, they expanded it subsequently to include other features as well, such as the restriction of virtually all evolutionary change to the process of speciation (Gould, 1985; Gould and Eldredge, 1977). The punctuated equilibrists have been opposed by many neo-Darwinists (e.g., Bown and Rose, 1987; Gingerich, 1985), who demonstrated stratigraphically controlled gradual change between mammalian species in the fossil record; such workers have come to be known as phyletic gradualists. Yet a third group reached a compromise position, suggesting that both patterns have operated, as already had been suggested in some cases by earlier workers (see Newman et al., 1985).

Issues involved in the debate cited above were summarized by Barnosky (1987), who examined results of various studies on Quaternary mammals. He pointed out that the Quaternary should be an ideal geologic interval for the testing of competing models because both time- and species-resolution are highly determinable, at least compared to the Mesozoic or Tertiary. Case-histories cited by Barnosky (1987) demonstrate that some species transitions appear to follow patterns of punctuated equilibrium, whereas others seem to fit more closely models of phyletic gradualism. No matter where the truth eventually may be shown to lie, all of these highly focused studies have depended upon elevated standards of detailed, stratigraphically documented collections made in the field at levels of thoroughness only imagined even when the new synthesis was being developed.

### *The Spectre of Heterochrony in Homotaxy*

Huxley (1870) recognized the spectre of heterochrony [i.e., "temporal overlap of assemblages assigned to successive, presumed non-overlapping ages, or assemblages assigned to the same age being time transgressive or not precisely time-equivalent" (Flynn et al., 1984)]. Huxley (1870) also appreciated that the possibility of heterochrony cannot be eliminated through application of standard paleontological techniques alone. Wisely, he suspected that fully homotaxic faunas (i.e., taxonomically *identical* assemblages), even when using the most closely spaced, stratigraphically controlled fossil collections, in reality, might be asynchronous. Therefore, it is possible that when comparing identically changing taxonomic assemblages between geographically separated areas, the usual assumption of synchrony of the assemblages may be incorrect. Instead, the geographically separated but homotaxic faunas may, for example, have been tracking, through time, shifting ecological regimes. Needless to say, anyone endeavoring to study the tempo and mode of evolutionary change must be able to recognize absolutely that no significant asynchrony exists between geographically separated, homotaxic faunal assemblages. As discussed by Flynn et al. (1984), two recent advances from the geological sciences provide capabilities, not available in the days of Huxley, to better evaluate the possibilities of heterochrony.

One advance involves detailed study of the record of polarity reversals of earth's magnetic field through orientation of ferromagnetic minerals in individual fossil localities (e.g., Lindsay et al., 1981). When polarity data are used in combination with other, independent dating techniques, it is often possible to identify particular brief intervals of earth's magnetic polarity history. The other advancement has been with radioisotopic dating, of which a multiplicity of suitable isotopes and variations in techniques is now known to exist. One particular variant that is especially promising for application to pre-Pleistocene, mammal-bearing units is the single-crystal, laser-fusion method, involving isotopes of argon (Swisher and Prothero, 1990). Through combination of detailed paleontology, magnetostratigraphy, and high-resolution radioisotopic dating, it is possible (Flynn et al., 1984) to recognize the existence of geographic migration of "age-defining" taxa through geologically significant intervals of time; however, no entire land-mammal fauna has yet been shown to be heterochronic.

### *The Nature of Extinction*

The phenomenon of extinction has intrigued scientists since its possibility was first proposed by Hooke in the 1670s (Dott and Batten, 1971). Although extinctions have occurred throughout the history of life, the times of major (or mass) extinctions, reputedly concentrated at major geologic boundaries, have received the most attention. Most of the recent study on extinctions by North American paleomammalogists has been on those in the proximity of the Cretaceous/Tertiary (K/T) and Pleistocene/Holocene (P/H) boundaries. In both cases, the majority of paleomammalogists has favored a conservative (i.e., rather gradualistic) point of view in explaining the extinctions; others, however, have suggested more dramatic scenarios.

A catastrophic perspective for the K/T boundary was presented initially by Alvarez et al. (1980), involving a presumed impact with earth of a major extraterrestrial body, probably an asteroid. Over the following decade, a variety of independent geological and paleontological evidence has been marshalled in support of the impact theory (see Izett, 1990). In simplest terms, the putative impact led to a kind of "nuclear winter" caused by fine-grained debris hurled into the atmosphere, initiating a complex series of events that essentially ended, through extensive marine and terrestrial extinctions, the unique biota that was characteristic of late Cretaceous time.

Most vertebrate paleontologists, in contrast, have been unconvinced. Archibald and Bryant (1990), for example, have examined the entirety of the extensive vertebrate faunas (including aquatic, semiaquatic, and terrestrial species) as stratigraphically represented below, at, and above the presumed K/T boundary of northeastern Montana. This is the world's only nonmarine section at which a detailed analysis of faunal change across the K/T boundary has been completed. Observed faunal changes across the boundary not only run contrary to ecological predictions for the effects of a nuclear winter but, according to Archibald and Bryant, are not even necessarily consistent with environmental catastrophy. They suggest the possibility of a more protracted interval (involving various extinctions and replacements). Such change could have been allied, for example, to alteration of habitat across the broad, latest Cretaceous coastal plain, resulting from retreat from North America of the Western Interior Seaway.

One suggested explanation of extinctions near the P/H boundary is that of overkill by invading humans (e.g., Martin, 1984). Chief evidence, at least in the Americas, involves the correlation, supported by radiometric dates, of extinctions of large ungulates (and their contemporaneous predators) with the first appearances of Man. Many archaeological sites across Eurasia and North America unequivocally document the prowess of late Pleistocene Man as a hunter, even of the largest contemporary mammals.

The idea of Man as the principal culprit in P/H extinctions has not, however, enjoyed unanimous acceptance, and all intergradations of viewpoints exist. Some workers have been willing to accept certain limited extinctions as having resulted from human overkill (principally through habitat destruction), particularly on oceanic islands. Widespread avian extinctions, for example, are well documented in the Hawaiian Islands (James et al., 1987) in association with arrival of the original Polynesians and their various commensals. Other workers (see Martin, 1967 for citations), in contrast, simply have found it difficult to accept the demise of vast herds of North American Pleistocene mammals at the hands of Man. This is especially true in light of the long coexistence of Man and mammalian megafaunas across Eurasia and Africa during all of Quaternary time.

As presumed for the K/T boundary, many workers have suggested that habitat changes were responsible for extinction of the latest Pleistocene megafaunas. Although evidence associated with local habitat (or global climatic) change may not be obvious for the latest Pleistocene, it is clear that climates became cooler overall and more seasonal in the interior through the latter half of the Cenozoic. Such changes caused dramatic shifts in distributions and types of plant communities. For example, Webb (1983) demonstrated changes in dominance of North American ungulates from browsing to grazing forms during late Miocene time. Workers such as Guthrie (1984) suggested that climatic changes accounting for the Miocene shift continued into Plio–Pleistocene time, thereby ultimately decreasing the net annual quality and quantity of food resources available to the megafauna. Graham and Lundelius (1984) suggested biotic disequilibrium as a possible reason for late Pleistocene extinctions.

In any case, no matter how the physical evidence itself may be interpreted, marriages among detailed biostratigraphy, magnetostratigraphy, radioisotopic dating, and even archaeology have led to greatly improved levels of focused inquiry associated with questions of causation in extinction. At least for the late Pleistocene and early Holocene, the levels of precision in dating made possible by $^{14}C$-technology have reached levels that make such age determinations of true relevance of biological considerations of extinction.

## *Epilogue*

We have summarized what we consider to be a broad sampling of major contributions by paleomammalogists to the field of mammalogy since the founding of the ASM 75 years ago. Many of these advancements have occurred in the last 25 years as new technologies, philosophies, and more workers have entered the field. As technologies continue to improve, philosophies mature, and information expands, we look forward to the spectacular additional progress that surely will be documented in the Centennial Volume of the society.

## Acknowledgments

We thank B. H. Breithaupt, J.-P. Cavigelli, R. W. Graham, L. E. Lillegraven, and R. W. Wilson for their help in the preparation of this manuscript. We thank W. A. Clemens, Jr. and M. R. Voorhies for their critical reviews.

## Literature Cited


Alvarez, L. W., W. Alvarez, F. Asaro, and H. V. Michel. 1980. Extraterrestrial cause for the Cretaceous-Tertiary extinction. Science, 208:1095–1108.

Archibald, J. D., and L. J. Bryant. 1990. Differential Cretaceous-Tertiary extinctions of non-marine vertebrates from northeastern Montana. Geological Society of America, Special Paper, 247:549–562.

Barnes, L. G., D. P. Domning, and C. E. Ray. 1985. Status of studies on fossil marine mammals. Marine Mammal Science, 1:15–53.

Barnosky, A. D. 1987. Punctuated equilibrium and phyletic gradualism: some facts from the Quaternary mammalian record. Current Mammalogy, 1:109–147.

Bayne, C. K. 1976. Early medial Pleistocene faunas of Meade County, Kansas. Kansas Geological Survey, Guidebook Series, 1:1–25.

Behrensmeyer, A. K., and A. P. Hill (eds.). 1980. Fossils in the making: vertebrate taphonomy and paleoecology. The University of Chicago Press, Chicago, 338 pp.

Benton, M. J. (ed.) 1988. The phylogeny and classification of the tetrapods. Volume 2: Mammals. The Systematics Association Special Volume, 35B:1–329.

Blackburn, D. G., J. M. Taylor, and H. A. Padykula. 1988. Trophoblast concept as applied to therian mammals. Journal of Morphology, 196: 127–136.

Bown, T. M., and K. D. Rose. 1987. Patterns of dental evolution in early Eocene anaptomorphine primates (Omomyidae) from the Bighorn Basin, Wyoming. Paleontological Society Memoir, 23:1–162.

Carleton, M. D., and R. E. Eshelman. 1979. A synopsis of fossil grasshopper mice, genus *Onychomys,* and their relationships to recent species. The University of Michigan, Museum of Paleontology, Papers on Paleontology, 21(C. W. Hibbard Memorial Volume 7):1–63.

Cifelli, R. L. 1990. Cretaceous mammals of southern Utah. IV. Eutherian mammals from the Wahweap (Aquilan) and Kaiparowits (Judithian) formations. Journal of Vertebrate Paleontology, 10:346–360.

Clemens, W. A., Jr. 1963. Fossil mammals of the type Lance formation Wyoming. Part I. Introduction and Multituberculata. University of California Publications in Geological Sciences, 48:1–105.

———. 1966. Fossil mammals of the type Lance formation Wyoming. Part II. Marsupialia. University of California Publications in Geological Sciences, 62: 1–122.

———. 1973. Fossil mammals of the type Lance formation, Wyoming. Part III. Eutheria and summary. University of California Publications in Geological Sciences, 94:1–102.

Cope, E. D. 1871. Preliminary report on the *Vertebrata* discovered in the Port Kennedy bone cave. Proceedings of the American Philosophical Society of Philadelphia, 12:73–102.

———. 1899. Vertebrate remains from Port Kennedy bone deposit. Journal of the Academy of Natural Sciences of Philadelphia, Second Series, 11:193–267.

Crompton, A. W. 1971. The origin of the tribosphenic molar. Pp. 65–87, *in* Early mammals (D. M. Kermack and K. A. Kermack, eds.). Zoological Journal of the Linnean Society, 50, suppl., 1:1–203.

Crompton, A. W., and A. L. Sun. 1985. Cranial structure and relationships of the Liassic mammal *Sinoconodon.* Zoological Journal of the Linnean Society, 85:99–119.

Damuth, J., and B. J. MacFadden (eds.). 1990. Body size in mammalian paleobiology: estimation and biological implications. Cambridge University Press, Cambridge, Great Britain, 397 pp.

Darwin, C. 1859. On the origin of species by means of natural selection. . . Murray, London, 490 pp.

Dodson, P., and D. Wexlar. 1979. Taphonomic investigations of owl pellets. Paleobiology, 5:275–284.

Domning, D. P., C. E. Ray, and M. C. McKenna. 1986. Two new Oligocene desmostylians and a discussion of Tethytherian systematics. Smithsonian Contributions to Paleobiology, 59, 56 pp.

Dorr, J. A., Jr., D. R. Spearing, and J. R. Steidtmann. 1977. Deformation and deposition between a foreland uplift and an impinging thrust belt: Hoback Basin, Wyoming. Geological Society of America, Special Paper, 177, 82 pp.

Dott, R. H., Jr., and R. L. Batten. 1971. Evolution of the Earth. McGraw-Hill Book Company, New York, 649 pp.

Edinger, T. 1948. Evolution of the horse brain. Geological Society of America, Memoir 25:1–174.

Eldredge, N., and S. J. Gould. 1972. Punctuated equilibria: an alternative to phyletic gradualism. Pp. 82–115, *in* Models in Paleobiology (T. J. M. Schopf, ed.). Freeman, Cooper & Company, San Francisco, 250 pp.

Emry, R. J. 1970. A North American Oligocene pangolin and other additions to the Pholidota. Bulletin of the American Museum of Natural History, 142: 455–510.

Engstrom, M. D., J. R. Choate, and H. H. Genoways. Taxonomy. Pp. 179–199, *in* Seventy-five years of mammalogy (1919–1994) (E. C. Birney and J. R. Choate, eds.). Special Publication, The American Society of Mammalogists, 11:1–433.

Evernden, J. F., D. E. Savage, G. H. Curtis, and G. T. James. 1964. Potassium-argon dates and the Cenozoic mammal chronology of North America. American Journal of Science, 262:145–198.

Flynn, J. J., B. J. MacFadden, and M. C. McKenna. 1984. Land-mammal ages, faunal heterochrony, and temporal resolution in Cenozoic terrestrial sequences. Journal of Geology, 92:687–705.

Fox, R. C. 1989. The Wounded Knee local fauna and mammalian evolution near the Cretaceous-Tertiary boundary, Saskatchewan, Canada. Paleontographica, Abstract A, 208:11–59.

Galusha, T., and J. C. Blick. 1971. Stratigraphy of the Santa Fe Group, New Mexico. Bulletin of the American Museum of Natural History, 144:1–127.

Gazin, C. L. 1953. The Tillodontia: an early order of mammals. Smithsonian Miscellaneous Collections, 121:1–110.

Gingerich, P. D. 1985. Species in the fossil record: concepts, trends, and transitions. Paleobiology, 11: 27–41.

———. 1986. George Gaylord Simpson: empirical theoretician. Pp. 3–9, *in* Vertebrates, phylogeny, and philosophy (K. M. Flanagan and J. A. Lillegraven, eds.). Contributions to Geology, University of Wyoming, Laramie, Special Paper, 3:1–361.

Gould, S. J. 1985. The paradox of the first tier: an agenda for paleobiology. Paleobiology, 11:2–12.

Gould, S. J., and N. Eldredge. 1977. Punctuated equilibria: the tempo and mode of evolution reconsidered. Paleobiology, 3:115–151.

Graham, R. W., and E. L. Lundelius, Jr. 1984. Coevolutionary disequilibrium and Pleistocene extinctions. Pp. 223–249, *in* Quaternary extinctions: a prehistoric revolution (P. S. Martin and R. G. Klein, eds.). University of Arizona Press, Tucson, 891 pp.

Gregory, J. T., J. A. Bacskai, G. V. Shkurkin, M. C. Winans, and B. H. Rauscher. 1992. Bibliography of fossil vertebrates 1989. Society of Vertebrate Paleontology, Lincoln, Nebraska, 495 pp.

Guilday, J. E. 1971. The Pleistocene history of the Appalachian mammal fauna. Pp. 233–262, *in* The distributional history of the biota of the southern Appalachians. Part III: Vertebrates (P. C. Holt, ed.). Virginia Polytechnic Institute and State University Research Division Monograph, Blacksburg, 4:1–306.

Guthrie, R. D. 1984. Mosaics, allelochemics and nutrients: an ecological theory of late Pleistocene megafaunal extinctions. Pp. 259–298, *in* Quaternary extinctions: a prehistoric revolution (P. S. Martin and R. G. Klein, eds.). University of Arizona Press, Tucson, 891 pp.

Hall, E. R. 1946. [Review of] Simpson, George Gaylord. The principles of classification and a classification of mammals. Journal of Mammalogy, 27:287–288..

Hennig, W. 1966. Phylogenetic systematics. University of Illinois Press, Urbana, 263 pp.

Hesse, C. 1941. [Review of] Nomenclature and correlation of the North American continental Tertiary (Report by H. E. Wood, II, et al.). Journal of Mammalogy, 22:458.

Hibbard, C. W. 1941. The Borchers fauna, a new Pleistocene interglacial fauna from Meade County, Kansas. Kansas Geological Survey Bulletin, 38:197–220.

———. 1947. The status of the genera Anaptogonia and Sycium Cope. Journal of Mammalogy, 28:67.

———. 1949. Techniques of collecting microvertebrate fossils. Contributions from the Museum of Paleontology, University of Michigan, 8:7–19.

Hopson, J. A., and H. R. Barghusen. 1986. An analysis of therapsid relationships. Pp. 83–106, *in* The ecology and biology of mammal-like reptiles (N. Hotton, III, P. D. MacLean, J. J. Roth, and E. C. Roth, eds.). Smithsonian Institution Press, Washington, D.C., 326 pp.

Huxley, T. H. 1870. The anniversary address of the president. Quarterly Journal of the Geological Society of London, 26:*xxix–lxiv*.

Izett, G. A. 1990. The Cretaceous/Tertiary boundary interval, Raton Basin, Colorado and New Mexico, and its content of shock-metamorphosed minerals; evidence relevant to the K/T boundary impact-extinction theory. Geological Society of America, Special Paper 249:1–100.

James, H. F., et al. 1987. Radiocarbon dates on bones of extinct birds from Hawaii. Proceedings of the National Academy of Sciences, USA, 84:2350–2354.

Jenkins, F. A., Jr. 1974. Tree shrew locomotion and the origin of primate arborealism. Pp. 85–115, *in* Primate locomotion (F. A. Jenkins, Jr., ed.). Academic Press, New York, 390 pp.

Jepsen, G. L. 1970. Bat origins and evolution. Pp. 1–64, *in* Biology of bats (W. A. Wimsatt, ed.). Academic Press, New York, 1:1–404.

Jerison, H. J. 1973. Evolution of the brain and intelligence. Academic Press, New York, 482 pp.

Kellogg, R. 1936. A review of the Archaeoceti. Carnegie Institution of Washington Publication, 482:1–366.

Korth, W. W. 1979. Taphonomy of microvertebrate fossil assemblages. Annals of Carnegie Museum, 48: 235–285.

Krause, D. W. 1982. Jaw movement, dental function, and diet in the Paleocene multituberculate *Ptilodus*. Paleobiology, 8:265–281.

Lillegraven, J. A. 1969. Latest Cretaceous mammals of upper part of Edmonton formation of Alberta, Canada, and review of marsupial-placental dichotomy in mammalian evolution. University of Kansas Paleontological Contributions, 50:1–122.

Lindsay, E. H., R. F. Butler, and N. M. Johnson. 1981. Magnetic polarity zonation and biostratigraphy of late Cretaceous and Paleocene continental deposits, San Juan Basin, New Mexico. American Journal of Science, 281:390–435.

Martin, P. S. 1967. Pleistocene overkill. Pp. 75–120, *in* Pleistocene extinctions, the search for a cause (P. S. Martin and H. E. Wright, Jr., eds.). Yale University Press, New Haven, Connecticut, 453 pp.

———. 1984. Prehistoric overkill: the global model. Pp. 354–403, *in* Quaternary extinctions: a prehistoric revolution (P. S. Martin and R. G. Klein, eds.). The University of Arizona Press, Tucson, 891 pp.

MATTHEW, W. D. 1915. Climate and evolution. Annals of the New York Academy of Sciences, 24:171–318.

———. 1939. Climate and evolution. Second ed. Special Publication of the New York Academy of Sciences, 1:1–223.

MCKENNA, M. C. 1962. Collecting small fossils by washing and screening. Curator, 3:221–235.

———. 1973. Sweepstakes, filters, corridors, Noah's arks, and beached Viking funeral ships in palaeogeography. Pp. 295–308, *in* Implications of continental drift to the Earth sciences (D. H. Tarling and S. K. Runcorn, eds.). Academic Press, London, 1:1–622.

———. 1975. Toward a phylogenetic classification of the Mammalia. Pp. 21–46, *in* Phylogeny of the Primates: a multidisciplinary approach (W. P. Luckett and F. S. Szalay, eds.). Plenum Press, New York, 483 pp.

———. 1983. Holarctic rearrangement, cosmic events, and Cenozoic terrestrial organisms. Annals of the Missouri Botanical Garden, 70:459–489.

MCNAB, B. K. 1978. The evolution of endothermy in the phylogeny of mammals. The American Naturalist, 112:1–21.

MELLETT, J. 1974. Scatological origin of microvertebrate fossil accumulations. Science, 185:349–350.

MIAO, D. 1991. On the origins of mammals. Pp. 579–597, *in* Origins of the higher groups of tetrapods: controversies and consensus (H.-P. Schultze and L. Trueb, eds.). Cornell University Press, Ithaca, 724 pp.

MILLER, G. S, AND J. W. GIDLEY. 1918. Synopsis of the supergeneric groups of rodents. Journal of the Washington Academy of Science, 8:431–448.

NEWMAN, C. M., J. E. COHEN, AND C. KIPNIS. 1985. Neo-Darwinian evolution implies punctuated equilibria. Nature, 315:400–401.

NOVACEK, M. J. 1987. Auditory features and affinities of the Eocene bats *Icaronycteris* and *Palaeochiropteryx* (Microchiroptera, *incertae sedis*). American Museum Novitates, 2877:1–18.

———. 1990. Morphology, paleontology, and the higher clades of mammals. Current Mammalogy, 2:507–543.

OLSON, E. C. 1980. Taphonomy: its history and role in community evolution. Pp. 5–19, *in* Fossils in the making: vertebrate taphonomy and paleoecology (A. K. Behrensmeyer and A. P. Hill, eds.). The University of Chicago Press, Chicago, 338 pp.

OSBORN, H. F. 1921. Resemblances and contrasts between zoologic and paleontologic research in mammalogy. Desirability of uniform standards and systems in classification, in description, in measurements, in reasoning. Journal of Mammalogy, 2:1–11.

PROTHERO, D. R., AND R. M. SCHOCH (EDS.). 1989. The evolution of perissodactyls. Oxford University Press, London, 537 pp.

RADINSKY, L. 1981. Brain evolution in extinct South American ungulates. Brain, Behavior and Evolution, 18:169–187.

REPENNING, C. A., C. E. RAY, AND D. GRIGORESCU. 1979. Pinniped biogeography. Pp. 357–369, *in* Historical biogeography, plate tectonics, and the changing environment (J. Gray and A. J. Boucot, eds.). Oregon State University Press, Corvallis, 500 pp.

ROWE, T. 1988. Definition, diagnosis, and origin of the Mammalia. Journal of Vertebrate Paleontology, 8:241–264.

SAVAGE, D. E. 1951. Late Cenozoic vertebrates of the San Francisco Bay region. University of California Publications in Geological Sciences, 28:215–314.

SAVAGE, D. E., AND D. E. RUSSELL. 1983. Mammalian paleofaunas of the world. Addison-Wesley Publishing Company, London, 432 pp.

SCHOCH, R. M. 1986. Systematics, functional morphology and macroevolution of the extinct mammalian order Taeniodontia. Bulletin of the Peabody Museum of Natural History, Yale University, New Haven, Connecticut, 42:1–307.

SIMONS, E. L., AND R. F. KAY. 1983. *Oatrania*, a new basal anthropoid primate from Fayum, Oligocene of Egypt. Nature, 304:624–626.

SIMPSON, G. G. 1928. A catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum. Oxford University Press, London, 215 pp.

———. 1929. American Mesozoic Mammalia. Memoir of the Peabody Museum of Yale University, 3:1–171.

———. 1944. Tempo and mode in evolution. Columbia University Press, New York, 237 pp.

———. 1945. The principles of classification and a classification of mammals. Bulletin of the American Museum of Natural History, 85:1–350.

———. 1952. Probabilities of dispersal in geologic time. Pp. 163–176, *in* The problem of land connections across the South Atlantic, with special reference to the Mesozoic (E. Mayr, et al., eds.). Bulletin of the American Museum of Natural History, 99:79–258.

———. 1953*a*. Evolution and geography. Oregon State System of Higher Education, Condon Lectures, Corvallis, 64 pp.

———. 1953*b*. The major features of evolution. Columbia University Press, New York, 434 pp.

———. 1971. Concluding remarks: Mesozoic mammals revisited. Pp. 181–198, *in* Early mammals (D. M. Kermack and K. A. Kermack, eds.). Zoological Journal of the Linnean Society, 50, suppl., 1:1–203.

SKINNER, M. F., S. M. SKINNER, AND R. J. GOORIS. 1977. Stratigraphy and biostratigraphy of late Cenozoic deposits in central Sioux County, western Nebraska. Bulletin of the American Museum of Natural History, 158:263–371.

SWISHER, C. C., III, AND D. R. PROTHERO. 1990. Single-crystal $^{40}Ar/^{39}Ar$ dating of the Eocene-Oligocene transition in North America. Science, 249:760–762.

SZALAY, F. S., M. J. NOVACEK, AND M. C. MCKENNA (EDS.). 1993. Mammal phylogeny. Springer-Verlag, New York, 1:1–249, 2:1–321.

TEDFORD, R. H. 1974. Marsupials and the new paleogeography. Pp. 109–126, *in* Paleogeographic provinces and provinciality (C. A. Ross, ed.). Society of Economic Paleontologists and Mineralogists, Special Publication, 21, 1–233.

VOORHIES, M. R. 1969. Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska. Contributions to Geology, University of Wyoming, Laramie, Special Paper, 1, 1–69.

Webb, S. D. 1983. The rise and fall of the late Miocene ungulate fauna in North America. Pp. 267–306, *in* Coevolution (M. H. Nitecki, ed.). The University of Chicago Press, Chicago, 392 pp.

———. 1985. Late Cenozoic mammal dispersals between the Americas. Pp. 357–386, *in* The great biotic interchange (F. G. Stehli and S. D. Webb, eds.). Plenum Press, New York, 532 pp.

White, J. A., and B. L. Keller. 1984. Evolutionary stability and ecological relationships of morphology in North American Lagomorpha. Pp. 58–66, *in* Papers in vertebrate paleontology honoring Robert Warren Wilson (R. M. Mengel, ed.). Special Publication, Carnegie Museum of Natural History, 9, 1–186.

Wible, J. R., and J. A. Hopson. 1993. Basicranial evidence for early mammal phylogeny. Pp. 45–62, *in* Mammal phylogeny: Mesozoic differentiation, multituberculates, monotremes, early therians, and marsupials (F. S. Szalay, M. J. Novacek, and M. C. McKenna, eds.). Springer-Verlag, New York, 249 pp.

Wilson, J. A. 1978. Stratigraphic occurrence and correlation of early Tertiary vertebrate faunas, Trans-Pecos Texas, Part I: Vieja area. Texas Memorial Museum Bulletin, 25:1–42.

Wilson, R. W. 1986. The Paleogene record of the rodents: fact and interpretation. Pp. 163–175, *in* Vertebrates, phylogeny, and philosophy (K. M. Flanagan and J. A. Lillegraven, eds.). Contributions to Geology, University of Wyoming, Laramie, Special Paper, 3:1–361.

Wood, A. E. 1955. A revised classification of the rodents. Journal of Mammalogy, 36:165–187.

Wood, H. E., II, et al. 1941. Nomenclature and correlation of the North American continental Tertiary. Bulletin of the Geological Society of America, 52:1–48.

Woodburne, M. O. (ed.). 1987. Cenozoic mammals of North America: geochronology and biostratigraphy. University of California Press, Berkeley, 336 pp.

Woodburne, M. O., and W. J. Zinsmeister. 1984. The first land mammal from Antarctica and its biogeographic implications. Journal of Paleontology, 58: 913–948.

Zakrzewski, R. J. 1975. Pleistocene stratigraphy and paleontology in western Kansas: the state of the art, 1974. Pp. 121–128, *in* Studies on Cenozoic paleontology and stratigraphy in honor of Claude W. Hibbard (G. R. Smith and N. E. Frieland, eds.). University of Michigan, Papers on Paleontology, 12 (C. W. Hibbard Memorial Volume 3), 143 pp.

# *BIOGEOGRAPHY*

SYDNEY ANDERSON AND BRUCE D. PATTERSON

## *Introduction*

Biogeography, the study of the distribution of life, seeks to comprehend an immense range and diversity of phenomena. Most broadly conceived, the field ranges from the domain of astrophysics (the distribution of matter in the universe and the physical laws of radiation, gravitation, and others which affect this) to ecological and behavioral interactions that govern the spatial distribution of individuals within local demes. For the purposes of this brief historical review, and in parallel with editorial opinion in biogeographic journals (see Blondel, 1987), however, we consider biogeographic patterns and processes ranging from global climates and drifting continents on the one hand to local communities and species responses at distributional limits on the other (e.g., Reichman, 1984). Conceptually, at least, our coverage transcends the fields now known as historical biogeography and landscape and geographical ecology, although space limitations preclude detailed treatment of all aspects.

Biogeographic patterns and processes are sensitive to variations in time, space, and biological organization. These patterns and processes may be categorized according to the scales of these crucial factors. "Ecological" time-periods may be contrasted with "evolutionary" ones—the former denotes the years, decades, and centuries over which ecological processes, such as dispersal, succession, altered resource-use patterns, and others take place. Evolutionary time periods may involve different types of organismal responses, including changing gene frequencies, local adaptation and genetic drift, and speciation. In similar fashion, processes that operate over local spatial scales differ from those involved in larger (regional or continental) patterns. Finally, the processes of environmental stimulus and organismal response are mediated in fundamentally different ways by species populations (through the genetics of reproduction and adaptation) and biotas (through competition, predation, and other community-level processes).

We attempt here to chronicle the development of mammalian biogeography over the last 75 years. After considering some trends that generally apply to all biogeographic subdisciplines, we use the different scales of time, space, and biological organization to organize our discussion of various topics. We first treat studies of species over ecological time, proceeding then to those on biotas (but emphasizing mammalian faunas) over ecological time, species over evolutionary time, and faunas over evolutionary time. Within each unit, we have attempted to arrange patterns and processes in order of increasing spatial scope.

## *Historical Trends*

By 1919 the discipline of biogeography was already vigorous and well established. That different plants and animals lived in different places was known in classical times, but elaboration and formalization of that recognition increased dramatically in the three centuries before the founding of the American Society of Mammalogists. Important contributions were made by early 19th Century workers, including von Humboldt and Bonpland, de Candolle, and Lyell (see Nelson, 1978). Sclater's (1858) classification of the world's avifauna into biogeographic regions and subregions ranks as a major biogeographic development of the 19th Century. This work, and the burgeoning inventories of worldwide faunas assembled by imperial Europe, permitted Lydekker (1986) to develop a strikingly accurate discussion of regionalism in mammalian faunas. The life-zone concept of Merriam (1890) was another major event, at least for understanding the ecological factors that affect the distribution of North American mammals. In addition, under Merriam's leadership, the U.S. Biological Survey had produced a growing series of taxonomic revisions and regional faunal accounts that were published mainly in the *North American Fauna* series—43 numbers had been published by 1919. Based on copious collections, many of these accounts included detailed distribution maps of species, vegetation types, and finally formal "life zones." Moreover, they contributed importantly to the developing polytypic species concept, with its explicit recognition of geographic variation, and thence eventually to the "modern synthesis" of evolutionary theory. Just before the founding of the society, Matthew's (1915) *Climate and Evolution* was published, postulating the northern origin and southward dispersal of many mammalian groups; Matthew's thesis emphasized the importance of history in interpreting biogeographic patterns. This paper had considerable influence on mammalian biogeography, in significant part through the work of his student G. G. Simpson. However, some of the details and major assumptions in Matthew's five-point thesis have required modification.

A more enduring contribution to this field was Wegener's hypothesis of drifting continents, originally presented in 1912. This revolutionary hypothesis was soundly rejected by Matthew and many other mammalogists, and its revival required the passage of half a century and the discovery of a geophysical mechanism, plate tectonics, to allow drift.

Since the founding of the ASM, a number of trends are discernable in the development of biogeography. Simple, general patterns were dissected to reveal more complex ones. Emphases shifted from purely descriptive accounts to increasingly quantitative and predictive ones. Models of biogeographic processes were developed, initially static and then increasingly more dynamic in character. Some of these trends have long been evident—in a mid-century appraisal, Hubbs (1958:470) noted "a shift from the classical, purely descriptive biogeography to a kinetic approach, which is more concerned with processes and explanations than with the classification of the earth into a hierarchy of biogeographical regions."

As biogeography matured, gains in analytical rigor have been achieved, sometimes at the expense of flexibility and breadth. In its infancy, biogeography had spanned all or most of natural history, but as it matured, rival schools developed around narrower concepts (e.g., island biogeography) or approaches (e.g., numerical biogeography). Biogeographers were themselves classified as champions of dispersal or vicariance, or devotees of equilibrium or historical schools. Even finer distinctions were thought necessary to reflect philosophical differences within these categories (e.g., vicariance biogeography, phylogenetic biogeography, and panbiogeography). For the most part, biogeographic discords reflected parallel acrimony in the sister disciplines of systematics and ecology, which also experienced philosophical and technological revolutions during the 1960s and 1970s (Hull, 1988; McIntosh, 1985). Perhaps because extended critical discussion has exposed the shortcomings of each approach, biogeography today is best carried out under a banner of pluralism (McIntosh, 1987).

## *Species Over Ecological Time Periods*

How is the distribution of a species related to its abundance? This relationship was explored, mostly from an ecological perspective, by Andrewartha and Birch (1954). The thesis of the book is that "distribution and abundance are but two aspects of one phenomenon." The book is replete with biogeographical implications. They showed that common species may be rare in marginal parts of their ranges and that there is no fundamental distinction between the extinction of a local population and the extinction of a species except that, in the latter case, the population becoming extinct happens to be the last one of the species.

How is the distribution of a species limited? Trying to understand those limits began simply enough with concepts such as Liebig's "law of the minimum" proposed for the limits to growth in plants (discussed by Hesse et al., 1937:21). This interesting question continues to attract speculation and investigation. A wholesale shift in distribution of a local fauna of mammals accompanying changes in local climates in the Pleistocene was described by Guilday et al. (1964).

The dynamic nature of species limits on a shorter time scale is indicated by numerous documented cases in which boundaries of individual species have expanded or contracted recently in North America over a relatively few years of time. For example, *Dasypus novemcinctus* (Fitch et al., 1952; Smith and Lawlor, 1964), *Baiomys taylori* (Baccus et al., 1971), and *Sigmodon hispidus* (Genoways and Schlitter, 1967), extended their ranges northward; *Marmota monax* extended westward in Kansas (Choate and Reed, 1986); *Lepus californicus* extended eastward in Texas (Packard, 1963); *Spermophilus richardsoni* (Hansen, 1962) extended southward in Colorado; and since 1960 *Sorex cinereus, Microtus pennsylvanicus, Mustela nivalis,* and *Zapus hudsonius* have extended southward in Kansas (Frey, 1992). It is more difficult to demonstrate retractions in ranges, but surely these have been occurring as well. The retractions in ranges of many larger mammals, such as grizzly bears, mountain lions, gray wolves, and wapiti in North America, need no further documentation here. Another recent mammalian example is the correlation of hours of darkness (about 7.3 hours in this case) needed for feeding with the northern limit of an Asian porcupine (Alkon and Saltz, 1988).

In 1957, Darlington's book *Zoogeography: the Geographical Distribution of Animals* summarized distribution of the major groups of terrestrial vertebrates. Questions posed (p. vii) were: (1) What is the main pattern of animal distributions? (2) How has the pattern been formed? (3) Why has the pattern been formed? and, (4) What does animal distribution tell about ancient lands and climates?

The answers (Darlington, 1957:618) were: (1) The main pattern is a "concentration of the largest, most diverse, least-limited faunas in the main tropical regions of the Old World; limitation caused by climate north of the tropics; and limitation and differentiation caused by barriers in South America and Australia." (2) The pattern has been formed by spread of successive dominant groups from the Old World tropics over much or all of the world, followed by zonation and differentiation according to climate and ocean barriers, and by retreat and replacement of old groups as new ones spread." (3) The pattern has been formed "because evolution has tended to produce the most dominant animals in the largest and most favorable areas, which for most vertebrates are in the main regions of the Old World tropics" (see Darlington, 1957: 569 for brief comments on probabilities and dominance). (4) Animal distribution tells us that "as far back as can be seen clearly, the main pattern of continents and climates seems to have been the same as now." From a slightly skeptical point of view, we may now judge that the compilation of summaries of distributions of different groups may have been a greater contribution than the set of answers or conclusions.

A hypothesis that dominant animals usually move to gain advantages rather than to escape disadvantages is repeatedly asserted in various contexts (e.g., Darlington, 1957: 620, 637, and ranging from major groups of vertebrates to races of humans). The concept lacks clear definition and has a teleological implication that is, at best, misleading. An interesting exchange on the application of the concept to human races was published in the *Journal of Mammalogy* (Hall, 1946; Hill, 1947).

In *The Mammals of North America* (Hall and Kelson, 1959) was a chapter (of 8 pages) on zoogeography (by Hall). The questions posed were: "What patterns emerge from the 500 maps showing the geographic distribution of North American mammals? What factors account for these patterns?" and, "Why are there fewer kinds of mammals in one area than in another?" The major patterns discussed are: (1) the distinction of three major regions with largely different faunas, namely boreal, temperate, and tropical; (2) the presence of more temperate than boreal species, and more tropical than temperate; (3) the presence of zonation within each of the major regions; (4) the presence in North America of more species thought to have come from Asia than vice versa, and the presence in South America of more species from North America than the reverse; and (5) the presence of an unusually large number of subspecies in the Southwest.

The major factors said to account for these patterns are: (1) temperature was regarded as a major factor in determining mammalian distributions from north to south; (2) the number of different habitats that are available is positively correlated with the number of species, both on the large spatial scale of regions and on the smaller scale of zones and local areas within zones; (3) the greater vigor of "mammals of a large land area [which] more often than not prevail over their counterparts of a small land area when the two are brought into competition" (p. xxix); and (4) advances and recessions of glaciation and accompanying aridity in areas from west to east within the temperate zone. The relevance of paleontological history was mentioned briefly. Hall (1981) shortened the original eight-page discussion of zoogeography to one page and included no basically different interpretations. Neither the patterns nor their explanations differed greatly from what could be found in earlier literature.

Returning to the hypothesis that animals from a greater land mass are more vigorous, we note that Hall in Hall and Kelson (1959) incidentally presented two other and contrary hypotheses. A probabilistic explanation appears in a footnote on p. xxvi, relating to the relative contributions of the South American and Central American tropics. Elsewhere (p. xxv) he noted that "North America and Eurasia might properly be thought of as one continuous region—the Holarctic region," which has only recently been broken by the barrier of the Bering Sea. In current terminology this is simply a vicariant event and the original hypothesis about different areas of different sizes and about vigor seems irrelevant, at least as it relates to Asia and North America. A probabilistic model was discussed by Horton (1974), basically as a null hypothesis, and the conclusion was reached that it is not necessary to invoke the concept of relative species dominance as a determinant of the direction of species movement in many cases. Frequently the term "dominance" has been used in the literature somewhat inconsistently and without careful definition, with resulting confusion.

A few years after the publication of Hall and Kelson (1959), Eduardo Rapoport came to the Department of Mammalogy at the American Museum of Natural History and asked one of us (Anderson) what similar works might exist for the mammals of other continents. Unfortunately, the answer was none. Since then a set of maps for Australian species has become available (Strahan, 1983) and has been the subject for biogeographical analysis from the standpoint of areography (Anderson and Marcus, 1992). A three volume work on South American mammals when completed will provide maps (two volumes have been published, Eisenberg, 1989, and Redford and Eisenberg, 1992). Another three-volume work with maps for South American mammals has been in preparation for many years (to be edited by S. Anderson, A. L. Gardner, and J. L. Patton). There is no comparable compilation with maps for Africa. Most of Eurasia lies in the Palaearctic Region, for which a set of maps was published by Corbet (1978), and the remainder lies within the Oriental or Indomalayan Region, recently treated by Corbet and Hill (1992) and including a set of maps. No subsequent biogeographical or areographic analyses based on these two sets of maps has been published yet. Incidentally, faunal lists, whether regional or on some more local scale, even when not accompanied by maps, have traditionally been basic sources for biogeographic data and their importance needs to be acknowledged here.

The set of maps for North American mammals in Hall and Kelson (1959) was used as the source of data in subsequent analyses by several authors. The question of how many species occur in different areas was addressed by Simpson (1964), who tallied numbers of species postulated (on the basis of the published range maps) to occur in each of the squares of a 150-mile grid. These sources were used in a more detailed examination of the relative contributions of different groups of mammals to the latitudinal gradient in species numbers by Wilson (1974). He noted "the lack of increase in species density" toward the tropics when quadrupedal mammals are considered alone, the major contributors to the latitudinal effect being the bats. He considered also the possible effect of the lesser amount of space available in Central America. Wilson's studies provided a much "finer grained" look than the tallies by three major regions in Halls' (1981) analysis. Even finer detail is worthy of analysis (but there is a limit to the ability of progressively smaller units of space to yield meaningful geographic information, as was discussed by Anderson, 1972). Willig and Sandlin (1991) compared the effects of quadrat and latitudinal band methodologies on detection of latitudinal gradients in species richness.

What is the frequency distribution of sizes of geographic ranges among all possible ranges for species of North American mammals? This question was addressed by Anderson (1977), using the same set of maps, and he noted that "it is clear that the species are not spread evenly, but that they are about an order of magnitude (10 times) less 'concentrated' in each successively larger order of magnitude of range" (Fig. 1).

Various analyses have focused on areas of distributions. For example, Armstrong (1972:354) noted that "Areographic analysis is of interest because it enables the provisional segregation of faunal elements of possible historical integrity from assemblages with compatible and complementary, yet coincidental ecology." The areographic analysis referred to was the sorting of species into groups with respect to the locations of their geographic ranges. Thus, in Colorado, Armstrong recognized nine "faunal elements" such as Cordilleran, Chihuahuan, Neotropical, and Great Basin.

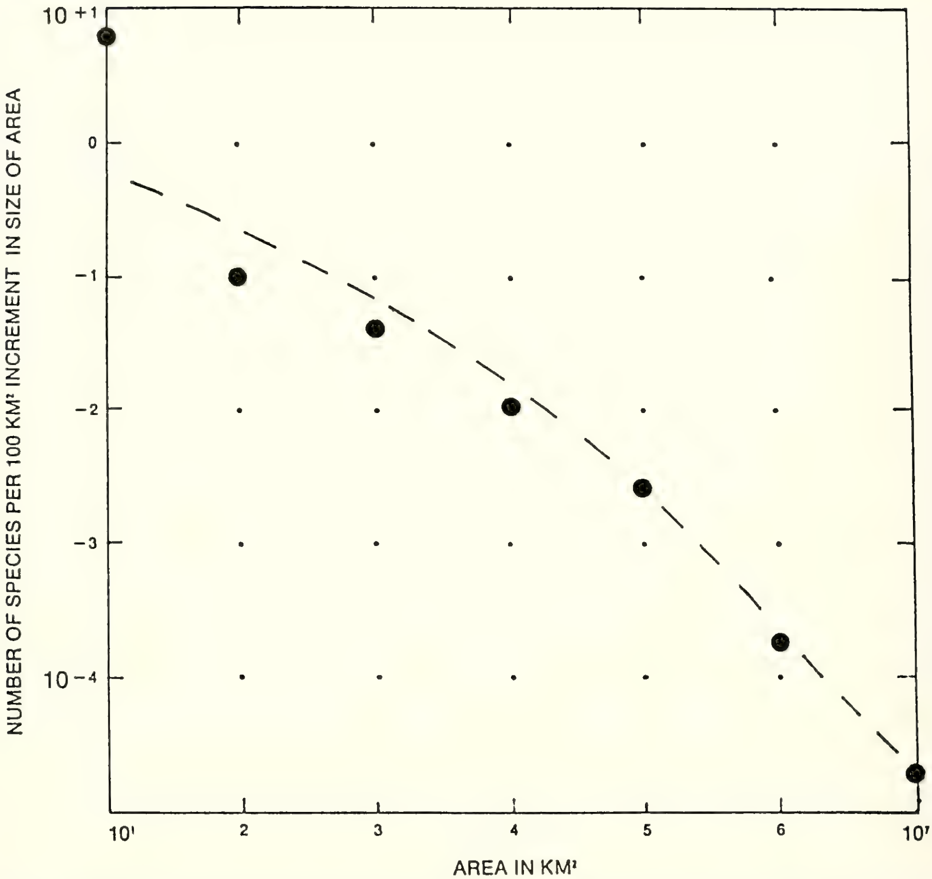



FIG. 1.—Graph for North American terrestrial mammals showing the number of species (averaged for each succeeding order of magnitude) having ranges of any given size. Counts are grouped in 100 km$^2$ increments. The negative values on the ordinate are powers of 10, thus $10^{-4}$ or 0.0001 species per 100 km$^2$ increment for a range of $10^6$ (1,000,000) km$^2$ means that there are so few species with ranges of this size that most increments or size-classes of 100 km$^2$ are unoccupied and, and on the average, there is about one species for each 10,000 size-classes (Anderson, 1977:12). It may be reasonably inferred from these data that at any range size a species has a greater probability of losing range than of increasing its range.

Most publications in mammalogy, or in biogeography, fit an existing mold. Although they contain new information, test an existing theory, or otherwise contribute to knowledge, they seem basically familiar as to topic, concept, assumptions, emphasis, and methodology. Occasionally a publication breaks new intellectual ground. *Areography* (Rapoport, 1982; an earlier Spanish edition, published in 1975, was not widely distributed) was such a publication. Clearly the author was thinking along new lines, developing new methods, and asking new questions. Let us briefly consider some of these.

Do North American species of mammals belonging to different orders and families have geographic ranges of different sizes (Rapoport, 1982:7)? Mean ranges were given for 9 orders and 14 families. Arithmetic means were used and differences noted. For example, the mean for Carnivora, the order with the largest ranges, was about eight times that of the Rodentia. Graphs of range size distributions for six orders were published by Anderson (1977:10). Rapoport used "square megametres" as his unit of measurement and defined a megametre (Mm) as 100 km. The prefix mega is usually used for million rather than 100 thousand, so these discrepant usages need to be taken into account when comparing data in Anderson's paper with those in Rapoport's. One square megameter as used by Rapoport is equal to $1 \times 10^4$ km$^2$ as used by Anderson, and Anderson used geometric means instead of arithmetic means.

What are the mean geographic ranges of bats with different feeding habits (Rapoport, 1982:9)? Those that eat animal food are more widespread than those that eat plant food. Whether this would remain true if their entire ranges are included, rather than just the parts of ranges within North America, remains to be tested.

What is the frequency distribution of the sizes of ranges of species among all possible sizes (Rapoport, 1982:13)? This question was investigated at about the same time, but independently of Anderson's work, which was published in 1972. Both authors pointed out the logarithmic or "hollow curve" distribution.

How are the ranges of subspecies distributed in space and in size relative to each other (Rapoport, 1982:27)? Various aspects of this were discussed and it was noted that "There is a tendency to increase the perimeter of the irregularity of the species' external frontiers when the number of subspecies increases."

How are numbers of subspecies with ranges surrounded by the ranges of other subspecies correlated with the total number of subspecies recognized within the species (Rapoport, 1982:31)? The correlation of internal subspecies and total number of subspecies in the species is +0.979.

Do the ranges of subspecies relative to each other differ among taxonomic groups (Rapoport, 1982:35)? The relative numbers that are considered to be contiguous, included, disjunct, and superimposed, differ some among the species of different orders, but the significance, both statistically and biologically, is unclear.

Does the size of the range of the most widespread subspecies agree with an equitable model or a random model (Rapoport, 1982:41)? A broken stick model was discussed and it was concluded that the division of lands among subspecies "seems to be a stochastic process" rather than an equitable one. This question was considered in some detail and with the same conclusion by Anderson and Evensen (1978).

Does the total size of the range of a species affect the way it is divided into subspecies (Rapoport, 1982:42)? "It seems that in the very widespread species the bigger landowners (sspp.) have a better chance of developing into very big landowners," and that as the size of a subspecies' range decreases it becomes less likely to fragment into two parts. As a result there is greater equitability among the ranges of smaller subspecies. The author noted that this poses more questions than it answers. [In a way this is more stimulating than the common procedure in which an author concludes that we now have "explained" something or other.]

The focus of areography on the areas of distribution or ranges of species, and on the sizes, shapes, and locations in space and time of these ranges, leads to other types of questions and answers. For example, Anderson (1977:11) was led to conclude that species "are about an order of magnitude (10 times) less 'concentrated' in each successively larger order of magnitude of range" (Fig. 1). This led Anderson (1985) to the conclusion that "the geographic range of a species, regardless of its size, is more likely to decrease than to increase." The former "conclusion" summarizes an observed pattern at one time, whereas the latter is an inference from that pattern and from theoretical assumptions and considerations and may well be true over time spans of different duration. These two conclusions seem to

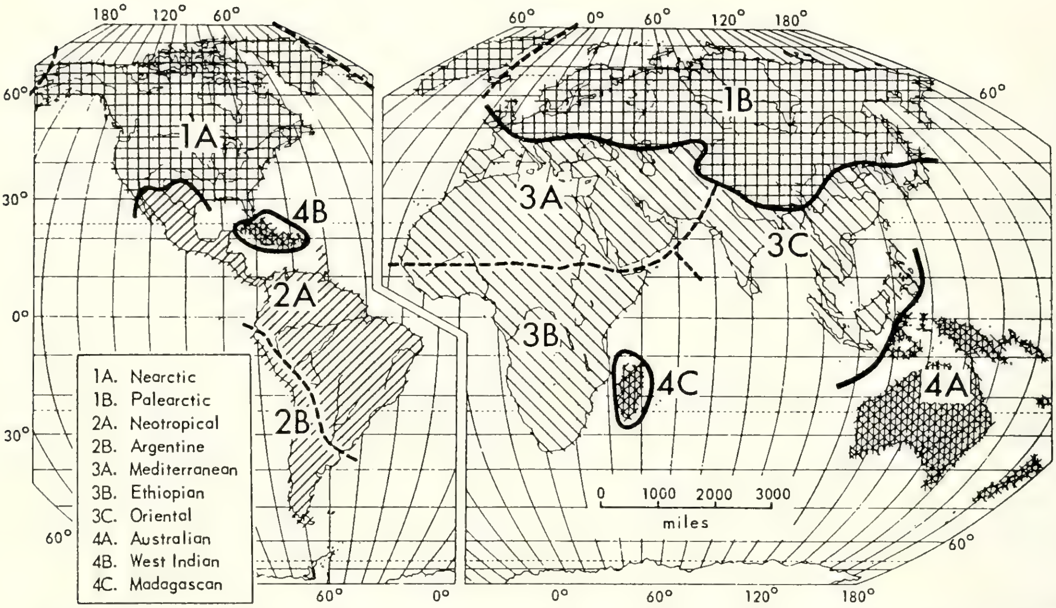



FIG. 2.—Four mammal faunal regions; (1) Holarctic, (2) Latin America, (3) Afro-Tethyan, and (4) Island, and ten subregions listed on map (Smith, 1983:462).

have escaped the attention of Pagel et al. (1991:796) when they wrote that "species with very small, and species with very large, geographic ranges are scarce." Only half of this is true. Large ranges are scarce, small ranges are not. The inference (discussed by Anderson, 1985) about the relative probabilities of increases and decreases of range sizes in a dynamic Markovian system over time was not mentioned in their discussion of ecological aspects of the distribution of range sizes of North American mammals.

## *Biotas Over Ecological Time Periods*

*Regions and subregions.*—Coincidence in the range limits of organisms points to broad biogeographic similarities among some local biotas and fundamental differences between others. Lydekker's (1896) account *A Geographical History of Mammals* served as a principal reference for mammalian geographical classifications. Lydekker (1896) divided the world into three realms: the Notogaeic (including Australian, Polynesian, Hawaiian, and Austro–Malayan regions), the Neogaeic (limited to the Neotropical region), and the Arctogaeic (including Malagasy, Ethiopian, Oriental, Holarctic, and Sonoran regions). Given the careful work represented in these early accounts, more recent contributions to the subject have involved either detailed analyses of biotic limits at the interface of such regions, or more quantitative approaches that create a fuller hierarchy of biogeographic regionalism. Additions to this hierarchy awaited better inventories, but simple classification is merely a first step in attempting to understand biogeographic patterns and processes.

On a world scale an analysis of terrestrial mammal faunal regions using multidimensional scaling produces a classification (Fig. 2) with four regions and ten subregions that is "more efficient and more internally consistent" than the classic Sclater-Wallace classification (Smith, 1983). Smith's analysis was based on maps for families of living mammals (Anderson and Jones, 1979).

How many faunal areas (whatever they may be named) should be recognized and where are their boundaries? This questions as it relates to mammals was addressed by Hagmeier and Stults (1964) and Hagmeier (1966), using squares in a 50-mile grid to tally boundaries of species from the set of North American distribution maps for mammals (from Hall and Kelson, 1959). A thoughtful critique of the analyses of Hagmeier and Simpson was written by Murray (1968). Many other detailed analyses attempting to define or recognize faunal regions, provinces, or similar areas have been conducted (for example Matson, 1982).

*Life zones.*—Life-zone concepts mostly date from Merriam's (1890) description of biotic associations on the San Francisco Mountains in northern Arizona. Merriam noted the resemblance between the replacement of communities as elevation decreased along a transect with the replacement observed as latitude decreased on a continental scale. Attributing the underlying causation to physical effects of temperature and precipitation gradients, Merriam (1894) proposed a large-scale classification of habitats that proved ultimately unsatisfactory when applied on a larger continental or global scale. Reasons for this were obvious to Lydekker (1896), who recognized that historical opportunity was also a fundamental factor. A clear correlation of faunas or biotas with elevation and latitude would only exist, as in North America, where mountain ranges tended to be north–south in orientation. East–west chains, such as the Pyrenees, Alps, and Himalayas, do not permit organisms that are restricted to the arctic or temperate zones of higher elevations to have direct access to corresponding belts at higher latitudes.

As early as 1923, Dice criticized the concept of life zones on the grounds that individual limitations of species ranges, and their common correlation with habitat, rendered this concept inaccurate and prone to error. Two other systems for delineating and naming biotic associations in North America were the biomes of Clements and Shelford (1939) and the biotic provinces of Blair and Hubbell (1938) and Dice (1943).

None of these specific systems is now in widespread use. Nevertheless, questions such as the following are fundamentally unresolved and continue to attract attention. In what ways is it useful to delineate and designate biotic or faunal areas? How should this be done, on ecological grounds, on spatial or areal grounds, or on some combined ecogeographical basis? What exactly do we represent by these schemes? What conclusions or what predictions can be drawn therefrom?

*Diversity patterns and their correlates.*—Early naturalists recognized that biotic diversity is unequally distributed over the planet, being greater in tropical regions. Hershkovitz (1987) has shown that 26% of the world's mammal fauna known to Linneaus in 1758, and 31% known to Buffon in his 1753–1789 compilations, came from the neotropics; corresponding figures for North America are 13% and 19%, respectively. Tropical "hotspots" of diversity attracted the attention of naturalist-explorers, whose collections continue to serve in the description and reappraisal of biotic diversity. It is a sad statement of modern science that, after 200 years, we still cannot estimate, to the nearest order of magnitude, the number of species coexisting on the planet (May, 1988).

Diversity has been related to a host of abiotic and biotic factors. A complete listing and discussion is beyond the scope of this work but includes spatial heterogeneity, competition, predation, stability, productivity, predictability, and seasonality (Emlen, 1973). Abiotic variables commonly correlated with these include area, latitude, longitude, elevation, precipitation, soils, and many others. Wright (1983) offered the "species-energy" relationship as an ultimate explanation for many of these more proximate factors.

Among numerous mammalian examples, several recent papers illustrate diverse ap-

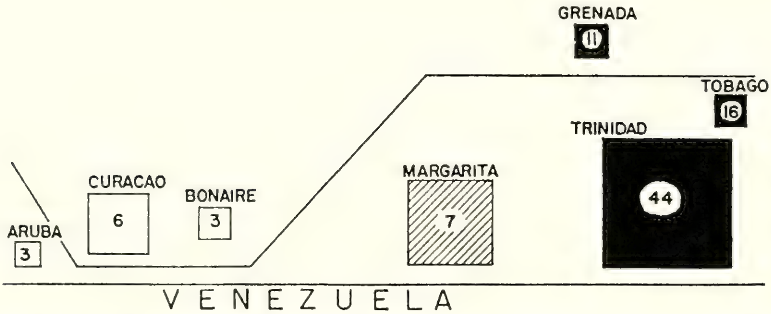



FIG. 3.—Diagrammatic comparison of islands off the north coast of South America. The size of each square is proportional to the size of the indicated island. The shading of each square indicates the vegetation type of the island (black—rain forest, diagonal lines—traces of rain forest, white—xerophytic vegetation only). The numbers refer to the number of bat species recorded from the island. The straight line near the bottom represents the Venezuelan coastline, the zigzag line above it the 100-fathom line (Koopman, 1958:432).

proaches to characterizing diversity and use specific analytical features to heighten their resolution, including Flessa (1975), McCoy and Connor (1980), and Willig and Sandlin (1991). References cited in these works illustrate the breadth of the field.

*Island biogeography.*—Knowledge of mammals on Mediterranean islands existed in classical Greek and Roman times. These studies were surprisingly contemporary in scope, identifying two of the most salient and prevalent properties of island life: (1) insular species often occur nowhere else and sometimes differ dramatically from mainland taxa; and (2) many insular forms are now extinct or endangered, illustrating their vulnerability to environmental and climatic changes. Such classical studies were known to both Darwin and Wallace in their pioneering works on evolution and biogeography. At the founding of the ASM, mammalian studies of island biogeography were relatively well integrated. One has only to consider the arguments of Grinnell and Swarth (1913), who published a truly modern analysis of the disjunct bird and mammal faunas inhabiting the isolated San Jacinto Mountains in southern California (see below).

Koopman (1958) examined the effects of island size, island isolation, former land connections, and ecological habitats on bats inhabiting islands off the north coast of South America. This multi-factorial approach is informative (Fig. 3), because it demonstrates that analyses at many different scales of space, time, and organic diversity are necessary. An analysis of nonvolant mammals in southeast Asia enabled Heaney (1986) to postulate changing extinction rates (Fig. 4) over time on a hypothetical island of 10,000 km$^2$.

Studies of island biogeography changed most dramatically with the publication of the "equilibrium theory" of island biogeography by MacArthur and Wilson (1963, 1967). This theory explained the species richness of any area as the product of two opposing rates: the migration of new species ($I$) and the extinction of existing ones ($E$). At a certain species richness, determined by an island's distance from colonization sources (affecting $I$) and its area (affecting $E$), the number of species tends toward a dynamic equilibrium—at this point, species composition changes ("turnover"), but species number is maintained at equilibrium. Mostly forgotten in the stormy debates engendered by the equilibrium theory was its authors' qualification (MacArthur and Wilson, 1967:20–21): "a perfect balance between immigration and extinction might never be reached . . . but to the extent that the assumption of a balance has enabled us

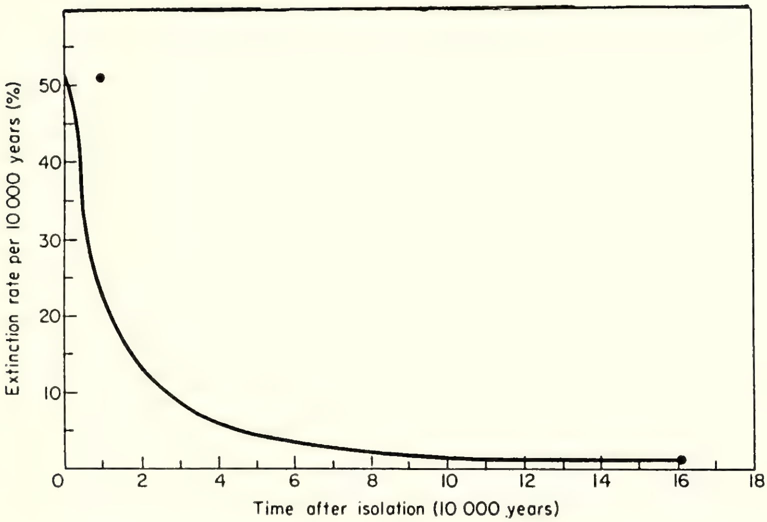



FIG. 4.—Extinction rate for non-volant mammal faunas in SE Asia. The two filled circles are data points discussed in Heaney's text; the curved line is an estimate of actual extinction rates for an island of 10,000 km² following isolation from the mainland. The exact shape of the curve is problematical (Heaney, 1986:155).

to make valid new predictions, the equilibrium concept is useful as a step. . . ."

The equilibrium model stimulated much research activity, including a substantial body focused on mammals (reviewed by Brown, 1986). Despite their limited number of species compared to some other animal groups, mammals exhibit an enormous range of vagilities, from volant migrators to sessile burrowers. Variation in body size and generation time is also immense. Thus, mammals show a broad spectrum of dispersal abilities and extinction proneness, and a correspondingly wide range of insular distributional patterns, all of which make this group well suited for tests of biogeographic theory.

Mammalian studies in island biogeography have critically altered basic paradigms within the field. Lomolino (1984, 1986) studied various aspects of mammalian dispersal as they relate to colonization of near-shore islands in the St. Lawrence Seaway, finding that the traits that lead to initial colonization of islands are not necessarily those promoting stable persistence there. Using this system and others, Lomolino (1986) showed that two principal variables of equilibrium theory, area and isolation, are not always independent in their effects on mammalian species richness but may interact to produce "compensatory effects." For example, small near-shore islands may have a surfeit of species, because high rates of colonization from the mainland sometimes overwhelm high extinction rates expected from their limited areas (see also Hanski, 1986).

The greatest revision of island biogeography since MacArthur and Wilson has been the recognition that history plays a critical role in the derivation and status of insular biotas, even over "ecological time." Empirical studies on many groups were to show that few archipelagos were actually at equilibrium (Gilbert, 1980); most appeared to be approaching a theoretical equilibrium, either from above ("biotic relaxation" via an excess of extinctions) or from below (under-saturation via an excess of colonizations). Brown (1971) was the first to place such "nonequilibrial" island systems in the theoretical context of the MacArthur-Wilson model. His now-classic study of mammals inhabiting Great Basin mountaintops presented in modern terms the arguments advanced by Grinnell and Swarth (1913) 58 years earlier, that isolated mountain ranges were freely populated during favorable Pleistocene episodes and, following their disjunction, have suffered an excess of area-dependent extinctions. Brown's (1971) interpretation of Great Basin faunal dynamics later received empirical support from Grayson's (1987) study of the Pleistocene fossils. Other studies have utilized Pleistocene records to substantiate inferences of historical derivation and dynamics of modern species richness (Ayer, 1936; Harris, 1990; Hope, 1973; Heaney, 1984, 1986, 1991; Morgan and Woods, 1986; Patterson, 1984).

The role of history in island biogeography is an area of considerable research activity, much of it involving mammals. Lawlor (1986) found significant differences in species-area slopes for mammalian faunas inhabiting "oceanic" archipelagos (populated de novo via overwater colonization) and "landbridge" archipelagos (fragments of formerly continuous areas subjected to local extinctions). Species-area slopes had previously been considered "devoid of biological meaning" (Connor and McCoy, 1979) because earlier analyses failed to take account of history. History also appears to influence patterns of insular species composition in predictable ways. Patterson and Atmar (1986) showed that, in landbridge island archipelagos, species composition shows a nested subset pattern in which smaller islands support nested subsets of the species present on larger islands. Oceanic islands rarely show this highly non-random pattern (see also Patterson, 1990).

## *Species Over Evolutionary Time Periods*

How should variability among populations on a geographic scale and within species be analyzed and expressed or represented? How should it be treated taxonomically? These are long-standing questions. The quality and quantity of basic data on variation have been increasing throughout this century. This has made it both possible and desirable to consider whether the traditional use of subspecies in taxonomy should be changed, whether by abandonment, modification, or supplementation. New methods of computation became readily available after 1950, and with the proliferation of electronic computers. New concepts, including phenetic analysis (in the form of numerical taxonomy and subsequently in clustering procedures in biogeographical analysis), phylogenetic systematics (growing chiefly from Hennig, 1966), and vicariance biogeography (rooted in the work of Croizat, 1976, and other papers as early as 1958, but rapidly mutating or splintering in various ways), have stimulated work also.

In the 1950s, concepts of subspecies and their nomenclature were discussed in a series of articles, mostly in the pages of *Systematic Zoology.* These included, in order of increasing perceived utility: Burt (1954), Hagmeier (1958), Doutt (1955), Lidicker (1962), Anderson (1966), Dillon (1961), and Durrant (1955). Today, subspecies have not been abandoned completely but are still in use at least in mammalogy and ornithology. There seem to have been some modifications in the concept in that subspecies may be used on the average a little more cautiously and at a bit higher level (in the continuum of degrees of difference between populations) (see also Engstrom et al., 1994). We feel that subspecies still have some use as a matter of convenience, but that the level in the continuum selected for subspecific recognition in any particular case is not inherently more interesting biologically than other possible levels. Supplementary methods are now in common use to deal with continuously varying degrees of difference, in both taxonomy and biogeography.

The role of vicariance, currently defined as the splitting of a formerly continuous range or area into two or more parts, has received considerable attention in recent decades. In a frequently cited paper on Caribbean biogeography, Rosen (1975) presented a vicariance model. It was said to have used data from mammals, but what data and how they were in fact used, or what the conclusions have to do with mammalian distribution is not clear; we are simply left with the implication that mammals conform to the vicariance model. The description of the method indicated that only monophyletic groups or individual species (which are regarded as monophyletic groups of populations) should be used. The author did not indicate which specific groups within the Mammalia were used in the analysis, nor which were hypothesized to be or demonstrated to be monophyletic. None of the five sources cited for mammalian data explicitly indicated which groups may be monophyletic.

Later studies of mammals in the Caribbean region have provided little to document the relevance of the vicariance model to the distribution of modern mammals. Based on their study of bats, Baker and Genoways (1978) reported that dispersal by flight seems to be the most logical explanation for the present Antillean bat fauna, but also noted that "the fact that the vicariance model is not the best one to explain the origin of the bat fauna should not be taken as an indictment against the model" (Baker and Genoways, 1978:72). MacFadden (1980) suggested that the insectivores *Nesophontes* and *Solenodon* may be relicts of an early continental fauna. MacPhee and Woods (1982) concluded in stronger terms that "on the whole, long-distance, over-water rafting from the Americas remains the most likely mechanism for past land vertebrate immigration into the Caribbean." Ernest Williams (in Woods, 1990) summarized the history of West Indian biogeography and the relative contributions of dispersalist and vicariance models. Because organisms do disperse and barriers do arise any model to be adequate in comprehensiveness must include both dispersal and vicariance. The problem is to evaluate the roles of both processes in particular situations as well as in general. In the same symposium volume, Karl Koopman (in Woods, 1990:639) was "in full agreement with Baker and Genoways (1978)," J. Knox Jones, Jr. (in Woods, 1990:653) also agreed "that overwater dispersal best explains present chiropteran distribution on Caribbean islands," and Charles Woods (1990:741) also postulated overwater dispersal and evolutionary radiation on the islands as the principal factors in the origin of the rodent fauna.

In the 1970s, interest in developing methods and actual applications of cladistic systematics to biogeography were increasing. This decade of activity culminated in a 1979 symposium at the American Museum of Natural History (Nelson and Rosen, 1981). In following years several text or reference books on this approach to biogeography were published (e.g., Humphries and Parenti, 1986; Nelson and Platnick, 1981; Wiley, 1988). Two special issues of *Systematic Zoology* (1988, nos. 3 and 4) included papers given at a later symposium on vicariance biogeography. There have not been many applications, successful or unsuccessful, specifically to mammalian biogeography. The magnitude and relative importance of vicariance biogeography to mammalian biogeography in the long term remains to be seen.

## *Biotas Over Evolutionary Time Periods*

Biotic processes involving mammalian faunas of sizeable areas over relatively long time periods have attracted interest from several quarters between 1919 and 1994. Among these processes (and conceptual schemes for dealing with them) are the following:

*Distributional "tracks."*—In his famous three-volume opus, Croizat (1958:74) opined "When we mention zoogeography, we most likely imagine a science of dispersal. . . . In reality, what we get today as 'zoogeography,' regardless of beauty of package and sound of label, is the lore originally broadcast by Darwin and later on refurbished by Matthew and his successors, Simpson, Mayr, etc." Croizat's solution to this was the formulation of "panbiogeography." Relying on graphical analyses of the geographic ranges of taxa (called tracks), panbiogeography seeks to identify ancestral patterns of spatial and temporal distribution, of which modern distributions are but relict fragments. Many of the 2,750 pages of *Panbiogeography* are devoted to mammalian examples and their interpretation by Croizat. There are many other ways of using spatial patterns to gain insight into faunal development and composition. For example, the simple and empirical superimposition of species boundaries on one map, whether showing a group with similar distributions such as those centering on the Chihuahuan desert or all of the species of a larger group such as mammals, can be informative (e.g., Anderson, 1972; Anderson and Marcus, 1992; Armstrong, 1972; Findley, 1969; and Jones et al., 1985).

*Continental stability.*—Simpson (1953) commented that "It remains possible that there were transoceanic continents or bridges or that continents drifted in the Triassic or earlier, but there is little good evidence that such was the fact. In any case such remote events would have little or no bearing on the present distribution of living things." Within a few years there was plenty of evidence that continents were drifting, not only in the Triassic but at present, and there was serious consideration of the bearing of continental drift on the present distribution of living things. Serious disagreements remain on the relative importance of that process compared to others.

*Centers of endemism.*—This term has appeared in the literature in recent years and has been related to the concept of refugia noted below. It is not always clear what an author may mean by a "center of endemism." In some cases it refers to a clustering of the centers of the geographic ranges of a number of species, especially species with rather small ranges. The occurrence of such a cluster is interpreted as evidence for a former refugium. In other cases a center of endemism refers to an area in which a relatively high percentage of the species are endemic thereto.

*Ecological complementarity of different regions.*—The extent to which (and the ways in which) faunas of similar major habitats, such as forests, deserts, or grasslands, are comparable has attracted recent interest and deserves more exploration. Such comparisons involve both ecological and evolutionary time scales and have as much to contribute to ecology, systematics, and functional morphology as to biogeography. The comparison of vertebrates in North American and South American deserts (the Sonoran and Monte, respectively) by Blair et al. (1976) is one example.

*Refugia.*—The idea that certain geographic regions have served as refugia for biotas against the vicissitudes of climate or competitors has been employed in various contexts. Over shorter Quaternary time scales, the somewhat controversial notion that warmer wet-dependent biotas endured Pleistocene cold or arid fluxes in isolated refugia has gained great application and acceptance throughout the world.

Findley (1969) applied this concept to interpreting distributions of montane and desert mammals in the southwestern part of the United States. The idea that refugia may have been important in tropical as well as temperate regions developed more recently. Cerquiera (1982) and Kinzey (1982) suggested that refugia applied to primate distributions in South America. Detailed map data for other mammalian groups have not been available to test this model. Most discussions and examples have centered on plants, birds, and butterflies for which map data were available (Whitmore and Prantz, 1987).

Over vast geologic time scales, the island continents of Australia and South America served as Tertiary and Quaternary refuges for various archaic groups of mammals, some still living, that were replaced by later lineages on other continents (e.g., Simpson, 1980).

*Interchange.*—Studies of faunal interchange analyze the patterns and processes involved when historically differentiated biotas intermingle. Different geographic theaters and faunas provide insights into various levels of this dynamic biogeography. Musser's continuing studies of mammals, especially murid rodents, from Sulawesi probe the limits of Wallace's line and its effects on biological evolution. Hoffmann, Vorontsov, and their coworkers focused more than a decade of work on the dynamic character of Beringia, a trans-oceanic landbridge that opened and closed repeatedly through the Pleistocene with the waxing and waning of continental glaciers, permitting interchange of Palearctic and Nearctic elements of the Holarctic biota. Surely the best studied example of biotic interchange involves the Nearctic and Neotropical faunas juxtaposed by the emergence of a Panamanian land bridge roughly 3 million years ago (e.g., Stehli and Webb, 1985). The strong differentiation of faunas isolated throughout the Cenozoic, their biotic diversity, and a detailed chronology of events derived from abundant fossil remains combine to produce this unparalleled record of biogeographic dynamics.

*Conservation biogeography.*—Of course, mammalogists were leading figures in the nascent conservation movement in North America, but much of their activity was in fields other than biogeography. "Applied biogeography" took root soon after the formulation of the Equilibrium Theory of Island Biogeography (MacArthur and Wilson, 1967). This theory was quickly applied to the conservation of species in habitat fragments, distilling a series of "geometrical rules" of reserve design (summarized by Diamond, 1976) that were at once the subjects of both acclaim and criticism. Mammalogists have contributed significantly to continued refinements of this field.

East (1981), Heaney (1986), and Newmark (1987) drew a series of conclusions about conservation of African, Philippine, and North American mammals, respectively, based on correlations between extinction rates and reserve or island area. Patterson and Atmar (1986) also argued that parks need to be large to fulfill their basic function, basing their conclusions on analyses of species composition. In a nested subset pattern, many small fragments each tend to support *the same* set of species; rare or narrowly restricted endemics most in need of protection are found only in the largest, richest fragments. Kitchener et al. (1980) developed a point-by-point assessment of the conservation value of heath fragments to small mammals of western Australia. The role of corridors between fragments in helping to sustain isolated populations of rainforest possums was examined by Laurance (1990), substantiating a "rescue effect" previously hypothesized by Brown and Kodric-Brown (1977); this subdiscipline is attracting much current attention. By showing that the majority of species in all higher taxa have small geographic ranges, Anderson (1985) underscored the vulnerability of most taxa to localized environmental changes. Literature on the role of biogeographic theory in conserving diverse tropical communities was recently reviewed by Patterson (1991).

Readers familiar with the biogeographic literature will readily appreciate how cursory this review has been. In fact, there are few aspects of biology that do not have biogeographic consequences, either by affecting geographic range limits, abundance within the range, or patterns of species coexistence. However, we hope that our survey succeeds in indicating the breadth and pluralistic nature of biogeographic research and its substantial role within mammalogy, past, present, and future.

## Literature Cited


Alkon, P. U., and D. Saltz. 1988. Foraging time and the northern range limits of Indian crested porcupines (*Hystrix indica* Kerr). Journal of Biogeography, 15:403–408.

Anderson, S. 1966. Taxonomy of gophers, especially *Thomomys* in Chihuahua. Systematic Zoology, 15: 189–198.

———. 1972. Mammals of Chihuahua, taxonomy and distribution. Bulletin of the American Museum of Natural History, 148:149–410.

———. 1977. Geographic ranges of North American terrestrial mammals. American Museum Novitates, 2629:1–15.

———. 1985. The theory of range-size (RS) distributions. American Museum Novitates, 2833:1–20.

Anderson, S., and M. K. Evensen. 1978. Randomness in allopatric speciation. Systematic Zoology, 27: 421–430.

Anderson, S., and J. K. Jones, Jr. 1979. Recent mammals of the world: a synopsis of families. Ronald Press, New York, 453 pp.

Anderson, S., and L. F. Marcus. 1992. Aerography [sic] of Australian tetrapods. Australian Journal of Zoology, 40:627–651.

Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University Chicago Press, Chicago, 782 pp.

Armstrong, D. M. 1972. Distribution of mammals in Colorado. Monograph of the Museum of Natural History, The University of Kansas, 3:x + 415 pp.

Ayer, M. Y. 1936. The archeological and faunal material from Williams Cave, Guadalupe Mountains, Texas. Proceedings of the Academy of Natural Science, Philadelphia, 88:599–618.

Baccus, J. T., R. E. Greer, and G. G. Raun. 1971. Additional records of *Baiomys taylori* (Rodentia: Cricetidae) for northern Texas. The Texas Journal of Science, 23:148–149.

Baker, R. J., and H. H. Genoways. 1978. Zoogeography of Antillean bats. Academy of Natural Sciences of Philadelphia, Special Publication, 13:53–97.

Blair, W. F., and T. H. Hubbell. 1938. The biotic districts of Oklahoma. The American Midland Naturalist, 20:425–454.

Blair, W. F., A. C. Hulse, and M. A. Mares. 1976. Origins and affinities of vertebrates of the North American Sonoran Desert and the Monte Desert of northwestern Argentina. Journal of Biogeography, 3:1–18.

Blondel, J. 1987. From biogeography to life history theory: a multithematic approach illustrated by the biogeography of vertebrates. Journal of Biogeography, 14:405–422.

Brown, J. H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. The American Naturalist, 105:467–478.

———. 1986. Two decades of interactions between the MacArthur–Wilson model and the complexities of mammalian distributions. Pp. 231–251, *in* Island biogeography of mammals (L. R. Heaney and B. D. Patterson, eds.). Biological Journal of the Linnean Society 28 (1&2) and Academic Press, London, 271 pp.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology, 58:445–449.

Burt, W. H. 1954. The subspecies category in mammals. Systematic Zoology, 3:99–104.

Cerquiera, R. 1982. South American landscapes and their mammals. Pp. 53–75, *in* Mammalian biology in South America (M. A. Mares and H. H. Genoways, eds.). Special Publication, Pymatuning Laboratory of Ecology, University of Pittsburgh, 6:1–539.

Choate, J. R., and K. M. Reed. 1986. Historical biogeography of the woodchuck in Kansas. Prairie Naturalist, 18:37–42.

Clements, F. E., and V. E. Shelford. 1939. Bio-ecology. J. Wiley & Sons, New York, vi + 425 pp.

Cockrum, E. L. 1948. The distribution of the hispid cotton rat in Kansas. Transactions of the Kansas Academy of Science, 51:306–312.

Connor, E. F., and E. D. McCoy. 1979. The statistics and biology of the species–area relationship. The American Naturalist, 113:791–833.

Corbet, G. B. 1978. The mammals of the Palaearctic Region: a taxonomic review. British Museum (Natural History), London, and Cornell University Press, Ithaca, 314 pp.

Corbet, G. B., and J. E. Hill. 1992. The mammals of the Indomalayan Region: a systematic review. Natural History Museum Publications, Oxford University Press, Oxford, 6 + 488 pp.

Croizat, L. 1958. Panbiogeography, or an introductory synthesis of zoogeography, phytogeography, and geology; with notes on evolution, systematics, ecology, anthropology, etc. Vol. 1—The New World, 1,018 pp. Vols. IIa and IIb—The Old World, by the author, Caracas, Venezuela, 1,731 pp.

Croizat-Chalen, L. C. M. 1976. Biogeografia analytica y sintetica ("Panbiogeografia") de los Americas. Biblioteca de la Academia de Ciencias Fisicas, Matematicas y Naturales (Caracas), vol. 15, 16, 1–454, 455–890.

Darlington, P. J., Jr. 1957. Zoogeography: the geographical distribution of animals. J. Wiley & Sons, New York, 675 pp.

Diamond, J. M. 1976. Relaxation and differential extinction on land-bridge islands: applications to natural preserves. Pp. 616–628, *in* Proceedings of the 16th International Ornithological Congress, Canberra, Australia.

Dice, L. R. 1923. Life zones and mammalian distribution. Journal of Mammalogy, 4:39–47.

———. 1943. The biotic provinces of North America. University of Michigan Press, Ann Arbor, 78 pp.

Dillon, L. S. 1961. Historical subspeciation in the North American marten. Systematic Zoology, 10: 49–64.

Doutt, J. K. 1955. Microgeographic races in mammals. Systematic Zoology, 4:179–185.

DURRANT, S. D. 1955. In defense of subspecies. Systematic Zoology, 4:186–190.

EAST, R. 1981. Species–area curves and populations of large mammals in African savanna reserves. Biological Conservation, 21:111–126.

EISENBERG, J. F. 1989. Mammals of the Neotropics, the northern Neotropics, vol. 1. University of Chicago Press, Chicago, 449 pp.

EMLEN, J. M. 1973. Ecology: an evolutionary approach. Addison-Wesley, Reading, Massachusetts, 493 pp.

ENGSTROM, M. D., J. R. CHOATE, AND H. H. GENOWAYS. 1994. Taxonomy. Pp. 179–199, *in* Seventy-five years of mammalogy (1919–1994) (E. C. Birney and J. R. Choate, eds.). Special Publication, The American Society of Mammalogists, 11:1–433.

FINDLEY, J. S. 1969. Biogeography of southwestern boreal and desert mammals. University of Kansas, Museum of Natural History Miscellaneous Publication, 51:113–128.

FITCH, H. S., P. GOODRUM, AND C. NEWMAN. 1952. The armadillo in the southeastern United States. Journal of Mammalogy, 33:21–37.

FLESSA, K. W. 1975. Area, continental drift, and mammalian diversity, Paleobiology, 1:189–194.

FREY, J. K. 1992. Response of a mammalian faunal element to climatic changes. Journal of Mammalogy, 73:43–50.

GENOWAYS, H. H., AND D. A. SCHLITTER. 1967. Northward dispersal of the hispid cotton rat in Nebraska and Missouri. Transactions of the Kansas Academy of Science, 69:3–4.

GILBERT, F. S. 1980. The equilibrium theory of island biogeography: fact or fiction? Journal of Biogeography, 7:209–235.

GRAYSON, D. K. 1987. The biogeographic history of small mammals in the Great Basin: observations on the last 20,000 years. Journal of Mammalogy, 68: 359–375.

GRINNELL, J., AND H. S. SWARTH. 1913. An account of the birds and mammals of the San Jacinto area of southern California [with remarks upon the behavior of geographic races on the margins of their habitats]. University of California, Publications in Zoology, 10:197–406.

GUILDAY, J. E., P. S. MARTIN, AND A. D. MCCRADY. 1964. New Paris No. 4: a late Pleistocene cave deposit in Bedford County, Pennsylvania. Bulletin of the National Speleological Society, 26:121–194 + 2 color pls.

HAGMEIER, E. M. 1958. Inapplicability of the subspecies concept to North American marten. Systematic Zoology, 7:1–7.

———. 1966. A numerical analysis of the distributional patterns of North American mammals. II. Reevaluation of the provinces. Systematic Zoology, 15: 279–299.

HAGMEIER, E. M., AND C. D. STULTZ. 1964. A numerical analysis of the distributional patterns of North American mammals. Systematic Zoology, 13:125–155.

HALL, E. R. 1946. Subspecies of man at the peace table. Journal of Mammalogy, 27:358–364.

———. 1981. The mammals of North America. Second ed. John Wiley & Sons, New York, 1:1–600 + *90,* 2:601–1181 + *90.*

HALL, E. R., AND K. R. KELSON. 1959. The mammals of North America. Ronald Press, New York, 2 vols, 1,083 pp + 79 pp. index.

HANSEN, R. M. 1962. Dispersal of Richardson ground squirrel in Colorado. The American Midland Naturalist, 68:58–66.

HANSKI, I. 1986. Population dynamics of shrews on small islands accord with the equilibrium model. Pp. 23–36, *in* Island biogeography of mammals (L. R. Heaney and B. D. Patterson, eds.). Biological Journal of the Linnean Society 28 (1&2) and Academic Press, London, 271 pp.

HARRIS, A. H. 1990. Fossil evidence bearing on Southwestern mammalian biogeography. Journal of Mammalogy, 71:219–229.

HEANEY, L. R. 1984. Mammalian species richness on islands on the Sunda Shelf, Southeast Asia. Oecologia, 61:11–17.

———. 1986. Biogeography of mammals in Asia: estimates of rates of colonization, extinction and speciation. Pp. 127–165, *in* Island biogeography of mammals (L. R. Heaney and B. D. Patterson, eds.). Biological Journal of the Linnean Society, 28 (1&2) and Academic Press, London, 271 pp.

———. 1991. An analysis of patterns of distribution and species richness among Philippine fruit bats (Pteropodidae). Bulletin of the American Museum of Natural History, 206:145–167.

HENNIG, W. 1966. Phylogenetic systematics. University of Illinois Press, Urbana, 263 pp.

HERSHKOVITZ, P. 1987. A history of the recent mammalogy of the Neotropical Region from 1492 to 1850. Pp. 11–98, *in* Studies in neotropical mammalogy: essays in honor of Philip Hershkovitz (B. D. Patterson and R. M. Timm, eds.). Fieldiana: Zoology, new series, number 39, 506 pp.

HESSE, R., W. C. ALLEE, AND K. P. SCHMIDT. 1937. Ecological animal geography. John Wiley & Sons, New York, xiv + 597 pp.

HILL, J. E. 1947. A zoologist looks at raciology: a reply to Dr. E. Raymond Hall's "Zoological subspecies of man at the Peace Table." Journal of Mammalogy, 28:87–89.

HOPE, J. H. 1973. Mammals of the Bass Straits Islands. Proceedings of the Royal Society of Victoria, 85:163–195.

HORTON, D. R. 1974. Species movement in zoogeography. Journal of Biogeography, 1:155–158.

HUBBS, C. L. (ED.). 1958. Zoogeography. American Association for the Advancement of Science, Publication 51, 509 pp.

HULL, D. 1988. Science as a process: an evolutionary account of the social and conceptual development of science. University of Chicago Press, Chicago, 586 pp.

HUMPHRIES, C. J., AND L. PARENTI. 1986. Cladistic biogeography. Oxford Monographs on Biogeography. Clarendon Press, Oxford, 98 pp.

JONES, J. K., JR., D. M. ARMSTRONG, AND J. R. CHOATE. 1985. Guide to mammals of the plains states. University of Nebraska Press, Lincoln, 371 pp.

KINZEY, W. G. 1982. Distribution of primates and forest refuges. Pp. 445–482, *in* Biological diversification in the tropics (G. T. Prance, ed.). Columbia University Press, New York, 714 pp.

KITCHENER, D. J., A. CHAPMAN, B. G. MUIR, AND M.

PALMER. 1980. The conservation value for mammals of reserves in the western Australian wheatbelt. Biological Conservation, 18:179–207.

KOOPMAN, K. F. 1958. Land bridges and ecology in bat distribution on islands off the northern coast of South America. Evolution, 12:429–439.

LAURANCE, W. F. 1990. Comparative responses of five arboreal marsupials to tropical forest fragmentation. Journal of Mammalogy, 71:641–653.

LAWLOR, T. E. 1986. Comparative biogeography of mammals on islands. Pp. 99–125, *in* Island biogeography of mammals (L. R. Heaney and B. D. Patterson, eds.). Biological Journal of the Linnean Society, 28 (1&2) and Academic Press, London, 271 pp.

LIDICKER, W. Z., JR. 1962. The nature of subspecies boundaries in a desert rodent and its implications for subspecies taxonomy. Systematic Zoology, 11: 160–171.

LOMOLINO, M. V. 1984. Immigrant selection, predation and the distributions of *Microtus pennsylvanicus* and *Blarina brevicauda* on islands. The American Naturalist, 123:468–483.

———. 1986. Mammalian community structure on islands: the importance of immigration, extinction, and interactive effects. Pp. 1–21, *in* Island biogeography of mammals (L. R. Heaney and B. D. Patterson, eds.). Biological Journal of the Linnean Society, 28 (1&2) and Academic Press, London, 271 pp.

LONG, C. A. 1963. Mathematical formulas expressing faunal resemblance. Transactions of the Kansas Academy of Science, 66:138–140.

LYDEKKER, R. 1896. A geographical history of mammals. Cambridge University Press, Cambridge, 400 pp.

MACARTHUR, R. H., AND E. O. WILSON. 1963. An equilibrium theory of island biogeography. Evolution, 17:373–387.

———. 1967. The theory of island biogeography. Monographs in Population Biology, Princeton University Press, Princeton, 1:1–203.

MACFADDEN, B. J. 1980. Rafting mammals or drifting islands?: biogeography of the Greater Antillean insectivores *Nesophontes* and *Solenodon*. Journal of Biogeography, 7:11–22.

MACPHEE, R. D. E., AND C. A. WOODS. 1982. A new fossil cebine from Hispaniola. American Journal of Physical Anthropology, 58:419–436.

MATSON, J. O. 1982. Numerical analysis of rodent distributional patterns in Zacatecas, México. Journal of Mammalogy, 63:73–84.

MATTHEW, W. D. 1915. Climate and evolution. Annals of the New York Academy of Science, 24:171–318.

MAY, R. M. 1988. How many species are there on Earth? Science, 241:1441–1449.

MCCOY, E. D., AND E. F. CONNOR. 1980. Latitudinal gradients in the species diversity of North American mammals. Evolution, 34:193–203.

MCINTOSH, R. P. 1985. The background of ecology. Cambridge studies in ecology. Cambridge University Press, Cambridge, 383 pp.

———. 1987. Pluralism in ecology. Annual Review of Ecology and Systematics, 18:321–342.

MERRIAM, C. H. 1890. Results of a biological survey of the San Francisco Mountain region and desert of the Little Colorado, Arizona. North American Fauna, 3:136 pp. + frontisp., 14 pls., and 5 maps [including one section by L. Stejneger].

———. 1894. Laws of temperature control of the geographic distribution of terrestrial animals and plants. National Geographic Magazine, 6:229–238.

MORGAN, G. S., AND C. A. WOODS. 1986. Extinction and the zoogeography of West Indian land mammals. Pp. 167–203, *in* Island biogeography of mammals (L. R. Heaney and B. D. Patterson, eds.). Biological Journal of the Linnean Society, 28 (1&2) and Academic Press, London, 271 pp.

MURRAY, K. F. 1968. Distribution of North American mammals. Systematic Zoology, 17:89–102.

NELSON, G. 1978. From Candolle to Croizat: comments on the history of biogeography. Journal of the History of Biology, 11:269–305.

NELSON, G., AND N. PLATNICK. 1981. Systematics and biogeography: cladistics and vicariance. Columbia University Press, New York, 567 pp.

NELSON, G., AND D. E. ROSEN (EDS.). 1981. Vicariance biogeography, a critique. Columbia University Press, New York, 593 pp.

NEWMARK, W. D. 1987. A land-bridge island perspective on mammalian extinctions in western North American parks. Nature, 325:430–432.

PACKARD, R. L. 1963. Distribution of the black-tailed jackrabbit in eastern Texas. The Texas Journal of Science, 15:107–110.

PAGEL, M. D., R. M. MAY, AND A. R. COLLIE. 1991. Ecological aspects of the geographical distribution and diversity of mammalian species. The American Naturalist, 137:791–815.

PATTERSON, B. D. 1984. Mammalian extinction and biogeography in the Southern Rocky Mountains. Pp. 247–293, *in* Extinctions (M. H. Nitecki, ed.). University of Chicago Press, Chicago, 354 pp.

———. 1990. On the temporal development of nested subsets patterns of species composition. Oikos, 59:330–342.

———. 1991. The integral role of biogeographic theory in the conservation of tropical forest diversity. Pp. 124–149, *in* Latin American mammalogy: history, biodiversity, and conservation (M. A. Mares and D. J. Schmidly, eds.). University of Oklahoma Press, Norman, xviii + 468 pp.

PATTERSON, B. D., AND W. ATMAR. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. Pp. 65–82, *in* Island biogeography of mammals (L. R. Heaney and B. D. Patterson, eds.). Biological Journal of the Linnean Society, 28 (1&2) and Academic Press, London, 271 pp.

PATTERSON, B. D., AND J. H. BROWN. 1986. Regionally nested patterns of species composition in granivorous rodent assemblages. Journal of Biogeography, 18:395–402.

RAPOPORT, E. H. 1982. Areography, geographical strategies of species. Pergamon Press, Oxford, xvi + 269 pp.

REDFORD, K. H., & J. F. EISENBERG. 1992. Mammals of the Neotropics, the southern cone, vol. 2., Chile, Argentina, Uruguay, and Paraguay. University of Chicago Press, 430 pp.

Reichman, O. J. 1984. Spatial and temporal variation of seed distributions in Sonoran desert soils. Journal of Biogeography, 11:1–11.

Rosen, D. E. 1975. A vicariance model of Caribbean biogeography. Systematic Zoology, 24:431–464.

Sclater, P. L. 1858. On the general geographical distribution of the members of the Class Aves. Proceedings of the Linnaean Society, London, 2:130–146.

Simpson, G. G. 1953. Evolution and geography, an essay on historical biogeography, with special reference to mammals. Condon Lectures, Oregon State System of Higher Education, 64 pp.

———. 1964. Species density of North American Recent mammals. Systematic Zoology, 13:57–73.

———. 1980. Splendid isolation: the curious history of South American mammals. Yale University Press, New Haven, Connecticut, 266 pp.

Smith, C. H. 1983. A system of world mammal faunal regions. I. Logical and statistical derivation of the regions. Journal of Biogeography, 10:455–466.

———. 1983. A system of world mammal faunal regions. II. The distance decay effect upon inter-regional affinities. Journal of Biogeography, 10:467–482.

Smith, J. D., and T. E. Lawlor. 1964. Additional records of the armadillo in Kansas. The Southwestern Naturalist, 9:48–49.

Stehli, F. G., and S. D. Webb (eds.). 1985. The great American biotic interchange. Plenum Press, New York, 532 pp.

Strahan, R. 1983. The Australian Museum complete book of Australian mammals. Angus & Robertson Publishers, Sydney, xvi + 530 pp.

Wegener, A. 1912. "Die Entstehung der Kontinente." Dr. A. Petermanns Mitteilungen aus Justus Perthes' Geographischer Anstart, year 58 (April), pp. 185–195; (May), pp. 253–256; (June), pp. 305–309.

Whitmore, T. C., and G. T. Prantz (eds.). 1987. Biogeography and Quaternary history in tropical America. Clarendon Press, New York, x + 214 pp.

Wiley, E. O. 1988. Vicariance biogeography. Annual Review of Ecology and Systematics, 19:513–542.

Willig, M. R., and E. A. Sandlin. 1991. Gradients of species density and species turnover in New World bats: a comparison of quadrat and band methodologies. Pp. 81–96, *in* Latin American mammalogy: history, biodiversity, and conservation (M. A. Mares and D. J. Schmidly, eds.). University of Oklahoma Press, Norman, Oklahoma, 468 pp.

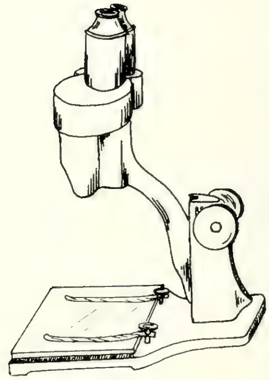
Wilson, J. W., III. 1974. Analytical zoogeography of North American mammals. Evolution, 28:124–140.

Woods, C. A. (ed.). 1990. Biogeography of the West Indies, past, present, and future. Sandhill Crane Press, Gainesville, Florida, 878 pp.

Wright, D. H. 1983. Species-energy theory: an extension of species–area theory. Oikos, 41:496–506.

# ANATOMY

CARLETON J. PHILLIPS



## Introduction

The Editors of this volume asked me to write about "*anatomy*" as it relates to mammalogy, using 1919 as a starting point. This seemed like a straight-forward task for a mammalogist interested in anatomy. After all, it is perfectly rational to believe that knowledge of structure-function complexes is an underpinning for understanding ecological, physiological, developmental, and behavioral patterns in mammals. Structure in static form is the cornerstone of systematics and structure in dynamic form is the cornerstone of understanding adaptive radiation. It also is reasonable to think that an historical perspective on mammalian anatomy could be developed with 1919 as the starting point. Indeed, D'Arcy Wentworth Thompson's treatise, *On Growth and Form,* had been published only a few years earlier, in 1917. This remarkable example of early 20th-Century scholarship still is a seminal source of ideas and hypotheses integrating anatomy, physiology, and development in an evolutionary setting (Bonner, 1966).

Regardless of the expectations of the Editors, the assigned task far exceeded what could be reviewed in a brief essay. After all, what is anatomy? In a broad sense it is an academic discipline that presently encompasses a stunning array of topics. At one extreme there is ultrastructure of mammalian cells and organelles, cell cytoskeletal features, intracellular localizations of secretory products and mRNAs, and three-dimensional configurations of basal laminae and neural networks; at the other extreme there is functional gross anatomy in the context of feeding, locomotion, physiology, or ecology.

Unlike some other scientific disciplines, the field of anatomy has expanded dramatically since 1919. So, while some research still retains the basic descriptive elements of earlier gross and microscopic anatomy (e.g., Brylski, 1933; Carleton, 1985; Forman and Phillips, 1993; Lay, 1993), technological advances in microscopy, cytochemistry, and immunohistochemistry, and foundation research in molecular biology and biochemistry have pushed the frontier of the discipline to the subcellular level (Phillips and Tandler, 1987). Today, a comparative anatomical study might involve immunohistochemical localization of neurotransmitters in the retina (e.g., Studholme et al., 1987), regulatory peptides in the digestive tract (Mennone et al., 1986), the geometry of neurons (Purves and Lichtman, 1985), somatotrophic mapping of the brain (Calford et al., 1985), comparative ultrastructure (Phillips, 1985*b*; Tandler et al., 1990) or morphological modifications to cellular organelles such as mitochondria (Tandler and Phillips, 1993*b*), or Golgi complexes in secretory cells (Tandler et al., in press *a*). Moreover, technology has converted the discipline from a largely descriptive enterprise to an experimental, function-oriented science. The latter being true at both gross and microscopic levels of anatomy, one finds functional analyses of gaits, climbing, swimming, and dentition (e.g., Cartmill, 1985; Fish, 1982; Hildebrand, 1985*a*, 1985*b*; Kiltie, 1981; Van de Graaff et al., 1982), integrations of gross and microscopic anatomy with physiology (Diamond, 1992; Rodriguez-Colunga et al., 1992; Sands et al., 1977), as well as analyses of the genetic basis of proteins composing the eye lens (Piatigorsky and Wistow, 1989), or genes responsible for the microanatomical structure of mammalian tooth enamel (Greenberg et al., 1984).

Collectively, a staggering amount of scientific and quasi-scientific information on mammalian anatomy has been accumulated since 1919. Thousands of journal articles, hundreds of institutional publications and monographs, and hundreds of books would qualify for consideration. Currently, Kent Van de Graaff has estimated that more than 80 journals carry anatomical articles about mammals (Van de Graaff, in litt.). Some of these are obvious: e.g., *Anatomy and Embryology*; *Journal of Morphology*; *Journal of Anatomy*; and *Anatomical Record.* However, most would be overlooked by an anatomist of 1919 vintage. For example, there are many with such unlikely titles as *The Journal of Wildlife Management*; *Journal of Ultrastructure Research*; *European Journal of Cell Biology*; *Microscopy Research and Techniques*; *Structural Biology*; *Differentiation*; *Cell and Tissue Research*; *Brain*; *Behavior and Evolution*; or *Growth.* All of these regularly publish articles with information that includes some aspect of mammalian anatomy, particularly microscopic and subcellular anatomy. So, it is apparent from the foregoing synopsis that only a very trimmed version of the subject proposed by the Editors would be manageable for the present essay.

Ultimately, I decided to focus on anatomy in the context of American mammalogy. Thus, I offer apologies to the large number of potential readers, especially my European colleagues and specialists in functional anatomy or cell structure, whose excellent work or specific interests in anatomy either are not mentioned or not cited extensively in this essay. Moreover, I trust that all readers will appreciate the fact that I have been very judicious in selecting citations: my intention has been to provide easily accessible examples, many taken from the *Journal of Mammalogy,* that could serve to illustrate a particular point. I should mention, however, that even with the many citations taken from the *Journal of Mammalogy,* there are at least three times more articles (including many of excellent quality) that might have been cited from this journal alone! I also have used the opportunity to introduce some literature from historians of science and philosophers of science, whose perspectives are welcome in any attempt to understand our present state as mammalogists. However, the fact remains that only a small fraction of the huge body of anatomical literature is mentioned herein.

Aside from narrowing the overall topic of anatomy to manageable proportions, a focus on anatomy in American mammalogy allowed me to explore, from a personal perspective, two observations about anatomy in terms of our discipline. First, while "mammalian anatomy" is a useful umbrella term, there appear to be at least three different kinds of anatomical research on mammals. One of these is conducted in the American medical school environment (and in dental and veterinary medical schools), another is conducted by persons who regard themselves as morphologists or experimental zoologists rather than anatomists or mammalogists, and yet another is conducted by persons who primarily were trained as museum-based systematic mammalogists. Writing about different kinds of mammalian anatomy may strike the reader as an exercise in semantic hair-splitting, but these categories of anatomy actually represent different scientific endeavors. I reached my conclusions about this subject in part from personal experience. For example, I have had opportunities to collaborate with anatomists such as Bernard Tandler and Carlin Pinkstaff who were based in medical or dental schools or trained primarily in zoology, and anatomists such as G. Lawrence Forman whose background, like mine, was fundamentally shaped by museum-based training in systematic mammalogy. I also have presented papers on mammalian anatomy at meetings of both the American Society of Mammalogists and the American Association of Anatomists. Finally, over the years (especially early in my career), I had numerous opportunities to visit with mammalogists such as E. Raymond Hall (The University of Kansas), Rollin H. Baker (Michigan State University), William H. Burt (University of Michigan), and David H. Johnson (United States National Museum), and zoologists such as Karl Stiles and H. R. Hunt (Michigan State University), and Tracy Storer (University of California, Davis), whose careers (excepting Baker) extended back nearly to the starting point of the present essay. My assertion, however, is not uniquely derived just from personal experience. Indeed, a number of historians of science who gathered in preparation for the Centennial Celebration of the American Society of Zoologists (held in 1989) more-or-less came to the same conclusion (Rainger et al., 1988). So, one objective of my essay will be to explore the history and intellectual or conceptual frameworks of what I term medical school anatomy, zoological morphology, and mammalogical anatomy.

My second observation is that there is some contradictory evidence about the role of anatomical research as it is conducted within the field of mammalogy. At one extreme, there is the obvious fact that nearly every taxonomic, or systematic, article on mammals has anatomical illustrations and, sometimes, novel anatomical descriptions. At the other extreme, anatomical research papers are cited only rarely in most general books or faunal accounts. Typical faunal accounts do not draw upon anatomical information and anatomical data are rarely included in geographic overviews. Standard reference works in mammalogy—say John Eisenberg's overview of the mammalian radiations (Eisenberg, 1981) or Terry Vaughan's classic mammalogy text (Vaughan, 1978) have attractive anatomical line drawings, but virtually none of the modern anatomical literature from non-mammalogical sources is cited in either book and little of the data from the various modern kinds of anatomical research, which range from cinematographic analyses of feeding or climbing to patterns of innervation, brain structure, and cell ultrastructure, have been integrated into the texts. Drawings of skulls and lower jaws, joint articulations, and dental cusp patterns are applications of anatomical illustration, but are not representative of "anatomy" in a modern scientific sense.

In contrast to the limited integration of anatomy into some seminal texts and faunal accounts, many high quality anatomical papers have been published in the *Journal of Mammalogy.* Authorship of these contributions has been international in scope and many of these papers, particularly those dealing with locomotion, dentition, glands, tongues and jaw systems and digestive systems, collectively, comprise an important, fundamental contribution to knowledge about mammals. In fact, the *Journal of Mammalogy* may be the best single source of information about integumentary glands in mammals (e.g., Atkeson and Marchinton, 1982; Dapson et al., 1977; Eadie, 1938; Estes et al., 1982; Jones and Plakke, 1981; Quay, 1965, 1968). Anatomical articles published in the *Journal of Mammalogy* are distinctive in two ways: most are comparative (i.e., more than one species is considered); and most are integrative (i.e., the anatomical data are in some way integrated with ecology or physiology or some other aspect of mammalian biology).

The ASM also has strongly supported the publication of anatomical contributions in its special publication series, sometimes as morphological monographs (Altenbach, 1979) and sometimes within books focused on the biology of particular taxa (e.g., Genoways and Brown, 1993; Tamarin, 1985). Museum-based publications constitute another significant portion of the North American literature in mammalogy. Historically, such publications frequently have contained specialized types of anatomical information about mammals: for example, in such publications one might find basic descriptive histology (Miller, 1895); discussion of anatomical adaptations in marine mammals (Howell, 1929); explanations of flight anatomy in bats (Vaughan, 1959); interspecific comparisons of the structure of the baculum (Burt, 1960); dental morphology and development (Phillips, 1971); the tragus in the ears of bats (Smith, 1972); bat skulls, dentitions, and skeletal features in context of ecology and evolution (Freeman, 1981; Freeman and Lemen, 1991); histomorphological comparisons of female reproductive tracts in bats (Hood and Smith, 1983); comparative histology, histochemistry, and ultrastructure of gastric mucosae in correlation with dietary habits (Forman, 1972; Phillips et al., 1984); ultrastructure of secretory cell products (Phillips et al., 1987*a*); comparative anatomy of hyoid musculature (Griffiths and Smith, 1991); comparative morphology of the cochlea in microchiropteran bats (Novacek, 1991); and comparative morphology of the glans penis in three genera of bats (Ryan, 1991).

## *Paradigms and Conceptual Frameworks*

Between 1890 and 1915, American academic biologists diverged into several distinctive professional subsets characterized, in part, by differences of opinion about what constituted "science." At one extreme the process of science was strictly descriptive, whereas at the other extreme it was strictly experimental (Benson, 1988; Rainger et al., 1988). By 1919, when the newly formed ASM first published the fledgling *Journal of Mammalogy,* this divergence was reflected among "anatomists" and "morphologists," both of whom investigated mammalian anatomy. The anatomists and morphologists of 1919 represented two very different academic camps. Anatomists largely favored descriptive work and typically were employed by medical schools where their academic function was to train young physicians (Appel, 1988). By way of contrast, the morphologists, whose studies were becoming more and more experimental, were employed by college and university academic departments of zoology or biology (Rainger et al., 1988).

Between the two academic camps, it was the anatomists rather than the morphologists per se who had the most influence on the early ASM and on the field of mammalogy before it was codified into an academic discipline. The reasons for this are twofold. First, some "founding fathers" of mammalogy were anatomists either by academic experience or by virtue of the medical profession. Harrison Allen and Gerrit S. Miller, Jr., are but two examples of early American mammalogists who could be identified as anatomists and both published excellent anatomical and microanatomical papers (e.g., Allen, 1880, 1885; Miller, 1895). Second, as an academic endeavor, anatomy was a largely descriptive mammal-oriented activity. Indeed, anatomists in 1919 did not necessarily focus on human beings or medicine as we know it today, and "laboratory" species of mammals still needed to be investigated in fundamental ways. Accordingly, descriptions of mammalian anatomical characteristics as provided by medical school faculty members were prominent features of the *Journal of Mammalogy* between 1925 and 1950.

In 1919, morphologists worked in the context of zoology and their research interests and teaching differed considerably from those of the medical school anatomists (Benson, 1988). Insofar as research is concerned, the morphologists investigated both invertebrates and vertebrates. Their work was somewhat comparative, but species of animals usually were valued for their utility as models for testing hypotheses rather than because of their intrinsic value or because of a curiosity about the species themselves. In the academic arena, the morphologist's pedagogic goals focused on graduate students and the challenge of research training rather than on teaching medical students the art of practicing medicine (Benson, 1988). Today, 75 years after the birth of the ASM, the fields of medical anatomy and zoological morphology still differ dramatically from each other and both are surprisingly different from mammalogical anatomy. Mammalogical anatomy developed as a unique form of scholarship within the broad context of "anatomy." This uniqueness is partly due to the fact that mammalogical anatomy was created within museum-based American mammalogy rather than within either medical school anatomy or zoology department morphology.

If the assertion that the subject matter of mammalian anatomy is shared by three separate academic groups seems remarkable, maybe even preposterous, one could substantiate it fairly easily by comparing contents and citation sources in the *American Journal of Anatomy, Anatomical Record, Journal of Morphology,* and *American Zoologist* with the contents and citation sources in the *Journal of Mammalogy.* There is remarkably little overlap among articles and sources of information between or among these journals. It is true, of course, that all of these journals publish articles about mammals. What impresses me, however, is the extent to which the articles reflect different scientific perspectives. These differences might suggest a lack of interchange or cognizance of one discipline for another, but perhaps they simply reflect the fact that the practitioners do not share a common scholarly heritage. My thesis is that modern mammalogical anatomy, medical school anatomy, and zoological morphology, as academic endeavors, differ in ways that are important to appreciate because these differences have served to influence, perhaps even channel, research over the past 75 years.

To the non-scientist, "*science*" often is regarded as a single enterprise conducted under a common set of rules referred to as the Scientific Method. Scientists generally understand, however, that their own work can differ in many ways from the scholarship of another scientific discipline. When confronted with the task of describing or explaining differences between their own and other scientific disciplines, many scientists find it difficult to articulate their perception of the difference. Indeed, sometimes there is little more than a vague sense that, "we do things differently." Even so, the sum of the differences just within the biological sciences is real enough to cause conflict, intradepartmental battles over college and university science curricula, and severe competition for funding. A philosopher of science, Thomas Kuhn, recognized the significance of these subtle non-uniformities within scientific disciplines. To write about this phenomenon, he (Kuhn, 1962) used the term "*paradigm*" to describe subunits of scholarship within broad fields of science; specifically he defined a paradigm as a coherent research tradition, including the rules and standards under which research is conducted. The components of a paradigm are varied, but could be expected to include an ethical perspective, cultural and academic origins, historical context, oral and written traditions, and the flavor of the personalities of the founders. Scholarly paradigms would be expected to incorporate a set of theories or assumptions and, although it may be difficult to define, one might expect a biological paradigm to espouse a particular concept of the nature of the world (Kuhn, 1962).

Finally, paradigms are defined implicitly rather than explicitly, so boundaries and membership often make more sense in retrospect than at a particular moment in time. The idea of scholarly paradigms can be applied readily to the subdivisions described within the broad subject of anatomical research on mammals. In the United States, medical school anatomy, zoological morphology, and mammalogical anatomy are different paradigms.

In the present essay, I explore some of the many components of a paradigm. However, one of the most important is what I term "*conceptual framework.*" A conceptual framework grows from the favorite theories and assumptions that underlie a scholarly paradigm. However, a conceptual framework to a large extent is the summation of how a paradigm deals with particular theories and assumptions and, therefore, the conceptual framework of one paradigm might differ from that of another, even though they are based on a single, common theory.

Conceptual frameworks are important because they root a scientist's research, link the results into some broader context, and influence the pathways of future research. Differences among conceptual frameworks unquestionably produce the most significant intellectual distinctions that can be made between scientists and, ultimately, paradigms. To many readers, Darwinian evolution is the single most obvious theory in all of biology, so it is constantly surprising to discover that evolution is not at the core of all scholarly paradigms in biology. Indeed, historically, Darwinian evolution was the central theoretical feature of zoological morphology, but was not central to either medical school anatomy or mammalogical anatomy.

The conceptual framework underlying the research of medical school anatomists could be described as a linear pathway within which the scientific method is applied to "questions" that unfold one after the other, often on the basis of technological advancement. By way of contrast, traditional taxonomy (ultimately systematics and cladistics) has provided the paradigm of mammalogical anatomy with a distinctive, non-linear type of conceptual framework. Taxonomic arrangements were the bases upon which interspecific anatomical comparisons were made at the time when museum-based mammalogical anatomy developed.

My assertion that evolutionary theory does not serve as the conceptual framework in medical school anatomy may not surprise many readers, but the same might not be true of my assertions about mammalogical anatomy and zoological morphology. Given the number of mammalogists presently interested in evolutionary biology, why were classification processes rather than evolutionary theory the original bases for the conceptual framework of mammalogical anatomy? The answer lies at least partly within the basic divergence between museum-based and laboratory-based natural science of the 19th Century (Benson, 1988; Kohlstedt, 1988). The museum-based branch, which strongly influenced many founders of modern mammalogy and mammalogical anatomy, was dominated by Louis Agassiz. This was significant because, as Kohlstedt (1988) has pointed out, Agassiz's 1848 textbook, *Principles of Zoölogy,* was used by his disciples in the museum community until late in the century. Agassiz wrote that the diversity of animal life was an "exhibition of the divine thought" and that human beings ". . . being made in the spiritual image of God . . . [are] competent to rise to the conception of His plan and purpose in the works of the Creation." Agassiz felt that the taxonomic activities that characterized museum-based research should include study of the "plan and purpose of God in His creation" (Kohlstedt, 1988). I do not mean to argue that early museum-based mammalogy was "creationist" in the modern sense. I simply wish to explain how as a museum-based science, mammalogical anatomy inherited an intellectual perspective and conceptual framework strikingly different from that of the morphologists employed in zoology departments at the turn of the century. The morphologists were not disciples of Agassiz: in the late 19th Century they actively avoided classification and focused instead on testing evolutionary theory, primarily through experimental research in embryology (Benson, 1988).

## *The Early History*

In order to appreciate fully mammalogical anatomy and its academic cousins, one must survey the foundations of anatomy, mammalogy, and morphology before 1919. It is difficult to imagine college and university life and academic structure in the 1880s, but it bore little resemblance to the present time. The subdisciplines within biology were as yet undefined. Aside from the need to educate another generation of teachers, the *raison d'être* of the professorate was unclear except at a few august institutions with philosophical scholars in the European tradition. Research and science as we know it—or as we use these terms—were very different from today and do not appear to have been the major foci of academic activity that they eventually became. The professorate was not yet a national cadre of researchers (Rainger et al., 1988). Instead of research, curriculum and curricular issues had priority.

In seeking individuals who affected the paradigms of mammalogical anatomy, medical school anatomy, and zoological morphology, we would find that many of the founders of medical school anatomy spent most of their time teaching young physicians (Appel, 1988). The founders of zoological morphology would be found among the self-described "*naturalists*" who taught various life science subjects in colleges and universities from the 1860s through the 1880s (Benson, 1988). By way of contrast, most of the academic grandfathers of North American mammalogy were among the "*natural historians*" of the 1870s through the 1880s. These forebearers of our discipline in North America concentrated on taxonomic studies of museum collections and used museum collections as the central pedagogic tool for training future teachers of natural science (Kohlstedt, 1988). When not at the museum, they were somewhere afield, gun and traps in hand (Sterling, 1991). The cultural component of mammalogical anatomy traces to the fact that many prominent early mammalogists spent as much time exploring and collecting as with college students, and more time skinning, cataloging, and identifying specimens than studying the revolutionary concepts of embryology, cytology, and evolution that occupied the thoughts of the zoological morphologists on the campuses of the Northeast and Midwest.

*The medical school anatomists.*—Generally speaking, the American anatomists did not spend time afield; they either were too busy with the medical arts or, more likely, did not regard the elemental activities of natural history as worthy of their time. They formally organized into an academic association in 1888 at the Congress of American Physicians and Surgeons held in Philadelphia. Throughout the 19th Century there was a certain elitism about natural science as conducted in the vicinity of Philadelphia so that the anatomists' selection of a city in which to organize themselves is telling. Indeed, the year before, in 1887, George B. Goode had addressed the Biological Society of Washington and paraphrased from Pickard's text on the *History of Zoology*. Pickard had asserted, ". . . zoology the world over, has sprung from the study of human anatomy, and. . . American zoology took its rise and was fostered chiefly in Philadelphia by the professors in the medical schools." Goode did not buy Pickard's idea, and went on to remark, ". . . there were good zoologists in America long before there were medical schools, and . . . Philadelphia was not the cradle of American natural history" (Kohlstedt, 1991). This quotation is telling because it not only illustrates the significance of Philadelphia in American science, but also because it underscores the sense of competition that forced the divergence between medical school anatomists and zoological morphologists.

The organizers of the first society of anatomists described themselves as the Association of American Anatomists, but changed their name to the American Association of Anatomists in 1909 (Appel, 1988). It is worth recalling that one of the prominent leaders of this founding group was Harrison Allen, who at the time was writing papers on the anatomy of bats and rodents and qualifies as an early figure in mammalogy. But, aside from Allen, who were these people and why did they formally organize themselves? Essentially, the anatomists may have been motivated by a desire to separate themselves from "physicians" in the sense of distinguishing between a scholarly pursuit—studying anatomy—and non-scholarly professional practice (see Appel, 1988). Strictly speaking, many of these anatomists were not just medical practitioners. Instead, many were faculty members at such medical schools as Harvard College, Yale, or Johns Hopkins. In this capacity they were charged with responsibility for educating young physicians. In retrospect they also seem to have been struggling to define their roles in ways that matched the prevailing ideas of scholarship. So, in modern terms they may have been seeking a vehicle by which their avocation—descriptive gross anatomy—could be incorporated into their job description as professors of anatomy.

*The zoological morphologists.*—Regardless of how one interprets the origins of the American Association of Anatomists, the most salient fact is extremely clear: the College of Physicians and Surgeons and its offspring association diverged from the academic milieu of the zoological morphologists, or naturalists. The relationship between the morphologists and medical school anatomists was not neutral; the morphologists openly regarded anatomy as a "dead" discipline. In the view of the morphologists, the basic structure of mammals, birds, and other vertebrates already had been described, so the principal task of anatomy had been completed (Appel, 1988; Benson, 1988). Why then would one wish to continue to pursue the subject? Indeed, the zoological morphologists and their colleagues were caught up in the sweeping philosophical issue of evolution and the practice of experimental "science." Additional gross anatomical descriptions probably seemed irrelevant. In terms of heritage, the American anatomists thus were excluded from the scholarship and ambiance of the life sciences as practiced in college and university zoology departments (Appel, 1988).

Ironically, however, it was microanatomy, embryology, histology, and cytology—all topics that eventually were studied by medical school anatomists—that attracted the attention of naturalists and served as early exemplars of 19th Century zoological morphology. The zoological morphologists pursued research projects that combined theoretical interests in evolution with new technology. In particular, they used the ever-improving technical skills of Germans who manufactured high quality lenses and provided rotary microtomes that could be used to slice tissues into thin, translucent sections suitable for the optical microscope (Benson, 1988). The cell theory of Schleiden and Schwann and the hypothesized relationship between ontogeny and evolution provided the zoological morphologists with conceptual frameworks for their research. This then was the academic heritage of the zoological morphologist: like their medical school counterparts they were laboratory-based, but unlike their medical school counterparts, their studies were rooted in evolutionary theory.

The zoological morphologists dominated development of college and university academic departments from the 1880s onward (Benson, 1988; Maienschein, 1988). Meanwhile, the traditional gross anatomists dominated the medical schools until Watson and Crick elucidated the structure of the DNA molecule, a feat that gave birth to cell and molecular biology and revolutionized the life sciences.

*The mammalogical anatomists.*—Strictly speaking, mammalogical anatomists—or the foundations of the science of mammalogy—were not included in the academic milieu of either the zoological morphologists or the anatomists. The academic origins of North American mammalogy and, ultimately, the paradigm of mammalogical anatomy, can be found within the culture of a third group—the museum-based natural historians. Superficially, it might seem that the natural historians were the forerunners of the naturalists and the naturalists were forerunners of all modern biologists. However, as Benson (1988) has explained, there was a striking divergence between natural historians and naturalists just as there was between the naturalists and anatomists. The natural historians collected and stored specimens of animals, which they used as the basis for instruction, exhibition, and personal taxonomic study. Because specimens were stored in museums, the museum environment was home to the natural historians who were founders of North American mammalogy. The naturalists deliberately diverged from the museum-based natural historians: instead of specimen-based instruction for future school teachers, public exhibitions, and taxonomy, the naturalists focused on research and research training and graduate education (Kohlstedt, 1988). The zoological morphologists who were derived from among these original naturalists thus held little in common with museum-based natural historians (Benson, 1988; Kohlstedt, 1988). Indeed, in the biology department at Johns Hopkins of the 1880s, the courses included histology, mammalian anatomy, comparative osteology, and embryology, but no taxonomy or classification (Benson, 1988).

In the first paragraph of this section of my essay, and elsewhere, I have used the term "culture" in reference to the origins of mammalogical anatomy. I selected this word because mammalogical anatomy was heavily influenced by factors other than traditional academic scholarship. In particular, hunting and trapping, exploration, collecting, and general "outdoorsmanship" underlie the origins of museum-based mammalogy and are some of the most fundamental reasons why anatomy in the context of mammalogy is totally different from the types of anatomy practiced by typical zoology department morphologists or by medical school faculty members. The field activites that characterized early mammalogy meant that future mammalogists would select wild mammals as research objects instead of laboratory species. The culture of exploration meant that mammalogists would be just as likely (maybe more likely) to investigate exotic species in the most remote places as they would be to investigate species that could be obtained near campus. Thus, in many ways the culture from which mammalogy grew is responsible for the broad perspectives of mammalogists and mammalogical anatomists. However, the primitive style in which field work was conducted also placed technical and intellectual limitations on what could or could not be investigated. By growing from, and then embracing, the culture of natural history, mammalogy both gained and lost. The discipline clearly was committed to a pathway that would diverge from whatever form of mammalogical science might be conducted by medical school anatomists and morphologists in zoology departments.

The cultural roots of North American natural history—and ultimately mammalogy—trace to Thomas Jefferson (Wilson and Eisenberg, 1990). In 1804, while serving as President of the United States, Jefferson sent Meriwether Lewis and William Clark on a lengthy collecting survey west of the Mississippi River. The motives behind the expedition have been debated by historians and some think that Jefferson's scientific interests merely covered his real intentions, which were territorial and political (Brodie, 1974). Considering Jefferson's personality, however, it seems obvious that his interest in natural science was a significant part of the story. Indeed, Jefferson was very interested in the possibility that unusual animals inhabited the continent. More importantly, perhaps, Jefferson made clear his intent that faunal survey was a goal of the expedition. Thus, the Lewis and Clark expedition was not merely an effort to carry forth the flag; it represented the beginning of the concept of government-sponsored science and served as the prototype for later major expeditions including J. W. Powell's extensive surveys (Kohlstedt, 1991; Powell, 1925). Under Jefferson's guidance, specimen collecting was planned as a major component of the Lewis and Clark expedition and consideration was given to the return and deposition of specimens.

Many of the progenitors of North American mammalogy preferred the gun and trap and the bedroll and camp fire to virtually anything else. An outdoor perspective and an emphasis on purposeful collecting were their twin legacies to mammalogy. Men such as E. W. Nelson and E. A. Goldman are part of the breeding stock of mammalogy. To be frank, they were neither scholars nor scientists. Given their limited educational experience and their interests (see Sterling, 1991), it is unlikely that they were aware of the emerging cell theory and the controversy about ontogeny and evolution that were being hotly debated in the hallways of academé.

In the late 19th Century and early 1900s, C. Hart Merriam sent Nelson and Goldman deep into Mexico, where they perfected the art of travel under adverse conditions, the strategy for collecting, and the techniques of field preservation. They developed ways of shipping specimens safely, habitually took notes, and became highly efficient at making camps (Sterling, 1991).

To appreciate fully the cultural importance of men like Nelson and Goldman, one must understand that they did more than set a tone for mammalogy. Aspects of their lives have been recapitulated to a remarkable degree by succeeding generations of mammalogists, including some of those who principally are mammalogical anatomists. Many living North American mammalogists have explored and collected mammals in every corner of the planet and, like Nelson and Goldman, have traveled on foot or horseback, lived in the rudest of conditions, and have endured the persistent assault of extremes in weather and countless insect and acarine pests. The pursuit of field work in the tradition of Nelson and Goldman has produced a certain outlook, a certain breed of scientist who, as Michael Mares put it, is ". . . accustomed to the hardships . . . including disrupted home lives, unsympathetic administrators, and frequent health problems [and therefore do] not suffer fools gladly" (Mares, 1991:63). Many modern mammalogists could have written the same lines as Nelson, who said, ". . . I often get thoroughly disgusted with [field work] and yet there is a fascination about the life I am leading that keeps me going despite myself" (from Sterling, 1991:40).

For many years, the technology of mammalogical anatomy was purely an extension of the art created by the 19th Century natural historians. Thus, even in the early 1960s the practice of field work and field collection differed little from the process as practiced in 1895 by Nelson and Goldman. So, insofar as anatomical studies are concerned, the museum laboratory portion of any research was destined to be archaic in comparison to what could be accomplished in the laboratories of a medical school anatomist. Although the adherence of mammalogists to their field and collecting traditions clearly limited the types of anatomical research that could be conducted, it also provided a remarkable platform for access to new data and the scientific future is bright with prospects for mammalogical contributions to cell and molecular biology and biochemistry.

By the late 1960s young mammalogists

began to pack hand-powered centrifuges and small microscopes in their baggage and by 1972, some 80 years after Nelson and Goldman explored and collected along the Pacific coast of Jalisco, Mexico, a new method of fixation of tissues for transmission electron microscopy was field-tested for the first time. In many ways nothing had changed; the fixative was formulated over a kerosene burner in a rude camp that resembled the one used by Nelson and Goldman in appearance, atmosphere, and geographic location. The fixative failed its first test, but was perfected and field-tested in Suriname by 1981 (Phillips, 1985*a*). Subsequently it has made possible the exploration of comparative cell ultrastructure and cytochemistry with virtually any species of mammal collected anywhere (e.g., Nagato et al., 1984; Phillips, 1985*b*; Tandler et al., 1986; Tandler and Phillips, 1993*a*). A process once reserved for the laboratories of medical school anatomists now can be applied in the conceptual framework of mammalogical anatomy. Thus, mammalogical anatomists have slowly acquired the technologies necessary for modernizing mammalogical field work (e.g., Forman and Phillips, 1988).

*The schism between natural historians and naturalists.*—Away from the field, the early natural historians mostly were associated with museums rather than college academic departments, and this distinction was more than administrative. Indeed, a deep philosophical schism separated the "laboratory-based" naturalists from the "museum-based" natural historians in the late 19th Century (Benson, 1988). While the naturalists debated ontogeny and evolution, the natural historians were captivated by diversity and focused their energy on collecting, cataloging, housing, and describing specimens.

As we look backward in time, it is apparent that these two camps were deliberate in their divergence. The laboratory-based naturalists controlled the college curricula and regarded the natural historians as nonscientific amateurs (Benson, 1988). The natural historians intellectually barricaded themselves in their museums and expressed concern that students were not receiving adequate training in taxonomy. To appreciate fully the significance of this schism, one need only examine an example of the academic pathways that ultimately led to the discipline of Zoology at the University of Chicago, and the development of the Museum of Vertebrate Zoology at the University of California, Berkeley.

When the prominent natural historian David Starr Jordan organized a new college at Palo Alto, California (now Stanford University), he received very specific advice from George W. Peckham. In 1881, in a letter to Jordan, Peckham wrote:

> ". . . it seems to me that Morphology and Embryology have usurped too much of the attention of the workers in the universities of America. I really believe that there has been more bad cell-making than bad species-making. The new Clark University under my friend Dr. Whitman [Charles Otis Whitman] will turn out numerous young morphologists, but not a man with any sympathy for general Natural History work" (Benson, 1988).

Jordan seems to have taken to heart the idea that natural history and cell-making could never co-exist, and this was reflected—reinforced—in his academic descendants who established their own institutions devoted to natural history and taxonomy. In particular, Jordan had a strong influence on Joseph Grinnell, who was to become the academic grandfather of mammalogy (Jones, 1991). Grinnell was perfect for the task. Although small in stature and reportedly shy by nature, he had a scholar's demeanor and was a demanding task master. E. Raymond Hall, one of Grinnell's many successful students, frequently told me of Grinnell's dogmatic, pedantic nature, which Hall himself had inherited. In keeping with the culture of mammalogy, Grinnell was born, in 1877, some 40 miles from Fort Sill in the "Indian Territory" now called Oklahoma. As a youngster, Grinnell went to the wilderness of Alaska where he developed a reputation as a collector, which ultimately served as one of his major credentials in securing his positions with Jordan and the Museum of Vertebrate Zoology at Berkeley (Dunlap, 1988; Jones, 1991).

While Jordan was following Peckham's advice, Charles Whitman retained his focus on evolutionary theory, morphology, and cytology. After leaving Clark University, Whitman essentially fathered zoology at the University of Chicago and his department became home to such luminaries as W. C. Allee, Sewall Wright, and zoological morphologists such as Libby H. Hyman (Maienschein, 1988).

The impact of Joseph Grinnell on the field of mammalogy and the paradigm of mammalogical anatomy hardly can be exaggerated; he and his academic descendants have published more than 5,000 scientific papers and books (Jones, 1991). Because he played so important a role in establishing and codifying our academic discipline in North America, it is noteworthy that Grinnell was remarkably narrow in academic ideology. Indeed, while college departments were diversifying and the naturalists of old were reorganizing into zoological morphologists, cytologists, embryologists, and geneticists, it almost seems as though Grinnell and other natural historians retrenched even further by actively restricting themselves and their students to more and more narrowly defined forms of taxonomy and zoogeography. Grinnell prohibited his students in the Museum of Vertebrate Zoology from taking courses or pursuing projects outside of the narrow confines of the museum environment. This suited some of his students just fine, but those possessed of broader interests in biology may have found the restraints an impediment to their personal intellectual development. For example, when Tracy Storer—a zoologist by any measure—wished to investigate ecological principles, he was pressured by Grinnell to refocus on museum-based taxonomic research with dead rather than living animals (Dunlap, 1988). The gap between the descendants of the original naturalists and the natural historians who gathered together in the natural history museums was further enforced by the fact that museums often were physically separated from academic departments and went so far as to create their own scientific publications to provide unspoiled outlets for the products of their research.

One of the interesting and historically relevant side-lights to the isolationism of the museum-based mammalogists occurred under E. Raymond Hall's directorship of the Museum of Natural History at The University of Kansas. Hall (E. R. Hall, pers. comm.) recognized the development of mammalogical anatomy as a distinctive paradigm and was convinced that medical school anatomy could profit from the introduction of mammalogical anatomists. Consequently, he fairly frequently suggested that students develop skills that would qualify them for employment on medical school faculties and one of his students, Phillip H. Krutzsch, became the first Chairman of Anatomy at the University of Arizona School of Medicine.

*Ethics, codification, and splintering of mammalogical anatomy.*—We have examined a variety of elements that contributed to the paradigm of mammalogical anatomy: the divergence of natural historians from the academic naturalists; the impact of outdoorsmanship and the tradition of exploration; the museum-based collection as a research and pedagogic resource; and the pervasive impact of taxonomy-systematics-cladistics as a conceptual framework. Before addressing the influences of taxonomy and natural history in more detail, we should briefly consider how ethical perspectives and codification processes occur in scholarly paradigms. In the case of mammalogical anatomy, codification of a coherent research process occurred over a lengthy period of time, but principally was in place by the time that the first generation of Grinnell's students departed from Berkeley to establish their own programs and museums.

There are many differences among the paradigms of mammalogical anatomy, medical anatomy, and zoological morphology, and one might presume that these differences tend to limit the direct competition that otherwise could occur. One of the more interesting examples is the extent to which the paradigms have subdivided the research subjects. Mammalogical anatomists are interested in most species of mammals, but tend not to be interested in the anatomy of either laboratory species or human beings. This characteristic of mammalogical anatomy has been codified, at least in part, through the *Journal of Mammalogy.* A review of articles published since 1919 reveals that articles on anatomy of laboratory mammals had become scarce by 1950 and that over the last 40 years they are essentially nonexistent. In effect, editorial policy (perhaps de facto) has restricted, or helped codify, the species that are suitable for anatomical studies in mammalogy. This codification did not originate within the ASM; it is reflected also in the museum-based anatomical publications from the time of Joseph Grinnell. As a comparison, the codification of using laboratory species or human tissues in medical school anatomy seemingly has been driven by a) restrictions on funding support for research, and b) the idea that a single example (possibly equivalent to a single species) is adequately representative of most mammals. In the paradigm of mammalogical anatomy, the selection of a few species appears equivalent to reducing mammalian diversity to a world of "the mouse," "the rat," and "the dog." It is far easier to describe paradigms than to allocate individuals to particular paradigms, and, in fact, some individuals very likely are able to shift from one paradigm to another. Thus, it should not be surprising that some of the prominent members of the medical school anatomy paradigm, for example Don Fawcett of Harvard Medical School, Carlin Pinkstaff of West Virginia University School of Medicine, and Frank Kallen of SUNY-Buffalo, are interested in wild species. Other scientists are more paradigm-bound, and it is their work that actually helps to define a paradigm. Moreover, in contrast to the *Journal of Mammalogy,* most anatomical journals welcome articles on the anatomy of non-laboratory species, so long as authors clearly explain why anatomical data from a "new" species might not be redundant to data from the mouse or rat.

The formation of paradigms is not preordained, does not appear to follow a set of rules, and generally is understandable only in historical terms. One important exception to this generalization may have occurred during the time that mammalogical anatomy was being codified. Not long after 1919, within mammalogy there was an internal clash over research and, especially, agreed-upon scientific ethics. [Although, the point should be made that "*ethics*" was not recognized as the issue at that time.] It is particularly interesting that this clash involved several of the original field collectors, especially E. A. Goldman, on the one hand and Grinnellian scholars on the other. The battle, which has been discussed and analyzed in historical detail by Thomas Dunlap (1988), centered on predator control policies and involved Goldman in his post-Mexico career as a Washington bureaucrat. In an ethical sense, Goldman and his supporters took the position that some species of mammals are more valuable than others. Value was dictated by human economy. The Grinnellian scholars, led primarily by E. Raymond Hall, essentially took the ethical position that all mammals have equal intrinsic value. As part of their strategy, Hall and his colleagues seized the academic high ground and, recalling Goldman's relatively weak academic credentials, they attacked Goldman's understanding of science and ability to interpret data (Dunlap, 1988; E.

R. Hall, pers. comm.). A successful effort was made to use the ASM and *Journal of Mammalogy* in the fight against predator control policies of the federal government (Dunlap, 1988), which ultimately was a fight that helped further define one paradigm and nearly created another.

The predator control conflict is relevant to our discussion because it illustrates how a paradigm can struggle for self-definition. In this case, the museum-based academic mammalogists codified their ethical position on the intrinsic value of all mammals and set their own standards for research. Moreover, the resulting split almost created a new paradigm for anatomical research on mammals—a paradigm based on wildlife biology or management. So it is that one can find a specialized type of anatomical information on selected species of mammals in *The Journal of Wildlife Management.* Studies of mammalian anatomy are a relatively small component of wildlife biology, but are distinctive enough to be contrasted with museum-based mammalogical anatomy. There are three major differences: absence of a taxonomic or systematic component; emphasis on application of data to management issues or biological foundations of management; and restriction of research to species judged to be of suitable economic (game) value. In terms of application, one finds articles in both *The Journal of Wildlife Management* and the *Journal of Mammalogy* on topics such as the following: use of anatomical features of teeth and skulls in age determination (e.g., Kirkpatrick and Sowls, 1962; Marks and Erickson, 1966); use of thymus, other glands, and the kidney as indicators of nutritional and developmental status (Hoffman and Robinson, 1966; Ozoga and Verme, 1978; Ransom, 1965); basic anatomy of game species (Short et al., 1965); the effects of environmental conditions and diet on growth and fat accretion in game species (Abbott et al., 1984; Holter and Hayes, 1977; Klein et al., 1987; Verme, 1979); and descriptive and morphometric data on physical morphology of different age classes (e.g., Lochmiller et al., 1987).

## *The Influence of Taxonomy*

Taxonomy has influenced mammalogical anatomy in three ways: 1) as mammalian taxonomy became codified into a predictable process, certain types of anatomical data were gathered and described; 2) certain types of descriptive information became "acceptable" matters for publication; and 3) any comparative anatomy undertaken by practitioners was conducted in terms of a taxonomic hierarchy. Because taxonomy was the mainstay of early 20th-century mammalogy, much of the early anatomical "research" by mammalogists resembled a series of practical exercises. Descriptions of certain structural elements, most notably the skeleton and dentition, were essential to taxonomy. Thus, early mammalogists spent much of their working time describing skulls, jaws, and teeth in careful detail. This procedure has not changed; the current version of this type of descriptive anatomy is virtually indistinguishable from that of 100 years ago.

It is important to understand that anatomy in the context of taxonomy was never intended to solve anatomical puzzles and certainly not intended to shed light on the sweeping theoretical concepts that attracted the zoological morphologists. When new information about structure was obtained by mammalogical anatomists, it was almost by accident and usually was treated as incidental to the main theme of the research. Taxonomy codified the pattern of observation so that the anatomical descriptions were tailored into a suitable format. In other words, the observations used for the written anatomical descriptions were predetermined by what was needed for comparisons to related species. An example of how this influenced anatomical descriptions by mammalogists can be seen in a paper by E. Raymond Hall. When Hall had an opportunity to examine the post-cranial skeleton from a rare species of bat, he did so only in the context of its comparison to a species in a related genus (Hall, 1935).

Observations born of taxonomy tend to deflect other anatomical issues. So, most mammalogical anatomy in the context of taxonomy is focused on pure comparisons and contrasts between species rather than functional concepts. The "channeled" practical anatomy derived from the taxonomic framework of North American mammalogy has continued on to this day, passsed down primarily through the Grinnellian academic lineage. An excellent example of this phenomenon may be seen in a summary paper by Jones and Genoways (1970), who reviewed new (ca. 1970) aspects of bat anatomy that could be used in modern types of systematic studies. Application of this approach, at the level of the light microscope, may be seen in an article in which Hood and Smith (1982) used histomorphological features in a cladistic analysis. One thus finds many examples of modern investigations in mammalogical anatomy, even some conducted with histochemical and ultrastructural methods, presented in a context and style familiar to taxonomists since 1885, but virtually unrecognizable to modern medical anatomists or zoological morphologists. One of the most striking recent examples can be seen in G. Lawrence Forman's Ph.D. dissertation at the University of Kansas. The histological and histochemical comparisons of gastric mucosa in species of microchiropteran bats duplicated the telegraphic style of taxonomic papers (Forman, 1972). Moreover, his research "laboratory" was housed in the museum penthouse so his slides were warmed by being placed on an empty tin of pipe tobacco that had been lined with aluminum foil. The slides then were warmed by a goose-neck lamp rather than by means of the slide warmers across campus in the departmental histology facility. Slides prepared by this means were then cleared, dehydrated, and stained in chemical solutions kept in empty baby-food jars that were stored on a nearby shelf.

A recognition of the importance of quantitation was another major impact of taxonomy on mammalogical anatomy. The correct way of taking and recording measurements of skeletal materials and teeth concerned everyone in taxonomy. One of the first papers published in the new *Journal of Mammalogy* was John C. Phillips' description of how to measure deer skulls (Phillips, 1919). The introduction of "dial" calipers was seen as a means of improving repeatability. This initiated a trend in which more and more measurable anatomical characters were sought. Both B. Elizabeth Horner (Horner, 1944) and Sydney Anderson (Anderson, 1968) described new types of craniometers that facilitated the process of taking skull and dental measurements. The use of morphometry and statistics to investigate geographic, populational, ontogenetic, and interspecific variation in skeletal elements evolved from this technology and from the availability of skeletal materials in museum collections. The measurement of cranial and dental characters used in taxonomy eventually resulted in efforts to separate variation due to inheritance from variation due to other factors (Bader, 1965; Strandskov, 1942); and to use allometric techniques for comparing skeletal anatomy (e.g., Goldstein, 1972; Nelson and Shump, 1978).

The value of dentition to taxonomy (and to paleontological mammalogy) is obvious and it is not surprising, therefore, to find that large numbers of papers on dental anatomy have been published by mammalogical anatomists. In addition to numerous descriptions of particular teeth in certain species or groups of mammals, the *Journal of Mammalogy* is an exceptionally rich resource of information about such disparate topics as genetics of tooth development (Gill and Bolles, 1982), dental homologies (Ziegler, 1971), eruption of teeth (Shadle, 1936; Slaughter et al., 1974), dental ontogeny (Birney and Timm, 1975), dental functions and coronal morphology (Chiasson, 1957; Kiltie, 1981), enamel structure (Flynn et al., 1987; Krause and Carlson, 1987), age determination and parturition (Klevezal and Myrick, 1984; Phillips et al., 1982), dental evolution (Gingerich and Rose, 1979; Klingener, 1963; Phillips and Oxberry, 1972), and quantitative variation (Gingerich and Winkler, 1979). Moreover, this interest in dentition has carried over to an interest in mastication (Herring, 1985; Reduker, 1983; Riley, 1985; Wilkins and Woods, 1983).

Museum-based mammalogical anatomy has appeared in investigations of tooth structure in many ways. One of the more unusual twists in the taxonomic trail led to the mouths of phyllostomid bats of the genus *Leptonycteris.* Periodontal disease and dissolution of mineralized tissue was observed in *L. nivalis,* but not in a broadly distributed relative, *L. sanborni.* This "taxonomic" character was traced to species-specific infestations of macronyssid mites (Phillips et al., 1969).

The search for new taxonomic characters also has led to one of the most distinctive topics in mammalogical anatomy seen within the covers of the *Journal of Mammalogy* and in museum publications. Beginning in 1940, the *Journal of Mammalogy* started publishing articles describing the os penis (baculum) and os clitorides of rodents and bats. The first article, on sciurid bacula (Wade and Gilbert, 1940), set the stage for a series of papers that described, compared, and, occasionally, offered functional hypotheses (e.g., Blair, 1942; Burt and Barkalow, 1942; Layne, 1952; Krutzsch, 1959, 1962; Patterson and Thaeler, 1982). Interest in the baculum and reproductive systems in general appears to have led to an interest in using the soft anatomy of the phallus in taxonomic studies (Lidicker, 1968). One such paper, based upon microscopic observations of the penis in species of bats and primates by a Grinnellian academic grandson, James D. Smith (Smith and Madkour, 1980), helped to touch off a sometimes bitter, sometimes anachronistic, international debate about the origin of bats (see Goodman, 1991, for an overview).

The use of microscopic data in mammalian taxonomy offers yet another set of examples of the unique nature of mammalogical anatomy. For instance, in keeping with the established pattern of mammalogical anatomy, Smith and Madkour (1980) did not publish their histological observations on the penis in bats in an anatomical journal. Instead, their findings were written in taxonomic style and published without any photomicrographs in the "*proceedings*" of a meeting hosted by The Museum, Texas Tech University. To a traditionally-trained microanatomist, photomicrographs are taken as "hard" data, so while Smith and Madkour's paper helped create a furor in taxonomist circles, it might have been unpublishable in more traditional anatomic circles. Comparative microanatomy of mammalian spermatozoa is another area in which mammalogical anatomists have influenced taxonomy. In turn, many of the articles on sperm morphology have been influenced more by the traditions of taxonomy than by the style of histological and histochemical data in other journals.

The taxonomic format gradually is being dropped by mammalogical anatomists in favor of formats more in keeping with the style in traditional anatomical journals. Examples of this conversion in mammalogical anatomy in the *Journal of Mammalogy* include articles based on scanning electron microscopy of hair structure (Brian et al., 1987; Homan and Genoways, 1978; Short, 1978) and transmission electron microscopy of the retina in rodents (Feldman and Phillips, 1984). Moreover, even the integration of mammalogical anatomy, systematics, and molecular evolution can be expected to occur in the coming decades (Phillips et al., 1993).

### *The Influence of Natural History*

Natural history, the linchpin of North American mammalogy, has influenced mammalogical anatomy in three ways. First, there is the fact that natural history involves field work and wild species in a natural setting. There is a tradition of exploration, collection, and faunal survey in mammalogy. Second, there is the semiformal codification of natural history (what to look at, what information to record, what to share with others). Third, within natural history it is acceptable to note bits and pieces of information—oddities and abnormalities.

Natural historians were regarded as amateurs by the early zoologist-naturalists who formed the nuclei of university and college zoology departments (Benson, 1988). In part this was due to the fact that many of the early survey personnel lacked advanced formal education. However, another aspect of this attitude was the hearsay aspect of the information disseminated by the natural historians. Indeed, at the end of the 19th Century and into the early 20th Century, writing in natural history was a curious amalgamation of fact and fiction, keen observation and anthropomorphism (see Dunlap, 1988). In effect, the Grinnellian era was devoted to a process that I have termed "*codification.*" That is, the ground rules and style of research in natural history were gradually organized into a format resembling what was accepted as "*science*" in biology. This process unfolds dramatically if one reads the *Journal of Mammalogy* from 1919 to 1945. Likewise, museum-based mammalogical anatomy inherited a natural history component that influenced the paradigm.

By tradition, the natural historians ancestral to mammalogical anatomists were keen observers who noticed virtually anything that was unusual in the field or in features of the specimens that they examined after their collecting trips. The idea of specifically recording observations of such features as integumentary glands, coats, special sensory structures, and abnormalities was codified early in the history of the ASM by Ernest Thompson Seton (Seton, 1919). In 1927, Joseph Grinnell presented a version of what should be acceptable in natural history studies, and this in turn formed the basis of E. Raymond Hall's version (Hall, 1955).

After a review of the *Journal of Mammalogy,* one is struck with the sensation that many of the mammalogical anatomists took seriously Seton's (1919) suggestion about noting the presence or absence and characteristics of glands. It almost seems as though Seton's paper, published in the first volume of the *Journal,* initiated an entire series of investigations of glands and gland structure. The *Journal* thus contains what may be the most extensive set of articles on this aspect of mammalian anatomy ever published. Indeed, the *Journal of Mammalogy* is by far the best single source of basic information about cutaneous and other integumentary glands in insectivores (Dryden and Conaway, 1967; Eadie, 1938), pikas (Harvey and Rosenberg, 1960), bats (Hood and Smith, 1984; Phillips et al., 1987*b*; Werner and Lay, 1963; Valdivieso and Tamsitt, 1964), rodents (Eriksson, 1981; Quay, 1962, 1965, 1968; Quay and Tomich, 1963), and ungulates (Quay and Müller-Schwarze, 1970).

Integumentary glands have attracted so much attention in part because they are often obvious to an observer. The most notable scientific reason, however, is that (as was apparent even to early natural historians) skin glands are important to mammalian biology. Observers in the field noted that individuals in some species seemed to react to each other based on olfactory cues; individuals frequently appeared to sniff certain areas of the skin on conspecifics. Observers also noted that glands were often more prominent in males than in females. Subsequently it was shown that mammalian skin glands typically are responsive to androgenic stimulation (Jannett, 1975; Quay, 1968), so secretions have the potential of being sex-specific. In addition to sex-specific secretions, integumentary glands sometimes harbor symbiotic bacteria that apparently are involved in scent production (Studier and Lavoie, 1984; Tandler et al., in press *b*). Although the histology and histochemistry of integumentary glands are not often discussed in detail in general texts, at least their roles in behavior now are widely appreciated (Müller-Schwarze, 1983).

Although many individuals have contributed to the knowledge of mammalian skin glands, William B. Quay heads the list. References to his extensive comparative analyses can be seen in articles ranging from modern reviews of knowledge about the integument and lipid-secretion in mammals to microanatomy of microtine rodents (see Quay, 1965, for example). It may not be surprising to discover that Quay's academic roots in part trace to the Museum of Zoology at the University of Michigan. The Museum of Zoology in Quay's time (late 1950s) was blessed with two of Joseph Grinnell's students, William H. Burt and Emmett T. Hooper. Quay's research, right from the beginning, exemplified both the taxonomic and the natural history components of mammalogical anatomy. Keeping in the tradition, some of his histological and histochemical articles appeared in Museum of Zoology publications. However, Quay was able to expand the border of his research beyond the traditions set by taxonomy and natural history. He proceeded to the experimental type of research favored by both medical anatomists and zoological morphologists; he was not satisfied with description and was willing to pursue his subject at a chemical level.

Feeding habits, diet, and feeding adaptations comprise another area that attracted the attention of the early natural historians and their observations help set that stage for detailed anatomical investigations of tongues, salivary glands, and digestive tracts in mammals (Doran and Allbrook, 1973; Golley, 1960; Greenbaum and Phillips, 1974; Horner et al., 1964; Kubota and Horiuchi, 1963; Phillips et al., 1987*b*).

In closing this section, it is worth mentioning briefly another aspect of the paradigm of mammalogical anatomy—an interest in the incidental or abnormal. The idea of noting small pieces of information, such as unusual skulls (Thorpe, 1930), was passed downward through the main academic lineages along with the formulae for describing skulls, jaws, teeth, and coat colors. The original notations, published in early volumes of the *Journal of Mammalogy,* were very informal and seemingly were regarded as "news" to be shared with colleagues. Only very slowly did such incidental notes evolve into a more formal presentation, reaching their zenith in the 1960s. Some articles focused on unusual features of anatomy that might have adaptive relevance (e.g., Breed, 1981), but many focused on "abnormal" anatomical characteristics. The most striking series of notes on anatomical abnormalities appeared in a 10-year period that began in 1963. In that period, at least 17 papers on dental abnormalities were published in the *Journal of Mammalogy.* A surprising number of these dealt with game species, especially cervids, and appear to have been incidental observations made in the course of other types of investigation. Since 1973, only two additional reports of dental abnormalities were published, suggesting either a change in interest or, perhaps, a new editorial policy. Indeed, the last decade apparently will mark the demise of the "note" as a means of recording incidental observations of anatomical oddities.

## *The Future of Mammalogical Anatomy*

In the previous sections I have described paradigms of academic anatomy practiced in North America and explained the origin of a special paradigm that I term mammalogical anatomy. As we have seen, mammalogical anatomy arose independently; the intellectual milieu, the format of presentation, the selection of topics, the expectations of the practitioners—in fact, the paradigm—is a conglomerate of collection, taxonomy, museum technique, and natural history. However, after 75 years, anatomy still has not been well-integrated into faunal mammalogy. That is to say, anatomy has a somewhat superficial relationship to mainline mammalogy. The general absence of anatomy in faunal mammalogy can be attributed to two factors: 1) the origins of mammalogical anatomy; and 2) the cultural and scientific gaps among mainline mammalogy and medical anatomy and zoological morphology. The first factor is indeed ironic because many of the scientific products of mammalogical anatomy are submerged in or identified with taxonomy and natural history. Mammalogical anatomists have unwittingly buried at least some of their work by publishing it in a taxonomic context or a taxonomic format. In a taxonomic context, descriptive anatomical data are relegated to the category of "characters" and, as a consequence, the data, or any discussion of functions or roles of anatomical features, are also lost in the body of the text. Mammalogical anatomy has been largely lost to medical anatomists and zoological morphologists for the same reasons that it has been overlooked by faunal mammalogists. Namely, articles in mammalogical anatomy often are misidentified as being of a purely taxonomic nature and thus are not consulted as sources of useful anatomical information.

Having a retrospective on the past 75 years might offer some hints as to the future of mammalogical anatomy. An understanding of the relationships among mammalogy, its anatomical offspring, and medical anatomy and zoological morphology, might be useful to the next generation of mammalogical anatomists. It seems clear that the next step is integration. By this, I mean more than just integrating mammalogical anatomy into faunal mammalogy (although that alone is a worthy challenge). More importantly, mammalogical anatomy should begin to profit from its own intellectual and academic heritage. The taxonomic perspective, for instance, should be employed to underscore the value of understanding relationships when designing experiments. Rather than being the instrument by which data are buried and forgotten, systematics should be the reason why data are understandable in an evolutionary context.

## *Acknowledgments*

I greatly appreciate the opportunity provided by my colleagues, E. C. Birney and J. R. Choate, to recount my understanding of the origins, history, and paradigm of anatomy in mammalogy. The views expressed in my essay are strictly my own and should not be misconstrued to represent those of the ASM, editors, or various colleagues who were helpful to me while I was writing the manuscript. I appreciated the editorial advice of G. Lawrence Forman of Rockford College. My own interest in microanatomy was largely stimulated by Larry, who very kindly shared his expertise in histology and histological technique when we both were graduate students at the Museum of Natural History at The University of Kansas. Bernard Tandler, formerly of the Department of Oral Biology, School of Dentistry, Case Western Reserve University, helped me gain insight to medical anatomy and zoological morphology by sharing his own experiences as both a student and scientist. Christopher Horvath of the Philosophy Department and Department of Biological Sciences at Illinois State University provided very valuable insight to philosophical and ethical issues. Some of my ideas and insight came from discussions with scientists who now are deceased, in particular E. R. Hall and J. K. Jones, Jr. I am grateful for the scholarly tradition that they so willingly shared. I also wish to thank N. Doss, Illinois State University, for her considerable assistance with the preparation of the manuscript. Finally, I wish to acknowledge the assistance of K. M. Van de Graaff of Brigham Young University in reviewing the anatomical literature in the *Journal of Mammalogy*.

## *Literature Cited*


ABBOTT, M. J., ET AL. 1984. Effect of photoperiod on growth and fat accretion in white-tailed doe fawns. The Journal of Wildlife Management, 48:776–787.

ALLEN, H. 1880. The ethmoid bone in bats. Bulletin of the Museum of Comparative Zoölogy, at Harvard College, 6:121–122.

———. 1885. On the embryos of bats. Contributions from the Zoological Laboratory of the University of Pennsylvania, 1:3–42.

ALTENBACH, J. S. 1979. Locomotor morphology of the vampire bat, *Desmodus rotundus*. Special Publication, American Society of Mammalogists, 6:1–137.

ANDERSON, S. 1968. New craniometer and suggestions for craniometry. Journal of Mammalogy, 49: 21–228.

APPEL, T. A. 1988. Organizing biology: The American Society of Naturalists and its "affiliated societies," 1883–1923. Pp. 87–120, *in* The American development of biology (R. Rainger, K. R. Benson, and J. Maienschein, eds.). University of Pennsylvania Press, Philadelphia, 380 pp.

ATKESON, T. D., AND R. L. MARCHINTON. 1982. Forehead glands of the white-tailed deer. Journal of Mammalogy, 63:613–617.

BADER, R. S. 1965. A partition of variance in dental traits of the house mouse. Journal of Mammalogy, 46:384–388.

BENSON, K. R. 1988. From museum research to laboratory research: the transformation of natural history into academic biology. Pp. 49–83, *in* The American development of biology (R. Rainger, K. R. Benson, and J. Maienschein, eds.). University of Pennsylvania Press, Philadelphia, 380 pp.

BIRNEY, E. C., AND R. M. TIMM. 1975. Dental ontogeny and adaptation in *Diphylla ecaudata*. Journal of Mammalogy, 56:204–206.

BLAIR, W. F. 1942. Systematic relationships of *Peromyscus* and several related genera as shown by the baculum. Journal of Mammalogy, 23:196–204.

BONNER, J. T. (ED). 1966. On growth and form by D'arcy Wentworth Thompson. Cambridge University Press, London, 346 pp.

BREED, W. G. 1981. Unusual anatomy of the male reproductive tract in *Notomys alexis* (Muridae). Journal of Mammalogy, 63:373–375.

BRIAN, M., C. HICKEY, AND M. B. FENTON. 1987. Scent-dispersing hairs (osmetricha) in some Pteropidae and Molossidae (Chiroptera). Journal of Mammalogy, 68:381–384.

BRODIE, F. W. 1974. Thomas Jefferson: an intimate history. W. W. Norton and Company, New York, 594 pp.

BRYLSKI, P. 1993. The evolutionary morphology of heteromyids. Pp. 357–385, *in* Biology of the Heteromyidae (H. H. Genoways and J. H. Brown, eds.). Special Publication, American Society of Mammalogists, 10:1–719.

BURT, W. H. 1960. Bacula of North American mammals. University of Michigan Museum of Zoology, Miscellaneous Publications, 113:1–76.

BURT, W. H., AND F. S. BARKALOW, JR. 1942. A comparative study of the bacula of woodrats. Journal of Mammalogy, 23:287–297.

CALFORD, M. B., GRAYDON, M. L., HUERTA, M. F., KAAS, J. H., AND J. D. PETTIGREW. 1985. A variant of the mammalian somatotrophic map in a bat. Nature, 313:477–479.

CARLETON, M. D. 1985. Macroanatomy. Pp. 116–175, *in* Biology of the New World *Microtus* (R. H. Tamarin, ed.). Special Publication, American Society of Mammalogists, 8:1–893.

CARTMILL, M. 1985. Climbing. Pp. 73–88, *in* Functional vertebrate morphology (M. Hildebrand, D. M. Bramble, K. F. Liem, and D. B. Wake, eds.). The Belknap Press of Harvard University Press, Cambridge, 430 pp.

CHIASSON, R. B. 1957. The dentition of the Alaskan fur seal. Journal of Mammalogy, 38:310–319.

DAPSON, R. W., STUDIER, E. H., BUCKINGHAM, M. J., AND A. L. STUDIER. 1977. Histochemistry of odoriferous secretions from integumentary glands in three species of bats. Journal of Mammalogy, 58:531–535.

DIAMOND, J. M. 1992. The red flag of optimality. Nature, 355:204–206.

DORAN, G. A., AND D. B. ALLBROOK. 1973. The tongue and associated structures in two species of African pangolins. Journal of Mammalogy, 54:909–923.

DRYDEN, G. L., AND C. H. CONAWAY. 1967. The origin and hormonal control of scent production in *Suncus murinus*. Journal of Mammalogy, 48:420–428.

DUNLAP, T. R. 1988. Saving America's wildlife. Princeton University Press, Princeton, New Jersey, 214 pp.

EADIE, W. R. 1938. The dermal glands of shrews. Journal of Mammalogy, 19:171–174.

EISENBERG, J. F. 1981. The mammalian radiations: an analysis of trends in evolution, adaptation, and behavior. University of Chicago Press, Chicago, 610 pp.

ERIKSSON, M. 1981. The bulbourethral gland of the wood mouse, *Apodemus sylvaticus*. Journal of Mammalogy, 62:375–378.

ESTES, R. D., CUMMING, D. H. M., AND G. W. HERN. 1982. New facial glands in domestic pig and warthog. Journal of Mammalogy, 63:618–624.

FELDMAN, J. L., AND C. J. PHILLIPS. 1984. Comparative retinal pigment epithelium and photoreceptor ultrastructure in nocturnal and fossorial rodents: the eastern woodrat and plains pocket gopher. Journal of Mammalogy, 65:231–245.

FISH, F. E. 1982. Function of the compressed tail of surface swimming muskrats (*Ondatra zibethicus*). Journal of Mammalogy, 63:591–597.

FLYNN, L. J., NEVO, E., AND G. HETH. 1987. Incisor enamel microstructure in blind mole rats: adaptive and phylogenetic significance. Journal of Mammalogy, 68:500–507.

FORMAN, G. L. 1972. Comparative morphological and histochemical studies of stomachs of selected American bats. University of Kansas Science Bulletin, 59:591–729.

FORMAN, G. L., AND C. J. PHILLIPS. 1988. Preparation and fixation of tissues for histological, histochemical, immunohistochemical, and electron microscopical studies. Pp. 405–424, *in* Ecological and behavioral methods for the study of bats (T. H. Kunz, ed.). Smithsonian Institution Press, Washington, D.C., 533 pp.

———. 1993. The proximal colon of heteromyid rodents: possible morphological correlates to enhanced water conservation. Pp. 491–508, *in* Biology of the Heteromyidae (H. H. Genoways and J. H. Brown, eds.). Special Publication, American Society of Mammalogists, 10:1–719.

Freeman, P. W. 1981. A multivariate study of the Family Molossidae (Mammalia, Chiroptera): morphology, ecology, and evolution. Fieldiana: Zoology, new series, 7:1–173.

Freeman, P. W., and C. A. Lemen. 1991. Morphometrics of the Family Emballonuridae. Pp. 54–61, *in* Contributions to mammalogy in honor of Karl F. Koopman (T. A. Griffiths and D. Klingener, eds.). Bulletin of the American Museum of Natural History, 432 pp.

Genoways, H. H., and J. H. Brown (eds.). 1993. Biology of the Heteromyidae. Special Publication, American Society of Mammalogists, 10:1–719.

Gill, A. E., and K. Bolles. 1982. A heritable tooth trait varying in two subspecies of *Microtus californicus* (Rodentia: Cricetidae). Journal of Mammalogy, 63:96–103.

Gingerich, P. D., and K. D. Rose. 1979. Anterior dentition of the Eocene condylarth: convergence with the tooth comb of lemurs. Journal of Mammalogy, 60:16–22.

Gingerich, P. D., and D. A. Winkler. 1979. Patterns of variation and correlation in the dentition of the red fox. Journal of Mammalogy, 60:691–704.

Goldstein, B. 1972. Allometric analysis of relative humerus width and olecranon length in some unspecialized burrowing mammals. Journal of Mammalogy, 53:148–156.

Golley, F. B. 1960. Anatomy of the digestive tract of *Microtus*. Journal of Mammalogy, 41:89–99.

Goodman, B. 1991. Holy phylogeny! Did bats evolve twice? Science, 253:36.

Greenbaum, I. F., and C. J. Phillips. 1974. Comparative anatomy and general histology of the tongues of long-nosed bats with reference to infestation of oral mites. Journal of Mammalogy, 55:489–504.

Greenberg, G., Bringas, P., Jr., and H. C. Slavkin. 1984. The epithelial genotype controls the pattern of extracellular enamel prism formation. Differentiation, 26:32–43.

Griffiths, T. A., and A. L. Smith. 1991. Systematics of emballonuroid bats (Chiroptera: Emballonuridae and Rhinopomatidae), based on hyoid morphology. Pp. 62–83, *in* Contributions to mammalogy in honor of Karl F. Koopman (T. A. Griffiths and D. Klingener, eds.). Bulletin of the American Museum of Natural History, 432 pp.

Hall, E. R. 1935. Certain osteological features of *Euderma maculatum*. Journal of Mammalogy, 15: 68–70.

———. 1955. Handbook of mammals of Kansas. Miscellaneous Publications, Museum of Natural History, University of Kansas, 7:1–303.

Harvey, E. B., and L. E. Rosenberg. 1960. An apocrine gland complex of the pike. Journal of Mammalogy, 41:213–219.

Herring, S. W. 1985. Morphological correlates of masticatory patterns in peccaries and pigs. Journal of Mammalogy, 66:603–617.

Hildebrand, M. 1985*a*. Walking and running. Pp. 38–57, *in* Functional vertebrate morphology (M. Hildebrand, D. M. Bramble, K. F. Liem, and D. B. Wake, eds.). The Belknap Press of Harvard University Press, Cambridge, 430 pp.

———. 1985*b*. Digging of quadrupeds. Pp. 89–109, *in* Functional vertebrate morphology (M. Hildebrand, D. M. Bramble, K. F. Liem, and D. B. Wake, eds.). The Belknap Press of Harvard University Press, Cambridge, 430 pp.

Hoffman, R. A., and P. F. Robinson. 1966. Changes in the endocrine glands of white-tailed deer as affected by season, sex, and age. Journal of Mammalogy, 47:266–280.

Holter, J. B., and H. H. Hayes. 1977. Growth in white-tailed deer fawns fed varying energy and constant protein. The Journal of Wildlife Management, 41:506–510.

Homan, J. A., and H. H. Genoways. 1978. An analysis of hair structure and its phylogenetic implications among heteromyid rodents. Journal of Mammalogy, 59:740–760.

Hood, C. S., and J. D. Smith. 1982. Cladistical analysis of female reproductive histomorphology in phyllostomatoid bats. Systematic Zoology, 31:241–251.

———. 1983. Histomorphology of the female reproductive tract in phyllostomoid bats. Occasional Papers, The Museum, Texas Tech University, 86:1–38.

———. 1984. Histology of a sexually dimorphic integumentary gland in *Macroglossus lagochilus*. Journal of Mammalogy, 65:1–9.

Horner, B. E. 1944. A new craniometer for carnivore and other mammalian crania. Journal of Mammalogy, 25:71–77.

Horner, B. E., J. M. Taylor, and H. H. Padykula. 1964. Food habits and gastric morphology of the grasshopper mouse. Journal of Mammalogy, 45:513–535.

Howell, A. B. 1929. Contributions to the comparative anatomy of the eared and earless seals (genera *Zalophus* and *Phoca*). United States National Museum, Proceedings, 73:1–142.

Jannett, F. J., Jr. 1975. "Hip glands" of *Microtus pennsylvanicus* and *M. longicaudus* (Rodentia: Muridae), voles "without" hip glands. Systematic Zoology, 24:171–175.

Jones, J. K., Jr. 1991. Genealogy of Twentieth-century systematic mammalogists in North America: the descendants of Joseph Grinnell. Pp. 48–56, *in* Latin American mammalogy: history, biodiversity, and conservation (M. A. Mares and D. J. Schmidley, eds.). University of Oklahoma Press, Norman, 468 pp.

Jones, J. K., Jr., and H. H. Genoways. 1970. Chiropteran systematics. Pp. 3–21, *in* About bats: a chiropteran biology symposium (B. H. Slaughter and D. W. Walton, eds.). Southern Methodist University Press, Dallas, 339 pp.

Jones, T. R., and R. K. Plakke. 1981. The histology and histochemistry of the perianal scent gland of the reproductively quiescent black-tailed prairie dog (*Cynomys ludovicianus*). Journal of Mammalogy, 62: 362–372.

KILTIE, R. A. 1981. The function of interlocking canines in rain forest peccaries (Tayassuidae). Journal of Mammalogy, 62:459–469.

KIRKPATRICK, R. D., AND L. K. SOWLS. 1962. Age determination of the collared peccary by tooth replacement pattern. The Journal of Wildlife Management, 26:214–217.

KLEIN, D. R., MELDGAARD, M., AND S. G. FANCY. 1987. Factors determining leg length in *Rangifer tarandus.* Journal of Mammalogy, 68:642–655.

KLEVEZAL, G. A., AND A. C. MYRICK, JR. 1984. Marks in tooth dentine of female dolphins as indicators of parturition. Journal of Mammalogy, 65:103–110.

KLINGENER, D. 1963. Dental evolution of *Zapus.* Journal of Mammalogy, 44:248–260.

KOHLSTEDT, S. G. 1988. Museums on campus: a tradition of inquiry and teaching. Pp. 15–47, *in* The American development of biology (R. Rainger, K. R. Benson, and J. Maienshein, eds.). University of Pennsylvania Press, Philadelphia, 380 pp.

KOHLSTEDT, S. G. (ED.). 1991. The origins of natural science in America: the essays of George Brown Goode. Smithsonian Institution Press, Washington, 411 pp.

KRAUSE, D. W., AND S. J. CARLSON. 1987. Prismatic enamel in multituberculate mammals: tests of homology and polarity. Journal of Mammalogy, 68: 755–765.

KRUTZSCH, P. H. 1959. Variation in the os penis of tropical fruit bats. Journal of Mammalogy, 40:387–392.

———. 1962. Additional data on the os penis of Megachiroptera. Journal of Mammalogy, 43:34–42.

KUBOTA, K., AND H. HORIUCHI. 1963. Anatomical studies of the salivary glands of the fur seal. Journal of Mammalogy, 44:349–364.

KUHN, T. 1962. Structure of the scientific revolution. University of Chicago Press, Chicago, 173 pp.

LAY, D. M. 1993. Anatomy of the heteromyid ear. Pp. 270–290, *in* Biology of the Heteromyidae (H. H. Genoways and J. H. Brown, eds.). Special Publication, American Society of Mammalogists, 10:1–719.

LAYNE, J. N. 1952. The os genitalia of the red squirrel, *Tamiasciurus.* Journal of Mammalogy, 33:457–459.

LIDICKER, W. Z. 1968. The phylogeny of New Guinea rodent genera based on phallic morphology. Journal of Mammalogy, 49:609–643.

LOCHMILLER, R. L., HELLGREN, E. C., AND W. E. GRANT. 1987. Physical characteristics of neonate, juvenile, and adult collared peccaries (*Tayassu tajacu angulatus*) from south Texas. Journal of Mammalogy, 68: 188–194.

MAIENSCHEIN, J. 1988. Whitman at Chicago: establishing a Chicago style of biology? Pp. 151–182, *in* The American development of biology (R. Rainger, K. R. Benson, and J. Maienschein, eds.). University of Pennsylvania Press, Philadelphia, 380 pp.

MARES, M. A. 1991. How scientists can impede the development of their discipline: egocentrism, small pool size, and the evolution of "sapismo." Pp. 57–75, *in* Latin American mammalogy: history, biodiversity, and conservation (M. A. Mares and D. J. Schmidley, eds.). University of Oklahoma Press, Norman, 468 pp.

MARKS, S. A., AND A. W. ERICKSON. 1966. Age determination in black bears. The Journal of Wildlife Management, 30:389–410.

MENNONE, A., C. J. PHILLIPS, AND D. E. PUMO. 1986. Evolutionary significance of interspecific differences in gastrin-like immunoreactivity in the pylorus of phyllostomid bats. Journal of Mammalogy, 67:373–384.

MILLER, G. S. 1895. On the introitus vaginae of certain Muridae. Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, 45:459–468.

MOSSING, T., AND L. KÄLLQUIST. 1981. Variation in cutaneous glandular structures in reindeer. Journal of Mammalogy, 62:606–612.

MÜLLER-SCHWARZE, D. 1983. Scent glands in mammals and their functions. Pp. 150–197, *in* Advances in the study of mammalian behavior (J. F. Eisenberg and D. G. Kleiman, eds.). Special Publication, American Society of Mammalogists, 7:1–753.

NAGATO, T., B. TANDLER, AND C. J. PHILLIPS. 1984. Unusual smooth endoplasmic reticulum in submandibular acinar cells in the male round-eared bat, *Tonatia sylvicola.* Journal of Ultrastructure Research, 87:275–284.

NELSON, T. W., AND K. A. SHUMP, JR. 1978. Cranial variation and size allometry in agouti paca from Ecuador. Journal of Mammalogy, 59:387–394.

NOVACEK, M. J. 1991. Aspects of the morphology of the cochlea in microchiropteran bats: an investigation of character transformation. Pp. 84–100, *in* Contributions to mammalogy in honor of Karl F. Koopman (T. A. Griffiths and D. Klingener, eds.). Bulletin of the American Museum of Natural History, 432 pp.

OZOGA, J. J., AND L. J. VERME. 1978. The thymus gland as a nutritional status indicator in deer. The Journal of Wildlife Management, 42:791–798.

PATTERSON, B. D., AND C. S. THAELER, JR. 1982. The mammalian baculum: hypotheses on the nature of bacular variation. Journal of Mammalogy, 63:1–15.

PHILLIPS, C. J. 1971. The dentition of glossophagine bats: development, morphological characteristics, variation, pathology, and evolution. Miscellaneous Publications, Museum of Natural History, University of Kansas, 54:1–138.

———. 1985*a*. Field fixation and storage of museum tissue collections suitable for electron microscopy. Acta Zoologica Fennica, 170:87–90.

———. 1985*b*. Microanatomy. Pp. 176–253, *in* Biology of the New World *Microtus* (R. H. Tamarin, ed.). Special Publication, American Society of Mammalogists, 8:1–893.

PHILLIPS, C. J., AND B. A. OXBERRY. 1972. Comparative histology of molar dentitions of *Microtus* and *Clethrionomys,* with comments on dental evolution. Journal of Mammalogy, 53:1–21.

PHILLIPS, C. J., AND B. TANDLER. 1987. Mammalian evolution at the cellular level. Pp. 1–66, *in* Current mammalogy (H. H. Genoways, ed.). Plenum Press, New York, 1:1–519.

PHILLIPS, C. J., J. K. JONES, JR., AND F. J. RADOVSKY. 1969. Macronyssid mites in the oral mucosa of long-nosed bats: notes on occurrence and associated pathology. Science, 165:1368–1369.

PHILLIPS, C. J., T. NAGATO, AND B. TANDLER. 1987*a*. Comparative ultrastructure and evolutionary patterns of acinar secretory product of parotid salivary glands in Neotropical bats. Pp. 213–229, *in* Studies in Neotropical mammalogy: essays in honor of Philip Hershkovitz (B. D. Patterson and R. M. Timm, eds.). Fieldiana: Zoology, new series no. 39, 506 pp.

PHILLIPS, C. J., B. TANDLER, AND C. A. PINKSTAFF. 1987*b*. Unique salivary glands in two genera of tropical microchiropteran bats: an example of evolutionary convergence in histology and histochemistry. Journal of Mammalogy, 68:235–242.

PHILLIPS, C. J., B. STEINBERG, AND T. H. KUNZ. 1982. Dentin, cementum, and age determination in bats: a critical evaluation. Journal of Mammalogy, 63: 197–207.

PHILLIPS, C. J., K. M. STUDHOLME, AND G. L. FORMAN. 1984. Results of the Alcoa Foundation Suriname expeditions. VIII. Comparative ultrastructure of gastric mucosae in four genera of bats (Mammalia: Chiroptera), with comments on gastric evolution. Annals of Carnegie Museum, 53:71–117.

PHILLIPS, C. J., B. TANDLER, AND T. NAGATO. 1993. Evolutionary divergence of salivary gland acinar cells: a format for understanding molecular evolution. Pp. 39–80, *in* Biology of the salivary glands (K. Dobrosielski-Verona, ed.). CRC Press, Boca Raton, 461 pp.

PHILLIPS, J. C. 1919. Skull measurements in the northern Virginia deer. Journal of Mammalogy, 1:130–133.

PIATIGORSKY, J., AND G. J. WISTOW. 1989. Enzyme/crystallins: gene sharing as an evolutionary strategy. Cell, 57:197–199.

POWELL, J. W. 1925. First through the Grand Canyon. The MacMillian Company, New York, 820 pp.

PURVES, D., AND J. W. LICHTMAN. 1985. Geometrical differences among homologous neurons in mammals. Science, 228:298–302.

QUAY, W. B. 1962. Apocrine sweat glands in the angulus oris of microtine rodents. Journal of Mammalogy, 43:303–310.

———. 1965. Comparative survey of the sebaceous and sudoriferous glands of the oral lips and angle in rodents. Journal of Mammalogy, 46:23–37.

———. 1968. The specialized posterolateral sebaceous glandular regions in microtine rodents. Journal of Mammalogy, 49:427–445.

QUAY, W. B., AND D. MÜLLER-SCHWARZE. 1970. Functional histology of integumentary glandular regions in the black-tailed deer. Journal of Mammalogy, 51:675–694.

QUAY, W. B., AND P. Q. TOMICH. 1963. A specialized midventral sebaceous glandular area in *Rattus exulans*. Journal of Mammalogy, 44:537–542.

RAINGER, R., K. R. BENSON, AND J. MAIENSCHEIN (EDS.). 1988. The American development of biology. University of Pennsylvania Press, Philadelphia, 380 pp.

RANSOM, A. G. 1965. Kidney and marrow fat as indicators of white-tailed deer condition. The Journal of Wildlife Management, 29:397–398.

REDUKER, D. W. 1983. Functional analysis of the masticatory apparatus in two species of *Myotis*. Journal of Mammalogy, 64:277–286.

RILEY, M. A. 1985. An analysis of masticatory form and function in three mustelids. Journal of Mammalogy, 66:519–528.

RODRIGUEZ-COLUNGA, M. J., C. FERNANDEZ, C. RODRIGUEZ, D. TOLIVIA, AND A. MENENDEZ-PELAEZ. 1992. Female Syrian hamster Harderian gland: development and effects of high environmental temperature and melatonin injections of histology and porphyrin deposits. The Anatomical Record, 232: 293–300.

RYAN, J. M. 1991. Comparative morphology of the glans penis in *Molossus, Promops*, and *Eumops* (Chiroptera: Molossidae). Pp. 122–137, *in* Contributions to mammalogy in honor of Karl F. Koopman (T. A. Griffiths and D. Klingener, eds.). Bulletin of the American Museum of Natural History, 432 pp.

SANDS, M. W., R. P. COPPINGER, AND C. J. PHILLIPS. 1977. Comparisons of thermal sweating and histology of sweat glands of selected canids. Journal of Mammalogy, 58:74–78.

SETON, E. T. 1919. For a methodic study of life-histories. Journal of Mammalogy, 1:67–69.

SHADLE, A. R. 1936. The attrition and extrusive growth of the four major incisor teeth of domestic rabbits. Journal of Mammalogy, 17:15–21.

SHORT, H. L. 1978. Analysis of cuticular scales on hairs using the scanning electron microscope. Journal of Mammalogy, 59:261–268.

SHORT, H. L., D. E. MEDIN, AND A. E. ANDERSON. 1965. Ruminoreticular characteristics of mule deer. Journal of Mammalogy, 46:196–199.

SLAUGHTER, B. H., R. M. PINE, AND N. E. PINE. 1974. Eruption of cheek teeth in Insectivora and Carnivora. Journal of Mammalogy, 55:115–125.

SMITH, J. D. 1972. Systematics of the chiropteran Family Mormoopidae. Miscellaneous Publications, Museum of Natural History, University of Kansas, 56:1–132.

SMITH, J. D., AND G. MADKOUR. 1980. Penial morphology and the question of chiropteran phylogeny. Pp. 347–365, *in* Proceedings of the Fifth International Bat Research Conference (D. E. Wilson and A. L. Gardner, eds.). Texas Tech University Press. pp.

STERLING, K. B. 1991. Two pioneering American mammalogists in Mexico: the field investigations of Edward William Nelson and Edward Alphonso Goldman, 1892–1906. Pp. 33–47, *in* Latin American mammalogy: history, biodiversity, and conservation (M. A. Mares and D. J. Schmidley, eds.). University of Oklahoma Press, Norman, 468 pp.

STRANDSKOV, H. M. 1942. Skeletal variations in guinea pigs and their inheritance. Journal of Mammalogy, 23:65–75.

STUDHOLME, K. M., S. YAZULLA, AND C. J. PHILLIPS. 1987. Interspecific differences in immunohistochemical localization of retinal neurotransmitters in four species of bats. Brain, Behavior and Evolution, 30:160–173.

STUDIER, E. H., AND K. H. LAVOIE. 1984. Microbial involvement in scent production in noctilionid bats. Journal of Mammalogy, 65:711–714.

TAMARIN, R. H. (ED). 1985. Biology of the New World

*Microtus*. Special Publication, American Society of Mammalogists, 8:1–893.

TANDLER, B., AND C. J. PHILLIPS. 1993*a*. Structure of serous cells in salivary glands. Microscopy Research and Techniques, 26:32–48.

———. 1993*b*. Giant mitochondria in the seromucous secretory cells of the accessory submandibular gland of the long-haired fruit bat, *Stenonycteris lanosus*. The Anatomical Record, 237:157–162.

TANDLER, B., T. NAGATO, AND C. J. PHILLIPS. 1986. Systematic implications of comparative ultrastructure of secretory acini in the submandibular salivary gland in *Artibeus* (Chiroptera: Phyllostomidae). Journal of Mammalogy, 67:81–90.

TANDLER, B., C. J. PHILLIPS, AND C. A. PINKSTAFF. In press *a*. Mucous droplets with multiple membranes in the accessory submandibular glands of long-winged bats. European Journal of Cell Biology.

TANDLER, B., K. TOYOSHIMA, AND C. J. PHILLIPS. In press *b*. Symbiotic bacteria in the accessory submandibular salivary gland of the club-footed bat, *Tylonycteris pachypus*. Journal of Dental Research.

TANDLER, B., C. J. PHILLIPS, T. NAGATO, AND K. TOYOSHIMA. 1990. Ultrastructure diversity in chiropteran salivary glands. Pp. 31–52, *in* Ultrastructure of the extraparietal glands of the digestive tract (A. Riva, P. M. Motta, and F. Testa Riva, eds.). Kluwer Academic Publishers, Boston, 278 pp.

THORPE, R. 1930. A remarkable woodchuck skull. Journal of Mammalogy, 11:67.

VALDIVIESO, D., AND J. R. TAMSITT. 1964. The histology of the chest gland of the pale spearnosed bat. Journal of Mammalogy, 45:536–539.

VAN DE GRAAFF, K. M., J. HARPER, AND G. E. GOSLOW, JR. 1982. Analysis of posture and gait selection during locomotion in the striped skunk (*Mephitis mephitis*). Journal of Mammalogy, 63:582–590.

VAUGHAN, T. A. 1959. Functional morphology of three bats: *Eumops*, *Myotis*, *Macrotus*. University of Kansas Publications, Museum of Natural History, 12:1–153.

———. 1978. Mammalogy. W. B. Saunders Company, Philadelphia, 522 pp.

VERME, L. J. 1979. Influence of nutrition on fetal organ development in deer. The Journal of Wildlife Management, 43:791–796.

WADE, O., AND P. T. GILBERT. 1940. The baculum of some Sciuridae and its significance in determining relationships. Journal of Mammalogy, 21:52–62.

WERNER, H. J., AND D. M. LAY. 1963. Morphological aspects of the chest gland of the bat, *Molossus ater*. Journal of Mammalogy, 44:552–555.

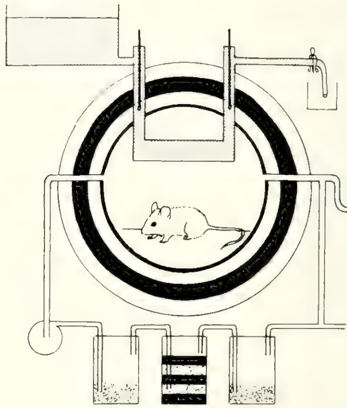
WILKINS, K. T., AND C. A. WOODS. 1983. Modes of mastication in pocket gophers. Journal of Mammalogy, 64:636–641.

WILSON, D. E., AND J. F. EISENBERG. 1990. Origin and applications of mammalogy in North America. Pp. 1–35, *in* Current mammalogy (H. H. Genoways, ed.). Plenum Press, New York, 2:1–577.

ZIEGLER, A. C. 1971. Dental homologies and possible relationships of Recent Talpidae. Journal of Mammalogy, 52:50–68.

# *PHYSIOLOGY*

Bruce A. Wunder and Gregory L. Florant



## *Introduction*

Physiology is at the same time a very old yet relatively new field of inquiry. Webster's New World Dictionary defines physiology as "The branch of biology dealing with the functions and vital processes of living organisms or their parts and organs." Karl Rothschuh (1973) has written a thorough history of physiological thought and the development of modern experimental methods in pursuing the subject. In it he notes that Aristotle (384–322 BC) used the term in its broadest sense to mean the study of knowledge about nature (from the Greek, *physis,* meaning knowledge of nature). Later, Greeks came to focus the meaning on the healing power of nature. Even as late as the 19th Century the term was still used in a broad sense. In 1848, Robley Dunglison defined "biology" as simply "physiology" and in the minds of most the term meant "hygiene" (Appel, 1987*a*). It was not until the 1850s or 1860s that experimentation became a tradition, and physiology came to take on the meaning given in Webster as defined above.

It is this topic, the study of organism function, which we will review here in the time frame of the founding and development of the ASM. The literature on the topic is huge so we will try to focus primarily on physiology as it relates to wild mammals, but will not make a clean distinction as we frequently need to reference what was being covered in the general physiological literature to put the wild mammal, or comparative studies, into perspective. Further, much of the earliest comparative literature comes from studies on invertebrates, as an early group of physiologists started work at the Woods Hole Marine Biological Labs and found invertebrates convenient forms for study.

## *Physiology Background*

Biologists, natural historians, and medical scientists dissected and reported on the anatomy of animals hundreds of years before they started to experiment on and understand the function of animals. Anatomy texts, with inferences to function, appeared in the time of the Greeks and the Middle Ages. However, the first texts in physiology, per se, were not written until the early 1800s in Europe. In North America, texts on physiology varied greatly from descriptive books on the human body intended primarily for medical students (e.g., Dunglison's Human

Physiology) to popular tracts on nutrition and hygiene. The first physiology text in North America was not published until 1896, 9 years after formation of the American Physiological Society (Appel, 1987*b*).

The concept of "experiment" to understand function was first pursued in a modern sense in Germany by Ludwig and others, and early U.S. physiologists typically studied there (Adolph, 1987; Rothschuh, 1973). These early studies (around the turn of the century) were necessarily descriptive and primarily of medical focus. Only later did investigators broaden their scope to include organisms other than humans or lab animals as models for humans. By 1887 there were several laboratories in North America where important research was being done and students could get good, thorough training in experimental methods. Thus, in 1887, 17 individuals decided to form the American Physiological Society (APS). Interestingly, one of the societies they used as their model was the American Society of Naturalists (ASN, formed in 1883), primarily because it was the first society that had restricted membership, a condition they felt was important. Further, at that time there was a closer tie between the disciplines of physiology and natural history. For example, the condition of membership in the ASN was "Membership in this society shall be limited to Instructors in Natural History, Officers of Museums and other Scientific Institutions, *Physicians* and other persons professionally engaged in some branch of Natural History" (italics ours). Indeed, half the original members of the APS were also members of the ASN and three of the organizers had been President of ASN!

Physiological journals of North America are relatively young, although a little older than the *Journal of Mammalogy* (begun in 1919–1920). The *American Journal of Physiology* was first published in 1898. The emphasis in stress physiology developed out of World War II brought the *Journal of Applied Physiology* in 1948. The *Journal of Comparative Physiology* was first published as *Zeitschrift für Vergleichende Physiologie* in 1924 and changed titles in 1972. *Physiological Zoology* started in 1928 and the early years focused primarily upon invertebrates; more vertebrate papers began to appear in the 1960s-1970s. As will be discussed below, comparative physiology began in earnest in the 1940s and truly flourished throughout the 1950s. Thus, many new specialty journals appeared after that (e.g., *Comparative Biochemistry and Physiology,* 1960; *Journal of Thermal Biology,* 1975). The later application of physiology to ecological questions was covered in ecological journals (e.g., *Ecology, Oikos, Oecologica,* and *Functional Ecology*).

## *Review Methods*

In order to evaluate how thought and subjects of investigation in physiology have changed over the 75 years since formation of the ASM, we reviewed several sources. There is a very informative history of the American Physiological Society that covers some aspects of this history (Brobeck et al., 1987). In addition, we reviewed articles in the *Journal of Mammalogy* and picked two review journals (*Physiological Reviews,* begun in 1921, and *Annual Review of Physiology,* begun in 1939) to give us some idea of what the leaders in the field during particular times thought were important topics to be reviewed and how authors approached and reviewed those topics. To focus on comparative physiology, we picked several journals in addition to the *Journal of Mammalogy* to evaluate for topical coverage—*Journal of Cellular and Comparative Physiology, Physiological Zoology,* and *Journal of Comparative Physiology.* We divided physiological topics into a number of categories (Table 1) following evaluation of the table of contents for chapter headings in six current physiology texts and placed papers into one of these categories. We realize this is not perfect but we found the list too large to be manageable otherwise. This necessarily led to some groupings; for example, the heading water balance includes some papers on ion balance, but if the paper was decidedly focused on the role of the kidney, then we placed it in kidney. Energetics includes papers on metabolism. Many papers covered temperature regulation and energetics (and may have touched on evaporation as a thermoregulatory mechanism). Here we tried to decide what the major focus of the paper was and categorize it accordingly. We started out with digestion as a single topic and found that we needed to group nutrition with it since they were frequently related. Early papers on the nervous system simply described brain electrical activity or brain waves and later papers emphasized cellular mechanisms related to neurotransmitters and ion channel function. Here, again, we needed to decide whether the focus of the paper was neuronal or some cellular function using neural tissue and that decided the category for us.

TABLE 1.—*Categories employed for grouping of physiological topics.*

| |
|---|
| Temperature Regulation |
| Energetics |
| Hibernation |
| Lipids |
| Water Balance (including ion regulation) |
| Urine |
| Kidney |
| Evaporation |
| Endocrinology |
| Reproduction (including the endocrinology thereof) |
| Digestion/Nutrition |
| Blood/Heart/Circulation |
| Respiration/Lung Function |
| CNS (neurophysiology in general) |
| Muscle |
| Cell (including molecular) |
| Other |

## *1920–1940*

During this period physiology bloomed as a discipline in North America. Several early physiologists who had been building their own apparatus for experimentation developed companies to produce that apparatus (e.g., W. T. Porter—the Harvard Apparatus Company; Ellen Robinson, who married Albert Grass, and founded the Grass Instrument Company) making expansion of certain fields possible in many labs simultaneously (Appel, 1987*c*). Much of the research during this period emphasized sanitation, temperature regulation, and nutrition as they related to human health. *Physiological Reviews* was initiated in 1921 and many early articles during the 1920s related to topics such as levels of blood components (e.g., sugar), vitamin research, digestion, and absorption of food. Much of this work had its genesis and direction focused from needs of World War I. The sanitation and nutritional requirements of armies directed many lines of research. In 1924, Boothby and Sandiford wrote a comprehensive paper in *Physiological Reviews* on basal metabolism in mammals emphasizing humans, but citing the vast literature (>100 articles) by Benedict on the subject. In 1922, at meetings of the American Physiological Society, F. G. Banting and C. H. Best presented their Nobel-winning research on the role of insulin in regulation of blood sugar. Work on the definition, role, and function of endocrine glands flourished. Most of the studies on such systems consisted of removing the gland to observe results and infer function from the resulting change in function.

In the physiological literature there was little emphasis on comparative physiology or using forms other than humans or animals as models for humans. Because there was so little emphasis on comparative aspects of physiology, very little work was reported on wild vertebrates in journals such as *Journal of Mammalogy*. In the *Journal* there are only about eight papers in the 1920s that could be defined generally as physiological, and five of those were on reproduction. Most of the work on reproduction emphasized description of reproductive cycles and timing of reproduction, which might be considered population biology today. Things expanded somewhat in the 1930s with ca. 35–40 papers appearing in the *Journal.* Most (16) of these concerned food habits with a little work on the actual physiology (digestibility) of digestion, but most simply listed food habits. Reproduction was still a strong field with 10 papers. Many articles described reproduction cycles, but a few pursued questions related to development. Benedict's study on the physiology of the elephant appeared in 1938, and there was early work on the role of the pineal in photoperiodic mechanisms. F. G. Hall's early work on adaptations to altitude was published in 1937, and there were ca. five papers on respiration in porpoises, as investigators pushed them as a novel system to understand respiration. Early work describing electrical activity and effects of shock on brains of beaver and kangaroo rats appeared. Studies of temperature regulation patterns and metabolism in humans were expanding due to interests in nutrition following World War I, and four papers on temperature regulation patterns and novel mechanisms (e.g., torpor) were published in the *Journal of Mammalogy.* Two of the papers were descriptions of low body temperatures in sloths by R. K. Enders from Swarthmore and one paper was on hibernation. As early as 1935, A. Brazier Howell and I. Gersh wrote a short paper indicating that kangaroo rats (given as *Dipodomys mohavensis*) could exist without free drinking water and speculated on the role of succulent vegetation and metabolic water in their adaptations. They even performed histological studies on the kidneys and speculated about reabsorption.

## *1940s*

The subject of comparative physiology expanded greatly in the 1940s. The early part of the decade saw a focus of physiology on national needs associated with the war efforts of World War II. This single event greatly expanded opportunity, support, and questions about physiology more than any other factor up to this time. With the development of aviation, new questions about adjustment to altitude arose. With more emphasis on submarine warfare, the Navy (through the Office of Naval Research) became interested in torpor (hence hibernation) as a possible way of maintaining crews underwater for long periods of time. The "off-duty" crew would use less oxygen in a reduced metabolic state, allowing submarines to remain under the sea for longer times. Thus, money became available for studies of metabolism, temperature regulation, and water balance (how could troops better adjust to desert or jungle conditions?). The standard topics of nutrition, digestion, circulation (especially hemodynamic shock), endocrine function, and neural control flourished with new and better equipment and support. These latter areas took on a more mechanistic flavor following the earlier descriptive work.

Two groups greatly spurred the work in comparative physiology. Laurence Irving was trying to build a program at Swarthmore and brought to the U.S. several students of the renowned Danish physiologist, August Krogh. In 1939, he helped Per Scholander obtain a Fulbright Fellowship and persuaded him to come to Swarthmore (Scholander, 1978). In 1946 Irving brought Bodil (Krogh's daughter) and Knut Schmidt-Nielsen to Swarthmore. Here, Scholander, always clever at designing and building equipment, developed the "Scholander syringe," which allowed gas analysis in very small samples of fluid (a "micro" Van Slyke apparatus). In 1947 Irving suggested that the group go to southern Arizona to study water metabolism in kangaroo rats. From that experience Bodil Schmidt-Nielsen went on to a distinguished career studying the physiology of the kidney and its role (along with other excretory organs) in regulating osmolality and volume of extra- and intracellular compartments. She served as President of the American Physiology Society from 1975 to 1976 (Brobeck, 1987). Knut Schmidt-Nielsen continued his outstanding career working on adaptations of a variety of animals to aridity focusing on temperature regulation and water balance. Irving himself founded and was the first Director of the Institute of Arctic Biology at the University of Alaska following a career focused on study of adaptations of mammals and birds to Arctic conditions. He became interested in the Arctic at the urging of Scholander, who previously had worked in Greenland doing botanical studies as a student. Scholander later became interested in questions related to diving physiology, which is what led him to Irving's lab (Scholander, 1978).

These collaborations resulted in the early classical papers describing how Arctic birds and mammals are better insulated than tropical forms, yet their patterns of metabolism and temperature regulation are similar (Scholander et al., 1950*a*, 1950 *b*, 1950*c*). At this time such studies consisted primarily of exposing animals to different ambient temperatures and measuring their body temperatures. However, Scholander also developed an experimental way to measure insulation via heat flow through skins using a hot plate as heat source. Metabolism was tediously measured using a spirometer and taking gas samples periodically for analysis with the Scholander syringe or Haldane apparatus. The primary focus was the use of comparative material to ask questions about how animals might be best adapted to particular, stressful environmental conditions.

About this same time (1945–1948), a group at Harvard consisting of O. P. Pearson, George Bartholomew, Peter Morrison, and G. E. Folk, Jr. was finishing their Ph.D.s and developed similar interests in asking questions about how animals were adapted to specific environmental stressors. Together with the Swarthmore group (Morrison went to Swarthmore before moving to the University of Wisconsin) they and their students were a dominant force in comparative physiology (especially mammals) for the next 30–40 years.

Morrison began studying temperature regulation of Central American mammals in the 1940s and went to Swarthmore where he interacted some with R. K. Enders. He quickly moved to the University of Wisconsin and later went to Alaska where he became Director of the Institute of Arctic Biology following Larry Irving in the late 1960s. In the 1940s, the emphasis was still upon measurement of temperature response patterns to varying environmental temperatures. Some labs began to look at mechanisms by which heat was conserved or lost (see Scholander et al., 1950*a,* 1950*b,* 1950*c*), but the methods were difficult and tedious. Pearson published some of the earliest papers on metabolism and temperature regulation of shrews, as did Morrison. Both were intrigued with the observation that the animals were reported to eat prodigious quantities and, hence, should have high metabolism. With small size they should have a large surface area for heat loss relative to their mass for active metabolism. Moving to southern California (UCLA), Bartholomew began work on desert forms using both birds and mammals, but emphasizing birds for his early work. However, in the 1950s he made trips to Alaska to study marine mammals. After some early reports on temperature and respiratory rates in these forms he emphasized study of behavior, a then emerging field. His mammal work, together with that of his students, focused on water balance and temperature regulation with attention to torpor as an energy-saving adaptation.

The field of temperature regulation was changing in the physiological arena also. In the early 1940s, the *Annual Review of Physiology* had a section entitled "Temperature Regulation," but starting in 1943 it was changed to "Heat and Cold" and in 1948 an entire paper on factors influencing sweating was published. Most of the studies then looked at factors that influenced body temperature, such as ambient temperature, ra-

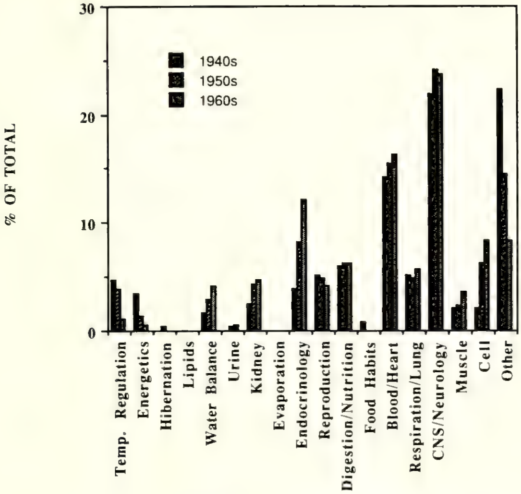



FIG. 1.—Percentage of papers published on various topics in the *Annual Review of Physiology* comparing the decades of the 1940s, 1950s, and 1960s.

diant heat loads, and effects of different clothing and activity levels on body temperature. These, of course, were in response to needs associated with World War II. The mid-1940s also produced papers on applied aviation medicine and anoxia in aviation.

## *1950s*

The impetus in comparative physiology begun in the 1940s continued into the 1950s. Much comparative work was done on water balance and thermoregulation of wild forms emphasizing Arctic and desert forms, with some studies on adaptation to high altitude. The general paradigm was to study an animal best adapted to deal with a particular environmental stressor. This work was a spin-off from the interest in stress physiology brought on by World War II and the available funding associated with that. In the "mechanistic" physiological literature there was a subtle shift in areas of emphasis. Figure 1 shows the relative percentage of papers in different subject areas published in the *Annual Review of Physiology* for the period 1940–1960 by decade. Temperature regulation made up ca. 5% of the literature in the 1940s and 1950s, then declined, while water balance (including ion balance) increased from 2% to 5% of the literature. The big increases were in work on endocrine systems and shifts to cellular approaches to mechanism. The dramatic change in endocrine coverage was a shift to specific gland function, their hormones, and mode of action versus "the endocrine system" discussed in earlier reviews. Early papers focused on the pituitary and its role in reproduction, along with thyroid and effects on growth and metabolism. These presaged the work on cellular mode of action that later were emphasized in the 1960s.

The comparative approach shows dramatically in the number and sorts of reviews written from the mid-1950s. Before this time, most studies emphasized the rat or humans, but in 1953 many papers with a comparative theme appeared in *Annual Review.* Starting in 1953, there was an article on comparative physiology of invertebrate muscle. From then to 1960 each issue had at least one paper with a definite comparative approach (e.g., sense organs, respiration in invertebrates, nutrition and feeding in vertebrates) with a comprehensive review by F. E. J. Fry on temperature compensation mechanisms for metabolism in poikilotherms in 1958. This followed a review on energetics in 1956 by Max Kleiber. In 1957 Kayser, who had worked on the subject since the 1930s, presented a definitive review on hibernation. Most of the work on hibernation to that point was descriptive regarding torpor patterns and body temperature shifts. Some early workers (e.g., Benedict and Lee, 1938; Lyman, 1948) had looked at metabolism in hibernators, but it was not until the 1950s and the development of the paramagnetic oxygen analyzer that such studies increased greatly in number. Charles P. Lyman and others reported on studies of nerve conduction, electrical activity of the cerebral cortex, circulation, and function of endocrine glands of hibernators.

The early work on water balance was expanded to include wild forms and total water budgets during the 1950s. Early work had focused on movement of water through skin, sweating mechanisms, and amounts of water needed by animals (Adolph and Dill, 1938; Dill et al., 1933; Tennent, 1946; Vorhies, 1945), and on structure and concentrating capacity of the kidney (Sperber, 1944). Although Howell and Gersh (1935 and see above) early pointed out that kangaroo rats needed little or no water, and the Schmidt-Nielsens expanded upon that in the late 1940s, it was not until the 1950s that studies focused on compartmentalizing water balance. Bodil and Knut Schmidt-Nielsen (see review in 1952) presented a "complete" account of water balance for "the" kangaroo rat and reported a value for pulmonary water loss (actually evaporative water loss). Later in the decade, Robert M. Chew expanded the work and included many other desert rodents, as did Bartholomew and his students (Dawson, Hudson, MacMillen).

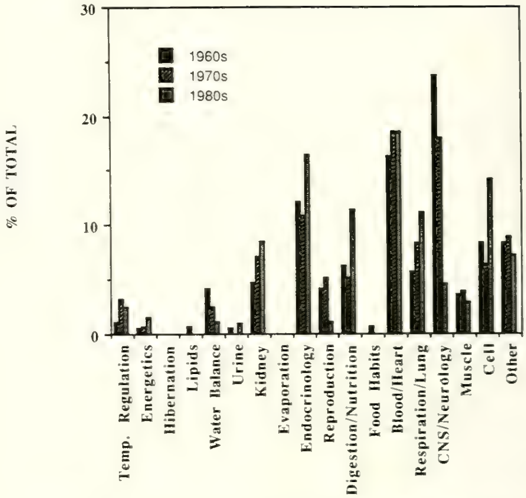



FIG. 2.—Percentage of papers published on various topics in the *Annual Review of Physiology* comparing the decades of the 1960s, 1970s, and 1980s.

## *1960s*

The comparative trend begun in the late 1940s expanded even more in the 1960s. Throughout the decade each volume of the *Annual Review of Physiology* had at least one article with a comparative approach, starting with Clyde Manwell's paper on blood pigments in 1960. An article by Don Farner on photoperiodic mechanisms in birds appeared in 1961 along with Florey's paper on comparative transmitter substances in neurophysiology (always a large topic for review). Vernberg reviewed what was known about adjustment to different geographic regions with a 1962 paper on latitudinal effects on physiological properties of populations (most of his work was on marine invertebrates, but it stimulated interest in vertebrates, including mammals) and it introduced a new technique—transplantation, which was used later in the decade by Ray Hock and others to study adaptation to altitude in deer mice. Articles on navigation by animals, comparative physiology of nutrition of vertebrates and invertebrates, and hormones in fish (by Hoar) added to J. Aschoff's classic paper on diurnal rhythms. Water and ion balance became more important topics than in the past. Bodil Schmidt-Nielsen reviewed mechanisms by which invertebrates dilute urine in the *Annual Review of Physiology* in 1963, a comparative paper on invertebrate excretory organs appeared in 1967, and G. Parry reviewed osmotic and ionic regulation (system level studies) in 1968. In 1961 Max Kleiber again reviewed energetics, emphasizing cellular energy transfer and metabolic control mechanisms over organismal metabolic rates, size, and ties to temperature regulation and food as in his 1956 review.

Studies of thermoregulatory patterns and mechanisms of thermoregulation under stress conditions for wild animals became more common. H. T. Hammel reviewed this topic in a 1968 paper in *Annual Review of Physiology*. In 1964 the first, and only, *Handbook of Physiology*: *Adaptation to the Environment* was published by the Ameri-

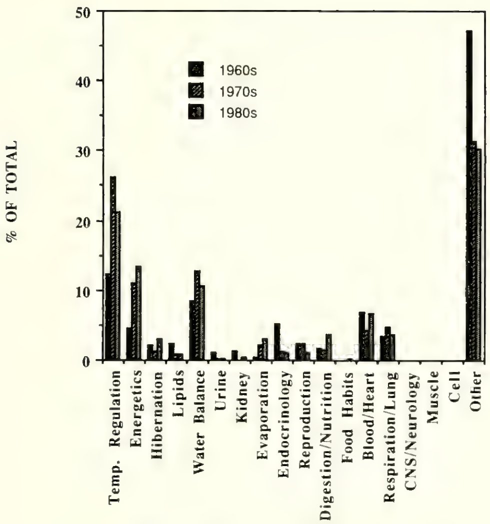



FIG. 3.—Percentage of papers published on various topics in *Physiological Zoology* comparing the decades of the 1960s, 1970s, and 1980s.

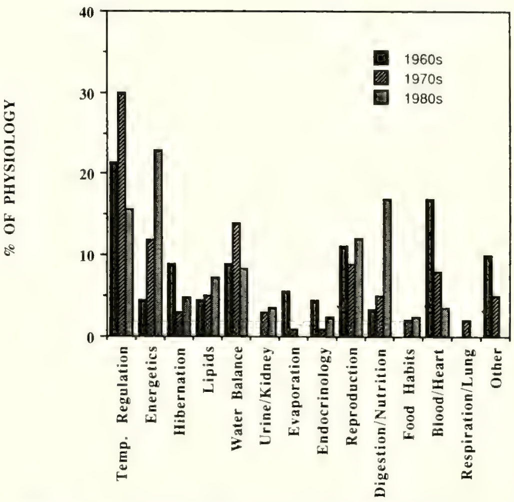



FIG. 4.—Percentage of papers published on various topics in physiology among the total papers on physiology published in the *Journal of Mammalogy* comparing the decades of the 1960s, 1970s, and 1980s.

can Physiological Society giving a state-of-the-art coverage for comparative physiology and human adjustment to stress brought on by environmental variables. In 1962 the first International Symposium of Hibernation and Cold Physiology was held in Aspen, Colorado (the 9th meeting was held in 1993 at Crested Butte, Colorado). Fig. 1 suggests that this topic of thermoregulation declined in coverage from the 1940s to the 1960s. Generally that is true with a reduction in human "stress" work after World War II, but Fig. 2 shows an increase in the 1970s and an increase in studies of energetics. The increase in 1970 reflects more papers on comparative topics (more wild species) and the increase in papers on energetics reflects an increase in papers investigating the mechanisms of thermoregulation and the role of metabolism in those. As noted, frequently it was difficult to separate a paper into one or the other category of thermoregulation or energetics. In the 1940s and early 1950s that was not so difficult because energetics papers usually related to total energy turnover, or need, and related more to nutrition and body size effects than to mechanisms of thermoregulation. Also many new journals appeared during this decade allowing more places for authors to submit work on these topics (e.g., *Journal of Comparative Biochemistry and Physiology, Journal of Thermal Biology*) and coverage of these topics in journals such as *Physiological Zoology* (Fig. 3) increased.

The increased coverage was reflected in the *Journal of Mammalogy* (Fig. 4). Over 20% of the papers in physiology concerned thermoregulation. Papers on energetics increased from 5% of all physiological coverage in the 1960s to 12% in the 1970s and 20% in the 1980s. During the 1960s investigators revived the paradigm of Justus von Leibig (from the 1800s) that physiology sets limits to distribution patterns. Thus, comparative physiology evolved into the fields of comparative (mechanistic) physiology, which selected organisms because they might best show the mechanisms at work in an organ system under stress, and physiological ecology, a new field developed to investigate how animal function and distribution might be restricted through physiological limitation to the environment. Thus, in 1963 Brian McNab's (a student of Peter Morrison) paper on the relation between home range and energy needs of mammals appeared. In the *Journal of Mammalogy* many papers published during this decade took on the emphasis of the interaction between physiology and "limitations." We find E. W. Jameson, Jr., writing about body mass effects and hibernation (how fat must individuals be before they can enter torpor?) and L. Getz investigating salt tolerance and aridity tolerance in voles and their relation to competition and habitat use and selection. Negus and Pinter published one of their first papers of a 15–20-year search for plant compounds that affect reproduction in voles (Negus was later joined by Berger in this work, which culminated in a 1981 paper in *Science* [Berger et al.] identifying the compound and a 1987 review of the topic). Further, Christian and Davis wrote about adrenal function, reproduction, stress, and vole cycles in *Microtus pennsylvanicus.* No matter what the physiological system (water balance-kidney; stress-adrenal; reproduction-endocrine/gonads), the paradigm for questions in this decade became limitation on some ecological parameter.

## *1970s*

As was the case in earlier decades, the strong topics for coverage in the physiological literature during the 1970s were endocrinology, circulation and respiration, and topics in neurobiology. The urinary system and kidney received less coverage than before. A look at Fig. 2 suggests that cell physiology received less attention in the 1970s than in the 1960s. However, that is misleading because much of the approach in endocrinology and neurobiology was molecular and cellular, with work on hormone receptors and mode of receptor function receiving much attention. In neurobiology, our understanding of impulse transmission and the cellular basis of nerve synapses and nerve/muscle interaction was being elucidated.

In comparative physiology there was a continuation of the ecological emphasis begun in the 1960s. Thermoregulation (including hibernation), energetics, water balance and kidney function, and reproduction continued strong or increased in coverage. At this time more papers on vertebrates in general, and mammals in particular, appeared in *Physiological Zoology.* Prior to 1960 much of the coverage in this journal was on invertebrates. As can be seen in Fig. 3, the topics listed above increased during the 1970s, just as they did among physiology papers published in the *Journal of Mammalogy* (Fig. 4). Thermoregulation, energetics, and water balance were all topics that expanded in coverage during this decade (Fig. 4). However, there were changes in approach and paradigms within which these physiological data were interpreted.

Within the field of thermoregulation and energetics, papers took on a new level of sophistication. Instead of just documenting more species for patterns of ability to thermoregulate in extreme environments (e.g., hot or cold, dry or wet), or evaluating the effects of body mass, there was a shift toward studying effects of, and cost for, various activities such as locomotion or reproduction, and an incorporation of broader factors influencing thermoregulation. The field of biophysics came of age following publication of David Gates' *Energy Exchange in the Biosphere* a decade earlier (Gates, 1962). Aaron Moen applied these techniques to deer and Heller and Gates used them to describe thermal physiology as a factor influencing chipmunk distribution along an altitudinal gradient on the eastern slope of the Sierra Nevada mountains in California. Here was use of physiology coupled with behavior to describe mechanisms of competitive exclusion for these distribution patterns. There was also increased emphasis on mechanisms of thermoregulation. Work on brown adipose tissue as a means of warming small mammals (first described as a heat generating tissue by Smith and Horwitz in 1969) took on more importance and was investigated by Heldmaier in Germany and Lynch and Wunder in the U.S. The role of various structures and mechanisms to modulate energy exchange with the environment (using biophysics and heat transfer concepts and equations) became more in vogue for study (e.g., Cena and Clark, 1973; Heller, 1972).

Energetics studies were applied more at a population level (following the lead of McNab, 1963) in an attempt to explain a variety of processes (e.g., home range sizes, reproductive costs, population growth). Energy became a currency to be used for describing behavior and to try to predict the consequences of population processes. The Polish school, led by Ladd Grodzinski, was quite active during this time writing on energetics, and reproduction and population growth in a variety of mammals varying in size from voles to roe deer. Grodzinski and Wunder (1975) reviewed the topic of energetics in small mammals. McNab continued in the vein of his 1960s work using energetics to discuss the distribution of vampire bats and other mammals. He then went on to develop ideas about how life history traits, such as food habits and body mass, might influence energetics in mammals.

There was also a shift during this decade to study energetics of animals in the field. While mechanistic studies still used metabolic rates measured as steady states during rest or some specific activity with oxygen analyzers in the lab, there was a new isotopic technique introduced to study integrated metabolism in the field. Much of the conceptual development and early validation work on these techniques to study metabolism and water turnover was done by Lifson in the 1950s and 1960s. However, the technique was expensive and required special equipment. Thus, few studies were undertaken until Ken Nagy, at UCLA, acquired access to the expensive isotopes and equipment to measure them. Much collaborative work was done, culminating in his review paper a decade later (Nagy, 1987) summarizing and scaling the allometric relationships of field metabolism in birds and mammals.

During this decade it was also realized that energy, per se, may not be the only limitation or major currency for evaluating performance of mammals in the field, and nutritional ecology took on a new importance. George Batzli became a dominant figure studying small herbivores. Realizing that energy is important to the lives of animals, these studies suggest that certain secondary chemicals in food may influence energy availability to mammals and some energy sources may have limited availability. For that reason most of the studies focused on herbivores, because they eat a high energy density food (plants) in which the energy is not readily available to mammals because it is tied up as cellulose and hemicellulose and vertebrates lack the enzymes necessary to break these down. Thus, digestion and digestive processes become critical to make these foods available for herbivores. There was a tremendous literature available from animal science where such processes had been studied for decades to enhance food production (e.g., Kleiber, Baldwin, Van Soest), but, with few exceptions, most studies of wild forms did not reference this literature to any great extent.

Studies of water balance still focused primarily upon animals living in arid regions (work by MacMillen and Hinds). Like the studies on energetics, however, there was a new push to learn how animals were truly challenged in the wild and, hence, radioisotopes were introduced to study water turnover in the field (see papers in the *Journal of Mammalogy* by Nagy and by Bradford). In the latter part of the decade and into the early 1980s, Christian (1979, 1980) investigated the role of water in reproduction, demographics, and habitat use by small desert rodents. Previously there was speculation that moisture may be important in these processes, but no one had sorted out moisture from energetics despite the fact that most desert forms obtain their moisture from their food. Christian simply introduced small watering stations in the field and found that the reproductive season was prolonged for some species, some actually showed numerical population increases, and there were habitat shifts to use of drier, more open habitat if moisture was present. Interestingly, little has been done with this technique in application to other species or habitats.

Overall during this decade there was a strong emphasis on environment factors and attempts to see how animals actually performed in the field. Tied to this was an interest in how performance of mammals shifts seasonally, regardless of whether one was studying temperature regulation, energetics, water balance, or reproduction.

## *1980s*

In the general physiological literature this was a time when many new, specialty journals were started or expanded having been initiated during the 1970s. Thus, papers in many fields were being shifted to these specialty journals and we found analysis of trends in a discipline harder to document using the standard review journals that we had used up to this decade. Endocrinology continued as a strong field with much more emphasis on molecular mechanism and ties to genetic control than had been the case earlier. Cardiac and circulatory function remained a strong area of research, with ca. 25% of the papers in *Physiological Review* being published in this area (Fig. 2). Most topics had molecular and cellular orientation and the general topic itself increased in coverage in *Physiological Review* from <10% to >15% of total papers.

*Physiological Zoology* changed editors in the 1970s from T. Park, who had been involved with the journal since its early days, to C. L. Prosser and J. E. Heath. Thus, many more papers on vertebrates, and mammals in particular, were published in the 1980s. The area of emphasis was energetics and, secondarily, thermoregulation (Fig. 3). Within thermoregulation there was a resurgence of interest in hibernation and torpor. This was a very topical subject in the 1950s and early 1960s, but seemed to lack focus in the late 1960s to late 1970s, except for papers on cellular mechanisms and tissue tolerance to cold. However, in the late 1970s there was renewed interest at the organismal level stimulated by work showing that the sorts of fuels burned during torpor may influence lengths of torpor bouts and that different kinds of fats (saturated versus polyunsaturated) might be used differentially during torpor periods. Thus, mammals may need to seek certain nutrients prior to hibernation. Kenagy and Geiser, Florant, and later Frank added to this area. French developed insight into the effects of body size on torpor bout lengths and optimal temperatures for torpidity. Many of the energetics papers of the decade relate to other aspects of a species' biology, such as population processes and costs for various behaviors or reproduction, adding to the information started in the 1970s. This was also a time when the field shifted to examine how body size (mass) influenced energetics and many other functions of organisms. Three major books on allometry were published emphasizing how body mass constrains and allows organisms (mammals in particular) to function (Calder, 1984; Peters, 1983; Schmidt-Nielsen, 1984).

Water balance of mammals became a topic of less emphasis, but some fine work on total water budgets and their significance for distribution limits or function was published by MacMillen, and MacMillen and Hinds. This work grew from the early studies of Bartholomew and Chew first published in the 1950s and 1960s. In these papers the relationship of water to thermoregulation was stressed as much as the use of water for general life processes and as a means of effecting ion balance.

Within the *Journal of Mammalogy,* papers on thermoregulation remained strong at >15% of the total papers in physiology published (Fig. 4). Energetics received renewed interest for investigation, increasing from around 10% to over 20% of the total physiology papers published. Reproduction remained steady at ca. 12%. The topic that truly took on a new interest was digestive biology and nutrition (Fig. 4). Many investigators began to study how the process of digestion might limit energy acquisition by mammals, especially small herbivores, and how nutrition might influence herbivore-plant interactions and animal performance.

Those studying thermoregulation continued the trends of the 1970s, applying this theme to limits on distribution and performance in mammals. Many studies linked thermoregulation to energetics so the shift to more energetics papers was, in part, a slightly different emphasis on thermoregulation. Many studies had, as part of their focus, adjustment to different seasons (work by Wunder and Merritt and colleagues), and mechanisms for those shifts (work by Hill, Kenagy, MacMillen, Wunder, French, Harlow, Dertin, McNab, and Cranford).

As mentioned above, along with these studies of energetics and the theme of limits to distribution and performance, many investigators began to study how energy sources and allocation pathways were fueled by animals. That is, what were their foods and how were nutrients obtained? George Batzli and his students had studied such questions for about two decades and, in the 1980s, began to look more closely at the role of secondary chemicals in food, in addition to rate processes and digestive efficiencies. Wunder and students showed that small herbivores (e.g., voles) could change gut size to better or more quickly process food, and many related papers followed. Two major texts on the topics of nutrition appeared, in addition to many symposia volumes, especially on ruminant herbivores. Peter Van Soest's book, *Nutritional Ecology of the Ruminant* (1982), set the stage for Charlie Robbins' book, *Wildlife Feeding and Nutrition* (1983). Both are used as a basis for posing questions about how various mammals adjust to novel foods or environments compared to more studied forms. Recent work is beginning to focus on limits to energy processing and the trade-off of the roles of digestion and assimilation with tissue utilization of substrates, or behavior of feeding. Over the next decade, we hope there will be a more complete understanding of how mammals, especially herbivores, utilize the myriad of plants available to them, and how plant–animal interactions are influenced by physical and biological factors such as thermoregulation, energy needs, and nutrient needs for reproduction.

## *Epilogue*

We have attempted to give a brief overview of how physiology in general, but especially comparative physiology of wild mammals, has shifted, waxed, and waned over the past 75 years as the ASM has grown. We suspect that the recent fervor for cell and molecular approaches will stimulate an understanding of not only mechanisms of process, but also how those processes relate to the fundamental biology (life histories) of the wild mammals possessing them. Such knowledge will be useful not only for understanding ourselves and our functions, but also how mammals function in ecosystems, and how they might adjust to changes in those ecosystems as we witness climatic and other environmental changes.

## *Literature Cited*

Adolph, E. F. 1987. Physiology flourishes in America. Pp. 1–10, *in* History of the American Physiological Society (J. R. Brobeck, O. E. Reynolds, and T. A. Appel, eds.). Waverly Press, Baltimore, Maryland, 533 pp.

Adolph, E. F., and D. B. Dill. 1938. Observations on water metabolism in the desert. American Journal of Physiology, 123:369–372.

Appel, T. A. 1987*a*. Founding. Pp. 11–29, *in* History of the American Physiological Society (J. R. Brobeck, O. E. Reynolds, and T. A. Appel, eds.). Waverly Press, Baltimore, Maryland, 533 pp.

———. 1987*b*. First quarter century, 1887–1912. Pp. 31–62, *in* History of the American Physiological Society (J. R. Brobeck, O. E. Reynolds, and T. A. Appel, eds.). Waverly Press, Baltimore, Maryland, 533 pp.

———. 1987*c*. Second quarter century, 1913–1937. Pp. 63–96, *in* History of the American Physiological Society (J. R. Brobeck, O. E. Reynolds, and T. A. Appel, eds.). Waverly Press, Baltimore, Maryland, 533 pp.

Benedict, F. G., and R. C. Lee. 1938. Hibernation and marmot physiology. Carnegie Institution of Washington Publication, 497:1–239.

Berger, P. J., N. C. Negus, E. H. Sanders, and P. D. Gardner. 1981. Chemical triggering of reproduction in *Microtus montanus*. Science, 214:69–70.

Brobeck, J. R. 1987. Presidents, 1963–1987. Pp. 177–280, *in* History of the American Physiological Society (J. R. Brobeck, O. E. Reynolds, and T. A. Appel, eds.). Waverly Press, Baltimore, Maryland, 533 pp.

Brobeck, J. R., O E. Reynolds, and T. A. Appel (eds.). 1987. History of the American Physiological Society. Waverly Press, Baltimore, Maryland, 533 pp.

Calder, W. A., III. 1984. Size, function, and life history. Harvard University Press, Cambridge, Massachusetts, 431 pp.

Cena, K., and J. A. Clark. 1973. Thermographic measurements of surface temperatures of animals. Journal of Mammalogy, 54:1003–1007.

Christian, D. P. 1979. Comparative demography of three namib desert rodents: responses to the provision of supplementary water. Journal of Mammalogy, 60:679–690.

———. 1980. Vegetative cover, water resources, and microdistributional patterns in a desert rodent community. Journal of Animal Ecology, 49:807–816.

Dill, D. B., A. V. Bock, and H. T. Edwards. 1933. Mechanisms for dissipating heat in man and dog. American Journal of Physiology, 104:36–43.

Gates, D. M. 1962. Energy exchange in the biosphere. Harper and Row Publishers, New York, 151 pp.

Grodzinski, W., and B. A. Wunder. 1975. Ecological energetics of small mammals. Pp. 173–204, *in* Small mammals: their productivity and population dynamics (F. B. Golley, K. Petrusewicz, and L. Ryszkowski, eds.). Cambridge University Press, Great Britain, 451 pp.

Heller, H. C. 1972. Measurements of convective and radiative heat transfer in small mammals. Journal of Mammalogy, 53:289–295.

Howell, A. B., and I. Gersh. 1935. Conservation of water by *Dipodomys*. Journal of Mammalogy, 16: 1–9.

Lyman, C. P. 1948. Oxygen consumption and temperature regulation of hibernating hamsters. Journal of Experimental Zoology, 109:55–78.

McNab, B. K. 1963. Bioenergetics and the determination of home range size. The American Naturalist, 97:133–140.

Nagy, K. A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. Ecological Monographs, 57:111–128.

Negus, N. C., and P. J. Berger. 1987. Mammalian reproductive physiology: adaptive responses to changing environments. Pp. 149–173, *in* Current mammalogy (H. H. Genoways, ed.). Plenum Publishing, New York, 1:1–519.

Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge, Great Britain, 328 pp.

Robbins, C. T. 1983. Wildlife feeding and nutrition. Academic Press, New York, 343 pp.

Rothschuh, K. 1973. History of physiology (Translated and edited by G. B. Risse). Robert E. Kriegen Publishing Co., Huntington, New York, 379 pp.

Schmidt-Nielsen, K. 1984. Scaling: why is animal size so important? Cambridge University Press, Cambridge, Great Britain, 241 pp.

Schmidt-Nielsen, K., and B. Schmidt-Nielsen. 1952. Water metabolism of desert mammals. Physiological Reviews, 32:135–166.

Scholander, P. F. 1978. Rhapsody in science. Annual Review of Physiology, 40:1–17.

Scholander, P. F., V. Walters, R. Hock, and L. Irving. 1950. Body insulation of some arctic and tropical mammals and birds. Biological Bulletin, 99: 225–236.

Scholander, P. F., R. Hock, V. Walters, F. Johnson, and L. Irving. 1950. Heat regulation in some arctic and tropical mammals and birds. Biological Bulletin, 99:237–258.

Scholander, P. F., R. Hock, V. Walters, and L. Irving. 1950. Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. Biological Bulletin: 99:259–271.

Smith, R. E., and B. A. Horwitz. 1969. Brown fat and thermogenesis. Physiological Review, 49:330–425.

Sperber, I. 1944. Studies on the mammalian kidney. Zool. Bidrag Fran Uppsala, 22:249–431.

Tennent, D. M. 1946. A study of the water losses through the skin in the rat. American Journal of Physiology, 145:436–440.

Van Soest, P. J. 1982. Nutritional ecology of the ruminant. Comstock Publishing Associates, Cornell University Press, Ithaca, New York, 373 pp.

Vorhies, C. T. 1945. Water requirements of desert animals in the southwest. University of Arizona Agricultural Experiment Station Technical Bulletin, 107: 487–525.

# REPRODUCTION

Oliver P. Pearson and G. J. Kenagy

### Introduction

We find ourselves in the early 1990s enriched by fascinating accounts of the reproductive biology of hundreds of kinds of mammals. We believe that we have a sophisticated understanding of the ways in which various reproductive mechanisms and strategies represent fitness. Almost all of this knowledge has been gained in the last 100 years.

When the ASM was founded in 1919, detailed information about reproductive patterns and mechanisms was available for only a handful of domesticated and wild animals, as well as for humans. Further understanding was severely handicapped by the primitive state of the science of endocrinology and the absence of yet-to-be-discovered insights in cell and molecular biology. In the years immediately following the founding of ASM, anatomists, physiologists, geneticists, psychologists, medical researchers, and biochemists all began contributing ideas and data to the emerging discipline of mammalian reproductive biology (Fig. 1).

To illustrate the relative collective effort that mammalogists have directed into studies of reproduction, we tallied all the articles published in every fifth volume of the *Journal of Mammalogy* from 1920 through 1990. Overall, 8% of the 1,846 papers dealt with reproduction. The percentage increased, however, during this 70-year interval. For the first 25 years only ca. 4% of the articles dealt with reproduction, but this increased to ca. 11% in the last 30 years (Fig. 2).

The development of our knowledge of the reproductive biology of mammals resulted from the vision of a few pioneers whose discoveries and teachings spread and multiplied while passing through a variety of institutions. The favorable climate for this flowering was found within institutions that drew their support from medical interests, agricultural and livestock interests, laboratory-animal needs, entrepreneurs who saw commercial opportunities, and surely, from the traditional "pure" scientists—those who could not rest until they found out whether some exotic species was an induced ovulator or why some other species had such a long gestation. We shall focus on only a few of the institutions and people who played important roles during the early decades of the 20th-Century flowering of reproductive biology. By mid-century, when the number of participating scientists became so numerous, we shall call attention to new ideas and approaches that have been shaped by

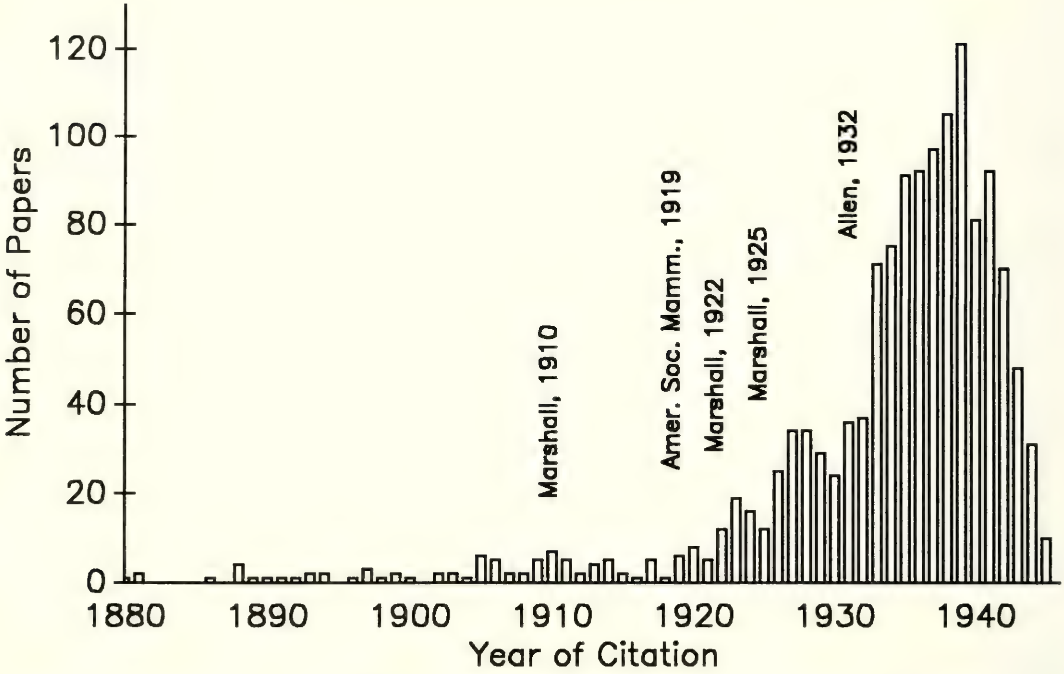



FIG. 1.—The growth of research on mammalian reproduction. Dates of appearance of 1,362 papers cited by Asdell (1946). Five significant publications or events are noted, as discussed in the text.

more recent generations of innovative people. In the more recent time period we have, for simplicity, been highly selective and general, indicating ideas of importance rather than describing them in detail, and we have not generally presented these modern trends in terms of specific people. More time will tell which recent approaches will have the most enduring value in the history of mammalian reproductive biology.

## EARLY 20TH CENTURY

### *The Cambridge Legacy*

The flowering of interest in mammalian reproduction reflected in Figure 1 can be traced to Great Britain, where a founding figure was Walter Heape. After a late start in science, Heape found himself teaching anatomy at Cambridge, where he co-authored a textbook of embryology. He soon obtained grant support and thereafter devoted himself full time to research. Working at a time when even the sex-determination mechanism of mammals was unknown, he successfully transplanted fertilized ova from one rabbit to another in the early 1890s, developed artificial insemination in 1897, and in 1901 published an impressive summary and synthesis (Heape, 1901). He fitted humans and dozens of species of wild and domesticated mammals into a common framework of reproductive categories using now-familiar terms (British spellings) such as oestrus, pro-oestrum, metoestrum, dioestrum, polyoestrous, and monoestrous. Had he remained longer in teaching, he no doubt would have become the leader of a "school"; but, his impact seems to have been mostly through his publications.

Heape's work inspired F. H. A. Marshall, a lecturer at the School of Agriculture in Cambridge, to publish his influential book on physiology of reproduction (1910). In the introduction, Marshall acknowledged, "I take this opportunity of recording my in-

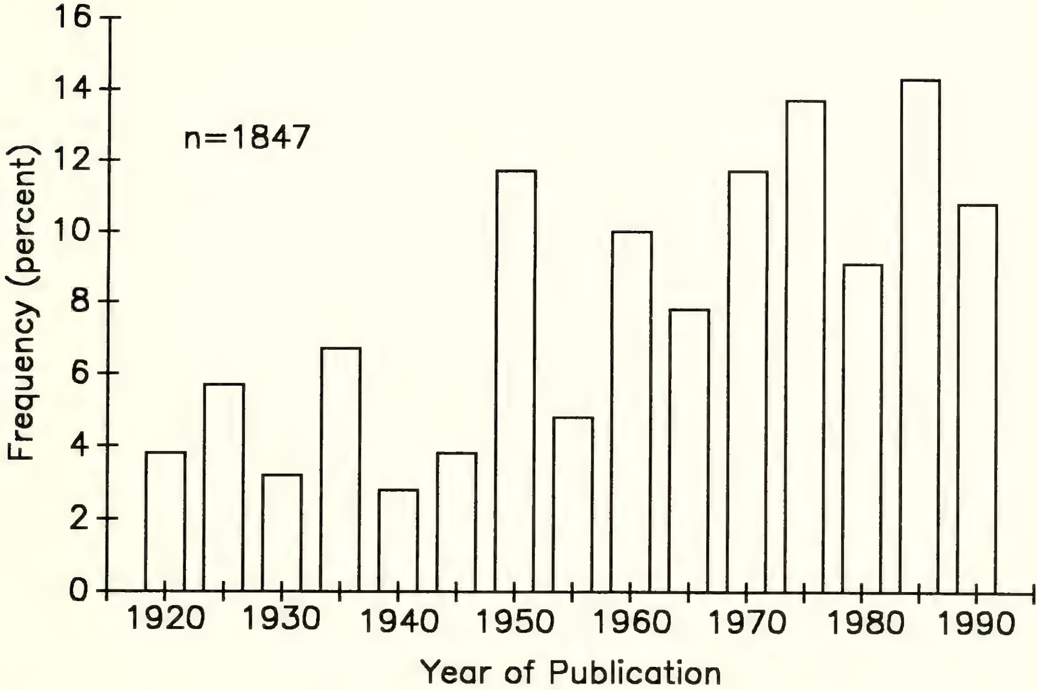



FIG. 2.—Increase in relative frequency of articles on reproduction appearing in the *Journal of Mammalogy*. Frequency distribution is shown for articles containing important information on reproduction ($n$ = 1,847), sampled every fifth year from 1920 through 1990.

debtedness to Mr. Walter Heape, through whose influence I was first led to realise the importance of generative physiology both in its purely scientific and in its practical aspects."

Marshall's book was a wide-ranging accumulation of information on breeding seasons, estrous cycles, uterine cycles, ovarian changes, spermatogenesis, the testes and ovaries as endocrine organs, the placenta, and other topics, all with reference to humans, laboratory animals, livestock, and wild animals. The 1910 and 1922 editions of this book became the "bible" to a generation of biologists who were to outline the diversity of reproductive strategies in mammals.

A second book by Marshall on reproductive physiology appeared in 1925. It appeared in time to influence the people, mostly British, who published reproductive studies in the 1930s and 1940s. The closing paragraphs of this second book call attention to global population concerns, Malthus, contraception, and eugenics. Reading those paragraphs two generations later brings one face to face with the fact that during the intervening 70 years we have not resolved those old yet vital ethical concerns. Furthermore, still newer discoveries have created yet more concerns undreamed of by Marshall.

Even before Marshall's books, British biologists were otherwise prepared for a flowering of reproductive studies. W. H. Caldwell, a Cambridge scholar on an expedition in 1884 to one of the colonies (Australia), sent the famous cable "Monotremes oviparous, ovum meroblastic" not to Great Britain or "the Continent," but to another outpost of the United Kingdom, Canada and the city of Montreal, where the British Association for the Advancement of Science was holding its annual meeting (Burrell, 1927). In this geographically widespread and receptive climate, Marshall's books provided a foundation on which subsequent generations could build. The pages of the *Proceedings of the Zoological Society of London,* the *Philosophical Transactions of the Royal Society of London,* and other prestigious publications are forever enriched by important reproductive studies by other luminaries such as E. C. Amoroso, J. R. Baker, F. W. R. Brambell, R. Deanesly, J. Hammond, J. P. Hill, L. H. Matthews, A. S. Parkes, I. W. Rowlands, and Sir Solly Zuckerman. Within little more than a decade in the 1930s and early 1940s they described the intricacies and novelties in the reproductive cycles of shrews and bats, hedgehogs and hyaenas, kangaroos and ferrets, wildcats and moles, and gibbons and rabbits. In the coming decades these researchers were followed by P. H. Leslie, J. L. Davies, B. Weir, and many others. A third edition of Marshall's book, delayed by World War II and published as three volumes with many chapter authors, appeared between 1952 and 1966 under the editorship of A. S. Parkes. Marshall had died in 1949, but he had contributed to many of the chapters. A fourth edition appeared in 1984, edited by G. E. Lamming.

The Zoological Society of London under the presidency of Sir Solly Zuckerman became one of the institutions that had a great impact on the development of studies of reproduction. In 1963, with support from industry (the Wellcome Trust), a research center was established, with an emphasis on studies of mammalian reproduction—I. W. Rowlands was its first director.

Perhaps the ultimate fruition of the Cambridge rootstock came in 1960, when the Society for the Study of Fertility, with support from the Wellcome Trust, founded the *Journal of Reproduction and Fertility.* C. R. Austin was editor and A. S. Parkes Chair of the Editorial Board. In the first issue, Parkes pointed out that the "output of literature on reproduction and fertility is mounting rapidly owing to the increasing number of scientifically based clinical studies, the greater importance attached to productivity in farm animals, the extension of field and laboratory studies to additional species, and the growing realization of the urgent need for finding means of controlling fertility in man." For three decades this journal has advanced in a distinguished manner the research interests of reproductive biologists. The first issue of volume 1 contains Hilda Bruce's description of a pheromonal influence on reproduction that came to be known as the Bruce Effect (Bruce, 1960). A recent number (1988, no. 1), edited in Cambridge by Barbara Weir, with E. J. C. Polge as Chair of the Executive Committee, contains articles on the reproduction of no less than 16 genera of mammals.

## *The Johns Hopkins Legacy*

Returning to 19th-Century North America, the Johns Hopkins University was established in Baltimore, Maryland, in 1876. The goal of the biology program was to provide students with hands-on, laboratory-oriented research training rather than the traditional lecture-til-full system; this successful model was eventually adopted by many North American universities (Benson, 1987). Thomas Huxley had been consulted extensively during the planning of the curriculum, and he recommended one of his proteges from Cambridge, H. Newell Martin, a physiologist, to be the first professor in the new Biology Department. The appointment of W. K. Brooks, a morphologist, followed immediately. The department subsequently produced an impressive array of scholars including E. B. Wilson, T. H. Morgan, E. G. Conklin, and R. G. Harrison, who all made a great impact on biology. The great influence of biology at Johns Hopkins on the discipline of mammalian reproduction was accomplished through a variety of the university's satellite programs, including the Medical School, the School of Hygiene and Public Health, the Institute for Biological Research, and, beyond the university itself, the Department of Embryology of the Carnegie Institution of Washington.

The Medical School opened in 1893. It was headed by Franklin Mall, who had been head of the Anatomy Department at the University of Chicago, an institution that had been modelled after Johns Hopkins. Many of the movers and shakers in the discipline of reproductive biology, such as Oscar Riddle, B. Bartelmez, Carl Moore, W. C. Young, Karl Lashley, and Frank Beach, were eventually trained at Johns Hopkins. Mall served as Professor of Anatomy at the Hopkins Medical School and encouraged development of at least 20 future professors of anatomy; three of them are especially pertinent to this review: George Wislocki, Herbert Evans, and George Corner.

Of these three, anatomist-histologist George Wislocki went from Johns Hopkins to the Medical School at Harvard University. He and his colleagues and students, such as Roy Greep, E. B. Astwood, E. W. Dempsey, Don Fawcett, Helen Deane, and William Wimsatt, spread the base of species studied to even more remote corners of the Class Mammalia.

Herbert Evans moved from Johns Hopkins to the Medical School of the University of California in Berkeley, where he founded the Institute of Experimental Biology. During nearly four decades he and members of the Institute accomplished a remarkable amount of important research. One of the first achievements was the 1922 monograph on the estrous cycle in the rat, coauthored by zoology professor Joseph Long (Long and Evans, 1922). They had created the Long-Evans strain of laboratory rat and, using the newly discovered vaginal smear technique, revealed the formerly unknown details of the estrous cycle of this laboratory animal. As pointed out by A. S. Parkes (1969), one has only to review the 10 abstracts by Long and Evans in the 1920 *Anatomical Record,* followed by 13 abstracts in the 1921 *Anatomical Record* by Evans and his associates, to be awed by the sweep of Evans' early contributions to reproductive anatomy and physiology. This was only a beginning, and was followed in 1931 by a monograph on reproduction in the dog (with H. H. Cole of the Department of Animal Sciences of the University of California at Davis), demonstrations of the pituitary gland as an endocrine organ, description of the growth hormone, and discovery of vitamin E and its role in reproduction (Parkes, 1969).

The third of this trio, George Corner, went to the Medical School at the University of Rochester, where he became widely known for his studies of the menstrual cycle of monkeys, the role of the corpus luteum as an endocrine organ and, with Willard Allen, the purification of the hormone progesterone. In 1940, Corner returned to Johns Hopkins and became Director of the Department of Embryology of the Carnegie Institution of Washington. His former professor, Mall, had been the first Director (1914), and two of his Hopkins teachers, Florence Sabin and Warren Lewis, also had distinguished careers at Carnegie.

The greatest impact of Johns Hopkins on the discipline of mammalian reproduction was through the Department of Embryology of the Carnegie Institution. It became the most important center of reproductive studies in the United States. At one time or another it included important anatomists and physiologists such as Warren Lewis, George Streeter, Oscar Riddle, Chester Heuser, Arthur Hertig, John Rock, Carl Hartman, George Bartelmez, Sam Reynolds, George Corner, Robert Enders, and Harland Mossman (Fig. 3).

Two other administrative units that added strength to the Johns Hopkins University were the School of Hygiene and Public Health, created in 1918, and its offshoot, the Institute of Biological Research. The latter was headed by Raymond Pearl and then was absorbed by the School of Hygiene and Public Health after Pearl's death in 1940. Pearl was a biometrician. He applied statistics to the birth, life, and death rates of populations, especially humans. He had wide-ranging influence through the two journals that he founded: *Human Biology* and *Quarterly Review of Biology.*

FIG. 3.—Photograph at the Carnegie Institution of Washington, Department of Embryology, Baltimore, 1931. Left to right: George Streeter, Robert Enders, Chester Heuser, Josephine Ball, Carl Hartman, P. Mihalic, Warren Lewis, Sam Reynolds.

The Carnegie group became known for exquisite studies of the embryology of humans, rhesus monkeys, and other mammals, published in the *Contributions to Embryology* of the Carnegie Institution. Many of the studies were beautifully illustrated by the noted medical illustrator James Didusch. Indeed, the first paper in volume 1 is by Mall himself (Mall, 1915). The Carnegie group moved inevitably into endocrine studies at a time when the exciting interplay of hormones produced by gonads, pituitary, and placenta was just being demonstrated.

## *Other Legacies*

The significant role played by anatomists at medical schools during the development of our understanding of mammalian reproduction is illustrated also by research and teaching at many such institutions. Much of the research was directed not at human problems but at a truly comparative understanding. While teaching at Cornell Medical College, Stockard and Papanicolaou (1917) discovered the utility of the vaginal smear in guinea pigs and in humans (the Pap smear). Harland Mossman, after a brief stay at Carnegie, had a long career of teaching and research at the Medical School at the University of Wisconsin, and published several influential books on human embryology (Hamilton et al., 1945, 1962); comparative morphology of the mammalian ovary (Mossman and Duke, 1973); and fetal membranes of vertebrates (Mossman, 1987). The potential of academic institutions was demonstrated by this small nucleus at Wisconsin; when an international symposium on the comparative biology of reproduction in mammals was convened in 1964 in London, eight of the 30 contributors held advanced degrees from the University of Wisconsin. Further aspects of the development of North American reproductive physiology in the early 20th Century are presented by Clarke (1987).

Another radiation directly traceable to the Carnegie group was into a government-sponsored program to understand the reproductive performance of commercially important fur-bearing mammals. This program was led by Frank Ashbrook in the Division of Fur Resources, U.S. Department of Agriculture (later Fish and Wildlife Service of the Department of Interior). Studies were conducted on the reproduction of fur seals, martens, minks, foxes, nutrias, and muskrats. Some of these studies were carried out at Swarthmore College near Philadelphia under the leadership of Robert Enders, who had spent a stimulating postdoctoral period at the Carnegie Institution. In addition to his own research on the mink and other fur-bearing animals, he used this major project, beginning in the 1940s, to introduce numerous students to research on mammalian reproduction. Some of them, chronologically, were David Bishop (sperm physiology), David Davis (rat populations, stress), Oliver Pearson (reproductive cycles), Bent Boving (implantation), Hewson Swift (Sertoli cells), Duncan Chiquoine (germ cells), Allen Enders (implantation), William Tietz (embryogenesis), Edward Wallach (ovarian physiology), Phil Myers (rodent and bat reproduction), and Anne Hirschfield (dynamics of ovarian follicles). Many of these students and more recently their own students continue searching for insights into reproductive biology.

### Further Notable Publications

North American researchers were influenced by the excitement over reproductive biology at Cambridge and other European sources in two ways—by reading the European literature and by direct contact with researchers in North America who had been exposed earlier to the ideas and approaches in Europe. For example, workers such as Asdell, Bissonnette, Chang, and Pincus spent early parts of their careers at Cambridge. Meanwhile, North Americans published most of their own work in American journals. Three journals of great importance to reproductive biology were the *American Journal of Anatomy* (founded 1901), the *Anatomical Record* (1908), and *The Journal of Experimental Zoology* (1904). All three were managed by the Wistar Institute in Philadelphia.

A book of undoubted importance in the development of reproductive biology appeared in 1932, with a second edition in 1939. Professor Edgar Allen at the University of Missouri, who had published on the early embryology of humans in the *Carnegie Institution Contributions to Embryology,* assembled a collection of coherent reviews by 21 distinguished collaborators that was published under the title of "Sex and Internal Secretions." It was dedicated to A. D. Mead, one of the members of the staff in anatomy at the University of Chicago in its early days. This book enabled a new generation of students to approach reproductive studies with a more solid foundation in the new science of endocrinology than was available to the generation weaned on Marshall's book. W. C. Young edited a third edition in 1961.

Studies of reproduction in farm livestock were conducted largely by federal agencies and by universities with an agricultural emphasis, both in Europe and the United States. A milestone of this radiation, which demonstrated the coming-of-age of comparative reproductive biology, was the appearance in 1946 of "Patterns of Mammalian Reproduction" by S. A. Asdell. Asdell came as a postdoc from England to Corner's laboratory at the University of Rochester Medical School, and later became a professor in the Department of Animal Husbandry at Cornell University. Asdell realized that "a beneficial purpose would be served if the available information on mammalian re-

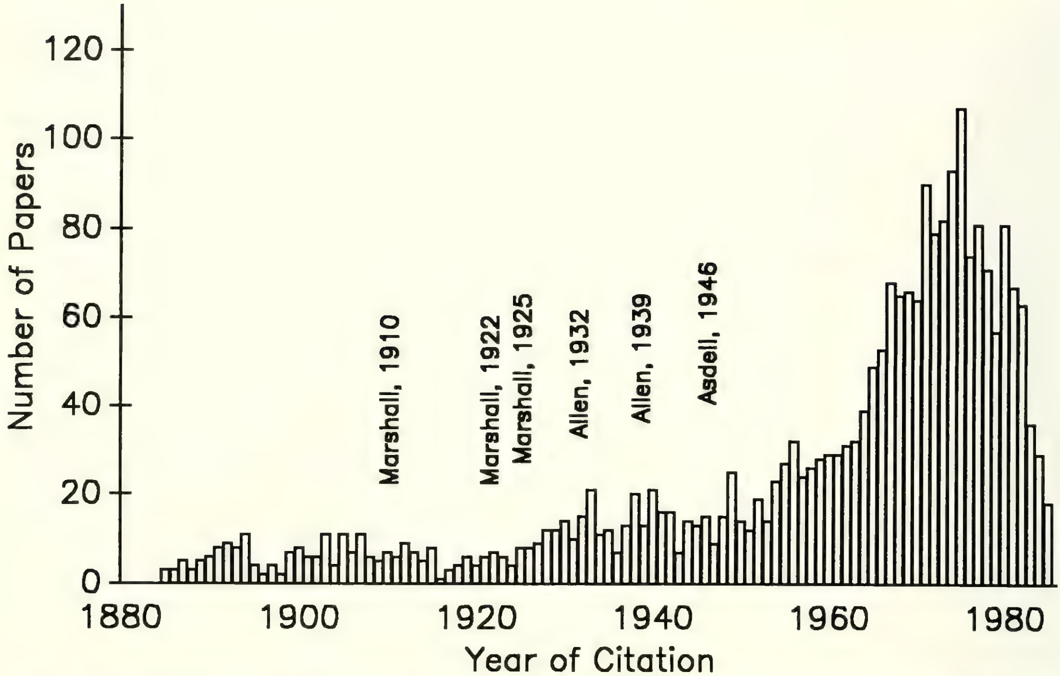



FIG. 4.—A century of research on mammalian reproduction. Dates of appearance of 2,346 papers cited by Mossman (1987). Significant publications or events are noted, as in Figure 1.

production were brought together, species by species. . . ." After paying tribute to his great predecessor at Cambridge, F. H. A. Marshall, Asdell displayed the fruits of the labors of hundreds of authors who had studied the reproduction of about 382 genera and 850 species of mammals. In those pages one could find information ranging from the unilateral functioning of platypus ovaries (page 37) to the number of spermatozoa in the ejaculate of the donkey (page 405). An expanded version of Asdell's book has appeared recently (Hayssen et al., 1993).

We have compiled a distribution of the dates of 1,362 literature citations in Asdell's 1946 book (Fig. 1), covering the late 19th and first half of the 20th centuries. Studies in mammalian reproduction clearly blossomed beginning in the 1920s. The dates of Marshall's books, of the founding of the ASM, and of Allen's book on sex and internal secretions are indicated as reference points. The decrease in number of citations in the mid-1940s is partially the result of World War II, in addition to the decline expected for bibliographic truncation at the approach of the publication date of Asdell's book. Figure 4 illustrates further proliferation of work in the 1960s and 1970s, following three-quarters of a century over which the early historical background was built.

Another serial, *Biology of Reproduction,* was started in the United States in 1969, edited by H. H. Cole. It too continues to publish scores of papers each year in comparative reproductive anatomy and physiology.

With growing audiences of university students, in addition to the research specialists, a parade of text books in reproductive biology arrived on the scene in the 1960s, 70s, and 80s. These books, mostly dealing with all vertebrates, rather than exclusively with mammals, are general and broad enough to be useful as texts for undergraduate zoology courses in reproduction, yet most of them also contain sufficient synthesis and overview along with the observational detail to make them useful in a personal research library. Sadleir's book (1969) on mammals emphasizes reproductive ecology, breeding patterns, and responses to environmental conditions; his later book (1973) on vertebrates is much broader in scope and surveys general reproductive patterns and comparative anatomy and physiology. Nalbandov's book (three editions: 1958, 1964, and 1976) emphasizes the reproductive physiology and anatomy of mammals and birds. Van Tienhoven (1968, 1983) treats the physiology and anatomy of all vertebrates. Two of the most recent books on vertebrate reproduction (Blüm, 1986; Jameson, 1988) are organized thematically, rather than taxonomically and, in addition to the usual information on reproductive patterns, anatomy, and physiology, provide a greater comparative and evolutionary perspective and greater integration of behavioral themes with all these areas.

Finally, and with exclusive attention to mammals, several well-produced text sources are available. Austin and Short (1972–1986, eight books, two editions) have produced a series of booklets that cover pretty much the full range of topics in mammalian reproductive biology, with well illustrated examples of research results along with the conceptual developments. Bronson's (1989) single-volume book offers an extensive and well laid out analysis of the regulatory processes that comprise mammalian reproductive physiology set in an environmental context. Flowerdew (1987) provides a useful blend of fundamentals of reproductive physiology with the biology of free-living mammalian populations. Clearly, and without our being able to mention all such existing books, a great variety of general reading has become available on mammalian reproductive biology. Probably one of the strongest recent areas of integrative bridging in the field of reproductive biology has been between physiology and behavior (see Eisenberg and Wolff, 1994).

Perhaps the most impressive evidence of the growth and vigor of reproductive biology as a general discipline is the appearance in 1963 and subsequent growth of the *Bibliography of Reproduction.* It is published monthly in Cambridge, England, by a consortium of reproductive societies in Great Britain, the United States, and Australia. The editors estimated that the annual production of papers (in 1990) on the reproductive biology and clinical sciences of vertebrates including humans may be on the order of 20,000.

In view of such a torrent of research, the impact of a relatively few institutions and individuals (as we have selected), along with their academic offspring, on the early development of the discipline of mammalian reproduction becomes quickly lost in the distal branches of the family trees. While emphasizing, and even exaggerating, the roles of only a few individuals, we have omitted untold other early researchers and teachers, many of whom worked in other countries. Thus we admit that it would be impossible to trace a balanced and objective presentation of all the research schools and their modern ramifications in a short article such as this. The rest of our review will thus simply identify the appearance of a selected series of what we believe to be important research trends in reproduction that have developed during the final third of the 20th Century.

## LATE 20TH CENTURY

We find ourselves at the end of the 20th Century in a stream of fast-moving developments and continued new discoveries in reproductive biology as we mark the 75th anniversary of the founding of the ASM. The most comprehensive new treatise on mammalian reproduction (Knobil and Neill, 1988) in the latter part of the century has appeared in two volumes, 2,413 pages, and 60 contributed chapters, each containing from several hundred to a thousand references. This new work, inspired by Allen's (1932) original "Sex and Internal Secretions," was edited and produced in the United States, with most of the authors from North America and many from elsewhere around the world. It provides a strong focus on cells, tissues, and neuroendocrine physiology, yet extends as far as reproductive behavior.

Our breadth of understanding of reproductive physiology and behavior in an evolutionary context can only continue to improve and become more meaningful. For the entire first century after Darwin's writings, challenges in the form of important questions in evolutionary theory resulted in important refinements and a maturity in our current view. Therefore, the potential relevance of integrative and evolutionary thinking at present is greater than ever. The tendency of so many scientists to specialize so narrowly offers a new challenge: to overcome narrow specialization by seeking breadth of understanding in the context of evolutionary biology.

As an example, a seemingly simple question remains of interest: why is reproduction typically sexual, rather than asexual, and why are there two, rather than some other number, of sexes (Short, 1994)? Ideas concerning this theoretical and evolutionary question can lead us in our search for the still unresolved issues of the mechaanisms of sex determination and sexual differentiation, which lie at the level of the molecular biology of gene function (McLaren, 1991).

## *Reproduction, Neuroendocrinology, and Molecular Biology*

Mammalian reproduction is comprised of a great array of processes: gamete production and release, mating behaviors, fertilization, implantation, development, placental function, parturition, lactation, and parental care. Our understanding of each of these processes has developed strongly in conjunction with the identification of hormones that control them (Knobil and Neill, 1988). Study of hormones has been a major paradigm of reproductive physiology since the middle of the century, with the advent of radioimmunoassays for measuring hormone concentrations and the perfection of biochemical techniques for characterizing hormone structure and function. Understanding the integration of nervous system output, including secretion by neurons of small peptide hormones that stimulate further hormonal signals that enter the blood stream, has provided the challenge to elucidate the role of the brain, hypothalamus, and pituitary in neuroendocrine regulation (Everett, 1988). Despite the general applicability of the neuroendocrine paradigm, it should also be useful in elucidating exceptional patterns and modes of reproduction. For example, the arrest and later reactivation of embryonic development occurs in special cases ("delayed implantation" and "embryonic diapause") where the delay may be associated with either lactation for earlier young that precede the arrested embryo(s), or with environmental factors that allow birth to occur at an appropriate time (Renfree and Calaby, 1981).

Through the extensive series of neuroendocrine regulatory schemes that have been unveiled by research on mammalian reproduction, the general field has served as a model for study of neuroendocrinology. One of the newest directions for this research has been the molecular neuroendocrinology of gene expression, i.e., identifying and quantifying the first gene products associated with hormone production. This new research trend amounts to another dimension in integrative reproductive biology, namely elucidating functional (physiological) aspects of molecular biology.

## *Environmental Physiology and Regulatory Processes*

Use of environmental information and environmental stimulation or inhibition of reproductive function represents one of the most popular themes in reproductive research. We will mention only a few highlights of our current understanding of this area, for which Bronson's (1989) book provides a useful view.

The time course over which seasonally breeding mammals respond and the cues used differ between the sexes and according to different stages in the overall reproductive program, beginning with activation of the gonads and extending through final aspects of postnatal care and termination of breeding condition (Wingfield and Kenagy, 1991). An enormous literature on the initial predictive effects of day length in stimulating gonadal recrudescence and thus preparing mammals for the onset of breeding (Bronson, 1989; Farner, 1985; Wingfield and Kenagy, 1991) has probably lead to an overimpression of the importance of "photoperiod" in breeding, at least in part because the effect is so consistent, easily obtainable, and the first to occur in a series of steps. Actually, not all mammals are "photoperiodic," i.e., capable of differential response to long versus short days. A small number of species (most notably ground squirrels and their relatives in the tribe Marmotini of the squirrel family Sciuridae) show persistent endogenous cycles of reproductive function in the experimental absence of seasonal changes in day length (Gwinner, 1986).

The mammalian mechanism of photoreception that drives the initial response of the reproductive system begins with the eyes and then a connection through the retinohypothalamic tract, a neural circuit from the retina to the brain that is distinct from the visual pathway (Rusak and Morin, 1976; Stetson and Watson-Whitmyre, 1976). The information on day length is processed in the suprachiasmatic nuclei of the hypothalamus, and signals are then sent through the brainstem and a spinal ganglion and back to another site in the brain, the pineal gland. Finally the daily rhythmic secretion of melatonin by the pineal plays an important role in the regulation of reproduction in response to changes in day length (Binkley, 1988; Hoffmann, 1981; Reiter, 1984). Some of the earliest pioneering work with the pineal was that of Wilbur Quay (1956), who studied seasonal and sexual variation in the pineal of *Peromyscus*.

Many aspects of environmental information besides day length, including the social context of an animal in its population, provide supplementary stimuli that synchronize, integrate, and modify the reproductive responses at all stages of the breeding cycle (Wingfield and Kenagy, 1991). Manipulations of simulated environmental conditions have been conducted to observe these responses, often including hormonal measurements, to environmental factors such as food supply (quantity and quality), water availability, temperature, and the social setting and attendant cues (Bronson, 1989; Wingfield and Kenagy, 1991). Some of the most useful research has involved species that can be studied both in the field, for correlative analysis, and in the laboratory, where simulation and manipulation can be carried out. Comparative field investigation of multiple species has illustrated that diverse patterns of breeding occur even in the same environment, and that body size, phylogeny, and specific adaptations of species account for the differences in timing and intensity of reproduction (Kenagy and Bartholomew, 1985). Such field observations have indicated the potential for each species to utilize different cues and to respond with different sensitivities to the entire range of environmental factors.

One of the most obvious and direct physiological responses that involves regulation of reproductive function is the availability of appropriate amounts and quality of nutrients and energy. Nutritional plane and energy balance act directly on the animal's metabolism and the assessment of body condition (I'Anson et al., 1991). Research in this area involves integration of data on general metabolism and metabolic hormones, as well as relevant organs such as the thyroid and adrenals, with the neuroendocrinology of the hypothalamic-pituitary-gonadal axis. The mammal's assessment of its nutritive plane and energy balance appears to play a direct day-by-day role in the onset and maintenance of reproductive function.

A mechanism of reproductive stimulation in mammalian herbivores that has remained an attractive research subject is the possibility that fresh green food contains a gonadotropic chemical signal (Friedman and Friedman, 1939). A natural plant compound, 6-methoxy-2 benzooxazolinone (6-MBOA), has more recently been identified and shown experimentally to stimulate reproductive function (Berger et al., 1981). Since the initial demonstration of this effect, similar results have been obtained in several rodent species. However, much remains to be learned about this effect, the extent of its occurrence among rodents, and the strength of interactions between the effect of 6-MBOA and other environmental factors that promote reproductive responses. It could be argued, for example, that because food is available already at the time it is being consumed, there would be no need for a predictive cue. The fact that a compound of interest has been identified has opened the door to new research possibilities.

## *Reproductive Energy Expenditures*

The study of energy relations in reproduction has continued to develop in popularity (Loudon and Racey, 1987). Energy is a meaningful reflection of allocation to reproduction and the relative functional significance of both physiological and behavioral work; it is often considered to be a currency that might represent fitness. The reproductive energy allocations of small mammals are of particular interest because of the extreme maternal intake and expenditure that must be required to support a litter whose requirements eventually far exceed those of the mother herself (Pearson, 1944). Considerable impetus to the analysis of energy use in animals came from the efforts of two researchers in American agricultural university settings at the middle of the 20th Century. Both S. Brody (1945) of the University of Missouri and Max Kleiber (1961) of the University of California at Davis produced important books that present the usefulness of energy analysis.

Attention recently focused on measuring the energy allocated to reproduction and growth in the context of life histories of free-living animals. It is clear that for many species the peak of all energy expenditures is reached by females during lactation (Oftedal, 1984). Some of the earlier attention to "reproductive energetics" that addressed only the basal, nonreproductive rates of energy expenditure will not remain as useful as newer, more explicit approaches (Loudon and Racey, 1987). A more direct approach that seeks to quantify reproductive energy expenditure and intake as they approach peaks may allow us to understand energetic bottlenecks associated with reproduction and even thereby the impact of reproductive expenditures on fitness costs (Daan et al., 1991; Kenagy et al., 1990).

## *Olfaction and Regulation of Reproduction*

Mammals generally rely to a much greater extent on the use of air-borne chemical information concerning their environment and their conspecifics than do most other vertebrates. Olfactory sensation and "pheromones" are particularly important in reproductive behavior and physiology, which has made mammals the most important research model for the study of olfaction (Booth and Signoret, 1992; Marchlewska-Koj, 1984; Vandenbergh, 1988). Next to research on mammalian olfaction, that on insects is far greater than on all the other vertebrate classes. The function of air-borne chemicals (pheromones) to prime other individuals by influencing their physiology and behavior probably extends across most mammalian orders; pheromones play a role not only in priming the initial (puberty or recrudescence) and mating stages of reproduction, but extend through the time of lactation and mother-young relations, and beyond that to the level of recognizing the identity of individuals within a population (Booth and Signoret, 1992).

Substantial documentation is available for pheromonal influences such as the cancellation of pregnancy due to the odors of a strange male (the classical "Bruce Effect"; Bruce, 1960), the accelerated onset of puberty in females due to the odors of males, and the inhibition of onset of female reproduction by the odors of other females or family (Vandenbergh, 1988). The impact of this field of research has been substantiated by study of these kinds of processes in the field, which represents an important contribution to population biology and behavior.

### *Behavior and Neuroendocrinology*

During the last quarter of the 20th Century the contributions of studies of neuroendocrine mechanisms to the understanding of reproductive behavior have become extremely important. The popularity of such research derives from its ability to address ecological and evolutionary questions with the approaches of neurobiology and molecular biology (Crews, 1992). Such a potential for integrative exploration with a focus at the organismal level reflects back to a view that prevailed at the founding of the ASM in 1919. It is gratifying, in light of the enormity and diversity of the modern biological research enterprise, that modern mammalogists have the opportunity to foster interest in the perspective of mammals as organisms.

Research on the diversity of reproductive patterns and their mechanisms of neuroendocrine control has produced valuable evolutionary insights. For example, certain bats have temporally dissociated the time of mating from the time of gametogenesis by allowing hibernation to intervene; the generation of neural and endocrine signals that direct this program modification illustrates the adaptive adjustments that can evolve within the constraints of the mammalian system (Crews, 1992). As another example, we have accumulated information on over 50 species of primates alone concerning various patterns of neuroendocrine regulation that sustain the diversity of sexual behavior strategies within this group (Dixson, 1983).

An area of mammalian reproductive biology that has relied on integration of physiological and neuroendocrine analyses going back to the middle of this century, and even earlier, is represented by the classic rodent population studies of Christian and Davis (1956). The potential interaction of the adrenal glands (and glucocorticoid hormones) with somatic and reproductive condition became apparent with the advent of the "stress" concept by Selye (1936). Neuroendocrine mechanisms of reproductive function and the interaction of this with stress physiology have thus been a long-standing aspect of research on small-mammal population regulation (Lee and McDonald, 1985). The most recent research has demonstrated the action of glucocorticoids in establishing a behavioral basis for differences among individuals within populations (Sapolsky, 1992).

### *Marsupials*

Mammalian diversity has provided a basis for comparative functional studies as well as evolutionary analysis. In this regard the marsupials represent a most remarkable payload of fascinating subject matter. J. P. Hill, C. G. Hartman, and G. B. Sharman were the earlier pioneers of marsupial reproductive biology. Since their time, research has been conducted by many others, especially in Australia, both at the universities and at other institutions, particularly the Commonwealth Scientific and Industrial Research Organization (CSIRO) and its Division of Wildlife and Ecology, known earlier by other names. "Reproductive Physiology of Marsupials" (Tyndale-Biscoe and Renfree, 1987) is an excellent monographic review of this research, answering many earlier questions concerning patterns and mechanisms, and raising new questions for future research. Many of the most remarkable contributions to marsupial reproductive endocrinology involve the process of embryonic diapause, originally identified by G. B. Sharman (1955). This process has since been shown in macropod marsupials to include simultaneous maintenance of two or three young of different ages by a mother and the production of milk of two different types out of different teats to support young of different ages (Tyndale-Biscoe and Renfree, 1987).

The evolutionary question as to why marsupials quickly pass through uterine embryonic life and then so greatly prolong lactation, as the major avenue of matrotrophy for development, remains open. One idea, now dispelled by recent immunological research (Rodger et al., 1985), was that marsupial mothers have a short gestation because the trophoblast lacks the immunosuppressive capability that would allow it to remain in the uterus without being rejected by the mother as "foreign" tissue. Fetal immunosuppression had already been recognized as a basis for eutherian maternal recognition of pregnancy and retention of young in the uterus, and was only demonstrated recently in marsupials (Rodger et al., 1985). New arguments for the evolutionary predilection of marsupials for lactation over placentation must be developed and supported. It is clear that the marsupial mode of reproduction is adaptive and should not be considered "primitive" or "inferior"—which was an inappropriate notion that dates back to the earliest discoveries of the pouch mode of nurturing extremely immature newborn.

## *Reproductive Technologies*

Experimental reproductive biology has both agricultural and medical applications. Manipulations of hormones, cells, and tissues were underway by the mid 20th Century, whereas genetic (transgenic) manipulation did not arise in the applied context until the 1980s.

Many aspects of reproduction have been manipulated to increase production by farm animals (Betteridge, 1986). These include artificial insemination, induction of estrus, synchronization of estrus or ovulation in groups, embryo transfer and manipulation, and in vitro fertilization; development of diagnostic tests has improved the usefulness of all these techniques. Genetic engineering, the insertion of specialized hormone-producing genes in transgenic animals, is being tested actively for applications such as enhancement of milk and meat production by growth hormone (Pursel et al., 1989).

Other manipulations of mammalian reproduction are being developed in wildlife conservation or management and in pest control. Captive breeding programs, which often include artificial insemination or embryo transfer, have been the only apparent alternative for maintaining some rare species, either in zoos or wildlife sanctuaries. On the other hand, explorations are being made of means to curb female reproduction, for example, in elephant populations that are overcrowded due to habitat destruction; in this case the antigestagenic steroid RU486 has been proposed as an abortion agent (Short, 1992). Finally, artificial steroid hormones that produce infertility or disturb normal function have recently been proposed to control pest populations of wild rodents (Gao and Short, 1993).

Human reproductive technology addressed birth control as a first priority and achieved this in the 1950s; control of the human population had been established as a goal of public planning (Austin and Short, 1986). Recently, immunological techniques have been applied to fertility control in the form of the "pregnancy vaccine" (Wang and Heap, 1992). Enhancement of fertility represents a growing enterprise of the 1980s and 1990s, with in vitro fertilization and manipulations of embryos becoming more important bases of attempted therapies. Finally, and with even greater ethical reservations, we are moving in the 1990s in the direction of genetic manipulations, gender manipulations, and transgenic innovation. Clearly the creativity of scientists and the demands of at least some members of society will drive us further. In this realm our ethical and legal systems have much catching up to do, as we struggle to deal with "what science has wrought."

## Natural History and the Future

Certainly scientific cleverness and creativity will spur us on to new vistas in reproductive biology. Approaching the end of the century, we are well equipped with technological potential to make new discoveries. It is reassuring to know that natural history and biodiversity remain part of the stuff from which we can extract discoveries. For example, this 75th anniversary year of the ASM we will learn of something that seems to violate a simple generality of mammalian parental care standards, and it was discovered serendipitously by unsuspecting investigators in Malaysia, who had set up mist nets for birds (Francis et al., 1994). The discovery was a population of fruit bats (*Dyacopterus spadiceus*) with males that had actively lactating mammary glands, yet also, later discovered, actively spermatogenic testes. Nature will certainly continue to surprise us and teach us, even as we enter the 21st Century.

We hope that the present historical synopsis of some of the highlights of mammalian reproductive biology over the past 75 years will offer some insights to mammalogists both young and old. From the standpoint of the ASM, some aspects of the early beginnings were provincially North American in scientific character. Another important trend in the history of science, along with the modernization of travel and communication, has been the internationalization of science. As modern scientists we have much available in the way of scientific resources to enhance our future pursuits and a whole world in which to do so, yet as mammalogists we also have our animals. Being oriented to the biology of the Class Mammalia, we can distinguish ourselves by continuing to seek the insights that will come from continued attention to these animals and their natural history and diversity.

## Acknowledgments

We thank K. Benson and M. Wake for historical references and A. Enders for providing Figure 3.

## Literature Cited

ALLEN, E. 1932. Sex and internal secretions. First ed. Williams and Wilkins, Baltimore, 951 pp.

———. 1939. Sex and internal secretions. Second ed. Williams and Wilkins, Baltimore, 1,346 pp.

ASDELL, S. A. 1946. Patterns of mammalian reproduction. Comstock Publishing Company, Ithaca, New York, 437 pp.

AUSTIN, C. R., AND R. V. SHORT. 1972–1986. Reproduction in mammals. First and second eds. Cambridge University Press, New York, Books 1–8.

———. 1986. Reproduction in mammals. Manipulating reproduction. Cambridge University Press, New York, Book 5, 235 pp.

BENSON, K. R. 1987. H. Newell Martin, W. K. Brooks, and the reformation of American biology. American Zoologist, 27:759–771.

BERGER, P. J., N. C. NEGUS, E. H. SANDERS, AND P. D. GARDNER. 1981. Chemical triggering of reproduction in *Microtus montanus*. Science, 214:69–70.

BETTERIDGE, K. J. 1986. Increasing productivity in farm animals. Pp. 1–47, *in* Reproduction in mammals. Manipulating reproduction (C. R. Austin and R. V. Short, eds.). Cambridge University Press, New York, Book 5, 235 pp.

BINKLEY, S. 1988. The pineal: endocrine and nonendocrine functions. Prentice-Hall, Englewood Cliffs, New Jersey, 304 pp.

BLÜM, V. 1986. Vertebrate reproduction. Springer-Verlag, Berlin, 405 pp.

BRODY, S. 1945. Bioenergetics and growth. Reinhold Publishing Corporation, New York, 1,023 pp.

BRONSON, F. H. 1989. Mammalian reproductive biology. University of Chicago Press, Chicago, 325 pp.

BRUCE, H. M. 1960. A block to pregnancy in the mouse caused by the proximity of strange males. Journal of Reproduction and Fertility, 1:96–103.

BURRELL, H. 1927. The platypus. Angus and Robertson, Sydney, 227 pp.

CHRISTIAN, J. J., AND D. E. DAVIS. 1956. The relationship between adrenal weights and population status in urban Norway rats. Journal of Mammalogy, 37:475–486.

Clarke, A. E. 1987. Research materials and reproductive science in the United States, 1910–1940. Pp. 323–350, *in* Physiology in the American context, 1850–1940 (G. L. Geison, ed.). American Physiological Society, Bethesda, Maryland, 403 pp.

Crews, D. 1992. Behavioral endocrinology and reproduction: an evolutionary perspective. Oxford Reviews in Reproductive Biology, 16:303–370.

Daan, S., D. Masman, A. M. Strijkstra, and G. J. Kenagy. 1991. Daily energy turnover during reproduction in birds and mammals: its relationship to basal metabolic rate. Acta XX Congressus Internationalis Ornithologici: 1976–1987.

Dixson, A. F. 1983. The hormonal control of sexual behavior in primates. Oxford Reviews of Reproductive Biology, 5:131–219.

Eisenberg, J. F., and J. O. Wolff. 1994. Behavior. Pp. 398–420, *in* Seventy-five years of mammalogy (1919–1994) (E. C. Birney and J. R. Choate, eds.). Special Publication. The American Society of Mammalogists, 11:1–433.

Evans, H. M., and H. H. Cole. 1931. An introduction to the study of the oestrous cycle of the dog. Memoirs of the University of California, 9:66–118.

Everett, J. W. 1988. Pituitary and hypothalamus: perspectives and overview. Pp. 1143–1233, *in* The physiology of reproduction (E. Knobil and J. D. Neill, eds.). Raven Press, New York (2 vols.), 2,413 pp.

Farner, D. S. 1985. Annual rhythms. Annual Review of Physiology, 47:65–82.

Francis, C. M., E. L. P. Anthony, J. A. Brunton, and T. H. Kunz. 1994. Lactation in male fruit bats (Pteropodidae). Nature.

Friedman, M. H., and G. S. Friedman. 1939. Gonadotrophic extracts from green leaves. American Journal of Physiology, 125:486–490.

Gao, Y., and R. V. Short. 1993. Use of an oestrogen, androgen or gestagen as a potential chemosterilant for control of rat and mouse populations. Journal of Reproduction and Fertility, 97:39–49.

Gwinner, E. 1986. Circannual rhythms. Springer-Verlag, Berlin, 154 pp.

Hamilton, W. J., J. D. Boyd, and H. W. Mossman. 1945. Human embryology. Williams and Wilkins, Baltimore, 366 pp.

Hayssen, V., Ari Van Tienhoven, and Ans Van Tienhoven. 1993. Asdell's patterns of mammalian reproduction. A compendium of species-specific data. Comstock Publishing Associates, Ithaca, New York, 1,023 pp.

Heape, W. 1901. The "sexual season" of mammals and the relation of "pro-estrum" to menstruation. Quarterly Journal of Microscopic Science, 44:1–70.

Hoffmann, K. 1981. Photoperiodism in vertebrates. Pp. 449–473, *in* Handbook of behavioral neurobiology. Biological rhythms (J. Aschoff, ed.). Plenum Press, New York, volume 4, 563 pp.

I'Anson, H., D. L. Foster, G. R. Foxcroft, and P. J. Booth. 1991. Nutrition and reproduction. Oxford Reviews of Reproductive Biology, 13:239–311.

Jameson, E. W. 1988. Vertebrate reproduction. Wiley, New York, 526 pp.

Kenagy, G. J., and G. A. Bartholomew. 1985. Seasonal reproductive patterns in five coexisting California desert rodent species. Ecological Monographs, 55:371–397.

Kenagy, G. J., D. Masman, S. M. Sharbaugh, and K. A. Nagy. 1990. Energy expenditure during lactation in relation to litter size in free-living golden-mantled ground squirrels. Journal of Animal Ecology, 59:73–88.

Kleiber, M. 1961. The fire of life. John Wiley & Sons, Inc., New York, 454 pp.

Knobil, E., and J. D. Neill (eds.). 1988. The physiology of reproduction. Raven Press, New York, 1:1–1390 + *90*, 2:1393–2413 + *90*.

Lamming, G. E. 1984. Marshall's physiology of reproduction. Volume 1, Reproductive cycles of vertebrates. Fourth ed. Churchill Livingstone, London, 842 pp.

Lee, A. K., and I. R. McDonald. 1985. Stress and population regulation in small mammals. Oxford Reviews in Reproductive Biology, 7:261–304.

Long, J. A., and H. M. Evans. 1922. The oestrous cycle in the rat and its associated phenomena. Memoirs of the University of California, 6:1–148.

Loudon, A. S. I., and P. A. Racey. 1987. Reproductive energetics in mammals. Symposia of the Zoological Society (London), 57:1–371.

McLaren, A. 1991. Sex determination in mammals. Oxford Reviews of Reproductive Biology, 13:1–33.

Mall, F. P. 1915. On the fate of the human embryo in tubal pregnancy. Contributions to Embryology, 1:3–104.

Marshall, F. H. A. 1910. The physiology of reproduction. First ed. Longmans, Green and Company, London, 706 pp.

———. 1922. The physiology of reproduction. Second ed. Longmans, Green and Company, London, 770 pp.

———. 1925. An introduction to sexual physiology for biological, medical and agricultural students. Longmans, Green and Company, London, 167 pp.

Mossman, H. W. 1987. Vertebrate fetal membranes. Rutgers University Press, New Brunswick, New Jersey, 383 pp.

Mossman, H. W., and K. Duke. 1973. Comparative morphology of the mammalian ovary. University of Wisconsin Press, Madison, 461 pp.

Nalbandov, A. V. 1958. Reproductive physiology: comparative reproductive physiology of domestic animals, laboratory animals and man. Freeman, San Francisco, 271 pp.

Oftedal, O. T. 1984. Milk composition, milk yield and energy output at peak lactation: a comparative review. Symposia of the Zoological Society (London), 51:33–85.

Parkes, A. S. 1969. Foreword: Dr. Herbert McLean Evans: an interview; selected publications; abstracts from *Anatomical Record*. Journal of Reproduction and Fertility, 19:1–49.

Pearson, O. P. 1944. Reproduction in the shrew (*Blarina brevicauda* Say). American Journal of Anatomy, 75:39–93.

Pursel, V. G., et al. 1989. Genetic engineering of livestock. Science, 244:1281–1288.

Quay, W. B. 1956. Volumetric and cytologic variation in the pineal body of *Peromyscus leucopus* (Rodentia) with respect to sex, captivity and day length. Journal of Morphology, 98:471–495.

Reiter, R. J. (ed.). 1984. The pineal gland. Raven Press, New York, 382 pp.

Renfree, M. B., and J. H. Calaby. 1981. Background to delayed implantation and embryonic diapause. Journal of Reproduction and Fertility (Supplement), 29:1–9.

Rodger, J. C., T. P. Fletcher, and C. H. Tyndale-Biscoe. 1985. Active anti-paternal immunization does not affect the success of marsupial pregnancy. Journal of Reproductive Immunology, 8:249–256.

Rusak, B., and L. P. Morin. 1976. Testicular responses to photoperiod are blocked by lesions of the suprachiasmatic nuclei in golden hamsters. Biology of Reproduction, 15:366–374.

Sadleir, R. M. F. S. 1969. The ecology of reproduction in wild and domestic mammals. Methuen, London, 321 pp.

———. 1973. The reproduction of vertebrates. Academic Press, New York, 227 pp.

Sapolsky, R. M. 1992. Stress, the aging brain, and the mechanisms of neuron death. MIT Press, Cambridge, Massachusetts, 429 pp.

Selye, H. 1936. A syndrome produced by diverse nocuous agents. Nature, 138:32.

Sharman, G. B. 1955. Studies on marsupial reproduction. III. Normal and delayed pregnancy in *Setonix brachyurus*. Australian Journal of Zoology, 3:56–70.

Short, R. V. 1992. Elephants and birth control. New Scientist, 1 August, 21–23.

———. 1994. Why sex? Pp. 3–22, *in* The differences between the sexes (R. V. Short and E. Balaban, eds.). Cambridge University Press, Cambridge, 465 pp.

Stetson, M. H., and M. Watson-Whitmyre. 1976. Nucleus suprachiasmaticus: the biological clock in the hamster? Science, 191:197–199.

Stockard, C. R., and G. N. Papanicolaou. 1917. The existence of a typical oestrous cycle in the guinea pig—with a study of its histological and physiological changes. American Journal of Anatomy, 22:225–265.

Tyndale-Biscoe, H., and M. Renfree. 1987. Reproductive physiology of marsupials. Cambridge University Press, Cambridge, 476 pp.

Vandenbergh, J. G. 1988. Pheromones and mammalian reproduction. Pp. 1679–1696, *in* The physiology of reproduction (E. Knobil and J. D. Neill, eds.). Raven Press, New York, 1:1–1390 + *90*, 2: 1393–2413 + *90*.

Van Tienhoven, A. 1968. Reproductive physiology of vertebrates. Saunders, Philadelphia, 498 pp.

———. 1983. Reproductive physiology of vertebrates. Second ed. Cornell University Press, Ithaca, New York, 491 pp.

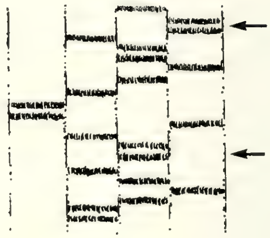
Wang, M.-W., and R. B. Heap. 1992. Vaccination against pregnancy. Oxford Reviews of Reproductive Biology, 14:303–370.

Wingfield, J. C., and G. J. Kenagy. 1991. Natural regulation of reproductive cycles. Vertebrate Endocrinology: Fundamentals and Biomedical Implications, 4(B):181–241.

Young, W. C., (ed.) 1961. Sex and internal secretions. Third ed. Williams and Wilkins, Baltimore, 2 volumes, 1,609 pp.

# *MOLECULAR SYSTEMATICS*

RODNEY L. HONEYCUTT AND TERRY L. YATES



### *Introduction*

Before the founding of the American Society of Mammalogists in 1919, Nuttall (1904) wrote a paper on the use of blood immunology in comparative studies of animals. This paper was the prelude to later comparative serological papers (see Boyden, 1942). By 1953 the molecular structure of DNA had been discovered (Watson and Crick, 1953), yet it was not until much later that systematists and evolutionary biologists capitalized on this discovery and the earlier serological findings. Molecular systematics is a young field that the founders of the ASM probably never imagined. Nevertheless, from the beginning, research on mammals played an important role in the development of the field of molecular systematics, and in many cases mammalian taxa were used to investigate the patterns and processes of molecular evolution. It was not until the middle to late 1970s, however, that mammalogists began to use cladistic methodology and molecular characters in phylogeny reconstruction and the study of evolutionary processes. Once the application of these techniques began, the field of molecular mammalian systematics exploded and has been rapidly growing as a result of increased access to molecular techniques and computer technologies.

The purpose of this chapter is to provide an historical account of mammalian molecular systematics. We present this information in three parts. First, we describe several molecular techniques and discuss how these have been used in mammalian systematics. Second, we discuss how mammals have been used to study the molecular evolutionary process, especially as it relates to the derivation of a molecular clock. Finally, we provide an overview of emerging issues and future directions in mammalian molecular systematics.

### *Molecular Techniques in Mammalian Systematics*

#### *Protein Electrophoresis*

For the past 30 years, protein electrophoresis has been the most extensively used method by those interested in patterns of genetic variation within and between populations and species. The method allows for the recognition and quantification of allozyme differences for both enzymatic and nonenzymatic proteins. These differences are observed as changes in migration of proteins across an electric field, primarily as a consequence of changes in net charge (size and shape are minor factors as well) of the protein. These changes are genetically based and reflect underlying changes in amino acid sequence between products of alleles at the same locus. As a result, genetic variation at multiple loci can be examined and used as characters in comparative studies.

The application of protein electrophoresis in evolutionary studies has been enhanced by a continual refinement of electrophoretic techniques (Harris and Hopkinson, 1976; Hunter and Markert, 1957; Murphy et al., 1990; Selander et al., 1971; Shaw and Prasad, 1970). Two early technique papers, Harris and Hopkinson (1976) on humans and Selander et al. (1971) on *Peromyscus polionotus,* have continued to be important contributions to mammalogy because they provided the detailed conditions (e.g., stains and buffers) for examination of electrophoretic variation at many loci in mammalian species. Michael H. Smith was a coauthor on the Selander et al. (1971) paper, and he has continued to promote protein electrophoresis by training and collaborating with a large number of mammalian systematists and evolutionary biologists.

Most electrophoretic studies during the 1960s and 1970s consisted of an examination of genetic variation within populations and species, with an emphasis on population genetics and the selectionist versus neutralist controversy (Harris, 1966; Hubby and Lewontin, 1966; Hubby and Throckmorton, 1965). As indicated by Selander and Whittam (1983), the neutral theory provided a null hypothesis for those interested in levels of diversity in structural genes. As a result, many of the earlier studies of allozyme variation attempted to interpret the observed levels of genetic heterozygosity and polymorphism found in species in light of neutral models as well as differences in selection pressures and life history strategies (Allendorf and Leary, 1986; Hedrick et al., 1976; Lewontin, 1974; Nei and Graur, 1984; Nevo, 1978; Selander, 1977; Selander and Kaufman, 1973). Research on genetic variation in mammals, using electrophoretic techniques, began in the middle 1960s and paralleled similar studies on other organisms. This research can be subdivided into: 1) microevolutionary studies and studies of geographic variation; and 2) macroevolutionary studies.

*Microevolutionary studies.*—The primary emphasis of early microevolutionary studies on mammals was on levels of genetic diversity within and between populations and the microevolutionary processes responsible for the variation observed (e.g., random genetic drift, migration, population bottlenecks, selection). One of the more interesting debates pertaining to mammals related to an interpretation of genetic variation within and between populations and species, especially in fossorial mammals (Baccus et al., 1983; Kilpatrick and Crowell, 1985; Nevo, 1985; Nevo and Shaw, 1972; Patton and Yang, 1977; Penny and Zimmerman, 1976; Sage et al., 1986; Schnell and Selander, 1981; Selander et al., 1974; Straney et al., 1976, 1979; Yates, 1983). Evitar Nevo and colleagues (Nevo, 1978, 1985; Nevo and Shaw, 1972; Nevo et al., 1974) found a correlation between biotic factors associated with the environment and allozyme polymorphism and heterozygosity in mammalian species, suggesting "adaptive relationships between genetic variability and spatial environmental heterogeneity." The low levels of genetic variation seen in fossorial mammals was interpreted as selection for homozygosity in a narrow subterranean niche. Other electrophoretic studies on primarily fossorial mammals disagreed with Nevo's interpretations (Patton and Yang, 1977; Penny and Zimmerman, 1976; Sage et al., 1986; Schnell and Selander, 1981; Selander et al., 1974). These studies revealed no positive relationship between "niche-width" and genetic variability in fossorial and non-fossorial mammals, supporting a more important role for historical factors related to fluctuating population size, founder events, and random drift. The data on this topic are still equivocal and little consensus has been achieved.

Some of the more interesting studies of microgeographic variation in mammals using electrophoresis have utilized genetic markers to examine both interactions between hybridizing species or chromosome races (Baker et al., 1989*a*; Cothran and Zimmerman, 1985; Gentz and Yates, 1986; Greenbaum, 1981; Greenbaum and Baker, 1976; Hafner et al., 1983; Heaney and Timm, 1985; Herd and Fenton, 1983; Nelson et al., 1987; Patton et al., 1972, 1979*a*, 1979*b*; Smith and Patton, 1984; Sullivan et al., 1986) and the structure of mammalian populations as a result of social organization and dispersal patterns (Chesser, 1983; Gaines and Krebs, 1971; McCracken and Bradbury, 1977, 1981; Scribner et al., 1983; Smith et al., 1983; Wilkinson, 1985). The most extensive research on mammalian hybrid zones has been conducted on hybridizing chromosomal races of *Peromyscus leucopus* (Adkins et al., 1991; Baker et al., 1983; Nelson et al., 1987; Stangl, 1986), *Uroderma bilobatum* (Baker, 1981; Greenbaum, 1981), and *Geomys bursarius* (Baker et al., 1989*a*; Bradley et al., 1991*a*, 1991*b*). These studies have characterized gene flow across hybrid zones using a combination of chromosomal and gene markers (both nuclear and mitochondrial) and have demonstrated that the dynamics of mammalian hybrid zones differ with respect to the origin of variation, the distribution of that variation, and the survival of hybrid individuals.

Finally, patterns of both microgeographic and macrogeographic variation have been used in studies of threatened and endangered species of mammals (Bonnell and Selander, 1974; Chesser et al., 1980; Dragoo et al., 1990; Forman et al., 1986; Hafner and Yates, 1983; Hamilton et al., 1987; Kilpatrick et al., 1986; Newman et al., 1985; Sullivan and Yates, in press; Wayne et al., 1986, 1991; Wayne and Jenks, 1991). Some of this research has focused on the overall level of genetic variation within species of mammals as a consequence of past population bottlenecks and other demographic features, and other studies have attempted to discuss conservation issues (e.g., identification of unique genetic stocks and determination of population status) in light of observed levels of genetic variation. The classic studies by Stephen J. O'Brien and colleagues on genetic variation in the cheetah (Newman et al., 1985; O'Brien et al., 1983; 1985, 1987*b*) and other felid species (O'Brien et al., 1986, 1987*a*, 1990; Packer et al., 1991; Roelke et al., 1993) have contributed greatly to our understanding of population bottlenecks and how genetics can be used in the conservation of mammalian species. These studies helped pave the way for a more routine use of genetic techniques and theory in conservation and management.

*Geographic variation.*—Protein electrophoresis also has been used to examine patterns of geographic variation in mammals, with the majority of the studies pertaining to patterns of variation in rodents. These geographic studies have focused on issues pertaining to the biogeographic history of relict populations (Hafner and Geluso, 1983; Smith et al., 1973), species such as pocket gophers that demonstrate fragmented populations and reduced gene flow (Hafner and Geluso, 1983; Hafner et al., 1987; Patton and Yang, 1977; Patton et al., 1979*b*; Smith et al., 1983), species demonstrating a montane distribution (Sullivan, 1985), the biogeography of species that have a more extended distribution (Nadler et al., 1973; Svoboda et al., 1985), and an examination of speciation patterns within a genus (Nevo et al., 1974; Patton, 1985). In more recent years, electrophoretic data have been combined with other genetic, morphologic, and ecologic data in an effort to identify recent or historical factors responsible for observed patterns of geographic variation (Avise et al., 1979*c*; Nelson et al., 1987; Nevo et al., 1993; Smith and Patton, 1988).

Allozyme variation has been used to compare differences in the overall level of genetic variation between island and mainland populations of the same species as well as taxa endemic to islands (Aquadro and Kilpatrick, 1981; Avise et al., 1974*b*; Berry, 1964; Kilpatrick, 1981; Patton, 1984). Again, most of these studies have involved rodent populations and, as indicated by Kilpatrick (1981), the overall pattern of variation is one whereby insular populations are more monomorphic than mainland populations. These results suggest that the level of variation on islands is related to the recency of colonization, the number of colonizations, the immigration rate between the island and mainland, and the effects of founder events and genetic drift. These conclusions may also hold true for insular populations on continental land masses as well.

*Macroevolutionary studies.*—As indicated by Avise (1974) and Buth (1984), protein electrophoresis is a valuable tool for addressing taxonomic issues in mammals and determining the relationships among taxa. A large number of electrophoretic studies have been used to identify species boundaries, identify cryptic species, compare sibling species, and determine the taxonomic status of particular species (some of which are threatened or endangered; Dragoo et al., 1990). For instance, Peter Baverstock and colleagues (Adams et al., 1982, 1987; Baverstock et al., 1977, 1983, 1984) have used protein electrophoresis to identify cryptic species of bats, rodents, and marsupials in Australia. Similar studies have been conducted on Nearctic mammal genera including *Lasiurus* (Baker et al., 1988), *Geomys* (Burns et al., 1985), *Spermophilus* (Cothran et al., 1977; Hafner and Yates, 1983; Nadler et al., 1982), *Blarina* (Tolliver and Robbins, 1987), and insectivores in general (Tolliver et al., 1985). Some studies, such as those on *Peromyscus comanche* (Johnson and Packard, 1974), *Peromyscus hooperi* (Schmidly et al., 1985), *Peromyscus maniculatus/Peromyscus melanotis* (Bowers et al., 1973), and arid-land foxes (Dragoo et al., 1990) were taxonomically focused with the primary role being the determination of the taxonomic status of a particular population or race.

Some of the earliest systematic studies employing protein electrophoresis pertained to the derivation of phylogenetic relationships among mammalian taxa. The rodent genus *Peromyscus* has received considerable attention over the years (Avise et al., 1974*a*, 1974*b*, 1979*c*; Bowers et al., 1973; Kilpatrick and Zimmerman, 1975; Patton et al., 1981; Rennert and Kilpatrick, 1986; Robbins et al., 1985; Schmidly et al., 1985; Zimmerman et al., 1975, 1978), and electrophoresis has helped resolve many taxonomic problems within this diverse genus. Robert Baker and colleagues (Arnold et al., 1982, 1983*a*; Baker et al., 1981; Koop and Baker, 1983) have conducted a large number of electrophoretic studies on phyllostomoid bats, both within and among genera. These studies are significant because they incorporated a cladistic approach (outgroup approach of Baverstock et al., 1979; Patton and Avise, 1983; Patton et al., 1981) to the analysis of allozyme data. In addition, these studies examined phylogenetic hypotheses using multiple data sets and discussed issues of taxonomic congruence (see Mickevich and Johnson, 1976). These studies, in combination with immunological, chromosomal, and morphological data, resulted in a revised phylogenetic classification for the bat family Phyllostomidae (Baker et al., 1989*b*).

Phylogenetic studies also have been conducted on a large number of other mammalian taxa, including rodents (Arnold et al., 1983*b*; Best et al., 1986; Cook and Yates, in press; Hafner, 1982; Hafner et al., 1981; Honeycutt and Williams, 1982; Janecek et al., 1992; Johnson and Selander, 1971; Nelson et al., 1984; Woods, 1982; Zimmerman and Nejtek, 1977), insectivores (George, 1986; Yates and Greenbaum, 1982; Yates and Moore, 1990), and carnivores (Wayne and O'Brien, 1987). Although these studies vary in the analytical approach chosen, the resultant phylogenies have been used to address hypotheses related to the biogeography and speciation. In this regard, studies designed to examine coevolution among mammalian hosts and their parasites are some of the more innovative in terms of using molecular phylogenies to examine evolutionary processes (Gardner, 1991; Hafner and Nadler, 1988, 1990; Reduker et al., 1987).

*Concluding remarks concerning electrophoresis.*—Protein electrophoresis is still the most cost-effective and rapid approach for assessing patterns of genetic variation, and it is very important in areas where little is known about the taxonomy of specific groups. In short, if one is interested in variation within a genus, electrophoresis has been and will continue to be the best starting point for the assessment of genetic variation and species-level differences. Having said this, we must add that the analysis of allozyme data has changed significantly over the past 20 years. Phenetic analyses utilizing distance estimates (Nei, 1972; Rogers, 1972) and clustering approaches that assume rate constancy have been shown to be inappropriate (Buth, 1984; Farris, 1972, 1985; Miyamoto and Cracraft, 1991; Swofford and Berlocher, 1987; Swofford and Olsen, 1990). Today, allozyme data can be analyzed more objectively using either distance approaches that do not assume rate constancy (Farris, 1972; Felsenstein, 1982, 1990; Fitch and Margoliash, 1967) or cladistic approaches (Farris, 1988; Patton et al., 1981; Swofford, 1990; Swofford and Berlocher, 1987; Swofford and Olsen, 1990) that treat loci (or alleles) as character states. If one peruses the papers that have been published on mammals over the past 20 years, the trend toward a cladistic approach in phylogeny reconstruction is apparent.

Finally, one of the major contributions that an interest in allozyme variation contributed to mammalogy is the formation of frozen tissue collections at several major museums including: 1) Texas Cooperative Wildlife Collection, Texas A&M University; 2) Museum of Vertebrate Zoology, University of California at Berkeley; 3) Museum of Southwestern Biology, University of New Mexico; 4) The Museum, Texas Tech University; 5) San Diego Zoo; 6) Section of Mammals, Carnegie Museum of Natural History; and 7) Natural History Museum, Louisiana State University. In addition, there are a large number of laboratories that have considerable frozen tissue holdings. One can affirm that frozen tissue collections are today an important resource to the mammalogical community (Dessauer et al., 1990) and more curatorial research, such as that conducted by Moore and Yates (1983), is needed. In addition, all those involved in studies that include collection of specimens, such as surveys and inventories, should be encouraged to collect tissue samples. Not only are resources limited and these specimens are valuable to continued molecular systematic efforts, but those values that apply to long term storage and maintenance of more traditional museum specimens apply to these specimens as well.

## *Immunology*

One of the oldest molecular techniques for evaluating relationships among mammalian taxa is comparative immunology (Boyden, 1942; Gerber and Leone, 1971; Goodman, 1963; Leone and Wiens, 1956; Levine and Moody, 1939; Nuttall, 1904), and this technique was perfected by Allan Wilson and Vincent Sarich at the University of California at Berkeley. Wilson, Sarich, and colleagues published a considerable number of papers on the rates of protein evolution and the relationships among mammals and other vertebrates (Carlson et al., 1978; Cronin and Sarich, 1975; Hafner, 1982; Honeycutt and Sarich, 1987*a*, 1987*b*; Honeycutt et al., 1981; Maxson et al., 1975; Pierson et al., 1986; Sarich, 1969*a*, 1969*b*, 1973, 1977, 1985; Sarich and Cronin, 1976; Sarich and Wilson, 1967*a*, 1967*b*; Wilson and Sarich, 1969). Most of these studies dealt with intraordinal relationships among mammalian genera and families and employed primarily the immunological techniques of precipitin and microcomplement fixation (MC'F). The two major molecules examined in these studies were albumin and transferrin, and an immunological distance, depicting the amount of amino acid difference between molecules from different taxa, was determined. This quantitative estimate of immunological distance was determined by the degree of reactivity between antibodies and antigens from different species based on comparisons of homologous and heterologous reactions (Maxson and Maxson, 1990).

In many cases both albumin and transferrin were shown to evolve in a clocklike manner within mammalian orders, and the early studies on primates employed this clock in estimating divergence times for specific taxa such as the hominoid primates (Sarich and Wilson, 1967*a,* 1967*b*; Wilson and Sarich, 1969). One exception to the albumin clock was found by Arnold et al. (1982) and Honeycutt and Sarich (1987*a*) for phyllostomoid bats, with considerable rate heterogeneity observed among lineages. Although immunological distance data have been criticized (Farris, 1985), the overall usefulness of these data to mammalian systematics has been verified, with phylogenies from albumin and transferrin being congruent, in most cases, with other molecular and non-molecular data (Arnold et al., 1982; Baker et al., 1989*a*; Dene et al., 1978; Prager and Wilson, in press; Sarich, 1985, in press; Sarich and Cronin, 1976). In at least two cases (Baker et al., 1989*b*; Kirsch, 1977), the phylogenetic trees shown by immunological data were used in combination with other data to revise the classification of mammalian groups.

### *Amino Acid Sequences*

The most thorough molecular studies of interordinal relationships in mammals have been conducted by Morris Goodman, Jaap Beintema, Wilfried De Jong, and colleagues using amino acid sequence data from approximately 10 polypeptides (Beintema et al., 1973, 1991; Beintema and Lenstra, 1982; Czelusniak et al., 1990; De Jong, 1982; De Jong et al., 1977, 1981; Dene et al., 1982; Goodman, 1976*a,* 1976*b*; Goodman et al., 1982, 1985, 1987; Miyamoto and Goodman, 1986; Romero-Herrera et al., 1978). One of the major strengths of amino acid sequences is that the data can be analyzed cladistically. A maximum parsimony procedure was introduced by Moore et al. (1973) to find ancestral codons which minimize the number of mutations over a given network of species. This approach operates on the principle that the genetic code is redundant and, therefore, the number of possible codons at a particular node in a network will be minimized. The procedure works backwards from a derived network and determines ancestral codons for particular nodes. The overall objective of this procedure is to obtain a network or phylogeny of sequences that minimizes the total number of nucleotide replacements (NR score). Goodman and colleagues have used this procedure for years to examine the relationships of eutherian mammals and primate taxa.

There have been criticisms of the maximum parsimony approach used by Goodman (Kimura, 1981), as well as the resultant trees derived from this approach or amino acid sequence data in general (Wyss et al., 1987). Goodman (1981) addressed some of Kimura's original criticisms. Issues raised by Wyss et al. (1987), concerning incongruence among phylogenies derived from different polypeptide sequences and between sequence phylogenies and those derived from morphological characters, are somewhat harder to address. As indicated by Honeycutt and Adkins (1993), one critical problem with amino acid sequence data is that the numbers and kinds of taxa represented by different genes vary. In addition, some genes are more conservative than others in terms of the overall amount of amino acid sequence differences between taxa, an observation related to functional constraints on the molecule. Both of these factors may contribute to a certain amount of incongruence.

More recent studies (Graur et al., 1991; Li et al., 1990, 1992) of relationships among eutherian orders still rely on amino acid sequence data. In one case, the issue of rodent monophyly has been challenged (Graur et al., 1991; Li et al., 1992). Honeycutt and Adkins (1993) discussed these data at length and suggested that in all of these recent studies the results are equivocal.

### *Nucleotide Sequences*

Most recent studies on the molecular systematics of mammals have focused on patterns of nucleotide sequence divergence in both the nuclear and mitochondrial genomes, and advances in molecular technology have made these studies considerably easier. These comparisons can be divided into two major categories, those using indirect estimates of nucleotide sequence divergence and those employing a direct sequencing method.

DNA/DNA hybridization provides a quantitative estimate of sequence differences between single copy nuclear DNAs from two or more taxa. This indirect estimate of sequence divergence is based on differences between the melting temperatures of a hybrid duplex DNA (heteroduplex) and DNA from a single species (homoduplex). The methodology used is based on earlier studies of reassociation kinetics (Britten and Kohne, 1968; Kohne et al., 1972), and in recent years this method has been employed extensively in studies of bird phylogenies (Sibley and Ahlquist, 1981). In fact, Sibley and Ahlquist have published numerous papers on avian systematics and have even provided a classification of birds based upon their findings (Sibley et al., 1988).

The results and interpretations of DNA/DNA hybridization studies have been challenged by several individuals (Cracraft, 1987; Sarich et al., 1989). Some of these criticisms arose in direct response to the findings of Sibley and Ahlquist (1984) on hominoid primate relationships. These criticisms pertained to the appropriateness of estimates of divergence based on $T_{50}H$, a measure of melting differences that includes the non-hybridizing portion of the melting profile. Although many of the issues raised by these criticisms have not been completely answered, DNA/DNA hybridization studies have been conducted on mammals (Arnason and Widegren, 1986; Brownell, 1983; Catzeflis et al., 1987; Kirsch et al., 1990*a,* 1990*b,* 1991, 1993; Springer and Kirsch, 1989, 1991; Springer and Krajewski, 1989). By far the most extensive research on mammals has been conducted by John Kirsch and colleagues at the University of Wisconsin on marsupials, and these studies have provided an excellent assessment of earlier criticisms and potential problems with the technique.

Another indirect method of estimating nucleotide sequence divergence involves an examination of restriction site variation in mitochondrial genomes and nuclear genes (for details, see Melnick et al., 1992). In this technique, DNA is digested with restriction endonucleases that specify combinations of primarily four and six base pair sequences. These restriction endonucleases cleave at specific sites and, when digested, the DNA is separated by gel electrophoresis and either labelled directly in the case of mitochondrial DNA (mtDNA) or probed with specific cloned DNA fragments. These resultant fragment patterns can be used directly to estimate sequence divergence or converted to restriction site maps, making the estimate of sequence divergence more straightforward (for more details see Li and Graur, 1991; Melnick et al., 1992).

The analysis of restriction fragment or site variation among mtDNAs has been the most popular approach in most studies involving mammals, and it is impossible to do justice in this review to the many studies that have been done. As indicated by several researchers (Avise et al., 1984; Brown, 1983, 1985;

Brown et al., 1979, 1982), mammalian mtDNA is maternally inherited and evolves, on average, much faster than nuclear genes. These features have made this molecule exceedingly useful in studies of geographic variation and the biogeography of mammals (Avise et al., 1979*a*, 1979*b*, 1987; Cann et al., 1987; Patton and Smith, 1992; Riddle et al., 1993; Riddle and Honeycutt, 1990; Wayne et al., 1992), patterns of speciation (Nevo et al., 1993), interactions among hybridizing taxa (Baker et al., 1989*a*; Carr et al., 1986; Nelson et al., 1984), and phylogenetic studies (Ferris et al., 1981, 1983; George and Ryder, 1986; Honeycutt et al., 1987). Although Allan Wilson, Wesley Brown, Robert Lansman, and John Avise introduced the technique of restriction enzyme analysis of mtDNA to evolutionary biologists, today there are laboratories all over the world involved in this type of research.

Restriction site analysis of mammalian nuclear DNA has not been as extensive, with most studies focusing on the ribosomal DNA (rDNA) repeat (see Hillis and Dixon, 1991, for a review). In terms of mammalian studies, two recent studies involving the higher level systematics of bats (Baker et al., 1991) and relationships among rodent taxa (Allard and Honeycutt, 1991) have been conducted. In both these studies, restriction site variation at the rDNA repeat provided little resolution, with most variation restricted to the nontranscribed spacer region.

Direct sequencing of mammalian mitochondrial and nuclear genes is fast becoming the method of choice for those interested in relationships at higher taxonomic levels (see review by Honeycutt and Adkins, 1993). By far, the bulk of data is from the mitochondrial cytochrome *c* oxidase subunit II gene (Adkins and Honeycutt, 1991, in press; Disotell et al., 1992; Ruvolo et al., 1991), the cytochrome b gene (Irwin et al., 1991; Sudman and Hafner, 1992), the ND4 and ND5 genes (Brown et al., 1982; Hayasaka et al., 1988), and the 12S and 16S ribosomal RNA genes (Allard and Honeycutt, 1992; Allard et al., 1991*b*, 1992; Hixson and Brown, 1986; Kraus and Miyamoto, 1991; Mindell et al., 1991; Miyamoto and Boyle, 1989; Miyamoto et al., 1989, 1990). These data have been used to address questions pertaining to relationships among taxa within primarily the orders Primates, Artiodactyla, and Rodentia, and in several cases issues pertaining to interordinal relationships were addressed. Two of the more interesting debates concerning ordinal level relationships involved the question of chiropteran monophyly and relationships among orders in the superorder Archonta, and in these studies both nuclear and mitochondrial gene sequences were used to test conflicting hypotheses (Adkins and Honeycutt, 1991; Ammerman and Hillis, 1992; Bailey et al., 1992; Honeycutt and Adkins, 1993; Mindell et al., 1991; Stanhope et al., 1992).

Research in molecular systematics on mammals using nuclear gene sequences has lagged behind studies of mitochondrial gene sequences. The most extensive data exist for rDNA genes, and these data have considerable potential for higher level questions (Hillis and Dixon, 1991; Mindell and Honeycutt, 1990). One exception to the more extensive rDNA studies has been the consistent research efforts of Morris Goodman and colleagues with respect to determining the relationships among eutherian mammalian orders using single copy genes or pseudogenes (Bailey et al., 1992; Koop and Goodman, 1988; Koop et al., 1986; Stanhope et al., 1992). As indicated by Honeycutt and Adkins (1993), morphology has not been able to resolve the relationships among eutherian orders (Novacek, 1992; Shoshani, 1986; Simpson, 1945) and, if nucleotide sequence data are to contribute to this issue, considerably more information is needed.

## Molecular Clock Concept

The analysis of morphological change in mammals has revealed irregularity in the evolutionary process, with different lineages demonstrating mosaic evolution in terms of the overall rate of morphological evolution. This mosaic evolution reflects the overall adaptive radiation observed for mammals, especially in terms of the diversity in form and function seen for higher categories. In contrast to phenotypic evolution, molecules (both proteins and nucleic acids) of mammals and other organisms presumably evolve in a neutral fashion, demonstrating a rather constant rate of change through evolutionary time and across diverse taxonomic groups (Brown et al., 1982; Easteal, 1985, 1990; Kimura, 1983; Sarich and Wilson, 1967*a,* 1967*b*; Wilson et al., 1977; Zukerkandl and Pauling, 1965). Some of the principles of the neutral theory were derived to distinguish between evolution at the morphological and molecular level. These principles relate to both the elimination of deleterious mutations and fixation of variation through selective neutrality as opposed to positive Darwinian selection and the overall rate of evolution observed for particular molecules as a consequence of the level of structural and functional constraints placed on these molecules.

An outgrowth of the neutral theory is the idea of a molecular clock, which sees the evolutionary process at the molecular level as a random process with a constant average rate of change (Fitch and Langley, 1976; Kimura, 1983; Li and Graur, 1991; Wilson et al., 1977; Zukerkandl and Pauling, 1965). In fact, one might say that the observation of a molecular clock has provided support for the neutral theory. By necessity, the molecular clock is a statistical clock, and it assumes a linear relationship between time since evolutionary divergence and molecular divergence. Obviously, the best test for a clock is one that evaluates the regularity of overall rates of divergence through time, and this test is best applied in a phylogenetic context (Fitch and Langley, 1976).

When evaluating rates of molecular evolution, several analytical approaches can be applied. One approach, the relative rate test, first introduced by Sarich and Wilson (1967*a,* 1967*b*) and expanded upon by others (Li and Graur, 1991; Li et al., 1987; Mindell and Honeycutt, 1990; Wu and Li, 1985), is a test for rate uniformity. It requires no knowledge of divergence times between species but does presuppose branching order in that an outside reference species or outgroup is required for the examination of lineages sharing a common point of divergence. The test is actually a comparison of the magnitude of change along two lineages subsequent to divergence from a common ancestor. It has been suggested that more than one outside reference species be used to minimize the effects of back mutations and convergent substitutions (Beverley and Wilson, 1984). The effects of such homoplasy increase over evolutionary time, thus the need for several calibration points (Gingerich, 1986).

Another method, the star phylogeny approach (Kimura, 1983), is a test that considers a case where all species diverge at the same point in time from a common ancestor and compares the observed and expected variances in rate under the Poisson process. This approach might be valid for mammalian orders but the estimates are probably minimal as a result of dichotomous branching (Nei, 1987). Gillespie (1986) has modified this approach to take into account branching.

Langley and Fitch (1974) introduced a third procedure that requires knowing the branching order. In this procedure expected branch lengths are calculated using maximum likelihood, and then a test for rate heterogeneity is employed using chi-square analysis.

Finally, the absolute rate can be estimated by calculating substitutions along each branch length in a phylogeny and calibrating the evolutionary rate based on dates from either the fossil record or biogeography (Beverly and Wilson, 1984; Maxson et al., 1975; Sarich and Wilson, 1967*a,* 1967*b*).

What is the evidence for a molecular clock? First, the evolutionary rate of divergence in amino acid sequence has been shown to be linear with time. This has been demonstrated for many proteins in mammals, including globins (Kimura, 1983; Li et al., 1985; Zukerkandl and Pauling, 1965). Although the overall rates between proteins may differ, this difference can be explained in terms of functional constraints and is consistent with the neutral theory (Kimura, 1983). Second, a large body of data on albumin immunology in mammals has revealed an overall relationship between rate of divergence and time (Carlson et al., 1978; Sarich, 1977), and this albumin/transferrin clock has been used extensively in comparisons of times of mammalian divergence. Finally, at the level of nucleotide sequence in both mitochondrial and nuclear genes, certain types of substitutions demonstrate clock-like behavior in terms of their divergence over time (Brown et al., 1982; Bulmer et al., 1991; Easteal, 1985, 1990; Hasegawa et al., 1985; Kimura, 1983; Mindell and Honeycutt, 1990; Miyamoto and Boyle, 1989; Vawter and Brown, 1986). In mammals there also is evidence of clock-like behavior of estimates of divergence derived from DNA/DNA hybridization (Catzeflis et al., 1987; Sibley and Ahlquist, 1984).

Although there is some confirmation of rates of amino acid and nucleotide substitutions being linear with time, there are many exceptions that challenge the generality of a molecular clock. First, differential rates of evolution have been observed for both nuclear and mitochondrial genes (Adkins and Honeycutt, 1991; Bajaj et al., 1984; Britten, 1986; Gillespie, 1991; Goodman et al., 1975; Holmes, 1991; Li and Graur, 1991; Li et al., 1985, 1987; Romero-Herrera et al., 1978; Wu and Li, 1985). Second, both distance estimates from DNA/DNA hybridization and synonymous substitution rates in genes suggest a generation time effect for mammals and other animals in terms of overall rates of divergence at the level of nucleotide substitutions (Britten, 1986; Li and Graur, 1991; Li et al., 1985; Wu and Li, 1985). Recently, a relationship between substitution rate differences, body size, and metabolic rates in mammals and other organisms has been found (Martin and Palumbi, 1993). Finally, in the case of an electrophoretic clock (Nei, 1971; Sarich, 1977; Smith and Coss, 1984), rates calculated from the same overall genetic distances from different mammals and other organisms vary as much as 20-fold (Avise and Aquadro, 1982). Therefore, the idea of using an albumin clock to set the electrophoretic clock is clearly suspect (Sarich, 1977).

As Hills and Moritz (1990*b*) pointed out, molecular divergence and time are correlated to an extent. The question, however, pertains to the amount of error associated with any time estimate derived from the magnitude of divergence separating taxa and the various means of clock calibration. In terms of the latter, paleontological and biogeographical estimates of time since divergence have associated errors and, in addition, using a calibrated rate from one set of taxa (e.g., between the rodent taxa *Mus* and *Rattus*) to determine time since divergence in an unrelated set of taxa (e.g., another order of mammals) can clearly create error if the overall rate or pattern of divergence differs for the same gene between the two unrelated groups. Although the error associated with an estimate of absolute time can be great, assessments of relative rates of molecular divergence are very useful to those interested in the processes of molecular evolution and the use of molecular characters in phylogeny reconstruction. Clearly, mammals provide an excellent model for studying either of these two aspects of evolution.

## Emerging Issues and Future Directions

Several major developments over the past three decades have had a profound impact on systematic and evolutionary biology. First, cladistic analysis has become the primary methodological approach used in phylogeny reconstruction, and it has provided an objective framework for deriving classifications, studying biogeography, and investigating speciation, cospeciation, and other evolutionary processes (Baker et al., 1989*a*; Brooks and McLennan, 1991; Eldredge and Cracraft, 1980; Hafner and Nadler, 1988, 1990; McKenna, 1975; Riddle and Honeycutt, 1990). Second, the ability to test hypotheses pertaining to the patterns and processes of evolution have been enhanced by the development of more sophisticated analytical procedures and more accessible computer software and hardware (Farris, 1988; Felsenstein, 1990; Miyamoto and Cracraft, 1991; Swofford, 1990; Swofford and Olsen, 1990). Third, genetics and molecular biology have provided information that has broadened our view as to the role of selection and neutrality in the evolutionary process (Gillespie, 1991; Kimura, 1983; Li and Graur, 1991; Nei, 1987). Finally, variation at the level of genes, gene products, and nucleotide sequences has provided a suite of literally thousands of independently evolving characters that can be used to examine diversity within populations, species, and higher taxa (Hillis and Moritz, 1990*a*; Honeycutt and Adkins, 1993). All of the above events have contributed directly to the ever increasing use of molecular characters in systematic and evolutionary studies, and today molecular systematics and molecular evolution are two of the fastest growing areas of research in systematic and evolutionary biology.

Recent advances in molecular biology have provided an easy-to-use set of tools for mammalogists interested in the origin and diversification of mammalian taxa. The polymerase chain reaction (Allard et al., 1991*a*; Higuchi and Ochman, 1989; Kocher et al., 1989; Saiki et al., 1988) and improved methods for obtaining nucleotide sequence information (Maxam and Gilbert, 1980; Sanger et al., 1977) are revolutionizing the fields of molecular evolutionary biology and systematics. Literally thousands of molecular characters can be used to address questions of higher level relationships among mammalian families and orders and, in combination with morphological data, one can begin to unravel the secret of the mammalian radiations. One of the most exciting areas of research is the use of ancient DNA, extracted from museum specimens and fossils, to provide a historical perspective on the genetics of populations and the relationships among extinct and extant forms of mammals (Higuchi et al., 1984; Paabo, 1989; Paabo et al., 1988, 1989; Shoshani et al., 1985; Thomas et al., 1990). As these techniques become more refined, we may one day be able to address questions pertaining to the early origin of mammals.

A major challenge to all mammalogists interested in molecular systematics pertains to data analysis, as can be seen by recent publications on the subject (Felsenstein, 1981, 1984, 1988; Miyamoto and Cracraft, 1991; Swofford and Olsen, 1990). This issue will become even more important as the amount of sequence data increases, and several questions pertaining to molecular data and the analysis of those data must be addressed. Some of these questions are (for a more detailed discussion on mammalian molecular systematics see Honeycutt and Adkins, 1993): 1) What criteria should be used in selecting the correct molecule and experimental approach? 2) Should one use equal or unequal weighting schemes in an analysis of molecular data? 3) How important is the selection of an outgroup, and what criteria should be used in selecting outgroups? 4) Which methodological approach to estimating evolutionary trees should be used, and are there situations when one particular method might be superior to the more accepted method? 5) How does one evaluate the reliability of trees derived from molecular sequences, and what factors can influence the accuracy of a cladogram? and 6) How does one consider total evidence when evaluating phylogenetic hypotheses, and what are some explanations for incongruence among trees derived from different molecular and non-molecular characters?

Finally, questions pertaining to the evolutionary process are being addressed using a phylogenetic framework (Brooks and McLennan, 1991). For instance, the organization and evolution of communities are being examined using a combination of biogeography, phylogenetics, and molecular characters (Avise et al., 1987; Riddle and Honeycutt, 1990; Riddle et al., 1993). As indicated earlier, the process of cospeciation is being studied by comparing the phylogenies of both the mammalian hosts and their parasites (Hafner and Nadler, 1988, 1990; Reduker et al., 1987). Phylogenies also offer a means of evaluating the evolution of complex behavior in mammals (Honeycutt, 1992). Aside from questions pertaining to organismal evolution, gene trees derived from mammals offer a means of examining convergent evolution at the molecular level (Stewart and Wilson, 1987) and the mechanisms responsible for producing variation (Bradley et al., 1993). Interest in all these areas will increase in the future, and as our knowledge of the molecular genetics of the developmental process increases, we may begin to examine the origin of morphological form and function of mammals by studying the underlying patterns of development at the level of genes and gene products.

## Acknowledgments

We thank R. D. Bradley, J. Salazar-Bravo, and an anonymous reviewer for helpful comments on this manuscript.

## Literature Cited

Adams, M., P. R. Baverstock, C. H. S. Watts, and T. Reardon. 1987. Electrophoretic resolution of species boundaries in Australian Microchiroptera. II. The *Pipistrellus* group (Chiroptera: Vespertilionidae). Australian Journal of Biological Science, 40: 163–170.

Adams, M., P. R. Baverstock, C. R. Tidemann, and D. P. Woodside. 1982. Large genetic differences between sibling species of bats, *Eptesicus*, from Australia. Heredity, 48:435–438.

Adkins, R. M., and R. L. Honeycutt. 1991. Molecular phylogeny of the superorder Archonta. Proceedings of the National Academy of Sciences (USA), 88:10317–10321.

———. In press. Evolution of the primate cytochrome *c* oxidase subunit II gene. Journal of Molecular Evolution, 38.

Adkins, R. M., K. McBee, C. A. Porter, and R. J. Baker. 1991. Hybrid breakdown in *Peromyscus leucopus* and examination of the recombinational-breakdown model. Journal of Mammalogy, 72:535–541.

Allard, M. W., and R. L. Honeycutt. 1991. Ribosomal DNA variation within and between species of rodents, with emphasis on the genus *Onychomys*. Molecular Biology and Evolution, 8:71–84.

Allard, M. W., and R. L. Honeycutt. 1992. Nucleotide sequence variation in the mitochondrial 12S rRNA gene and the phylogeny of African mole-rats (Rodentia: Bathyergidae). Molecular Biology and Evolution, 9:27–40.

Allard, M. W., D. L. Ellsworth, and R. L. Honeycutt. 1991*a*. The production of single-stranded DNA suitable for sequencing using the polymerase chain reaction. BioTechniques, 10:24–26.

Allard, M. W., M. M. Miyamoto, and R. L. Honeycutt. 1991*b*. Tests for rodent polyphyly. Nature, 353:610–611.

Allard, M. W., M. M. Miyamoto, L. Jarecki, F. Kraus, and M. R. Tennant. 1992. DNA systematics and evolution of the artiodactyl family Bovidae. Proceedings of the National Academy of Sciences (USA), 89:3972–3976.

Allendorf, F. W., and R. F. Leary. 1986. Heterozygosity and fitness in natural populations of animals. Pp. 57–76, *in* Conservation biology: the science of scarcity and diversity (M. E. Soule, ed.). Sinauer Associates, Sunderland, 584 pp.

Ammerman, L. K., and D. M. Hillis. 1992. A molecular test of bat relationships: monophyly or diphyly? Systematic Biology, 41:222–232.

Aquadro, D. F., and C. W. Kilpatrick. 1981. Morphological and biochemical variation and differentiation in insular and mainland deer mice (*Peromyscus maniculatus*). Pp. 214–230, *in* Mammalian population genetics (M. H. Smith and J. Joule, eds.). University of Georgia Press, Athens, 380 pp.

Arnason, U., and B. Widegren. 1986. Pinniped phylogeny enlightened by molecular hybridization using highly repetitive DNA. Molecular Biology and Evolution, 3:356–365.

Arnold, M. L., R. J. Baker, and R. L. Honeycutt. 1983*a*. Genic differentiation and phylogenetic relationships within two New World bat genera. Biochemical Systematics and Ecology, 11:295–303.

Arnold, M. L., L. W. Robbins, R. K. Chesser, and J. C. Patton. 1983*b*. Phylogenetic relationships among six species of *Reithrodontomys*. Journal of Mammalogy, 64:128–132.

Arnold, M. L., R. L. Honeycutt, R. J. Baker, V. M. Sarich, and J. K. Jones, Jr. 1982. Resolving a phylogeny with multiple data sets: a systematic study of phyllostomoid bats. Occasional Papers, The Museum, Texas Tech University, 77:1–15.

Avise, J. C. 1974. Systematic value of electrophoretic data. Systematic Zoology, 23:137–148.

AVISE, J. C., AND C. F. AQUADRO. 1982. A comparative summary of genetic distances in the vertebrates. Patterns and correlations. Evolutionary Biology, 15:151–185.

AVISE, J. C., R. A. LANSMAN, AND R. O. SHADE. 1979*b*. The use of restriction endonucleases to measure mitochondrial DNA sequence relatedness in natural populations. I. Population structure and evolution in the genus *Peromyscus*. Genetics, 92:279–295.

AVISE, J. C., J. E. NEIGEL, AND J. ARNOLD. 1984. Demographic influences on mitochondrial DNA lineage survivorship in animal populations. Journal of Molecular Evolution, 20:99–105.

AVISE, J. C., M. H. SMITH, AND R. K. SELANDER. 1974*a*. Biochemical polymorphism and systematics in the genus *Peromyscus*. VI. The *boylii* species group. Journal of Mammalogy, 55:751–763.

AVISE, J. C., M. H. SMITH, AND R. K. SELANDER. 1979*c*. Biochemical polymorphism and systematics in the genus *Peromyscus*. VII. Geographic differentiation in members of the *truei* and *maniculatus* species groups. Journal of Mammalogy, 60:177–192.

AVISE, J. C., C. GIBLIN-DAVIDSON, J. LAERM, J. C. PATTON, AND R. A. LANSMAN. 1979*a*. Mitochondrial DNA clones and matriarchal phylogeny within and among geographic populations of the pocket gopher, *Geomys pinetis*. Proceedings of the National Academy of Sciences (USA), 76:6694–6698.

AVISE, J. C., J. F. SHAPIRA, S. W. DANIEL, C. F. AQUADRO, AND R. A. LANSMAN. 1983. Mitochondrial DNA differentiation during the speciation process in *Peromyscus*. Molecular Biology and Evolution, 1:38–56.

AVISE, J. C., M. H. SMITH, R. K. SELANDER, T. E. LAWLOR, AND P. R. RAMSEY. 1974*b*. Biochemical polymorphism and systematics in the genus *Peromyscus*. V. Insular and mainland species of the subgenus *Haplomylomys*. Systematic Zoology, 23:226–238.

AVISE, J. C., ET AL. 1987. Intraspecific phylogeography: the mitochondrial bridge between population genetics and systematics. Annual Review of Ecology and Systematics, 18:489–522.

BACCUS, R., N. RYMAN, M. H. SMITH, C. REUTERWALL, AND D. CAMERON. 1983. Genetic variability and differentiation of large grazing mammals. Journal of Mammalogy, 64:109–120.

BAILEY, W. J., J. L. SLIGHTOM, AND M. GOODMAN. 1992. Rejection of the "flying primate" hypothesis by phylogenetic evidence from the e-globin gene. Science, 256:86–89.

BAJAJ, M., T. BLUNDELL, AND S. WOOD. 1984. Evolution in the insulin family: molecular clocks that tell the wrong time. Biochemical Society Symposium, 49:45–54.

BAKER, R. J. 1981. Chromosome flow between chromosomally characterized taxa of a volant mammal, *Uroderma bilobatum* (Chiroptera: Phyllostomatidae). Evolution, 35:296–305.

BAKER, R. J., R. L. HONEYCUTT, AND R. A. VAN DEN BUSSCHE. 1991. Examination of monophyly of bats: restriction map of the ribosomal DNA cistron. Bulletin of the American Museum of Natural History, 206:42–53.

BAKER, R. J., C. S. HOOD, AND R. L. HONEYCUTT. 1989*b*. Phylogenetic relationships and classification of the higher categories of the New World bat family Phyllostomidae. Systematic Zoology, 38:228–238.

BAKER, R. J., J. C. PATTON, H. H. GENOWAYS, AND J. W. BICKHAM. 1988. Genic studies of *Lasiurus* (Chiroptera: Vespertilionidae). Occasional Papers, The Museum, Texas Tech University, 117:1–15.

BAKER, R. J., L. W. ROBBINS, F. B. STANGL, JR., AND E. C. BIRNEY. 1983. Chromosomal evidence for a major subdivision in *Peromyscus leucopus*. Journal of Mammalogy, 64:356–359.

BAKER, R. J., S. K. DAVIS, R. D. BRADLEY, M. J. HAMILTON, AND R. A. VAN DEN BUSSCHE. 1989*a*. Ribosomal-DNA, mitochondrial-DNA, chromosomal, and allozymic studies on a contact zone in the pocket gopher, *Geomys*. Evolution, 43:63–75.

BAKER, R. J., R. L. HONEYCUTT, M. L. ARNOLD, V. M. SARICH, AND H. H. GENOWAYS. 1981. Electrophoretic and immunological studies of the relationship of the Brachyphyllinae and the Glossophaginae. Journal of Mammalogy, 62:665–672.

BAVERSTOCK, P. R., M. ADAMS, AND M. ARCHER. 1984. Electrophoretic resolution of species boundaries in the *Smithopsis murina* complex (Dasyuridae). Australian Journal of Zoology, 32:823–832.

BAVERSTOCK, P. R., C. H. S. WATTS, AND S. R. COLE. 1977. Electrophoretic comparisons between the allopatric populations of five Australian pseudomyine rodents (Muridae). Australian Journal of Biological Science, 30:471–485.

BAVERSTOCK, P. R., S. R. COLE, B. J. RICHARDSON, AND C. H. WATTS. 1979. Electrophoresis and cladistics. Systematic Zoology, 28:214–219.

BAVERSTOCK, P. R., M. ADAMS, M. ARCHER, N. L. MCKENZIE, AND R. HOW. 1983. An electrophoretic and chromosomal study of the dasyurid marsupial genus *Ningaui archer*. Australian Journal of Zoology, 31:381–392.

BEINTEMA, J. J., AND J. A. LENSTRA. 1982. Evolution of mammalian pancreatic ribonucleases. Pp. 43–73, *in* Macromolecular sequences in systematics and evolutionary biology (M. Goodman, ed.). Plenum Press, New York, 418 pp.

BEINTEMA, J. J., K. RODEWALD, G. BRAUNITZER, J. CZELUSNIAK, AND M. GOODMAN. 1991. Studies on the phylogenetic position of the Ctenodactylidae (Rodentia). Molecular Biology and Evolution, 8:151–154.

BEINTEMA, J. J., A. J. SCHEFFER, H. VAN DIJK, G. W. WELLING, AND H. ZWIERS. 1973. Pancreatic ribonuclease: distribution and comparisons in mammals. Nature New Biology, 241:76–78.

BERRY, R. J. 1964. The evolution of an island population of the house mouse. Evolution, 18:468–483.

BEST, T. L., R. M. SULLIVAN, J. A. COOK, AND T. L. YATES. 1986. Chromosomal, genic, and morphologic variation in the agile kangaroo rat, *Dipodomys agilis* (Rodentia: Heteromyidae). Systematic Zoology, 35:311–324.

BEVERLEY, S. M., AND A. C. WILSON. 1984. Molecular evolution of *Drosophila* and the higher Diptera. II. A time scale for fly evolution. Journal of Molecular Evolution, 21:1–13.

BONNELL, M. L., AND R. K. SELANDER. 1974. Elephant seals: genetic variation and near extinction. Science, 184:908–909.

BOWERS, J. H., R. J. BAKER, AND M. H. SMITH. 1973. Chromosomal, electrophoretic, and breeding studies of selected populations of deer mice (*Peromyscus maniculatus*) and black-eared mice (*P. melanotis*). Journal of Mammalogy, 27:378–386.

BOYDEN, A. 1942. Systematic serology: a critical appreciation. Part I. Systematic serology and its relation to general biology. Physiological Zoology, 25: 109–145.

BRADLEY, R. D., J. J. BULL, A. D. JOHNSON, AND D. M. HILLIS. 1993. Origin of a novel allele in a mammalian hybrid zone. Proceedings of the National Academy of Sciences (USA), 90:8939–8941.

BRADLEY, R. D., S. K. DAVIS, AND R. J. BAKER. 1991*a*. Genetic control of premating-isolating behavior: Kaneshiro's hypothesis and asymmetrical sexual selection in pocket gophers. Journal of Heredity, 82:192–196.

BRADLEY, R. D., S. K. DAVIS, S. F. LOCKWOOD, J. W. BICKHAM, AND R. J. BAKER. 1991*b*. Hybrid breakdown and cellular-DNA content in a contact zone between two species of pocket gophers (*Geomys*). Journal of Mammalogy, 72:697–705.

BRITTEN, R. J. 1986. Rates of DNA sequence evolution differ between taxonomic groups. Science, 231: 1393–1398.

BRITTEN, R. J., AND D. E. KOHNE. 1968. Repeated sequences in DNA. Science, 161:529–540.

BROOKS, D. R., AND D. A. MCLENNAN. 1991. Phylogeny, ecology, and behavior. University of Chicago Press, Chicago, 434 pp.

BROWN, W. M. 1983. Evolution of animal mitochondrial DNA. Pp. 62–88, *in* Evolution of genes and proteins (M. Nei and R. K. Koehn, eds.). Sinauer Associates, Sunderland, Massachusetts, 331 pp.

———. 1985. The mitochondrial genome of animals. Pp. 95–130, *in* Molecular evolutionary genetics (R. MacIntyre, ed.). Plenum Press, New York, 610 pp.

BROWN, W. M., M. GEORGE, JR., AND A. C. WILSON. 1979. Rapid evolution of animal mitochondrial DNA. Proceedings of the National Academy of Sciences (USA), 76:1967–1971.

BROWN, W. M., E. M. PRAGER, A. WANG, AND A. C. WILSON. 1982. Mitochondrial DNA sequences of primates: tempo and mode of evolution. Journal of Molecular Evolution, 18:225–239.

BROWNELL, E. 1983. DNA/DNA hybridization studies of muroid rodents: symmetry and rates of molecular evolution. Evolution, 38:1034–1051.

BULMER, M., K. H. WOLFE, AND P. M. SHARP. 1991. Synonymous nucleotide substitution rates in mammalian genes: implications for the molecular clock and the relationships of mammalian orders. Proceedings of the National Academy of Sciences (USA), 88:5974–5978.

BURNS, J. C., J. R. CHOATE, AND E. G. ZIMMERMAN. 1985. Systematic relationships of pocket gophers (genus *Geomys*) on the central Great Plains. Journal of Mammalogy, 66:102–118.

BUTH, D. G. 1984. The application of electrophoretic data in systematic studies. Annual Review of Ecology and Systematics, 15:501–522.

CANN, R. L., M. STONEKING, AND A. C. WILSON. 1987. Mitochondrial DNA and human evolution. Nature, 325:31–36.

CARLSON, S. S., A. C. WILSON, AND R. D. MAXSON. 1978. Do albumin clocks run on time? Science, 200: 1183–1185.

CARR, S. M., S. W. BALLINGER, J. N. DERR, L. H. BLANKENSHIP, AND J. W. BICKHAM. 1986. Mitochondrial DNA analysis of hybridization between sympatric white-tailed deer and mule deer in West Texas. Proceedings of the National Academy of Sciences (USA), 83:9576–9580.

CATZEFLIS, F. M., F. H. SHELDON, J. E. ALQUIST, AND C. S. SIBLEY. 1987. DNA-DNA hybridization evidence of the rapid rate of rodent DNA evolution. Molecular Biology and Evolution, 4:242–253.

CHESSER, R. K. 1983. Genetic variability within and among populations of the black-tailed prairie dog. Evolution, 37:320–331.

CHESSER, R. K., M. H. SMITH, AND I. L. BRISBIN, JR. 1980. Management and maintenance of genetic variability in endangered species. International Zoo Yearbook, 20:146–154.

COOK, J. A., AND T. L. YATES. In press. Systematic relationships of the Bolivian Tuco-tucos, genus *Ctenomys* (Rodentia: Ctenomyidae). Journal of Mammalogy.

COTHRAN, E. G., AND E. G. ZIMMERMAN. 1985. Electrophoretic analysis of the contact zone between *Geomys breviceps* and *Geomys bursarius*. Journal of Mammalogy, 66:489–497.

COTHRAN, E. G., E. G. ZIMMERMAN, AND C. F. NADLER. 1977. Genic differentiation and evolution in ground squirrel subgenus *Ictidomys* (genus *Spermophilus*). Journal of Mammalogy, 58:610–622.

CRACRAFT, J. 1987. DNA hybridization and avian phylogenetics. Evolutionary Biology, 21:47–96.

CRONIN, J. E., AND V. M. SARICH. 1975. Molecular systematics of the New World monkeys. Journal of Human Evolution, 4:357–375.

CZELUSNIAK, J., ET AL. 1990. Perspectives from amino acid and nucleotide sequences on cladistic relationships among higher taxa of Eutheria. Current Mammalogy, 2:541–567.

DE JONG, W. W. 1982. Eye lens proteins and vertebrate phylogeny. Pp. 75–114, *in* Macromolecular sequences in systematics and evolutionary biology (M. Goodman, ed.). Plenum Press, New York, 418 pp.

DE JONG, W. W., J. T. GLEAVES, AND D. BOULTER. 1977. Evolutionary changes of a-crystallin and the phylogeny of mammalian orders. Journal of Molecular Evolution, 10:123–135.

DE JONG, W. W., A. ZWEERS, AND M. GOODMAN. 1981. Relationship of aardvark to elephants, hyraxes and sea cows from a-crystallin sequences. Nature, 292: 117–119.

DENE, H., M. GOODMAN, M. C. MCKENNA, AND A. E. ROMERO-HERRERA. 1982. *Ochotona princeps* (pika) myoglobin: an appraisal of lagomorph phylogeny. Proceedings of the National Academy of Sciences (USA), 79:1917–1920.

DENE, H., M. GOODMAN, AND W. S. PRYCHODKO. 1978. An immunological examination of the systematics of the Tupaioidea. Journal of Mammalogy, 59:697–706.

DESSAUER, H. C., C. J. COLE, AND M. A. HAFNER. 1990. Collection and storage of tissues. Pp. 25–41, *in* Molecular systematics (D. M. Hillis and C. Moritz, eds.).

Sinauer Associates, Sunderland, Massachusetts, 588 pp.

Disotell, T. R., R. L. Honeycutt, and M. Ruvolo. 1992. Mitochondrial DNA phylogeny of the Old World monkey tribe Papionini. Molecular Biology and Evolution, 9:1–13.

Dragoo, J. W., J. R. Choate, and T. L. Yates. 1990. Evolutionary and taxonomic relationships among North American arid-land foxes. Journal of Mammalogy, 71:318–332.

Easteal, S. 1985. Generation time and the rate of molecular evolution. Molecular Biology and Evolution, 2:450–453.

———. 1990. The pattern of mammalian evolution and the relative rate of molecular evolution. Genetics, 124:165–173.

Eldredge, N., and J. Cracraft. 1980. Phylogenetic patterns and the evolutionary process: method and theory in comparative biology. Columbia University Press, New York.

Farris, J. S. 1972. Estimating phylogenetic trees from distance matrices. American Naturalist, 106:645–668.

———. 1985. Distance data revisited. Cladistics, 2:144–157.

———. 1988. HENNIG86: program and documentation. State University of New York, New York.

Felsenstein, J. 1981. Evolutionary trees from DNA sequences: a maximum likelihood approach. Journal of Molecular Evolution, 17:368–376.

———. 1982. Numerical methods for inferring evolutionary trees. Quarterly Review of Biology, 57:379–404.

———. 1984. Distance methods for inferring phylogenies: a justification. Evolution, 38:16–24.

———. 1988. Phylogenies for molecular sequences: inference and reliability. Annual Review of Genetics, 22:521–565.

———. 1990. PHYLIP: phylogenetic inference package, version 3.3. Program and documentation. Department of Genetics, University of Washington, Seattle, Washington.

Ferris, S. D., A. C. Wilson, and W. M. Brown. 1981. Evolutionary trees for apes and humans based on cleavage maps of mitochondrial DNA. Proceedings of the National Academy of Sciences (USA), 78: 2432–2436.

Ferris, S. D., R. D. Sage, E. M. Prager, U. Ritte, and A. C. Wilson. 1983. Mitochondrial DNA evolution in mice. Genetics, 105:681–721.

Fitch, W. M., and C. H. Langley. 1976. Evolutionary rates in proteins: neutral mutations and the molecular clock. Pp. 197–219, *in* Molecular anthropology (M. Goodman, R. E. Tashian, and J. H. Tashian, eds.). Plenum Press, New York, 466 pp.

Fitch, W. M., and E. Margoliash. 1967. Construction of phylogenetic trees. Science, 155:279–284.

Forman, L., et al.. 1986. Genetic variation within and among lion tamarins. American Journal of Physical Anthropology, 71:1–11.

Gaines, M. S., and C. J. Krebs. 1971. Genetic changes in fluctuating vole populations. Evolution, 25:702–723.

Gardner, S. L. 1991. Phyletic coevolution between subterranean rodents of the genus *Ctenomys* (Rodentia: Hystricognathi) and nematodes of the genus *Paraspidodera* (Heterakoidea: Aspidoderidae) in the Neotropics: temporal and evolutionary implications. Zoological Journal of the Linnean Society, 102: 169–201.

Gentz, E. J., and T. L. Yates. 1986. Genetic identification of hybrid camelids. Zoo Biology, 5:349–354.

George, M., Jr., and O. A. Ryder. 1986. Mitochondrial DNA evolution in the genus *Equus*. Molecular Biology and Evolution, 3:535–546.

George, S. B. 1986. Evolution and historical biogeography of soricine shrews. Systematic Zoology, 35:153–162.

Gerber, J. D., and C. A. Leone. 1971. Immunologic comparisons of the sera of certain phyllostomatid bats. Systematic Zoology, 20:160–166.

Gillespie, J. H. 1986. Variability of evolutionary rates of DNA. Genetics, 113:1077–1091.

———. 1991. The causes of molecular evolution. Oxford University Press, New York, 336 pp.

Gingerich, P. D. 1986. Temporal scaling of molecular evolution in primates and other mammals. Molecular Biology and Evolution, 3:205–221.

Goodman, M. 1963. Serological analysis of the systematics of recent hominoids. Human Biology, 35: 377–424.

———. 1976*a*. Protein sequences in phylogeny. Pp. 141–159, *in* Molecular evolution (F. J. Ayala, ed.). Sinauer Associates, Sunderland, Massachusetts, 277 pp.

———. 1976*b*. Toward a genealogical description of the primates. Pp. 321–353, *in* Molecular anthropology (M. Goodman, R. E. Tashian, and J. H. Tashian, eds.). Plenum Press, New York, 466 pp.

———. 1981. Globin evolution was apparently very rapid in early vertebrates: a reasonable case against the rate-constancy hypothesis. Journal of Molecular Evolution, 17:114–120.

Goodman, M., J. Czelusniak, and J. E. Beeber. 1985. Phylogeny of Primates and other eutherian orders: a cladistic analysis using amino acid and nucleotide sequence data. Cladistics, 1:171–185.

Goodman, M., G. W. Moore, and G. Matsuda. 1975. Darwinian evolution in the genealogy of hemoglobin. Nature, 253:603–608.

Goodman, M., J. Czelusniak, B. F. Koop, D. A. Tagle, and J. L. Slightom. 1987. Globins: a case study in molecular phylogeny. Cold Spring Harbor Symposium on Quantitative Biology, 52:875–890.

Goodman, M., A. E. Romero-Herrera, H. Dene, J. Czelusniak, and R. E. Tashian. 1982. Amino acid sequence evidence on the phylogeny of primates and other eutherians. Pp. 115–191, *in* Macromolecular sequences in systematic and evolutionary biology (M. Goodman, ed.). Plenum Press, New York, 418 pp.

Graur, D., W. A. Hide, and W.-H. Li. 1991. Is the guinea-pig a rodent? Nature, 351:649–652.

Greenbaum, I. F. 1981. Genetic interactions between hybridizing cytotypes of the tent-making bat (*Uroderma bilobatum*). Evolution, 35:306–321.

Greenbaum, I. F., and R. J. Baker. 1976. Evolutionary relationships in *Macrotus* (Mammalia: Chiroptera): biochemical variation and karyology. Systematic Zoology, 25:15–25.

Hafner, D. J., and K. N. Geluso. 1983. Systematic relationships and historical zoogeography of the desert pocket gopher, *Geomys arenarius*. Journal of Mammalogy, 64:405–413.

Hafner, D. J., K. E. Petersen, and T. L. Yates. 1981. Evolutionary relationships of jumping mice (genus *Zapus*) of the Southwestern United States. Journal of Mammalogy, 62:501–512.

Hafner, D. J., and T. L. Yates. 1983. Systematic status of the Mojave ground squirrel, *Spermophilus mohavensis* (subgenus *Xenospermophilus*). Journal of Mammalogy, 64:397–404.

Hafner, J. C., D. J. Hafner, J. L. Patton, and M. F. Smith. 1983. Contact zones and the genetics of differentiation in the pocket gopher *Thomomys bottae* (Rodentia: Geomyidae). Systematic Zoology, 32: 1–20.

Hafner, M. S. 1982. A biochemical investigation of geomyoid systematics (Mammalia: Rodentia). Sonderdruck aus Zoologie fur zoologischen Systematik und Evolutionforschung, 20:118–130.

Hafner, M. S., J. C. Hafner, J. L. Patton, and M. F. Smith. 1987. Macrogeographic patterns of genetic differentiation in the pocket gopher *Thomomys umbrinus*. Systematic Zoology, 36:18–34.

Hafner, M. S., and S. A. Nadler. 1988. Phylogenetic trees support the coevolution of parasites and their hosts. Nature, 332:258–259.

———. 1990. Cospeciation in host-parasite assemblages: comparative analysis of rates of evolution and timing of cospeciation events. Systematic Zoology, 39:192–204.

Hamilton, M. J., R. K. Chesser, and T. L. Best. 1987. Genetic variation in the Texas kangaroo rat, *Dipodomys elator* Merriam. Journal of Mammalogy, 68:775–781.

Harris, H. 1966. Enzyme polymorphism in man. Proceedings of the Royal Society London Series B, 164:298–310.

Harris, H., and D. A. Hopkinson. 1976. Handbook of enzyme electrophoresis. North-Holland Publishing Company, Amsterdam, Netherlands, looseleaf, unpaged.

Hasegawa, M., H. Kishino, and T.-A. Yano. 1985. Dating the human-ape splitting by a molecular clock of mitochondrial DNA. Journal of Molecular Evolution, 22:160–174.

Hayasaka, K., T. Gojobori, and S. Horai. 1988. Molecular phylogeny and evolution of primate mitochondrial DNA. Molecular Biology and Evolution, 5:626–644.

Heaney, L. R., and R. M. Timm. 1985. Morphology, genetics, and ecology of pocket gophers (genus *Geomys*) in a narrow hybrid zone. Biological Journal of the Linnean Society, 25:301–317.

Hedrick, P. W., M. E. Ginevan, and E. P. Ewing. 1976. Genetic polymorphism in heterogeneous environments. Annual Review of Ecology and Systematics, 7:1–32.

Herd, R. M., and M. B. Fenton. 1983. An electrophoretic, morphological, and ecological investigation of a putative hybrid zone between *Myotis lucifugus* and *Myotis yumanensis* (Chiroptera: Vespertilionidae). Canadian Journal of Zoology, 61: 2029–2050.

Higuchi, R., B. Bowman, M. Freiberger, O. A. Ryder, and A. C. Wilson. 1984. DNA sequences from the quagga, an extinct member of the horse family. Nature, 312:282–284.

Higuchi, R. G., and H. Ochman. 1989. Production of single-stranded DNA templates by exonuclease digestion following the polymerase chain reaction. Nucleic Acids Research, 17:5865.

Hillis, D. M., and M. T. Dixon. 1991. Ribosomal DNA: molecular evolution and phylogenetic inference. The Quarterly Review of Biology, 66:411–453.

Hillis, D. M., and C. Moritz (eds.). 1990*a*. Molecular systematics. Sinauer Associates, Sunderland, Massachusetts, 588 pp.

Hillis, D. M., and C. Moritz. 1990*b*. An overview of applications of molecular systematics. Pp. 502–515, *in* Molecular systematics (D. M. Hillis and C. Moritz, eds.). Sinauer Associates, Sunderland, Massachusetts, 588 pp.

Hixson, J. E., and W. M. Brown. 1986. A comparison of the small ribosomal RNA genes from the mitochondrial DNA of the great apes and humans: sequence, structure, evolution, and phylogenetic implications. Molecular Biology and Evolution, 3:1–18.

Holmes, E. C. 1991. Different rates of substitution may produce different phylogenies of the eutherian mammals. Journal of Molecular Evolution, 33:209–215.

Honeycutt, R. L. 1992. Naked mole-rats. American Scientist, 80:43–53.

Honeycutt, R. L., and R. M. Adkins. 1993. Higher level systematics of eutherian mammals: an assessment of molecular characters and phylogenetic hypotheses. Annual Review of Ecology and Systematics, 24:279–305.

Honeycutt, R. L., and V. M. Sarich. 1987*a*. Albumin evolution and subfamilial relationships among New World leaf-nosed bats (family Phyllostomidae). Journal of Mammalogy, 68:508–517.

———. 1987*b*. Monophyly and molecular evolution within three phyllostomid bat genera. Journal of Mammalogy, 68:518–525.

Honeycutt, R. L., and S. L. Williams. 1982. Genic differentiation in pocket gophers of the genus *Pappogeomys*, with comments on intergeneric relationships in the subfamily Geomyinae. Journal of Mammalogy, 63:208–217.

Honeycutt, R. L., S. Y. Edwards, K. Nelson, and E. Nevo. 1987. Mitochondrial DNA variation and the phylogeny of African mole rats (Rodentia: Bathyergidae). Systematic Zoology, 36:280–293.

Honeycutt, R. L., I. F. Greenbaum, R. J. Baker, and V. M. Sarich. 1981. Molecular evolution of vampire bats. Journal of Mammalogy, 62:805–811.

Hubby, J. L., and R. C. Lewontin. 1966. A molecular approach to the study of genic heterozygosity in natural populations. I. The number of alleles at a different loci in *Drosophila pseudoobscura*. Genetics, 54:577–594.

Hubby, J. L., and L. H. Throckmorton. 1965. Protein differences in *Drosophila*. II. Comparative species genetics and evolutionary problems. Genetics, 52:203–215.

Hunter, R. L., and C. L. Markert. 1957. Histochemical demonstration of enzymes separated by zone electrophoresis in starch gels. Science, 125:1294–1295.

Irwin, D. M., T. D. Kocher, and A. C. Wilson. 1991. Evolution of the cytochrome b gene in mammals. Journal of Molecular Evolution, 32:128–144.

Janecek, L. L., R. L. Honeycutt, I. L. Rautenbach, B. H. Erasmus, S. Reig, and D. A. Schlitter. 1992. Allozyme variation and systematics of African mole-rats (Rodentia:Bathyergidae). Biochemical Systematics and Ecology, 20:401–416.

Johnson, G. L., and R. L. Packard. 1974. Electrophoretic analysis of *Peromyscus comanche* Blair, with comments on its systematic status. Occasional Papers, The Museum, Texas Tech University, 24:1–16.

Johnson, W. E., and R. K. Selander. 1971. Protein variation and systematics in kangaroo rats (genus *Dipodomys*). Systematic Zoology, 20:377–405.

Kilpatrick, C. W. 1981. Genetic structure of insular populations. Pp. 28–60, *in* Mammalian population genetics (M. H. Smith and J. Joule, eds.). University of Georgia Press, Athens, 380 pp.

Kilpatrick, C. W., and K. L. Crowell. 1985. Genic variation of the rock vole, *Microtus chrotorrhinus.* Journal of Mammalogy, 66:94–101.

Kilpatrick, C. W., and E. G. Zimmerman. 1975. Genetic variation and systematics of four species of mice of the *Peromyscus boylii* species group. Systematic Zoology, 24:143–162.

Kilpatrick, C. W., S. C. Forrest, and T. W. Clark. 1986. Estimating genetic variation in the black-footed ferret—a first attempt. Great Basin Naturalist, 8:145–149.

Kimura, M. 1981. Was globin evolution very rapid in its early stages? A dubious case against the rate-constancy hypothesis. Journal of Molecular Evolution, 17:110–113.

———. 1983. The neutral theory of molecular evolution. Cambridge University Press, Cambridge, England, 367 pp.

Kirsch, J. A. W. 1977. The comparative serology of Marsupialia, and a classification of marsupials. Australian Journal of Zoology, Supplementary Series, 52:1–152.

Kirsch, J. A. W., R. E. Bleisweiss, and A. W. Dickerman. 1993. DNA/DNA hybridization studies of carnivorous marsupials. III. Relationships among species of *Didelphis* (Didelphidae). Journal of Mammalian Evolution, 1:75–97.

Kirsch, J. A. W., A. W. Dickerman, O. A. Reig, and M. S. Springer. 1991. DNA hybridization evidence for the Australian affinity of the American marsupial *Dromiciops australis.* Proceedings of the National Academy of Sciences (USA), 88:10465–10469.

Kirsch, J. A. W., C. Krajewski, M. S. Springer, and M. Archer. 1990*a*. DNA-DNA hybridization studies of carnivorous marsupials. II. Relationships among dasyurids (Marsupialia: Dasyuridae). Australian Journal of Zoology, 38:673–696.

Kirsch, J. A. W., M. S. Springer, C. Krajewski, M. Archer, K. Aplin, and A. W. Dickerman. 1990*b*. DNA/DNA hybridization studies of carnivorous marsupials. I: The intergeneric relationships of bandicoots (Marsupialia: Perameloidea). Journal of Molecular Evolution, 30:434–448.

Kocher, T. D., et al. 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. Proceedings of the National Academy of Sciences (USA), 86: 6196–6200.

Kohne, D. E., J. A. Chiscon, and B. H. Hoyer. 1972. Evolution of primate DNA sequences. Journal of Human Evolution, 1:627–644.

Koop, B. F., and R. J. Baker. 1983. Electrophoretic studies of relationships of six species of *Artibeus* (Chiroptera: Phyllostomidae). Occasional Papers, The Museum, Texas Tech University, 83:1–12.

Koop, B. F., and M. Goodman. 1988. Evolutionary and developmental aspects of two hemoglobin B-chain genes ($e^M$ and $B^M$) of opossum. Proceedings of the National Academy of Sciences (USA), 85: 3893–3897.

Koop, B., M. Goodman, P. Xu, K. Chan, and J. L. Slightom. 1986. Primate n-globin DNA sequences and man's place among the great apes. Nature, 319:234–238.

Kraus, F., and M. M. Miyamoto. 1991. Rapid cladogenesis among the pecoran ruminants: evidence from mitochondrial DNA sequences. Systematic Zoology, 40:117–130.

Langley, C. H., and W. M. Fitch. 1974. An examination of the constancy of the rate of molecular evolution. Journal of Molecular Evolution, 3:161–177.

Leone, C. A., and A. L Wiens. 1956. Comparative serology of carnivores. Journal of Mammalogy, 37: 11–23.

Levine, H. P., and P. A. Moody. 1939. Serological investigation of rodent relationships. Physiological Zoology, 12:400–411.

Lewontin, R. C. 1974. The genetic basis of evolutionary change. Columbia University Press, New York, 346 pp.

Li, W.-H., and D. Graur. 1991. Fundamentals of molecular evolution. Sinauer Associates, Sunderland, Massachusetts, 284 pp.

Li, W.-H., C.-C. Luo, and C.-I. Wu. 1985. Evolution of DNA sequences. Pp. 1–84, *in* Molecular evolutionary genetics (R. J. MacIntyre, ed.). Plenum Press, New York, 610 pp.

Li, W.-H., M. Tanimura, and P. M. Sharp. 1987. An evaluation of the molecular clock hypothesis using mammalian DNA sequences. Journal of Molecular Evolution, 25:330–342.

Li, W.-H., M. Gouy, P. M. Sharp, C. O'Huigin, and Y.-W. Yang. 1990. Molecular phylogeny of Rodentia, Lagomorpha, Primates, Artiodactyla, and Carnivora and molecular clocks. Proceedings of the National Academy of Sciences (USA), 87:6703–6707.

Li, W.-H., W. A. Hide, A. Zharkikh, D.-P. Ma, and D. Graur. 1992. The molecular taxonomy and evolution of the guinea pig. Journal of Heredity, 83: 174–181.

Martin, A. P., and S. R. Palumbi. 1993. Body size, metabolic rate, generation time, and the molecular clock. Proceedings of the National Academy of Sciences (USA), 90:4087–4091.

MAXAM, A. M., AND W. GILBERT. 1980. Sequencing end-labeled DNA with base-specific chemical cleavages. Methods of Enzymology, 65:499–559.

MAXSON, L. R., AND R. D. MAXSON. 1990. Proteins II: immunological techniques. Pp. 127–155, *in* Molecular systematics (D. M. Hillis and C. Moritz, eds.). Sinauer Associates, Sunderland, Massachusetts, 588 pp.

MAXSON, L. R., V. M. SARICH, AND A. C. WILSON. 1975. Continental drift and the use of albumin as an evolutionary clock. Nature, 255:397–399.

MCCRACKEN, G. F., AND J. W. BRADBURY. 1977. Paternity and genetic heterozygosity in the polygynous bat, *Phyllostomus hastatus.* Science, 198:303–306.

———. 1981. Social organization and kinship in the polygynous bat *Phyllostomus hastatus.* Behavioral Ecology and Sociobiology, 8:11–34.

MCKENNA, M. C. 1975. Toward a phylogenetic classification of Mammalia. Pp. 21–46, *in* Phylogeny of the Primates (W. P. Luckett and F. S. Szalay, eds.). Plenum, New York, 483 pp.

MELNICK, D. J., G. A. HOELZER, AND R. L. HONEYCUTT. 1992. Mitochondrial DNA: its uses in anthropological research. Pp. 179–233, *in* Molecular applications in biological anthropology (E. J. Devor, ed.). Cambridge University Press, Cambridge, England, 258 pp.

MICKEVICH, M. F., AND M. S. JOHNSON. 1976. Congruence between morphological and allozyme data in evolutionary inference and character evolution. Systematic Zoology, 25:260–270.

MINDELL, D. P., AND R. L. HONEYCUTT. 1990. Ribosomal RNA in vertebrates: evolution and phylogenetic applications. Annual Review of Ecology and Systematics, 21:541–566.

MINDELL, D. P., C. W. DICK, AND R. J. BAKER. 1991. Phylogenetic relationships among megabats, microbats, and primates. Proceedings of the National Academy of Sciences (USA), 88:10322–10326.

MIYAMOTO, M. M., AND S. M. BOYLE. 1989. The potential importance of mitochondrial DNA sequence data to eutherian mammal phylogeny. Pp. 437–450, *in* The hierarchy of life (B. Fernholm, K. Bremer, and H. Jornvall, eds.). Elsevier, New York, 500 pp.

MIYAMOTO, M. M., AND J. CRACRAFT (EDS.). 1991. Phylogenetic analysis of DNA sequences. Oxford Press, New York, 358 pp.

MIYAMOTO, M. M., AND M. GOODMAN. 1986. Biomolecular systematics of eutherian mammals: phylogenetic patterns and classification. Systematic Zoology, 35:230–240.

MIYAMOTO, M. M., F. KRAUS, AND O. Z. RYDER. 1990. Phylogeny and evolution of antlered deer determined from mitochondrial DNA sequences. Proceedings of the National Academy of Sciences (USA), 87:6127–6131.

MIYAMOTO, M. M., S. M. TANHAUSER, AND P. J. LAIPIS. 1989. Systematic relationships in the artiodactyl tribe Bovini (family Bovidae), as determined from mitochondrial DNA sequences. Systematic Zoology, 38: 342–349.

MOORE, D. W., AND T. L. YATES. 1983. Rate of protein inactivation in selected mammals following death. Journal of Wildlife Management, 47:1166–1169.

MOORE, G. W., J. BARNABAS, AND M. GOODMAN. 1973. A method for constructing maximum parsimony ancestral amino acid sequences on a given network. Journal of Theoretical Biology, 38:459–485.

MURPHY, ROBERT W., J. W. SITES, D. G. BUTH, AND C. H. HAUFLER. 1990. Proteins I: isozyme electrophoresis. Pp. 45–126, *in* Molecular systematics (D. M. Hillis and C. Moritz, eds.). Sinauer Associates, Sunderland, Massachusetts, 588 pp.

NADLER, C. F., N. N. VORONTSOV, R. S. HOFFMANN, I. I. FORMICHOVA, AND C. F. NADLER, JR. 1973. Zoogeography of transferrins in Arctic and long-tailed ground squirrel populations. Comparative Biochemistry and Physiology, B. Comparative Biochemistry, 44:33–40.

NADLER, C. F., R. S. HOFFMAN, N. N. VORONTSOV, J. W. KOWPPL, L. DEUTSCHAND, AND I. SUKERKNIK. 1982. Evolution in ground squirrels. II. Biochemical comparisons on Holartic populations of *Spermophilus.* Zeitschrift Saugetierkund, 47:198–215.

NEI, M. 1971. Interspecific gene differences and evolutionary time estimated from electrophoretic data on protein identity. American Naturalist, 105:385–398.

———. 1972. Genetic distance between populations. The American Naturalist, 106:283–292.

———. 1987. Molecular evolutionary genetics. Columbia University Press, New York, 512 pp.

NEI, M., AND D. GRAUR. 1984. Extent of protein polymorphism and the neutral mutation theory. Evolutionary Biology, 17:73–118.

NELSON, K., R. J. BAKER, AND R. L. HONEYCUTT. 1987. Mitochondrial DNA and protein differentiation between hybridizing cytotypes of the white-footed mouse, *Peromyscus leucopus.* Evolution, 41:864–872.

NELSON, K., R. J. BAKER, AND H. S. SHELLHAMMER. 1984. Test of alternative hypotheses concerning the origin of *Reithrodontomys raviventris*: genetic analysis. Journal of Mammalogy, 65:668–673.

NEVO, E. 1978. Genetic variation in natural populations: patterns and theory. Theoretical Population Biology, 13:121–177.

———. 1985. Ecological and populational correlates of allozyme polymorphisms in mammals. Acta Zoologica Fennica, 170:25–29.

NEVO, E., AND C. R. SHAW. 1972. Genetic variation in a subterranean mammal, *Spalax ehrenbergi.* Biochemical Genetics, 7:235–241.

NEVO, E., Y. J. KIM, C. R. SHAW, AND C. S. THAELER, JR. 1974. Genetic variation, selection, and speciation in *Thomomys talpoides* pocket gophers. Evolution, 28:1–23.

NEVO, E., R. L. HONEYCUTT, H. YONEKAWA, K. NELSON, AND N. HANZAWA. 1993. Mitochondrial DNA polymorphism in subterranean mole-rats of the *Spalax ehrenbergi* superspecies in Israel, and its peripheral isolates. Molecular Biology and Evolution, 10: 590–604.

NEWMAN, A., ET AL. 1985. Biochemical genetic variation in eight endangered or threatened felid species. Journal of Mammalogy, 66:256–267.

NOVACEK, M. J. 1992. Mammalian phylogeny: shaking the tree. Nature, 356:121–125.

NUTTALL, G. H. F. 1904. Blood immunity and blood relationships. Cambridge University Press, Cambridge, England.

O'BRIEN, S. J., D. E. WILDT, AND M. BUSH. 1986. The cheetah in genetic peril. Scientific American, May, 1986:84–92.

O'BRIEN, S. J., D. E. WILDT, D. GOLDMAN, C. R. MERRIL, AND M. BUSH. 1983. The cheetah is depauperate in genetic variation. Science, 221:459–462.

O'BRIEN, S. J., ET AL. 1987*b*. East African cheetahs: evidence for two population bottlenecks? Proceedings of the National Academy of Sciences (USA), 84: 508–511.

O'BRIEN, S. J., ET AL. 1987*a*. Biochemical genetic variation in geographic isolates of African and Asiatic lions. National Geographic Research, 3:114–124.

O'BRIEN, S. J., ET AL. 1985. Genetic basis for species vulnerability in the cheetah. Science, 227:1428–1434.

O'BRIEN, S. J., ET AL. 1990. Genetic introgression within the Florida panther *Felis concolor coryi*. National Geographic Research, 6:485–494.

PAABO, S. 1989. Ancient DNA: extraction, characterization, molecular cloning, and enzymatic amplification. Proceedings of the National Academy of Sciences (USA), 86:1939–1943.

PAABO, S., J. A. GIFFORD, AND A. C. WILSON. 1988. Mitochondrial DNA sequences from a 7000-year-old brain. Nucleic Acid Research, 16:9775–9787.

PAABO, S., R. HIGUCHI, AND A. C. WILSON. 1989. Ancient DNA and the polymerase chain reaction. Journal of Biological Chemistry, 264:9709–9712.

PACKER, C., A. E. PUSEY, H. ROWLEY, D. A. GILBERT, J. MARTENSON, AND S. J. O'BRIEN. 1991. Case study of a population bottleneck: lions of the Ngorongoro Crater. Conservation Biology, 5:219–230.

PATTON, J. L. 1984. Genetical processes in the Galapagos. Biological Journal of the Linnean Society, 21:97–111.

———. 1985. Population structure and the genetics of speciation in pocket gophers, genus *Thomomys*. Acta Zoologica Fennica, 170:109–114.

PATTON, J. C., AND J. C. AVISE. 1983. An empirical evaluation of qualitative Hennigian analyses of protein electrophoretic data. Journal of Molecular Evolution, 19:244–254.

PATTON, J. L., AND M. F. SMITH. 1992. MtDNA phylogeny of Andean mice: a test of diversification across ecological gradients. Evolution, 46:174–183.

PATTON, J. L., AND S. Y. YANG. 1977. Genetic variation in *Thomomys bottae* pocket gophers: macrogeographic patterns. Evolution, 31:697–720.

PATTON, J. C., R. J. BAKER, AND J. C. AVISE. 1981. Phenetic and cladistic analyses of biochemical evolution in peromyscine rodents. Pp. 288–308, *in* Mammalian population genetics (M. H. Smith and J. Joule, eds.). University of Georgia Press, Athens, Georgia, 380 pp.

PATTON, J. L., R. K. SELANDER, AND M. H. SMITH. 1972. Genic variation in hybridizing populations of gophers (genus *Thomomys*). Systematic Zoology, 21:263–270.

PATTON, J. L., J. C. HAFNER, AND M. S. HAFNER. 1979*a*. Hybrid zones in *Thomomys bottae* pocket gophers: genetic, phenetic, and ecologic concordance patterns. Evolution, 33:860–876.

PATTON, J. L., M. S. HAFNER, J. C. HAFNER, AND M. F. SMITH. 1979*b*. Hybrid zones in *Thomomys bottae* pocket gophers: genetic, phenetic, and ecologic concordance patterns. Evolution, 33:860–876.

PENNY, D. F., AND E. G. ZIMMERMAN. 1976. Genic divergence and local population differentiation by random drift in the pocket gopher genus *Geomys*. Evolution, 30:473–483.

PIERSON, E. D., V. M. SARICH, J. M. LOWENSTEIN, M. J. DANIEL, AND W. E. RAINEY. 1986. A molecular link between the bats of New Zealand and South America. Nature, 323:60–63.

PRAGER, E. M., AND A. C. WILSON. In press. Information content of immunological distances. Methods In Enzymology.

REDUKER, D. W., D. W. DUSZYNSKI, AND T. L. YATES. 1987. Evolutionary relationships among *Eimeria* spp. (*Apicomplexa*) infecting cricetid rodents. Canadian Journal of Zoology, 65:722–735.

RENNERT, P. D., AND C. W. KILPATRICK. 1986. Biochemical systematics of populations of *Peromyscus boylii*. I. Populations from east-central Mexico with low fundamental numbers. Journal of Mammalogy, 67:481–488.

RIDDLE, B. R., AND R. L. HONEYCUTT. 1990. Historical biogeography in North American arid regions: an approach using mitochondrial-DNA phylogeny in grasshopper mice (genus *Onychomys*). Evolution, 44:1–15.

RIDDLE, B. R., R. L. HONEYCUTT, AND P. L. LEE. 1993. Mitochondrial DNA phylogeography in northern grasshopper mice (*Onychomys leucogaster*): the influence of Quaternary climatic oscillations on population dispersion and divergence. Molecular Ecology, 2:183–193.

ROBBINS, L. W., M. H. SMITH, M. C. WOOTEN, AND R. K. SELANDER. 1985. Biochemical polymorphism and its relationship to chromosomal and morphological variation in *Peromyscus leucopus* and *Peromyscus gossypinus*. Journal of Mammalogy, 66:498–510.

ROELKE, M. E., J. S. MARTENSON, AND S. J. O'BRIEN. 1993. The consequences of demographic reduction and genetic depletion in the endangered Florida panther. Current Biology, 3:340–350.

ROGERS, J. S. 1972. Measures of genetic similarity and genetic distance. Studies in genetics VII. University of Texas Publications, 7213:145–153.

ROMERO-HERRERA, A. E., H. LEHMANN, K. A. JOYSEY, AND A. E. FRIDAY. 1978. On the evolution of myoglobin. Philosophical Transactions of the Royal Society of London, 283:61–163.

RUVOLO, M., T. R. DISOTELL, M. W. ALLARD, W. M. BROWN, AND R. L. HONEYCUTT. 1991. Resolution of the African hominoid trichotomy by use of a mitochondrial gene sequence. Proceedings of the National Academy of Sciences (USA), 88:1570–1574.

SAGE, R. D., J. R. CONTRERAS, V. G. ROIG, AND J. L. PATTON. 1986. Genetic variation in the South American burrowing rodents of the genus *Ctenomys* (Rodentia: Ctenomyidae). Zeitschrift Saugetierkunde, 51:158–172.

SAIKI, R. K., ET AL. 1988. Primer-directed enzymatic amplification of DNA with a thermostable DNA polymerase. Science, 239:487–491.

Sanger, F., S. Nicklen, and A. R. Coulson. 1977. DNA sequencing with chain terminating inhibitors. Proceedings of the National Academy of Sciences (USA), 74:5463–5467.

Sarich, V. M. 1969*a*. Pinniped origins and the rate of evolution of carnivore albumins. Systematic Zoology, 18:286–295.

———. 1969*b*. Pinniped phylogeny. Systematic Zoology, 18:416–422.

———. 1973. The giant panda is a bear. Nature, 245: 218–220.

———. 1977. Rates, sample sizes, and the neutrality hypothesis for electrophoresis in evolutionary studies. Nature, 256:24–28.

———. 1985. Rodent macromolecular systematics. Pp. 423–452, *in* Evolutionary relationships among rodents: a multidisciplinary analysis (W. P. Luckett and J.-L. Hartenberger, eds.). Plenum, New York, 721 pp.

———. In press. Some results of 25 years with the blood of mammals. *In* Mammal phylogeny: placentals (F. S. Szalay, M. J. Novacek, and M. C. McKenna, eds.). Springer-Verlag, New York.

Sarich, V. M., and J. E. Cronin. 1976. Molecular systematics of the primates. Pp. 141–170, *in* Molecular anthropology (M. Goodman, R. E. Tashian, and J. H. Tashian, eds.). Plenum Press, New York, 466 pp.

Sarich, V. M., and A. C. Wilson. 1967*a*. Rates of albumin evolution in primates. Proceedings of the National Academy of Sciences (USA), 58:142–148.

———. 1967*b*. Immunological time scale for hominid evolution. Science, 158:1200–1203.

Sarich, V. M., C. W. Schmid, and J. Marks. 1989. DNA hybridization as a guide and phylogenies: a critical analysis. Cladistics, 5:3–32.

Schmidly, D. J., M. R. Lee, W. S. Modi, and E. G. Zimmerman. 1985. Systematics and notes on the biology of *Peromyscus hooperi*. Occasional Papers, The Museum, Texas Tech University, 97:1–40.

Schnell, G. D., and R. K. Selander. 1981. Environmental and morphological correlates of genetic variation in mammals. Pp. 60–99, *in* Mammalian population genetics (M. H. Smith and J. Joule, eds.). University of Georgia Press, Athens, 380 pp.

Scribner, K. T., R. K. Chesser, and R. J. Warren. 1983. Spatial and temporal genetic variability of the eastern cottontail on west Texas playa basins. Journal of Mammalogy, 64:287–294.

Selander, R. K. 1977. Genic variation in natural populations. Pp. 21–45, *in* Molecular evolution (F. J. Ayala, ed.). Sinauer Associates, Sunderland, Massachusetts, 277 pp.

Selander, R. K., and D. W. Kaufman. 1973. Genic variability and strategies of adaptation in animals. Proceedings of the National Academy of Sciences (USA), 70:1875–1877.

Selander, R. K., and T. S. Whittam. 1983. Protein polymorphism and the genetic structure of populations. Pp. 89–114, *in* Evolution of genes and proteins (M. Nei and R. K. Koehn, eds.). Sinauer Associates, Sunderland, Massachusetts, 331 pp.

Selander, R. K., D. W. Kaufman, R. J. Baker, and S. L. Williams. 1974. Genic and chromosomal differentiation in pocket gophers of the *Geomys bursarius* group. Evolution, 28:557–564.

Selander, R. K., M. H. Smith, S. Y. Yang, W. E. Johnson, and J. R. Gentry. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old-field mouse (*Peromyscus polionotus*). Studies in genetics VI. University of Texas Publications, 7103:49–90.

Shaw, C. R., and R. Prasad. 1970. Starch gel electrophoresis of enzymes: a compilation of recipes. Biochemical Genetics, 4:297–320.

Shoshani, J. 1986. Mammalian phylogeny: comparison of morphological and molecular results. Molecular Biology and Evolution, 3:222–242.

Shoshani, J., J. M. Lowenstein, D. A. Walz, and M. Goodman. 1985. Proboscidean origins of mastodon and woolly mammoth demonstrated immunologically. Paleobiology, 11:429–437.

Sibley, C. G., and J. E. Ahlquist. 1981. The phylogeny and relationships of the ratite birds as indicated by DNA-DNA hybridization. Pp. 301–335, *in* Evolution today (G. G. E. Scudder and J. L. Reveal, eds.). Carnegie–Mellon University, Pittsburgh, Pennsylvania.

Sibley, C. G., and J. E. Ahlquist. 1984. The phylogeny of the hominoid primates, as indicated by DNA-DNA hybridization. Journal of Molecular Evolution, 20:2–15.

Sibley, C. G., J. E. Ahlquist, and B. L. Monroe, Jr. 1988. A classification of the living birds of the world, based on DNA/DNA hybridization studies. Auk, 105: 409–423.

Simpson, G. G. 1945. The principles of classification and a classification of mammals. Bulletin of the American Museum of Natural History, 85:1–350.

Smith, D. G., and R. G. Coss. 1984. Calibrating the molecular clock: estimates of ground squirrel divergence made using fossil and geological time markers. Molecular Biology and Evolution, 1:249–259.

Smith, M. F., and J. L. Patton. 1984. Dynamics of morphological differentiation: temporal impact of gene flow in pocket gopher populations. Evolution, 38:1079–1087.

———. 1988. Subspecies of pocket gophers: causal bases for geographic differentiation in *Thomomys bottae*. Systematic Zoology, 37:163–178.

Smith, M. H., R. K. Selander, and W. E. Johnson. 1973. Biochemical polymorphism and systematics in the genus *Peromyscus*. III. Variation in the Florida deer mouse (*Peromyscus floridanus*), a Pleistocene relict. Journal of Mammalogy, 54:1–13.

Smith, M. F., J. L. Patton, J. C. Hafner, and D. J. Hafner. 1983. *Thomomys bottae* pocket gophers of the central Rio Grande Valley, New Mexico: local differentiation, gene flow, and historical biogeography. Occasional Papers, Museum Southwestern Biology, 2:1–16.

Springer, M. S., and J. A. W. Kirsch. 1989. Rates of single-copy DNA evolution in phalangeriform marsupials. Molecular Biology and Evolution, 6:331–341.

———. 1991. DNA hybridization, the compression effect, and the radiation of diprotodontian marsupials. Systematic Zoology, 40:131–151.

Springer, M. S., and C. Krajewski. 1989. DNA hybridization in animal taxonomy: a critique from first principles. Quarterly Review of Biology, 64:291–318.

Stangl, F. G., Jr. 1986. Aspects of a contact zone between two chromosomal races of *Peromyscus leucopus* (Rodentia: Cricetidae). Journal of Mammalogy, 67:465–473.

Stanhope, M. J., J. Czelusniak, J.-S. Si, J. Nickerson, and M. Goodman. 1992. A molecular perspective on mammalian evolution from the gene encoding interphotoreceptor retinoid binding protein, with convincing evidence for bat monophyly. Molecular Phylogenetics and Evolution, 1:148–160.

Stewart, C.-B., and A. C. Wilson. 1987. Sequence convergence and functional adaptation of stomach lysozymes from foregut fermenters. Cold Spring Harbor Symposium Quantitative Biology, 52:891–899.

Straney, D. O., M. H. Smith, R. J. Baker, and I. F. Greenbaum. 1976. Biochemical variation and genic similarity of *Myotis velifer* and *Macrotus californicus*. Comparative Biochemistry and Physiology, A. Comparative Biochemistry, 54:243–248.

Straney, D. O., M. H. Smith, I. F. Greenbaum, and R. J. Baker. 1979. Biochemical genetics. Pp. 157–176, *in* Biology of bats of the New World family Phyllostomatidae, Part III (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.). Special Publications, The Museum, Texas Tech University, 16:1–441.

Sudman, P. D., and M. S. Hafner. 1992. Phylogenetic relationships among Middle American pocket gophers (genus *Orthogeomys*) based on mitochondrial DNA sequences. Molecular Phylogenetics and Evolution, 1:17–25.

Sullivan, R. M. 1985. Phyletic, biogeographic, and ecologic relationships among montane populations of least chipmunks (*Eutamias minimus*) in the southwest. Systematic Zoology, 34:419–448.

Sullivan, R. M., D. J. Hafner, and T. L. Yates. 1986. Genetics of a contact zone between two chromosomal forms of the grasshopper mouse (genus *Onychomys*): a reassessment. Journal of Mammalogy, 67:640–659.

Sullivan, R. M., and T. L. Yates. In press. Population genetics and conservation of relict populations of the red squirrel (genus *Tamiasciurus*). Special Publications, Smithsonian Institution.

Svoboda, P. L., J. R. Choate, and R. K. Chesser. 1985. Genetic relationships among southwestern populations of the Brasilian free-tailed bat. Journal of Mammalogy, 66:444–450.

Swofford, D. L. 1990. PAUP: phylogenetic analysis using parsimony, version 3.0. Illinois Natural History Survey, Champaign, Illinois.

Swofford, D. L., and S. H. Berlocher. 1987. Inferring evolutionary trees from gene frequency data under the principle of maximum parsimony. Systematic Zoology, 36:293–325.

Swofford, D. L., and G. J. Olsen. 1990. Phylogeny reconstruction. Pp. 411–501, *in* Molecular systematics (D. M. Hillis and C. Moritz, eds.). Sinauer Associates, Sunderland, Massachusetts, 588 pp.

Thomas, W. K., S. Paabo, F. X. Villablanca, and A. C. Wilson. 1990. Spatial and temporal continuity of kangaroo rat populations shown by sequencing mitochondrial DNA from museum specimens. Journal of Molecular Evolution, 31:101–112.

Tolliver, D. K., and L. W. Robbins. 1987. Genetic variability within *Blarina carolinensis*, and among three sympatric species of shrews (Insectivora: Soricidae). Journal of Mammalogy, 68:387–390.

Tolliver, D. K., M. H. Smith, and R. H. Leftwich. 1985. Genetic variability in Insectivora. Journal of Mammalogy, 66:405–410.

Vawter, L., and W. M. Brown. 1986. Nuclear and mitochondrial DNA comparisons reveal extreme rate variation in the molecular clock. Science, 234:194–196.

Watson, J. D., and F. H. C. Crick. 1953. Molecular structure of nucleic acids. Nature, 25:737.

Wayne, R. K., and S. M. Jenks. 1991. Mitochondrial DNA analysis implying extensive hybridization of the endangered red wolf *Canis rufus*. Nature, 351: 365–368.

Wayne, R. K., and S. J. O'Brien. 1987. Allozyme divergence within the Canidae. Systematic Zoology, 36:339–355.

Wayne, R. K., N. Lehman, M. W. Allard, and R. L. Honeycutt. 1992. Mitochondrial DNA variability of the gray wolf: genetic consequences of population decline and habitat fragmentation. Conservation Biology, 6:558–569.

Wayne, R. K., L. Forman, A. K. Newman, J. M. Simonson, and S. J. O'Brien. 1986. Genetic monitors of zoo populations: morphological and electrophoretic assays. Zoo Biology, 5:215–232.

Wayne, R. K., et al. 1991. Conservation genetics of the endangered Isle Royale gray wolf. Conservation Biology, 5:41–51.

Wiley, E. O. 1981. Phylogenetics: the theory and practice of phylogenetic systematics. John Wiley & Sons, New York, 439 pp.
divergence within the Canidae. Systematic Zoology, 36:339–355.

Wiley, E. O. 1981. Phylogenetics: the theory and practice of phylogenetic systematics. John Wiley & Sons, New York, 439 pp.
Wilkinson, G. S. 1985. The social organization of the common vampire bat. II. Mating system, genetic structure, and relatedness. Behavioral Ecology and Sociobiology, 17:123–134.

Wilson, A. C., S. S. Carlson, and T. J. White. 1977. Biochemical evolution. Annual Review of Biochemistry, 46:573–639.

Wilson, A. C., and V. M. Sarich. 1969. A molecular time scale for hominid evolution. Proceedings of the National Academy of Sciences (USA), 63:1088–1093.

Woods, C. A. 1982. The history and classification of South American hystricognath rodents: reflections on the far away and long ago. Pp. 377–392, *in* Mammalian biology in South America (M. A. Mares and H. H. Genoways, eds.). University of Pittsburgh Press, Pittsburgh, Pennsylvania, 539 pp.

Wu, C.-I., and W.-H. Li. 1985. Evidence for higher rates of nucleotide substitution in rodents than in man. Proceedings of the National Academy of Sciences (USA), 82:1741–1745.

Wyss, A. R., M. J. Novacek, and M. C. McKenna. 1987. Amino acid sequence versus morphological data and the interordinal relationships of mammals. Molecular Biology and Evolution, 4:99–116.

YATES, T. L. 1983. The mole that keeps its nose clean. Natural History, 92:54–61.

YATES, T. L., AND I. F. GREENBAUM. 1982. Biochemical systematics of North American moles (Insectivora: Talpidae). Journal of Mammalogy, 63:368–374.

YATES, T. L., AND D. W. MOORE. 1990. Speciation and evolution in the family Talpidae (Mammalia: Insectivora). Pp. 1–22, *in* Evolution of subterranean mammals at the organismal and molecular levels (E. Nevo and O. Reig, eds.). Liss/Wiley, New York, 422 pp.

ZIMMERMAN, E. G., B. J. HART, AND C. W. KILPATRICK. 1975. Biochemical genetics of *truei* and *boylei* groups of the genus *Peromyscus* (Rodentia). Comparative Biochemistry and Physiology, B. Comparative Biochemistry, 52:541–545.

ZIMMERMAN, E. G., C. W. KILPATRICK, AND B. J. HART. 1978. The genetics of speciation in the rodent genus *Peromyscus*. Evolution, 32:565–579.

ZIMMERMAN, E. G., AND M. E. NEJTEK. 1977. Genetics and speciation of three semispecies of *Neotoma*. Journal of Mammalogy, 587:391–402.

ZUKERKANDL, E., AND L. PAULING. 1965. Evolutionary divergence and convergence in proteins. Pp. 97–166, *in* Evolving genes and proteins (V. Bryson and H. J. Vogel, eds.). Academic Press, New York, 629 pp.

# *CYTOGENETICS*

ROBERT J. BAKER AND MARK S. HAFNER


### *Introduction*

When we were invited to prepare a review of the field of cytogenetics for the 75th anniversary of the ASM we had several discussions on the breadth and nature of the subject. This sent us scurrying to *A Dictionary of Genetics* (King and Stansfield, 1990:98) to determine the exact definition of the word cytogenetics: cytogenetics—the science that combines the methods and findings of cytology and genetics. This definition failed to provide us with the resolution that we desired. Pertaining to the field of mammalogy, the word cytogenetics is a synonym for karyology, chromosomal evolution, or chromosome biology.

Chromosomes, or collectively, the karyotype, are subcellular morphological entities, and this chapter on cytogenetics is the only such chapter devoted to a single cellular organelle. Why then is the karyotype accorded such an important position in mammalogy? Several books have been written on this subject, of which two of the best are M. J. D. White's *Animal Cytology and Evolution* (1973) and *Modes of Speciation* (1978*b*). This organelle (the chromosome) has been implicated in many biological phenomena including speciation (Baker and Bickham, 1986; Bush et al., 1977; White, 1968, 1978*a*), rapid morphological change (Wilson et al., 1974), gene duplication (White, 1978*b*), and sex determination (Bull, 1983; Ohno, 1967). However, there may even be more basic reasons that the karyotype has been important to mammalogy. Before the advent of molecular biology, there were few easily quantified characters that provided systematic resolution among closely related species. The karyotype represents such a character. In addition, most karyological techniques are adaptable to field conditions and require minimal expense; therefore, it is not surprising that a number of mammalogists have chosen to specialize in this area. As is the case with many other subdisciplines, the field of cytogenetics extends far beyond the classical limits of mammalogy. For example, cytogenetics has important implications in the fields of carcinogenesis, mutagenesis, and medicine. Herein, however, we restrict our report to cytogenetics as related to the science of mammalogy.

### *Conceptual Development of the Field*

The field of cytogenetics was essentially nonexistent prior to 1919. Until the 1950s, no reliable methods were available to determine diploid number or morphology of chromosomes. Although the theory that heredity was chromosomally based was developed in the 1890s, this discovery had little immediate impact on the field of mammalogy. A brief review of the history of our understanding of the karyotype of the human provides insight into the state of the methods available during this time. In the early 1920s, the diploid number for *Homo sapiens* was commonly described as 24. In 1923, T. S. Painter reported the diploid number was 48 with an XX/XY sex-determining system (Painter, 1923). Not until 1956 (Tjio and Levan, 1956) was the correct diploid number (46) determined. The significance of the difficulty in documenting the human karyotype is that early methods were tedious, subjective, and labor intensive, and they could not be adapted easily to the type of survey work that mammalogists usually conduct. Nevertheless, by 1951, two significant lists of chromosomal data had been generated that together described the diploid or haploid numbers of approximately 175 species of mammals (Makino, 1951; Matthey, 1950). As verified by more recent studies, the majority of these descriptions were reasonably accurate.

Even though technical aspects of the field of cytogenetics were rather primitive until the mid-1950s, some theoretical and conceptual aspects of the field were remarkably current as early as the 1920s. The following quote is from Painter (1925:407–408):

"In the present paper a good deal of attention has been given to chromosome numbers, yet at the same time it has been fully realized that numbers per se are of secondary importance. The significant point is that as far as we can gauge it, the total amount of chromatin in the different mammalian groups is about the same, and there has been a remarkable stability in the chromosome associations. Inferentially, we may surmise that the total number of genes is about the same in all groups. In their chromosome constitution, the mammals have shown themselves, so far at least, comparable to an order of insects.

If my general conclusion is a valid one, then we may expect that the plotting of chromosome maps in the eutheria will go forward with comparative rapidity, because linkage values established in one group or species can be applied to other forms. . . . Transverse fragmentation or end to end fusion will occasionally upset these relations, but on the whole they should prove the same in different forms, and enable us eventually to plot the chromosome maps of the eutheria. . . ."

Painter's (1925) insights into chromosomal evolution and the future of mammalian cytogenetics were remarkably prescient, especially considering the dearth of actual data that existed in the field of cytogenetics in the mid-1920s. We encourage the student of cytogenetics to review Painter's article in its entirety.

In the 1960s, there was a burst of activity in the field of cytogenetics that produced accurate diploid numbers and descriptions of karyotypes for a wide variety of mammalian taxa. Interpretation of these new data was influenced strongly by prevailing views of chromosome evolution in the 1950s and 1960s. For example, it was widely held that most or all chromosome rearrangements reduced fertility (i.e., fitness); hence, karyotypic differences were generally viewed as indicators of species distinctiveness. For this reason, the first examples of chromosomal polymorphism discovered within taxa that behaved otherwise as biological species (Ford et al., 1957) received considerable attention. Of course there are several examples where numerous chromosomal polymorphisms exist in naturally occurring populations and these demonstrate rather conclusively that fitness reduction in heterozygotes can be minimal if not nonexistent (Koop et al., 1983; Nachman, 1992*a*, 1992*b*; Nachman and Myers, 1989; Stangl, 1986).

Most mammalian cytogeneticists of the 1960s also assumed that karyotypes identical in gross morphology were also identical at the level of gene order. Of course G-banding has shown that similar nonbanded karyotypes may underestimate amounts of chromosomal evolution by several orders of magnitude (Baker and Bickham, 1980; Haiduk et al., 1981). Breakage points in chromosomes were assumed to be stochastic, such that the independent occurrence of the same rearrangement in separate lineages was considered highly improbable and convergent evolution would not be a problem in cytogenetics. The significance of this conclusion is that when two taxa shared a chromosomal rearrangement identified by G-bands, its usefulness as a synapomorphy was almost beyond question. This too has been shown to be inaccurate by several examples, including chromosome 6 in 30 species of *Peromyscus,* which may have been rearranged as many as seven times (Stangl and Baker, 1984). The strongest evidence that the same chromosomal rearrangement can occur repeatedly comes from studies of human families that have unusual rearrangements (such as the 11q;22q; Fraccaro et al., 1980) that have arisen independently in many families from widely separated geographic origins. Chromosomal evolution was thought to be a highly ordered and time-dependent process (John and Lewis, 1966; for review see Baker et al., 1987). Therefore, taxa distinguished by a large number of chromosomal differences were thought to be distantly related. Examples such as the following two document that little time or genetic distance is required in some cases where extensive chromosomal evolution has occurred. 1) Despite the karyotypic differences between the species of *Muntiacus* (one with $2n = 6, 7$ and the other with $2n = 46$), viable offspring are produced by interspecific crosses of the two (Wurster and Benirschke, 1970). 2) *Reithrodontomys megalotis* and *R. zacatacae* have widely divergent karyotypes distinguished by over 30 rearrangements, but the two are not distinguished by any differences in allozymes at 30 loci (Hood et al., 1984; Nelson et al., 1984).

In the 1960s, chromosomes were believed to be stable structures and exchanges between nonhomologous chromosomes were thought to be rare. Barbara McClintock's Nobel Prize-winning work (1978) provided the first insights into an exceptionally dynamic process of exchange among nonhomologous chromosomes. Although the syntenic groups shared by various orders of mammals (O'Brien et al., 1985) indicate a measure of stability in the karyotype, nonetheless it is widely documented that the exchange of transposable elements, heterochromatin, and other pieces of DNA, such as ribosomal genes, between nonhomologous chromosomes is a common process (Arnheim et al., 1980; Dover, 1982; Hamilton et al., 1990, 1992; Wichman et al., 1991, 1992). Concepts about chromosomal evolution and the forces that result in chromosomal conservatism in some lineages and rapid change in others are being revised continually (Baker et al., 1987; Bradley and Wichman, in press; Graphodatsky, 1989; Patton and Sherwood, 1983; Wichman et al., 1991, 1992). The primary focus at this time reflects recent technological advances associated with molecular biology, which has permitted more sophisticated experiments and testing of the molecular based hypotheses associated with cytogenetics.

## *Technological Advances*

Although the microscope was invented in 1590 by Hans and Zacharias Janssen in Holland (King and Stansfield, 1990), instruments powerful enough to observe chromosomes were not designed until the 1800s. It was not until 1888 that the term chromosome was introduced by Wilhelm Waldeyer. The X chromosome was documented in 1891 by Henking, who also described its meiotic behavior. Henking (1891) used the term "X" because the function of the chromosome was unknown. The concept of the X chromosome's involvement in sex determination was developed by McClung (1901, 1902). The Y chromosome was first described by Wilson (1909). In 1901, Montgomery associated maternal and paternal chromosomes into pairs (homologous chromosomes) and related this to Mendel's genetic laws. By 1903 the role of the chromosome in heredity was demonstrated conclusively by Sutton (1902, 1903).

One technical difficulty in examining chromosome morphology and number stems from the fact that the cellular space is small and the methods used to examine chromosomes before 1960 involved squashing cells between a microscope slide and a coverslip (Hsu, 1979). The end result of this procedure was poorly spread masses of chromosomes whose depth extended beyond the normal field of focus for light microscopes. Therefore, chromosomal counts were made by following within the mass of chromosomes an individual chromosome through several focal lengths. Needless to say, this process was exceedingly tedious and often inaccurate.

A technical breakthrough that was of paramount importance in determining chromosomal morphology was the hypotonic pretreatment of cells to enlarge the cells and aid in the ability to see each chromosome of the karyotype as an independent unit in a single field of focus. Hsu (1979) calls this the hypotonic miracle in his well-written documentation of this discovery. Although the effects of hypotonic treatment of cells were described by Slifer in 1934, the significance of her discovery to the field of cytogenetics went unnoticed for almost two decades. In 1952, three papers (Hsu, 1952; Hughes, 1952; Makino and Nishimura, 1952) were published describing the hypotonic pretreatment phenomenon. Ultimately, hypotonic pretreatment was combined with another methodological breakthrough, the blaze-dry method (Scherz, 1962), to spread the chromosomes effectively from a single cell into a broader field for easier viewing of chromosomal detail. Students of cytogenetics who are interested in the history and development of this field should read Hsu's (1979) account.

Another major methodological breakthrough in the field of cytogenetics was Krishnan's (1968) discovery that mitotic inhibitors such as Colchicine and vinblastine sulfate (Velban) arrest cell division at the metaphase plate. Mitotic inhibitors had been used commonly in plant genetics long before they were applied to mammalian cytogenetics. For example, Blakeslee and Avery demonstrated as early as 1937 that Colchicine induced polyploidy in plants.

Techniques for preferential staining of particular regions of chromosomes (collectively called "banding" techniques) stemmed from work by Caspersson et al. (1968, 1970) and Pardue and Gall (1970). Those generally acknowledged as producing the first Q-bands are Caspersson et al. (1968, 1970), and production of the first C-bands is credited to Pardue and Gall (1970) and Arrighi and Hsu (1971). G-bands were first documented by Seabright (1971) and Sumner et al. (1971), R-bands were developed by Dutrillaux and Lejeune (1971), and stains specific for nucleolar organizing regions (NORs) are credited to Matsui and Sasaki (1973). Modern techniques for in situ hybridization stemmed from work by Gall and Pardue (1969) and John et al. (1969). In situ hybridization techniques advanced even further with the introduction of nonradioactive antibody probes visualized with enzymes or fluorescent dyes (Frommer et al., 1988; Langer et al., 1981; Manuelidis et al., 1982; Pinkel et al., 1986). A modern review of chromosome banding and other cytogenetic methods was provided by Sumner (1990).

## *Cytogenetic Studies: Insights from the Journal of Mammalogy*

There are more than 9,000 scientific journals that deal with the biological sciences.

In 1992 alone, nearly 7,000 articles in the field of cytogenetics were published in no fewer than 627 different journals (Macgregor, 1993). Because of the revolution in molecular biology, the scope of cytogenetics is ever expanding. We feel that valuable insights into the nature of the science of mammalogy can be gained by examination of publications in the *Journal of Mammalogy* that appeared during this period of expansion of the science of cytogenetics. Approximately 130 studies emphasizing chromosomes or using cytogenetic data or techniques have been published in the *Journal of Mammalogy* since its inception. Included in these studies are the first descriptions of karyotypes of roughly 284 species of mammals, including the first karyotypes reported for many mammalian genera and several families. As the following account will document, the *Journal of Mammalogy* played only a minor role in the early history of the field of cytogenetics. However, in 1967 it was thrust into the mainstream of mammal cytogenetic research, largely due to the improvement of karyotyping techniques such as use of mitotic inhibitors and blaze-dry methods that improved the spreading of chromosomes. Since 1966 (Nadler, 1966; Nadler and Hughes, 1966; Singh and McMillan, 1966), the *Journal of Mammalogy* has played an important role in the field of mammal cytogenetics, especially in the subfields of cytotaxonomy and cytosystematics.

Readers of the *Journal of Mammalogy* were introduced to the nascent field of cytogenetics in L. C. Dunn's (1921) study of coat-color inheritance in rodents. This study, which also introduced many mammalogists to Mendelian genetics, reported that diploid numbers were known at that time for only four species of rodents: the mouse (*Mus*); the rat (*Rattus*); the guinea pig (*Cavia*); and the Old World rabbit (*Oryctolagus*; rabbits were then classified as rodents). Based on this fragmentary evidence, Dunn (1921:139) made a remarkably insightful speculation, ". . . there is some slight evidence that in the evolution of rodents a fractionation of chromosomes may have occurred, for the mice and rats have 19 (haploid) while the guinea-pigs have 28." This comment was all the more remarkable considering that the entire concept of organic evolution was open to question when Dunn published this work. With reference to the haploid-number similarity between *Mus* and *Rattus*, Dunn (1921: 139) commented: "Whether this is due to a community of descent in the terms of current evolutionary theory or to relationship through some other cause is one of the questions which genetics, aided by the chromosome notation, may be expected at some time to answer."

Seventy-two years later *Science* published a genome issue showing a genetic linkage map of *Mus* (Copeland et al., 1993) documenting exactly the kinds of results predicted by Dunn (1921). Copeland et al. (1993) calculated that based on linkage maps, the mouse and the human have undergone approximately 150 chromosomal rearrangements since they last shared a common ancestor (Nadeau and Taylor, 1984).

The first figure of chromosomes published in the *Journal of Mammalogy* was a camera lucida drawing of meiotic prophase tetrads of the house mouse, *Mus musculus* (Hoy and Berkowitz, 1931). Although this article described a relatively simple method for fixation and preservation of chromosomes in the field, it did not catalyze the intense interest in mammalian chromosomes anticipated by its authors. To the contrary, this article was followed by a hiatus of almost 30 years, during which time no cytogenetic paper was published in the *Journal of Mammalogy*.

As noted above, two landmark books were published during this time in the rapidly expanding field of cytogenetics: Matthey's (1950) *Les Chromosomes des Vertebres,* and Makino's (1951) *An Atlas of the Chromosome Numbers in Animals.* Although these books were primarily compendia of diploid and fundamental numbers known at that time, Matthey (1950) speculated on the potential systematic value of chromosomes in the Mammalia. Johnson and Ostenson (1959) were the first to publish a paper in the *Journal of Mammalogy* that emphasized the potential usefulness of chromosomes as taxonomic characters. Their study was primarily a review of taxonomic methods available in 1959, and they reported no new mammalian karyotypes. However, Johnson and Ostenson (1959:573) referred to Matthey's (1952) pioneering studies of microtine chromosomes and stated: "Such a fundamental difference as in chromosomes [between two voles, *Microtus agrestis* and *M. pennsylvanicus*] must be regarded as strong evidence of species difference." This was the first of many such statements to appear in the *Journal of Mammalogy* signaling the taxonomic importance of cytogenetic characters.

The first figure of a mitotic-metaphase karyotype to be published in the *Journal of Mammalogy* appeared in volume 47 (Nadler and Hughes, 1966). This karyotype of a ground squirrel (*Spermophilus spilosoma*) was remarkably clear and showed in considerable detail individual chromosomal elements. The same year, Nadler (1966) published the first diagram to appear in the *Journal* showing hypothetical chromosomal changes that occurred during the evolutionary history of a mammalian lineage (in this case, the ground squirrel subgenus *Spermophilus*). Nadler's (1966) paper was among the first to bring cytogenetic evidence to bear on higher-order questions in the field of mammalian systematics, a field that, before that time, had been dominated by morphological and paleontological studies.

Before 1967, articles on mammalian cytogenetics were published in a wide variety of outlets including *The American Naturalist, Anatomical Record, Chromosoma, Experientia, Journal of Genetics, Journal of Morphology, Proceedings of the Society of Experimental Biology and Medicine,* and a myriad of other books, journals, proceedings, and reports. In an effort to organize the rapidly expanding literature in this field, Hsu and Benirschke published in 1967 their important compendium titled, *An Atlas of Mammalian Chromosomes.*

Methodological breakthroughs in the field of cytogenetics in 1967 triggered a major thrust in this research area worldwide. Instrumental in development of these new methods was James L. Patton, then a graduate student at the University of Arizona. The University of Arizona was a nucleus for this type of activity at this time with Patton and Robert J. Baker focusing on mammalian cytogenetics. Fortunately, Patton and Baker chose to publish many of their earliest cytogenetic studies in the *Journal of Mammalogy* (e.g., Baker and Patton, 1967; Patton, 1967; Patton and Hsu, 1967), which in concert with others (Nadler, 1966; Nadler and Hughes, 1966; Singh and McMillan, 1966) brought the *Journal* into the mainstream of cytogenetics research. Baker and Patton's seminal contributions to the field of mammalian cytogenetics and, in particular, their development of convenient techniques for use in the field (e.g., Baker, 1970; Patton, 1967), are still widely cited in the cytogenetics literature.

An analysis of the rate of publication of cytogenetic studies in the *Journal of Mammalogy* from the time of the journal's inception (1920) to the present (Fig. 1) illustrates the enormous surge in this field that began in the 1960s. For example, no cytogenetic studies appeared in the *Journal* between 1961 and 1965; in contrast, 22 such articles appeared for the time period of 1966 to 1970. Similarly, no new karyotypes were described in the *Journal* during the first half of the 1960s, whereas the karyotypes of 85 species of mammals were reported there for the first time between 1966 and 1970.

Most cytogenetic studies published in the *Journal of Mammalogy* in the late 1960s and early 1970s were descriptive in nature, and most authors linked—explicitly or implicitly—chromosomal differentiation with taxonomic distinctness. For example, Shellhammer (1967:549) stated (with respect to two species of harvest mice, *Reithrodonto-*

*mys*) that: "the karyotypes . . . are different enough to suggest that the two are in the terminal stages of speciation." However, as the karyotypes of more and more species of mammals were reported in the *Journal* and elsewhere, it became apparent that chromosomal variation in mammals was not necessarily linked to the process of speciation and that chromosomal variation, in general, was much more complex than had been envisioned by earlier workers in the field. In a study that described the karyotypes of 32 species of vespertilionid bats, Baker and Patton (1967:283) stated: "From the few studies of mammalian karyotypes that have thus far been made, it appears obvious that the degree of karyotypic variation encountered at a given taxonomic level . . . is in itself highly variable from mammalian group to group."

Thus began a period of intensive surveys of chromosomal variation in mammals, which was the subject of several articles published in the *Journal* beginning in 1968 (e.g., Blanks and Shellhammer, 1968; Lee and Zimmerman, 1969; Nelson-Rees et al., 1968). Although intraspecific chromosomal polymorphism had been known since Ford et al.'s (1957) classic study of shrews (*Sorex araneus*), the genetic consequences and evolutionary significance of chromosomal polymorphism were only poorly understood even a decade later. For example, Blanks and Shellhammer (1968:729), whose article in the *Journal of Mammalogy* was the first report of supernumerary chromosomes in mammals, stated candidly: "We do not understand the mode of inheritance of the small chromosomes . . . ." Not surprisingly, this period of intensive karyological surveys (1966–1970) generated a large gap between data and theory in the field of mammalian cytogenetics. This, in turn, led to a certain amount of disillusionment on the part of workers attempting to solve taxonomic problems using chromosomal evidence. For example, Sutton and Nadler (1969:534) stated: "Chromosomes are of limited value for the solution of taxonomic problems and they are of little help in establishing relationships between species and subspecies of the genus *Eutamias* [chipmunks]."

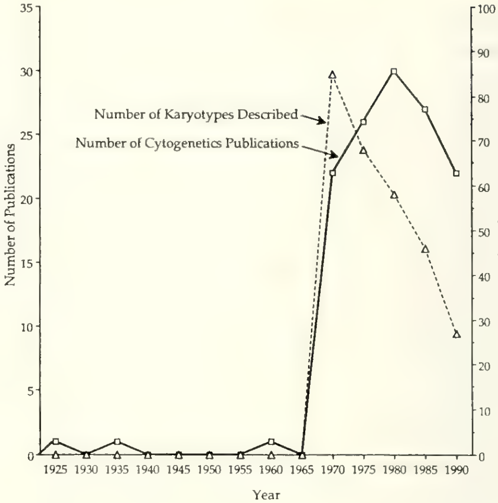



FIG. 1.—Number of cytogenetics publications and number of new karyotypes described in the *Journal of Mammalogy* from 1919 to 1990. The axes are scaled differently to show that the rate of publication of cytogenetics research increased throughout the 1970s, whereas the rate of publication of new karyotypes has declined consistently since 1970.

As the number of studies reporting intraspecific chromosomal variation in mammals increased, there was growing confusion in the literature with respect to the terms "geographic variation" and "polymorphism." Fortunately, Lee and Zimmerman's (1969) chromosomal study of cotton rats (*Sigmodon*) stemmed the tide of growing confusion by carefully distinguishing between geographic variation (". . . differences in karyotype between [presumably conspecific] organisms from different localities . . .") and chromosomal polymorphism (". . . variation within a geographically localized, panmictic population.") (Lee and Zimmerman, 1969:335–336).

Patton and Dingman's (1968) cytogenetic study of natural hybridization between the pocket gophers *Thomomys bottae* and *T. umbrinus* was published in volume 49 of the *Journal of Mammalogy*. Although their taxonomic conclusion (that *T. bottae* and *T. umbrinus* are distinct species) was controversial and was rejected by certain leading mammalogists of the time (e.g., Hall, 1981: 469), they demonstrated for the first time the value of chromosomes in analyses of genetic introgression in mammals. Patton and Dingman's (1968) taxonomic conclusion was bolstered 5 years later by a detailed analysis of meiosis in *bottae* × *umbrinus* hybrids (Patton, 1973). This work set the standard for cytogenetic studies of mammal hybrid zones for many years.

From 1967 through 1972, most major publications in the field of mammalian cytogenetics and reports of significant methodological and conceptual breakthroughs in the field were published in the journals *Chromosoma, Cytogenetics, Experientia, Science,* and *Nature*. During the same period, most studies describing the karyotypes of mammal species were published in *Mammalian Chromosomes Newsletter*. Perhaps as a result, the number of karyotypes described in the *Journal of Mammalogy* began to decline in the early 1970s (from its peak in the late 1960s) and has continued to decline (Fig. 1). However, as more and more chromosomal data accumulated in the early 1970s making large-scale syntheses possible, noteworthy publications in the field of mammalian cytogenetics began to appear with increasing frequency in the journals *Evolution, Hereditas, Systematic Zoology,* and *Journal of Mammalogy* (Fig. 1). One particularly important contribution that appeared in the *Journal of Mammalogy* during this period was Nadler et al.'s (1971) study of prairie dog (*Cynomys*) evolution; this was the first of many studies published in the *Journal* that used combined chromosomal and biochemical evidence to address a systematic problem.

The early 1970s witnessed a renaissance in the field of cytogenetics that was catalyzed by the development of techniques for banding chromosomes that increased dramatically the taxonomic usefulness of karyotypes. In his chromosomal study of kangaroo rats (*Dipodomys*), Stock (1974) published the first figure of a metaphase karyotype stained for constitutive heterochromatin ("C-bands") and the first figure of a Geimsa-banded karyotype ("G-bands") to appear in the *Journal*. Stock's contribution was followed soon thereafter by a study that used banded karyotypes to document chromosomal conservatism in rodents (Mascarello et al., 1974*a*), and another that used banded karyotypes to confirm the role of Robertsonian mechanisms in the origin of chromosomal diversity in woodrats (*Neotoma*; Mascarello et al., 1974*b*). Four years later, Mascarello (1978) introduced readers of the *Journal of Mammalogy* to yet another staining procedure (Ag-As silver staining), which was used to visualize nucleolus organizing regions on individual chromosomes.

Development of these new staining procedures in the mid-1970s triggered a burst of activity on the part of mammalian cytosystematists, and as a result the number of cytogenetic studies published in the *Journal of Mammalogy* peaked between 1976 and 1980 (Fig. 1). During this period, Greenbaum and Baker (1978) published the first article in the *Journal* that used C- and G-banded karyotypes to deduce the primitive karyotype for a group of mammals (in this case, white-footed mice of the genus *Peromyscus*). This was among the first studies published anywhere in which a cytogenetic analysis was viewed in the context of phylogenetic systematics. Bickham's (1979) study of the chromosomal variation in vespertilionid bats used cladistic methods to produce a phylogeny of these taxa using G-banded karyotypes.

The frequency of appearance of cytogenetic publications in the *Journal of Mammalogy* declined steadily during the 1980s and continues to decline today (Fig. 1). This trend probably reflects the general shift away from morphological and cytogenetic methods toward use of molecular methods by large numbers of mammalian biologists. This decline in frequency of cytogenetic studies during the 1980s has occurred despite the recent introduction of new and promising cytogenetic techniques. Notable among these new techniques are fluorescent-banding procedures (Bickham, 1987) and flow cytometric studies of nuclear-DNA content (Burton and Bickham, 1989). The first color photo published in the *Journal of Mammalogy* appeared in an article by Baker et al. (1992) that documented the number of ribosomal gene sites in bats using fluorescent in situ hybridization. Although these new developments have failed, thus far, to reinvigorate the field of mammalian cytogenetics within the pages of the *Journal of Mammalogy,* there is little doubt that the next generation of mammalogists will rediscover the value of cytogenetic characters for genetic and systematic inquiry.

*Geographic and taxonomic coverage.*—Published literature in the *Journal of Mammalogy* shows a strong emphasis on North American species. This geographic bias is likewise reflected in the set of 130 studies categorized herein as cytogenetic research. For example, 102 of the 130 studies (78%) published between 1920 and 1990 in the field of cytogenetics have dealt exclusively with North American species. Of the remaining 35 studies, 22 (17%) have involved Central or South American species, 6 (5%) have focused on African species, 5 (4%) on Asian species, and 2 (2%) on Australian or New Zealand species.

All 79 karyotypes published in the *Journal of Mammalogy* during its initial 50 years of existence (1920–1969) were from either rodents (14 studies/45 species) or bats (three studies/34 species). This trend was broken in 1970 when Holden and Eabry published the karyotypes of two species of rabbits (*Sylvilagus*). The first cetacean (Kulu et al., 1971) and artiodactyl (Nadler, 1971) karyotypes were published in volume 52, and the first carnivore karyotype appeared a year later (Wurster-Hill, 1973). Yates and Schmidly

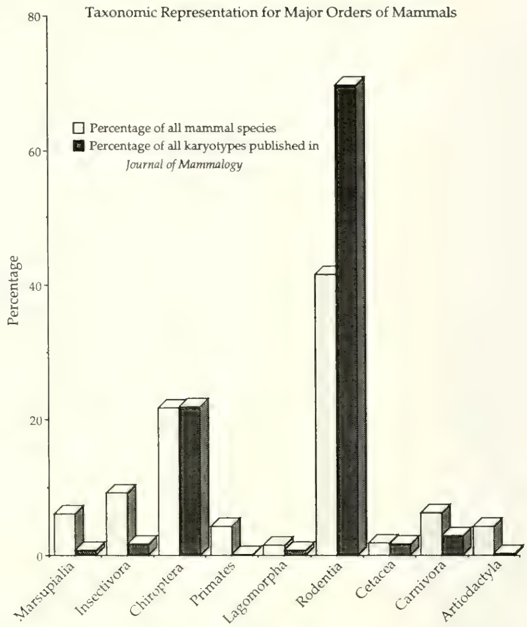



FIG. 2.—Taxonomic bias in the cytogenetics literature published in the *Journal of Mammalogy.* For each of the nine orders of mammals listed, the bar on the left represents the percentage of all extant mammalian species that belong to that order and the bar on the right indicates the percentage of all karyotypes published in the *Journal of Mammalogy* relating to species of that order. Note that rodents are over-represented in the cytogenetics literature, whereas all other groups, except bats, are under-represented relative to their species abundance.

(1975) reported the first insectivore karyotype, and the first marsupial karyotype appeared almost a decade later (Seluja et al., 1984). Surprisingly, no other mammalian order is represented by karyotypes published in the *Journal.*

Considering that bat species (Chiroptera) comprise approximately 22% of all living species of mammals (Anderson and Jones, 1984), it seems appropriate that roughly 22% of all karyotypes that have appeared in the *Journal of Mammalogy* are from species of bats (Fig. 2). In contrast, rodents comprise approximately 42% of extant mammal species, yet nearly 70% of all karyotypes reported in the *Journal* are of rodents. This striking taxonomic bias in favor of rodents is probably a consequence of the fact that most rodents are small and easily captured and karyotyped.

## *Summary and Conclusions*

The field of cytogenetics was in its infancy when the ASM was founded in 1919. Perhaps in part because the *Journal of Mammalogy* was not yet widely known in international circles, early workers in the field of mammalian cytogenetics chose to publish results of their studies in journals with wider readership; hence the *Journal* played only a minor role in the early development of the field. In the 1960s, methodological advances developed by several mammalogists, including Charles F. Nadler, James L. Patton, and Robert J. Baker, finally brought the *Journal of Mammalogy* into the mainstream of cytogenetics research.

The future of cytogenetic studies is especially promising. Recent advances in chromosome painting (Lengauer et al., 1990, 1991), which can provide resolution to homologous chromosomal regions among distantly related taxa, should permit survey type work among various groups of mammals. Polymerase chain reaction amplification of chromosomal loci with conserved primers (Koch et al., 1991; Terkelsen et al., 1993) should also be readily adaptable to the types of investigations that are valuable to the science of mammalogy. The use of multi-color in situ hybridizations (Reid et al., 1992; Scherthan et al., 1992) will permit examination of the order of genes on a chromosome during a single experiment. Chromosomal banding through computerized images using fluorescent dyes (K. L. Bowers, pers. comm.; Volpi and Baldini, 1993; Ward et al., 1991) will greatly facilitate identification of chromosomes without the numerous replications required by the old trypsin methods. The development of in situ probes from DNA libraries should provide countless loci to be mapped. These advances indicate that we are only beginning to see the methodological improvements that will aid in cytogenetic analyses. Amid this technological growth, we note that there is a tremendous number of mammals for which karyotypic data are not available. Survey work in these areas is also desirable.

## *Literature Cited*


Anderson, S., and J. K. Jones, Jr. (eds.). 1984. Orders and families of Recent mammals of the world. John Wiley & Sons, New York, 686 pp.

Arnheim, N., M. Krystal, R. Schmickel, G. Wilson, O. Ryder, and E. Zimmer. 1980. Molecular evidence for genetic exchange among ribosomal genes on nonhomologous chromosomes in man and apes. Proceedings of the National Academy of Sciences, USA, 77:7323–7327.

Arrighi, F. E., and T. C. Hsu. 1971. Localization of heterochromatin in human chromosomes. Cytogenetics, 10:81–86.

Baker, R. J. 1970. Karyotype trends in bats. Pp. 65–96, *in* Biology of bats (W. A. Wimsatt, ed.). Academic Press, New York, 1:1–406.

Baker, R. J., and J. W. Bickham. 1980. Karyotypic evolution in bats: evidence of extensive and conservative chromosomal evolution in closely related taxa. Systematic Zoology, 29:239–251.

———. 1986. Speciation by monobrachial centric fusions. Proceedings of the National Academy of Sciences, USA, 83:8245–8248.

Baker, R. J., and J. L. Patton. 1967. Karyotypes and karyotypic variation of North American vespertilionid bats. Journal of Mammalogy, 48:270–286.

Baker, R. J., M. B. Qumsiyeh, and C. S. Hood. 1987. Role of chromosomal banding patterns in understanding mammalian evolution. Pp. 67–96, *in* Current mammalogy (H. H. Genoways, ed.). Plenum Press, New York, 1:1–519.

Baker, R. J., M. Maltbie, J. G. Owen, M. J. Hamilton, and R. D. Bradley. 1992. Reduced number of ribosomal sites in bats: evidence for a mechanism to contain genome size. Journal of Mammalogy, 73:847–858.

Bickham, J. W. 1979. Chromosomal variation and evolutionary relationships of vespertilionid bats. Journal of Mammalogy, 60:350–363.

———. 1987. Chromosomal variation among seven species of lasiurine bats (Chiroptera: Vespertilionidae). Journal of Mammalogy, 68:837–842.

Blakeslee, A. F., and A. G. Avery. 1937. Methods of inducing doubling in chromosomes in plants. Journal of Heredity, 28:392–411.

Blanks, G. A., and H. S. Shellhammer. 1968. Chromosome polymorphism in California populations of harvest mice. Journal of Mammalogy, 49:726–731.

Bradley, R. D., and H. A. Wichman. In press. Rapidly evolving repetitive DNAs in a conservative genome: a test of factors that affect chromosomal evolution. Chromosome Research.

Bull, J. J. 1983. Evolution of sex determining mechanisms. Benjamin/Cummings, London, 316 pp.

Burton, D. W., and J. W. Bickham. 1989. Heterochromatin variation and DNA content conservatism in *Geomys attwateri* and *Geomys breviceps* (Rodentia: Geomyidae). Journal of Mammalogy, 70:580–591.

Bush, G. L., S. M. Case, A. C. Wilson, and J. L. Patton. 1977. Rapid speciation and chromosomal evolution in mammals. Proceedings of the National Academy of Sciences, USA, 74:3942–3946.

Caspersson, T., L. Zech, and C. Johanson. 1970. Differential banding of alkylating fluorochromes in human chromosomes. Experimental Cell Research, 60:315–319.

Caspersson, T., et al. 1968. Chemical differentiation along metaphase chromosomes. Experimental Cell Research, 49:219–222.

Copeland, N. G., et al. 1993. A genetic linkage map of the mouse: current applications and future prospects. Science, 262:57–66.

Dover, G. A. 1982. Molecular drive: a cohesive mode of species evolution. Nature, 299:111–117.

Dunn, L. C. 1921. Unit character variation in rodents. Journal of Mammalogy, 2:125–140.

Dutrillaux, B., and J. Lejeune. 1971. Sur une nouvelle technique d'analyse du caryotype humain. Comptes Rendus de l'Academie des Sciences (Paris) D, 272:2638–2640.

Ford, C. E., J. L. Hamerton, and G. B. Sharman. 1957. Chromosome polymorphism in the common shrew. Nature, 180:392–393.

Fraccaro, M., et al. 1980. The 11q;22q translocation: a European collaborative analysis of 43 cases. Human Genetics, 56:21–51.

Frommer, M., C. Paul, and P. C. Vincent. 1988. Localization of satellite DNA sequences on human metaphase chromosomes using bromodeoxyuridine-labelled probes. Chromosoma, 97:11–18.

Gall, J. G., and M. L. Pardue. 1969. Formation and detection of RNA-DNA hybrid molecules in cytological preparations. Proceedings of the National Academy of Sciences, USA, 63:378–383.

Graphodatsky, A. S. 1989. Conserved and variable elements of mammalian chromosomes. Pp. 95–123, *in* Cytogenetics of animals (C. R. E. Halnan, ed.). CAB International Press, Wallingford, Oxon, United Kingdom, 519 pp.

Greenbaum, I. F., and R. J. Baker. 1978. Determination of the primitive karyotype for *Peromyscus*. Journal of Mammalogy, 59:820–834.

Haiduk, M. W., R. J. Baker, L. W. Robbins, and D. A. Schlitter. 1981. Chromosomal evolution in African Megachiroptera: G- and C-band assessment of the magnitude of change in similar standard karyotypes. Cytogenetics and Cell Genetics, 29:221–232.

Hall, E. R. 1981. The mammals of North America. Second ed. John Wiley & Sons, New York, 1:1–600 + *90*.

Hamilton, M. J., R. L. Honeycutt, and R. J. Baker. 1990. Intragenomic movement, sequence amplification and concerted evolution in satellite DNA in harvest mice, *Reithrodontomys*: evidence from in situ hybridization. Chromosoma, 99:321–329.

Hamilton, M. J., G. Hong, and H. A. Wichman. 1992. Intragenomic movement and concerted evolution of satellite DNA in *Peromyscus*: evidence from in situ hybridization. Cytogenetics and Cell Genetics, 60:40–44.

Henking, H. 1891. Über Spermatogenese bei *Pyrrhocoris apterus*. Z. wiss. Zoology, 51:685.

Holden, E., and H. S. Eabry. 1970. Chromosomes of *Sylvilagus floridanus* and *Sylvilagus transitionalis*. Journal of Mammalogy, 51:166–168.

Hood, C. S., L. W. Robbins, R. J. Baker, and H. S. Shellhammer. 1984. Chromosomal studies and evolutionary relationships of an endangered species, *Reithrodontomys raviventris*. Journal of Mammalogy, 65:655–667.

Hoy, W. E., Jr., and K. Berlowitz. 1931. A method for the fixation of mammalian chromosomes in the field. Journal of Mammalogy, 12:397–400.

Hsu, T. C. 1952. Mammalian chromosomes in vitro. I. The karyotype of man. Journal of Heredity, 43: 172.

———. 1979. Human and mammalian cytogenetics: an historical perspective. Springer-Verlag, New York, 186 pp.

Hsu, T. C., and K. Benirschke (eds.). 1967. An atlas of mammalian chromosomes. Volumes 1–4. Springer-Verlag, New York, 1967–1970.

Hughes, A. 1952. Some effects of abnormal tonicity on dividing cells in chick tissue cultures. Quarterly Journal of Microscopical Science, 93:207–220.

John, B., and K. R. Lewis. 1966. Chromosome variability and geographic distribution in insects. Science, 152:711–721.

John, H., M. L. Birnsteil, and K. W. Jones. 1969. RNA-DNA hybrids at cytological levels. Nature, 223: 582–587.

Johnson, M. L., and B. T. Ostenson. 1959. Comments on the nomenclature of some mammals of the Pacific northwest. Journal of Mammalogy, 40:571–577.

King, R. C., and W. D. Stansfield. 1990. A dictionary of genetics. Fourth ed. Oxford University Press, New York, 406 pp.

Koch, J., J. Hindkjær, J. Morgensen, S. Kølvraa, and L. Bolund. 1991. An improved method for chromosome specific labeling of alpha satellite DNA in situ using denatured double stranded DNA probes as primers in a PRimed IN Situ labeling (PRINS) procedure. Genetic Analysis and Technical Applications, 8:171–178.

Koop, B. F., R. J. Baker, and H. H. Genoways. 1983. Numerous chromosomal polymorphisms in a natural population of rice rats (*Oryzomys*: Cricetidae). Cytogenetics and Cell Genetics, 35:131–135.

Krishnan, A. 1968. Time-lapse and ultrastructure studies on the reversal of mitotic arrest induced by vinblastine sulfate in Earle's L cells. Journal of National Cancer Institute, 41:581–596.

Kulu, D. D., I. Veomat, and R. S. Sparkes. 1971. Cytogenetic comparisons of four species of cetaceans. Journal of Mammalogy, 52:828–832.

Langer, P. R., A. A. Waldrop, and D. C. Ward. 1981. Enzymatic synthesis of biotin-labeled polynucleotides: novel nucleic acid affinity probes. Proceedings of the National Academy of Sciences, USA, 78:6633–6637.

LEE, M. R., AND E. G. ZIMMERMAN. 1969. Robertsonian polymorphism in the cotton rat, *Sigmodon fulviventer.* Journal of Mammalogy, 50:333–339.

LENGAUER, C., ET AL. 1991. Painting of defined chromosomal regions by in situ suppression hybridization of libraries from laser-microdissected chromosomes. Cytogenetics and Cell Genetics, 56:27–30.

LENGAUER, C., H. RIETHMAN, AND T. CREMER. 1990. Painting of human chromosomes with probes generated from hybrid cell lines by PCR with Alu and L1 primers. Human Genetics, 86:1–6.

MACGREGOR, H. S. 1993. Chromosome research-look forward to 2001. Chromosome Research, 1:5–7.

MAKINO, S. 1951. An atlas of the chromosome numbers in animals. The Iowa State College Press, Ames, 290 pp.

MAKINO, S., AND I. NISHIMURA. 1952. Water pretreatment squash technic: a new and simple practical method for the chromosome study of animals. Stain Technology, 27:1–7

MANUELIDIS, L., P. R. LANGER-SAFER, AND D. C. WARD. 1982. High-resolution mapping of satellite DNA using biotin-labeled DNA probes. Journal of Cell Biology, 95:619–625.

MASCARELLO, J. T. 1978. Chromosomal, biochemical, mensural, penile, and cranial variation in desert woodland woodrats (*Neotoma lepida*). Journal of Mammalogy, 59:477–495.

MASCARELLO, J. T., A. D. STOCK, AND S. PATHAK. 1974*a*. Conservatism in the arrangement of genetic material in rodents. Journal of Mammalogy, 55:695–704.

MASCARELLO, J. T., J. W. WARNER, AND R. J. BAKER. 1974*b*. A chromosome banding analysis of the mechanisms involved in the karyological divergence of *Neotoma phenax* (Merriam) and *Neotoma microps* Baird. Journal of Mammalogy, 55:831–834.

MATSUI, S., AND M. SASAKI. 1973. Differential staining of nucleolus organizers in mammalian chromosomes. Nature, 246:148–150.

MATTHEY, R. 1950. Les chromosomes des vertébrés. Université F. Rouge-Lausanne, 356 pp.

———. 1952. Chromosomes de Muridae (Microtinae et Cricetinae). Chromosoma, 5:113–138.

MCCLINTOCK, B. 1978. Mechanisms that rapidly reorganize the genome. Stadler Symposium, 10:25–47.

MCCLUNG, C. E. 1901. Notes on the accessory chromosome. Anatomischer Anzeiger, 20:220–226.

———. 1902. The accessory chromosome-sex determinant. Biological Bulletin, 3:43–84.

MONTGOMERY, T. H. 1901. A study of the chromosomes of the germ cells of the Metazoa. Transactions of the American Philosophical Society, 20:154–236.

NACHMAN, M. W. 1992*a*. Geographic patterns of chromosomal variation in South American marsh rats, *Holochilus brasiliensis* and *H. vulpinus.* Cytogenetics and Cell Genetics, 61:10–16.

———. 1992*b*. Meiotic studies of Robertsonian polymorphisms in the South American marsh rat, *Holichilus* (sic) *brasiliensis.* Cytogenetics and Cell Genetics, 61:17–24.

NACHMAN, M. W., AND P. MYERS. 1989. Exceptional chromosomal mutations in a rodent population are not strongly underdominant. Proceedings of the National Academy of Sciences, USA, 86:6666–6668.

NADEAU, J. H., AND B. A. TAYLOR. 1984. Length of chromosomal segments conserved since divergence of man and mouse. Proceedings of the National Academy of Sciences, USA, 81:814–818.

NADLER, C. F. 1966. Chromosomes and systematics of American ground squirrels of the subgenus *Spermophilus.* Journal of Mammalogy, 47:579–596.

———. 1971. Chromosomes of the Dall sheep, *Ovis dalli dalli* (Nelson). Journal of Mammalogy, 52:461–463.

NADLER, C. F., AND C. E. HUGHES. 1966. Chromosomes and taxonomy of the ground squirrel subgenus *Ictidomys.* Journal of Mammalogy, 47:46–53.

NADLER, C. F., R. S. HOFFMANN, AND J. J. PIZZIMENTI. 1971. Chromosomes and serum proteins of prairie dogs and a model of *Cynomys* evolution. Journal of Mammalogy, 52:545–555.

NELSON, K., R. J. BAKER, H. S. SHELLHAMMER, AND R. K. CHESSER. 1984. Test of alternative hypotheses concerning the origin of *Reithrodontomys raviventris*: genetic analysis. Journal of Mammalogy, 65: 668–673.

NELSON-REES, W. A., A. J. KNIAZEFF, R. J. BAKER, AND J. L. PATTON. 1968. Intraspecific chromosome variation in the bat, *Macrotus waterhousii* Gray. Journal of Mammalogy, 49:706–712.

O'BRIEN, S. J., H. N. SEUANEZ, AND J. E. WOMACK. 1985. On the evolution of genome organization in mammals. Pp. 519–589, *in* Molecular evolution genetics (R. S. MacIntyre, ed.). Plenum Press, New York, 610 pp.

OHNO, S. 1967. Sex chromosomes and sex-linked genes. Springer-Verlag, New York, 192 pp.

PAINTER, T. S. 1923. Studies in mammalian spermatogenesis. II. The spermatogenesis of man. Journal of Experimental Zoology, 37:291–336.

———. 1925. A comparative study of chromosomes in mammals. The American Naturalist, 59:385–408.

PARDUE, M. L., AND J. G. GALL. 1970. Chromosomal localization of mouse satellite DNA. Science, 168: 1356–1358.

PATTON, J. L. 1967. Chromosome studies of certain pocket mice, genus *Perognathus* (Rodentia, Heteromyidae). Journal of Mammalogy, 48:27–37.

———. 1973. An analysis of natural hybridization between the pocket gophers, *Thomomys bottae* and *Thomomys umbrinus,* in Arizona. Journal of Mammalogy, 54:561–584.

PATTON, J. L., AND R. E. DINGMAN. 1968. Chromosome studies of pocket gophers, genus *Thomomys.* I. The specific status of *Thomomys umbrinus* (Richardson) in Arizona. Journal of Mammalogy, 49:1–13.

PATTON, J. L., AND T. C. HSU. 1967. Chromosomes of the golden mouse *Peromyscus* (*Ochrotomys*) *nuttalli* (Harlan). Journal of Mammalogy, 48:637–639.

PATTON, J. L., AND S. W. SHERWOOD. 1983. Chromosome evolution and speciation in rodents. Annual Review of Ecology and Systematics, 14:139–158.

PINKEL, D., T. STRAUME, AND J. W. GRAY. 1986. Cytogenetic analysis using quantitative, high-sensitivity, fluorescence hybridization. Proceedings of the National Academy of Sciences, USA, 83:2934–2938.

REID, T., A. BALDINI, T. C. RAND, AND D. C. WARD.

1992. Simultaneous visualization of seven different DNA probes by in situ hybridization using combinatorial fluorescence and digital imaging microscopy. Proceedings of the National Academy of Sciences, USA, 89:1388–1392.

Scherthan, H., M. Köhler, P. Vogt, K. von Malsch, and D. Schweizer. 1992. Chromosomal in situ hybridization with double-labeled DNA: signal amplification at the probe level. Cytogenetics and Cell Genetics, 60:4–7.

Scherz, R. G. 1962. Blaze drying, by igniting the fixative, for improved spreads of chromosomes in leucocytes. Stain Technology, 37:386.

Seabright, M. 1971. A rapid banding technique for human chromosomes. Lancet, 2:971–972.

Seluja, G. A., M. V. Di Tomaso, N. Brum-Zorrilla, and H. Cardoso. 1984. Low karyotypic variation in two didelphids (Marsupialia): karyogram and chromosome banding analysis. Journal of Mammalogy, 65:702–707.

Shellhammer, H. S. 1967. Cytotaxonomic studies of the harvest mice of the San Francisco Bay region. Journal of Mammalogy, 48:549–556.

Singh, R. P., and D. B. McMillan. 1966. Karyotypes of three subspecies of *Peromyscus*. Journal of Mammalogy, 47:261–265.

Slifer, E. H. 1934. Insect development: VI. The behavior of grasshopper embryos in anisotonic, balanced salt solution. Journal of Experimental Zoology, 67:137–157.

Stangl, F. B., Jr. 1986. Aspects of a contact zone between two chromosomal races of *Peromyscus leucopus* (Rodentia: Cricetidae). Journal of Mammalogy, 67:465–473.

Stangl, F. B., Jr., and R. J. Baker. 1984. Evolutionary relationships in *Peromyscus*: congruence in chromosomal, genic, and classical data sets. Journal of Mammalogy, 65:643–654.

Stock, A. D. 1974. Chromosome evolution in the genus *Dipodomys* and its taxonomic and phylogenetic implications. Journal of Mammalogy, 55:505–526.

Sumner, A. T. 1990. Chromosome banding. Unwin Hyman, London, 434 pp.

Sumner, A. T., E. H. Evans, and R. A. Buckland. 1971. New technique for distinguishing between human chromosomes. Nature, New Biology, 232:31–32.

Sutton, D. A., and C. F. Nadler. 1969. Chromosomes of the North American chipmunk genus *Eutamias*. Journal of Mammalogy, 50:524–535.

Sutton, W. S. 1902. On the morphology of the chromosome group in *Brachystola magna*. Biological Bulletin, 4:24–39.

———. 1903. The chromosomes in heredity. Biological Bulletin, 4:231–251.

Terkelsen, C., J. Koch, S. Kølvraa, J. Hindkjær, S. Pedersen, and L. Bolund. 1993. Repeated primed in situ labeling: formation and labeling of specific DNA sequences in chromosomes and nuclei. Cytogenetics and Cell Genetics, 63:235–237.

Tjio, J. H., and A. Levan. 1956. The chromosome number of man. Hereditas, 42:1–6.

Volpi, E. V., and A. Baldini. 1993. MULTIPRINS: a method for multicolor primed in situ labeling. Chromosome Research, 1:257–260.

Waldeyer, W. 1888. Über Karyokinese und ihre Beziehung zu den Befruchtungsvorgängen. Archiv für Mikroskopische Anatomie und Entwicklungsmechanik, 32:1.

Ward, D. C., P. Lichter, A. Boyle, A. Baldini, J. Menninger, and S. G. Ballard. 1991. Gene mapping by fluorescent in situ hybridization and digital imaging microscopy. Pp. 291–303 *in* Etiology of human disease at the DNA level (J. Lindsten and U. Petersson, eds.). Raven Press, Limited, New York, 316 pp.

White, M. J. D. 1968. Models of speciation. Science, 159:1065–1070.

———. 1973. Animal cytology and evolution. William Clowes and Sons, London, 961 pp.

———. 1978*a*. Chain processes in chromosomal speciation. Systematic Zoology, 27:285–298.

———. 1978*b*. Modes of speciation. Freeman, San Francisco, 455 pp.

Wichman, H. A., R. A. Van Den Bussche, M. J. Hamilton, and R. J. Baker. 1992. Tranposable elements and the evolution of genome organization in mammals. Genetica, 86:287–293.

Wichman, H. A., C. T. Payne, O. A. Ryder, M. J. Hamilton, M. Maltbie, and R. J. Baker. 1991. Genomic distribution of heterochromatic sequences in equids: implications to rapid chromosomal evolution. Journal of Heredity, 82:369–377.

Wilson, A. C., V. M. Sarich, and L. R. Maxson. 1974. The importance of gene rearrangement in evolution: evidence from studies on rates of chromosomal, protein, and anatomical evolution. Proceedings of the National Academy of Sciences, USA, 71:3028–3030.

Wilson, E. B. 1909. Recent researchers on the determination and heredity of sex. Science, 29:53.

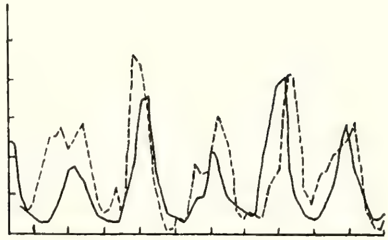
Wurster, D. H., and K. Benirschke. 1970. Indian muntjac, *Muntiacus muntijak*: a deer with a low diploid chromosome number. Science, 168:1364–1366.

Wurster-Hill, D. 1973. Chromosomes of eight species from five families of Carnivora. Journal of Mammalogy, 54:753–760.

Yates, T. L., and D. J. Schmidly. 1975. Karyotype of the eastern mole (*Scalopus aquaticus*), with comments on the karyology of the family Talpidae. Journal of Mammalogy, 56:902–905.

# *POPULATION ECOLOGY*

WILLIAM Z. LIDICKER, JR.



### *Introduction*

The term "population" traces its roots to "people" (Latin populus), which is a collection of human beings. Later it took on the meaning of collections of (usually similar) things. In biology it defines a group of individuals of the same species (kind). Often such groups live in a prescribed place and can be distinguished operationally from other similar groups by partial or complete discontinuities in space or time or both. It is important, however, to recognize that such "natural" groupings are not essential to the "concept" of population; any arbitrarily designated group of individuals of the same species is sufficient. Once a population is designated, it is then possible to investigate whether it can also be defined by spatial or temporal discontinuities. Much confusion results from confounding these two objectives.

Increasingly, biologists find it useful to view the living world (the biosphere) as being organized on different levels of complexity that can be hierarchically arranged. Such a holistic perspective is by no means universally accepted as useful, and in fact this view has progressed rather slowly and fitfully over the past century. The history of population ecology as an intellectual discipline is inextricably connected to that development (Allen and Starr, 1982; McIntosh, 1985; O'Neill et al., 1986).

The concept population fits into the hierarchy of biotic complexity above the level of the individual organism and below that of the community. The concept community is biotically much more complex than population because it concerns a universe (system) that includes more than one species (kind) of living organism. It is often difficult to distinguish studies at the population and community levels because populations almost universally live with and interact with other kinds of living organisms. Nevertheless, a distinction can generally be made on the basis of whether the study is focused on a single species or more than one. This is the same distinction made by the old terms "autecology" and "synecology." Moreover, populations can be viewed conceptually in isolation even if this is rarely realistic, and one can certainly focus attention on one species at a time. A bacterial culture in a test tube is an example of the former and a study of the causes of mortality in a population of deer is an example of the latter. The concept population also fits into a hierarchy of evolutionary units (Brandon and Burian, 1984; Eldridge, 1985; Lewontin, 1970; Salthe, 1985; Vrba and Eldridge, 1984).

This chapter reviews how research on mammals over the last 75 years has influenced population ecology and considers how developments in ecology generally have impacted mammalogy. One of the central issues in population ecology is that of population regulation, and this will therefore constitute a major thread through this chapter. A second theme will concern maturation of the concept "population" along with the recognition of population processes as being real biological phenomena above the level of the individual organism. I use the metaphor of a tree to organize this chapter. First I discuss the historical underpinnings (roots: pre-1930), followed by a review of the early research on population processes in mammals (trunk: 1930–1070). Next is an overview of modern foci in the field (branches: 1970 forward), and finally, I give brief comments on future perspectives (buds). Note that flowers and fruit are left for the future. In the context of this book, the emphasis has been on North American contributions, although I fully acknowledge the immense importance of others to this history.

## *Roots: Initial Thoughts*

The question of what regulates the numbers of organisms all began of course with a focus on a mammal, *Homo sapiens.* Thomas Malthus (1798) pointed out that populations have the capacity to increase exponentially but, except for brief episodes, do not do so. Therefore, negative forces (checks and balances) must operate on populations so as to counter the tendency to increase toward infinity. This insight was critical to the ontogeny of Charles Darwin's thinking about evolution, and an essential ingredient in the development of our understanding of evolution by natural selection. In ecology, however, Malthus' pioneering contribution to the analysis of population processes languished until early in the 20th Century when ecology really started to blossom as a discipline (McIntosh, 1985).

Like the roots of a majestic chestnut, the origins of mammalian population ecology are deep, intricate, numerous, and nourishing. Formal discussions of population birth, death, and growth rates were published in the first few years of this century (Lotka, 1907, and references therein). One influential paper that is often credited with the beginning of modern population theory (at least in North America) was published in 1911 by two economic entomologists working on gypsy moths (Howard and Fiske, 1911). They clearly defined density equilibrium and attributed its achievement to "facultative agents" that increased proportionally in their suppressing effects as density increased. Thus, it was an interest in economically important insects and their control that was the impetus for quantitative thinking about population growth. Entomologists were soon joined by mathematical theorists in the development of quantitative models for population processes (Lotka, 1925; Pearl, 1927; Volterra, 1926, 1931), but these efforts were slow to influence ecologists generally and mammalogists in particular. Early ecology texts hardly mentioned population regulation at all (Chapman, 1931; Shelford, 1913, 1929).

In the early part of this century, mammalogists were preoccupied with faunal surveys and documenting the occurrences and distribution of species and subspecies of mammals (Hamilton, 1955; Miller, 1929). Population-level thinking was not much in evidence, and in fact most systematists harbored a typological philosophy. A common view was that if a specimen were demonstrably different from "typical" individuals, it should be given a formal scientific name so that the fact of its uniqueness would not be lost to the scientific community. As information accumulated on geographic variation within species and within populations, these views were gradually replaced by the realization that populations are not collections of identical individuals, and that these assemblages of individuals also have features beyond those of the individuals that make them up.

Mammalogists also gradually became more interested in ecological questions, especially as information on life histories was acquired. In this they were encouraged by several leaders including Cabrera (1922), Seton (1929), Hamilton (1939), and Bourlière (1951). Wildlife managers also played a critical role in this transition, because they were interested in questions of population regulation and control. Their approach, however, was normally to identify important mortality factors, and not to view populations in any quantitative way (Leopold, 1933; Trippensee, 1948). They also popularized the notion of "optimal density," not only as an ideal of management technology, but also as a natural state of some populations (Bates, 1950; Dasmann, 1964; Elton, 1927; Howard, 1965; Leopold, 1933). The idea was that densities stabilized below a subsistence level so that body size, health, growth, and fecundity would be maximal. There was no recognition of the difficulties such idealism posed for natural selection at the individual level, although professional managers could strive for such a goal.

Another root of critical importance to future population ecology was the gradual development of holistic philosophy. The name and formal description date from Smuts (1926), but the roots are deep and pervasive (Forbes, 1880; Semper, 1881), and include Forbes' "microcosm" (1887) and the infamous "vitalism" of earlier times. Also holistic philosophy has been a dominant thread in many Eastern cultures for at least 2,500 years (Barnett, 1982; Konishi and Îto, 1973; Lidicker, 1988*b*). A few well-known early ecologists struggled with holistic notions (Clements and Shelford, 1939; Elton, 1930: 30; Friederichs, 1927, 1930; Gause, 1934: 2; Thienemann, 1939), but were largely unsuccessful because of a combination of the difficulty of the idea, lack of formal terminology for systems concepts, lack of a data base for population and community processes, and the spectacular successes of reductionist approaches to research (Lidicker, 1978). One example will illustrate this situation. When Clements (1905, 1916) and especially Clements and Shelford (1939) used the metaphor of "complex organism" to express the idea that communities represented a higher order of biological organization than that of individuals, the idea was received with hostility. Today we recognize their supra-organism as an expedient metaphor for an idea almost all ecologists now accept, but only in the suitable format of modern jargon. E. P. Odum deserves considerable credit for encouraging holistic thinking, especially through his influential ecology texts beginning in 1953 (Odum, 1953).

The final major "root" to be mentioned is that of genetics and evolution. These two disciplines developed independently of ecology until recent decades. Of course, there were notable exceptions such as Charles Elton, who was very much an evolutionary biologist as well as an ecologist (Crowcroft, 1991; McIntosh, 1985). For the most part mammalogists thought about evolution in terms of phylogenies and adaptations, but not much about population-level processes. With the "modern synthesis" in the 1940s, evolution and genetics (especially population genetics) were brought together and provided a more appropriate framework for synthesis with ecology (Brown and Wilson, 1994). Still, the entrenched notion that ecological time frames are very much shorter than evolutionary time is still hampering us today. In 1969, I started to teach a lecture course in genetic ecology for graduate students, and remember well that for a number of years I spent the first lecture explaining and justifying such a radical interdisciplinary notion.

## *The Trunk: Early Research on Population Processes*

Early research (1930s and 1940s) on mammalian population ecology emerged from research on life histories and on wildlife and forest management. Hamilton (1955), in his review of American mammalogy, pointed out how important the invention and widespread use of the snap-trap was in encouraging life history studies and in making possible large collections of specimens. Still, populations were not viewed as entities with growth rates, birth rates, and the like. In Hamilton's (1939) classic treatise on American mammals, only one brief chapter is devoted to populations. In this he debunked the "balance of nature" as a fiction pointing to the ubiquitous variability in species numbers. Most of the chapter is devoted to cycles and mass outbreaks. Twelve years later, Gabrielson (1951) similarly allocated only one chapter to "population controls" in his wildlife management text. He also attacked the balance of nature ideal, especially where human influences are present, and briefly discussed interspecific competition, predation, damage to crops and habitat by wildlife, and the control of introduced plants. Trippensee's text (1948) mainly discussed individual game species, followed by a section called "Miscellaneous Wildlife Relationships," with a chapter on "variations in numbers of wild animals" and one on "predator-prey relationships."

Toward the end of this period, mainstream ecologists at least were clear on the components of the population growth equation (Allee et al., 1949; Cole, 1948; Park, 1946). However, no coherent concept of populations being regulated by the quantitative interplay of births, deaths, and dispersal rates was generally expressed. Trippensee (1948:386), for example, seems to have been unaware that an unrestrained positive biotic potential will produce exponential growth toward infinity. Of course, any concept of community processes was even more vaguely perceived. While interspecific competition, predation, and diseases were clearly thought important, no interacting network of interspecific interactions was envisioned. Trippensee (1948: 398), nonetheless, did warn readers that "Predator relationships are complex and cannot be dealt with as simple phenomena," and then illustrated the prevailing simplified viewpoint with a table from Mendall (1944) classifying species of predators into four categories from "distinctly beneficial" to "primarily detrimental."

It is interesting that "cycles" played such a prominent role in discussions of populations even before Elton's (1942) classic work on this subject. Hamilton's (1939) analysis of multi-annual cycles is particularly thorough. He gives most space to sunspots as the causal agent, but in the end finds the evidence inadequate. Paraphrasing his views at that time, cyclic increases seemed to be the result of "abnormal" reproduction, and declines were caused by disease. In Trippensee's (1948) chapter on variations in numbers, four out of 19 references cited have sunspots in the title, and he gives serious support to "cosmic factors" as causative agents. Surprisingly, food was not considered a critical factor at that time, except for lynx (*Lynx canadensis*) during crashes in snowshoe hares (*Lepus americanus*). Generally the feeling was that population growth usually was checked far short of subsistence limitations (McAtee, 1936), a view that was consistent with the prevalent notion of "optimal densities." Hamilton (1939:253) did, however, speculate that the "abnormal" reproduction that led to rodent outbreaks may have been abetted by a vitamin.

The importance given to predation and disease as significant mortality agents went through an interesting transition at that time. Early wildlife biologists (e.g., Leopold, 1933) generally accepted predation and disease as major mortality agents. In this they were supported by the prevailing opinion among insect ecologists that parasites (including parasitoids) were the most important biotic mortality agents. A major shift in thinking can be attributed to the classical work of Errington (1946), whose primary research was on muskrats (*Ondatra zibethicus*). He professed that predators generally took only surplus prey, and therefore had no influence on density levels. This view of benign predation gained rapid popularity, possibly fueled by a reaction to the vehement anti-predator stance of ranchers and government agencies. It reached an extreme form in the Cartwright Principle, which proclaimed that predators could save gallinaceous birds from extinction because when first nests were destroyed, birds re-nested at a more favorable time of the year and hence were more productive (Trippensee, 1948:392). This Erringtonian principle dominated thinking about predation among mammalian ecologists almost to the present day, although, as I will point out, in recent decades important modifications have been advanced.

While mammalogical ecologists were thus occupied, insect ecologists were moving rapidly toward more rigorous and quantitative approaches to population regulation (Lidicker, 1978). Strongly influenced by the mathematical theorists active early in the century, they sought to fit environmental complexities into the relatively simple population models that were being developed. They thus began to think clearly about how various factors can interact quantitatively to bring about changes in population numbers. Some early and spectacular successes in biological control abetted this approach (Dunlap, 1981:31–35). The inherent risk in this path was that simple models led to simple concepts of reality, and investigators were seduced into looking for single factor explanations of population changes. Tremendous advances in experimental biology made possible by reductionist approaches to research made the search for general and elegant explanations of biological phenomena especially tantalizing (Lidicker, 1988*b*). Mammalogists were, of course, not completely isolated from this ferment. Hamilton (1939), for example, quotes the entomologist Uvarov (1931) at length regarding the balance of nature idea, and by the 1950s vertebrate ecologists generally had joined the fray. The Bureau of Population at Oxford under Charles Elton's leadership was one of the centers of ferment and excitement that contributed to the developing synthesis (Crowcroft, 1991).

As changes in numbers were seen increasingly clearly as the product of rate changes in the influences of various environmental "factors," controversies quickly developed. It became widely appreciated in the 1930s that control of numbers required that negative processes (environmental resistance) be positively related to population densities. Some, however, were convinced that the relevant forces were abiotic factors and others were just as sure that they had to be biotic (Lidicker, 1978). On the one side were those most impressed with climate, weather, habitat, fire, and the like as determining numbers, with biotic factors being incidental. Others were sure that biotic factors such as intra-specific competition, food, parasites, and predators were all important, with the abiotic environment simply setting the stage for their actions. Advocates of the former tended to view population densities as strongly variable, even stochastic, with local extinctions common. Champions of biotic control usually saw densities as carefully regulated about an equilibrium that, while not constant, was not random.

Because of the association between abiotic factors and failure to establish a fairly constant equilibrium density, and the corresponding association between biotic factors and density regulation, the term "density independent factor" came to be applied to the abiotic and "density dependent factor" to biotic influences. These terms were introduced by Smith (1935) and quickly became widely used. Unfortunately, they took on so many shades of meaning and innuendo that semantic problems have plagued the subject ever since (Lidicker, 1978; Solomon, 1958). To summarize briefly, density dependence sometimes meant biotic factors, sometimes density regulating, sometimes simply that the factor's effect changed with density, sometimes positively, sometimes negatively, sometimes absolutely and sometimes proportionately, and sometimes it meant that the factor itself (not its effect) changed with density (responsiveness). Similarly, density independence meant whatever density dependence did not: abiotic factors, non-regulating effects, effects that were unrelated to density, were constant numerically or proportionately, or were factors that were simply unresponsive themselves to density changes. Valiant efforts by leading ecologists failed to untangle this muddle (Schwertfeger, 1941; Solomon, 1949; Thompson, 1939).

Clarifying data were slow to accumulate. Because the questions were semantically mired, so were the answers. This was after all before the era of field experiments and hypothesis testing. Excellent laboratory studies were reported that clearly established that both biotic and abiotic factors could regulate numbers, but such information was easily dismissed by field ecologists as irrelevant. Field researchers were generally searching for evidence to support their particular biases and almost always they succeeded. This situation led to a lot of argument and excitement, but little progress toward clarifying the issues of the relative importance of abiotic and biotic influences, how they interacted, and how decimating effects changed quantitatively with density in field populations.

A second circumstance that strongly influenced the way that research on populations was done in this era, and how ecologists thought about the issues was the predominance of reductionist approaches. Not that very many ecologists thought explicitly about what they were doing in these terms but, as already alluded to, holistic thinking was still embryonic and quite difficult. Reductionism was achieving fantastic successes in cell and molecular biology, as well as physiology and medicine. All science students were taught that in good science one asks only "how" something works and not "why" it works the way it does. Naturally, ecologists wanted to be good scientists too.

The emphasis on reductionism had several beneficial effects. It led to many good field and laboratory experiments and it encouraged the practice of carefully studying the effects of various factors on a subject population one by one. This was, and remains, a powerful protocol. To suggest that it had its limitations remains controversial indeed (Gaines et al., 1991; Lidicker, 1991). In my view, however, the single-minded reductionist approach, without a complementary systems (holistic) framework to guide it, ultimately limits understanding (Lidicker, 1988*a*, 1988*b*; Macfadyen, 1975; Odum, 1977). For the time and subject under discussion, the important effect was to encourage investigators to expect simple mechanisms for density regulation to be found. Not only were single key factors regulating densities sought, but it was optimistically hoped that the answer once found could be extrapolated across time, across populations to the entire species, and then across species and even larger taxonomic groupings. After all, general properties of cells, biotic molecules, and genetic codes, were being reported regularly. In retrospect, we now know that this approach failed because density regulation machinery turned out to be generally not simple, and single factor hypotheses are not amenable to this discovery (Hilborn and Stearns, 1982; Lidicker, 1978:133; Smith, 1952). It is analogous to the futile search for *the* cause of cancer.

With various investigators focusing on different aspects of density regulation, new controversies emerged. An important one that is only just now fading is whether extrinsic or intrinsic factors were most important. That is, some argued that factors in the environment directly imposed regulation on the subject population, while others felt that changes in the organisms that constitute the population were the essential variables. It is surprising that ecologists could be so oblivious to the basic paradigm of their discipline, namely the organism-environment interaction system, and to the truism that both the properties of the organisms and the environment change over space and time. Thus, while the intrinsic versus extrinsic argument was ultimately sterile, it did call attention to the importance of looking at the properties of both organism and environment in trying to understand population processes (Lidicker, 1978).

Another development in the 1940s to which mammalogists made critical contributions was the acceptance of the life table concept in population ecology (Deevey, 1947). It was, of course, introduced much earlier (Pearl, 1922), but failed to make much of an impact on vertebrate ecologists, probably because the required data were too difficult to acquire with existing technologies. Life tables served to focus attention on the attributes of various age and sex groups within populations, and eventually led to an appreciation for the age and sex structure of populations. The Leslie Matrix (Leslie, 1945) for calculation of population growth is a familiar manifestation of this development. Thus intra-population demographic variation was added to the increasing appreciation for genetic variation within populations to generate an increasingly realistic image of population phenomena. Modern population modelers continue to invoke structured populations in their models (Boyce, 1977; Łomnicki, 1980; Schaffer, 1974). One negative aspect of the enthusiasm for life tables was the easy assumption that a particular life table characterized each species. In strict terms, a life table applies to a particular cohort of individuals born over a specified, and usually quite limited, time and space. Confusion on this point continues.

In the 1950s and 1960s, proponents of various classes of density-regulating factors tended to be viewed as "schools of thought." The climatic school was not very popular among vertebrate ecologists (once sunspots were abandoned), but it was sometimes conceded that climatic factors could be critical on the edges of species' ranges. The availability of cover and nest sites were admittedly part of what determined a species' habitat, but were not often considered in determination of densities. Predation and parasitism had their champions, but mammalian ecologists generally seemed to have lost interest in disease and the Erringtonian Principle diminished faith in the efficacy of predators (Errington, 1963; Howard, 1953).

The extrinsic factor with the most widespread support was that of food. Lack (1954, 1966) had eloquently argued for food limitation being the primary regulating factor. It was logical (all organisms required nutrition), and it fit into the emerging synthesis of evolutionary thinking in ecology (organisms should evolve so as to maximally use their food supplies). Detractors, however, pointed to contradictory evidence in specific cases, to the potential (and frequently to evidence as well) for regulation by nonfood factors, and to the necessity that consistent regulation by food requires optimal tracking by a population of its food resources. The food theory also became more sophisticated. While food quantity was stressed at first, nutrients later became recognized as potentially limiting (Pitelka and Schultz, 1964).

Other researchers turned their attention to intrinsic mechanisms. For some, self-regulation made sense in that organisms would seem to be better off if they were not always at the point of exhausting their resources (e.g., Wynne-Edwards, 1962, 1965). Prudence demanded some measure of self control. Others were disappointed that no extrinsic factor was found that fulfilled the hope of a general regulating factor. A technique that became widely utilized at this time was to grow populations of small mammals in laboratory or outdoor enclosures. In this way a bridge between the laboratory and field was forged, and population processes could be studied in a circumstance such that either intrinsic or extrinsic factors could be manipulated individually.

One class of intrinsic factors that was studied extensively was that of physiological change associated with varying densities. An early hypothesis of Chitty (1952, 1955, 1958) that high densities led to physiological damage that increased mortality rates and moreover could be passed on to offspring during gestation or lactation was later abandoned by him (Chitty, 1960, 1967). Christian (1950) introduced the intriguing idea that exhaustion of the adreno-pituitary system may be involved in population declines. High densities would feature a variety of stressors, he suggested, and hence the proximate causes of mortality would be non-specific. Later (Christian, 1955*a*, 1955*b*, 1959, 1961; Christian and Davis, 1955) he expanded the model to suggest that high densities activated the stress resistance mechanisms of the body, eventually resulting in their exhaustion. Reduced reproductive competence and death soon followed. A related phenomenon was the "shock disease" widely associated with population crashes in snowshoe hares. As this was known to involve hypoglycemia and non-specific mortality agents, it could easily be fitted into the stress hypothesis. Trippensee (1948:392), however, thought shock disease was caused by a lack of minerals in the diet. Many researchers pursued these ideas, and by the end of the 1960s the situation could be summarized as follows (Lidicker, 1978): the stress syndrome was real in laboratory situations, but was not found to be generally applicable to field populations.

A second class of intrinsic factors to be proposed was that of behavioral changes with density. Territoriality, fighting, dispersal, and cannibalism all could change with density and may be expected to have demographic consequences. Wynne-Edwards (1962, 1965, 1986) proposed that "epideictic displays" were a mechanism by which individuals communicated their density circumstances to each other. As such, this notion was criticized for not making sense in the context of individual selection, but could be defended by involving group selection mechanisms (Wynne-Edwards, 1986). The use of enclosed populations led to the discovery of behaviorally-mediated reproductive inhibition (Calhoun, 1949, 1962; Crowcroft and Rowe, 1957; Davis, 1949; Lidicker, 1965; Petrusewicz, 1957; Southwick, 1955). In fact, Petrusewicz (1957) startled ecologists with his evidence that in laboratory colonies of house mice (*Mus musculus*), a socially-inhibited group can be induced to resume reproduction simply by moving it to a new cage, even a smaller one. Otherwise, phenotypic behavioral changes with density were mainly studied in more recent decades.

Genotypic shifts in populations with density changes were the third class of intrinsic factors contemplated seriously as regulating mechanisms. Led by Chitty (1960, 1967) and Krebs (1964, 1971), the stimulating idea was proposed that selective pressures varying with density favored different genotypes at high versus low densities, and the corresponding shifts in gene frequencies led to predictable demographic consequences. Such ideas had been suggested earlier for insect populations (Turner, 1960; Wellington, 1960; Wilbert, 1963), but Chitty and Krebs applied them specifically to density cycles of microtine rodents and suggested that aggressive versus docile behavior was the relevant behavior being selected. Later they hypothesized that, instead of aggression, the behavior being selected was spacing behavior including dispersal (Krebs, 1979*a*; Krebs et al., 1973). These ideas were so important that they strongly influenced the character and direction of research on small-mammal populations in subsequent decades.

Over the roughly four decades covered in this section (1930s through 1960s), some general trends in the relative importance of mortality, natality, and movements in and out of populations (immigration and emigration, respectively; Lidicker, 1975) can be discerned. Of course, early in this period, mammalian researchers did not usually think of these processes as interacting variables in a growth equation. Early emphasis was on mortality; reproduction was thought to be almost always "normal," i.e., nonvarying. In fact, Smith (1935), in his seminal paper defining density dependence and independence, referred to density dependent factors as mortality agents only. Even Dasmann (1964) discussed density dependence only in terms of mortality. Gradually, the importance of reproduction gained appreciation, especially as data accumulated showing that it too could vary with density. At first, "abnormally" good reproduction was thought to produce population outbreaks (Hamilton, 1939:274), but then it became apparent that reproduction often declines with increasing density as well (see Howell, 1923, for a pioneering example). This new focus on reproduction reaches an extreme with demographers who tend to view human population growth rates as mainly influenced by birth rates and hardly at all by mortality, a tradition going back at least to Pearl (1925).

Movements in and out of populations were not given much attention (but see Hamilton, 1953). Early on, dispersal was viewed as destabilizing because individuals were visualized as moving about in search of favorable circumstances, thus increasing the variability of local densities. Then, as growth equations entered the arena, growth rates were defined as birth rates minus death rates ($r$). This dogma swept through the text books and assured that immigration and emigration would not be considered seriously. When they were mentioned at all, they were dismissed as trivial or balanced between imports and exports and therefore ignorable. If significant emigration was acknowledged, it was lumped with mortality under the rubric "gross mortality." Except for the paper by Howard (1960) postulating that both "genetic" and "environmental" dispersal may occur, and my own paper (Lidicker, 1962) suggesting that emigration should be examined for its possible effects in density regulation, the fervor of interest in dispersal came in later decades.

I end this section with a caveat and mention of two exceptional individuals. For the four decades covered here, I have tried to portray major themes of intellectual development. As time progressed through the period, it becomes increasingly difficult to follow one thread. Our disciplinary "trunk" forms major branches and many more researchers are involved. Moreover, the average intellect that one tries to describe is a statistical artifact drawn from a fairly small sample size. Each individual investigator is of course exceptional in at least some respects. An important exception to this average intellect was Charles Elton, who some consider the father of mammalian population ecology (Berry, 1987). Not only was he an early architect of community concepts (e.g., Eltonian pyramids), but he was an advocate of incorporating evolutionary thinking in ecology long before this was routine. As early as 1930, he expressed the holistic view that a whole biological community could act as a unit of selection (Elton, 1930: 30), and warned that ". . . the modern ecologist runs a risk of . . . falling back upon a severely mechanistic view . . . based on the laws of physics and chemistry, solid in themselves, but unsatisfactory as a complete explanation of the life and mind of animals" (1930:9). Secondly, for the mammalian ecologist, Elton's treatise on voles, mice, and lemmings (1942) was where it all began. His Bureau of Population at Oxford was, moreover, the gestation site for notables such as Dennis Chitty, Peter Crowcroft, Richard Miller, and Mick (H. M.) Southern, and also strongly influenced long-term visitors like Frank Pitelka (see also Crowcroft, 1991).

A second exceptional individual in this formative era was Kazimierz Petrusewicz (Lidicker, 1984). He established in 1952, in the rubble of World War II, a Department of Ecology within the Polish Academy of Sciences, which was elevated in 1971 to the status of an Institute. Petrusewicz was director from 1956 to 1973, during which time Polish ecology became an internationally recognized center of excellence, with important work on mammals. Mammalian research extended from the analysis of population processes in laboratory settings to energetics, production, population regulation, dispersal, social behavior, and wildlife management. Petrusewicz himself was intensely interested in relating evolution to ecological processes, had a sophisticated holistic philosophy, and contemporaneously with Elton was writing papers on concepts of community structure. His influence on population ecology in Poland, eastern Europe, and the world community was profound and long lasting (Lidicker, 1984). He was elected an Honorary Member of the American Society of Mammalogists in 1975 (Taylor and Schlitter, 1994).

## *The Modern Era: The Last Two Dozen Years*

Alluding to our botanical metaphor, we have now reached the stage in the development of our subject where we have branches, lots of branches, both major supports, and idiosyncratic twigs. No longer can we imagine that there is but a single path or even a few major paths of intellectual ontogeny, and it becomes increasingly difficult to review intellectual history by tracing the origin and transmission of key ideas and the influence of especially significant leaders in the process. Of course, there were these, but the abbreviated hindsight of history and the huge dimensions and the establishment make these leaders seem for now more like extenders of intellectual pseudopodia than creaters of new paradigms.

Mammalian population ecology had in this period not only joined the mainstream (I should say maelstrom) of population ecology, but was providing a leading voice. It was and is vigorous, diverse, incredibly interdisciplinary, and has nurtured the germination of new subdisciplines such as evolutionary ecology, behavioral ecology, community ecology, landscape ecology, and conservation biology. Still our enthusiasm cannot quite match that of R. J. Berry who wrote (1987:1) that "... the proper study of biology inevitably involves an investigation of the processes which affect populations."

*ASM programs.*—The increasing attention given to populations and community level phenomena, as well as the expanding diversity of subdisciplines in this field, are reflected in the programs of the annual meetings of the ASM. These programs allow us to monitor and assess the prevailing paradigms over time among working mammalogists, and thus to measure the net progressions of the field (Also see Gill and Wozencraft, 1994).

For this purpose, I classified all the papers in 16 programs covering 1926 to 1991. The classification was subjective and used 10 major categories plus a number of subcategories. There were, or course, a few ambiguous or cryptic titles, and some papers could be placed into more than one category. Because of the scope of this chapter, I focused particularly on papers that seemed to reflect a population or community concept. Ecological papers judged to be at the organismal level were assigned to a "general life history" or "physiology and morphology" category. The few titles with a landscape perspective were lumped with community ecology. A category of "behavioral ecology" was also recognized to include papers that related behavior to ecological processes and that included group behavior such as mating systems or other social behavior. This scheme of categorization allows for the monitoring of research activities at the population or higher levels, which is the subject of this chapter. Otherwise, the plethora of papers in general life history phenomena would obscure these patterns.

The percentage of papers in ecology at the population or higher level is plotted over a 66-year period (Fig. 1). There were no papers in this category in 1926 and only two in 1938. These first in our sample were an address by Joseph Grinnell on "Effects of a wet year on mammalian populations," and one by W. P. Taylor on "Significance of numbers in mammalian ecology." There was

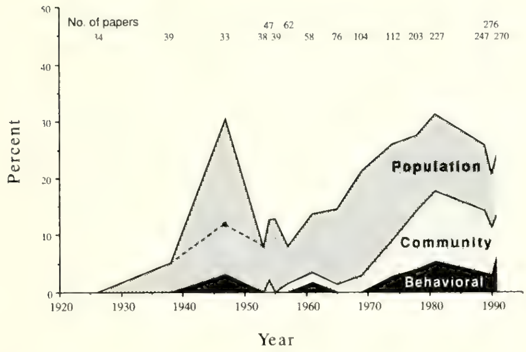



FIG. 1. Percentages of papers on ecological subjects presented at annual meetings of the ASM, based on 16 programs from 1926 to 1991. Ecological papers are allocated to behavioral, population, and community categories based on their primary conceptual level. The dashed line for 1947 indicates the percent of papers in population ecology when six papers in a symposium on populations are omitted.

an increase to nine papers in 1947, but this was almost entirely the result of a symposium on "Population, home range, and territories in mammals." Interestingly, five out of the nine papers were on techniques and another (by Durward L. Allen) was titled "Purposes of population studies." If these six are subtracted, the percentage of ecology papers drops from 30.3 to 12.1% (Fig. 1). This symposium and one at the society's 1950 meeting on the dynamics of mammalian populations mark the beginning of a steady increase in the proportion of papers given on these topics, which reached a peak of 31.3% in 1981 and declined moderately after that.

Papers recognizable as community-level started in the 1954 program and increased rapidly after 1969. One paper was assigned to behavioral ecology in 1947, but the next one was not until 1961, and the third was in 1974. After 1947, the proportion of population-level papers varied hardly at all (6.5–18.3%), with changes in the ecological offerings being due to the addition of community and behavioral ecology contributions (Fig. 1).

*Importance of new techniques.*—An important contributor to the success of population research in this period was the arrival of new and powerful techniques. Whereas the snaptrap and livetrap were the technical "work horses" of the previous era, they were soon supplemented by an impressive list of innovations. Following World War II, radioactive isotopes became readily available and were used to follow individuals, determine pedigrees, reveal movements, and measure various demographic parameters (Stenseth and Lidicker, 1992*a*). Because of health hazards to the investigators as well as to the research subjects and their environments, however, such isotopes are less commonly used now.

A second technique was that of radio-tracking (Amlaner and MacDonald, 1980; McShea and Madison, 1992). At first this approach was restricted to large mammals, but with the increasing miniaturization of transmitters, radios with batteries have shrunk to where even mice can carry them successfully. Telemetry has provided a wonderful opportunity to follow the movements and activities of individual mammals, even through the guts of predators. When numerous individuals in the same population are being followed simultaneously, it is also possible to reveal social interactions, and thereby to understand why certain movements are occurring in addition to describing them.

A more recent development is the use of fluorescent powders to track movements of nocturnal species (Kaufman, 1989). Under favorable circumstances these powders can reveal paths of movement by reflection of ultra-violet light. They have also been used to determine social bonds such as mother-juvenile and adult male-female relationships by detection of the transfer of small amounts of the powder between individuals (Ribble and Salvioni, 1990).

Critically important has been the development of various biochemical techniques. Electrophoresis of blood and tissue proteins and enzymes has been used widely since the late 1960s, and has been an effective tool in assessing the genetic architecture of populations and in measuring relatedness among groups. The analysis of mitochondrial DNA restriction enzyme fragments has also been useful for measuring relationships over a shorter time span than is usually possible with the allozymic variants coded by nuclear DNA. This is because the mutation rate, and hence biochemical drift, is faster with certain sections of mitochondrial DNA than with nuclear. As of this writing, the most exciting new development is that of DNA-fingerprinting. Although a more difficult and laborious technique, it has the potential for unequivocal individual identification as well as for parental exclusion analysis. Thus it has tremendous promise in investigations requiring individual recognition and knowledge of pedigrees. Another new development with great promise is the polymerization chain reaction (PCR), which allows for amplification (multiplication) of small sections of DNA so that such fragments can be sequenced, compared, and relatedness judged. It has also opened up the possibility of using small amounts of DNA surviving in museum specimens and near-fossils to assess relationships among taxa, and perhaps more relevant to the ecologist, is the possibility of charting genetic change in populations over relatively short periods of time. PCR techniques utilizing dinucleotide repeats called "microsatellites" that are widely distributed throughout the mammalian genome may be rich sources of polymorphisms and hence information on relatedness among individuals because of their extensive and presumably neutral variability. New developments useful to the population biologist can be predicted confidently.

Finally, it is appropriate to call attention to the vast improvement in quantitative techniques available to the population biologists. These include powerful computer software packages for organizing and analyzing data, using multivariate statistics, clustering techniques, and the like. Even field methodologies for gathering demographic and other data are greatly improved (Hammond, 1987; Hiby and Jeffery, 1987; Montgomery, 1987; Smith et al., 1975; Ward et al., 1987). Mathematical modeling, both analytical and computer simulation, has benefited our understanding of population processes (Conley and Nichols, 1978; Dekker, 1975; Hestbeck, 1988; Stenseth, 1981, 1983, 1986; Stenseth and Lidicker, 1992*b*), and undoubtedly will play a large role in the future. It helps us to think clearly, to test the quantitative consequences of our ideas, and allows us to synthesize quantities of facts and relationships that would otherwise push beyond the limits of our mental capacities. Modeling only threatens progress when we view mathematical expressions as templates of reality, or as substitutes for data, or confuse mathematical proof with careful testing of hypotheses.

*Intellectual foci.*—I have divided the intellectual history of our subject in the modern era into six interconnected and overlapping foci or themes. A single branch of inquiry is no longer realistic, and, moreover, the order in which I discuss them is completely arbitrary. These vignettes are in no way attempts to review these topics, each of which is a vast subject in itself. The most I can do here is attempt to connect each theme with the previous historical period, and to suggest major intellectual trends. As I have been a participant in this process, the risks of personal biases creeping into the analysis are greater than for the earlier periods. My intention, nevertheless, is to be as objective as possible. One major area omitted here is that of life history evolution (Boyce, 1988). This is because I think of this field as more at the organismal than population level of analysis. Clearly, however, the study of life history extends into the population level especially where gender differences in life history strategy or other polymorphisms occur.

1) Spatial structuring of populations. As mentioned, population ecologists were generally aware of the importance of age and sex structure within populations, continued

to gather data on this, constructed life tables, and increasingly emphasized cohort analysis rather than extrapolation over time or to species as a whole. Appreciation of spatial structure, however, was slower in coming.

Contrary to common sense, populations of organisms were, at the beginning of this modern period, conceptualized as infinite in size and generally panmictic. Such approximations were consistent with the theory of population genetics and evolution then prevailing and with the ubiquitous maps of species' ranges. Although mammalian ecologists generally realized that these simplifications were unrealistic, they did not, I think, appreciate that it mattered very much. In the summer of 1967, P. K. Anderson traveled extensively in the Soviet Union, and learned first hand about the views of several leading Soviet ecologists (particularly B. K. Fenyuk, T. V. Koshkina, N. P. Naumov, P. A. Panteleyev, I. Ya Polyakov, and S. S. Shvarts) concerning the spatial structuring of mammalian populations and the ecological and genetic importance attributed to this structuring. Inspired by these insights (as well as recent research on *Mus musculus*), Anderson (1970) wrote an important review on ecological structure and gene flow in small mammals in which he proposed that genetic and social fragmentation was indeed the rule for species of small mammals and that this implied a dramatic change in the way we should view population biology. Shortly thereafter, Shvarts' book (1969) on the evolutionary ecology of animals was translated into English by A. E. Gill (Shvarts, 1977), and Hansson (1977) wrote his influential paper on the importance of heterogeneous landscapes in the ecology of small mammals. It is important that these contributions appeared in an intellectual environment in which notions of environmental grain (Levins, 1968) were being widely discussed, at least by evolutionary theorists.

In 1978, a symposium on mammalian population genetics was held in conjunction with the annual meetings of the ASM. In reviewing the published volume from this symposium (Smith and Joule, 1981), it is apparent that even at this time, most attention was given to temporal variation in genetic constitution of populations (e.g., Gaines, 1981) and the causes and significance of genetic variation within populations (e.g., Schnell and Selander, 1981). Only one paper gave significant attention to spatial variation on the scale of habitat patches (Massey and Joule, 1981).

Subsequently, the importance of spatial structuring became increasingly recognized as a critical demographic and genetic influence. Currently, it is an extremely fashionable topic of investigation (Hansson and Stenseth, 1988). Even models of density cycles of microtines now are incorporating habitat heterogeneity as a relevant variable (Bondrup-Nielsen and Ims, 1988; Gaines et al., 1991; Lidicker, 1985*a,* 1988*a,* 1991; Ostfeld et al., 1985).

The culmination of this trend is the emergence of the subdiscipline of landscape ecology (Forman and Godron, 1986; Lidicker, 1988*b*), and its application to mammalian ecology (Bauchau and LeBoulengé, 1991; Lidicker et al., 1991; Merriam, 1990, 1991; Szacki and Liro, 1991; Wegner and Merriam, 1990; Wolff, 1980). At this level of biological complexity, systems composed of two or more habitat patches (community-types) are the subject of inquiry. Thus, the role of patch size, edge-to-area ratios, connectedness, and inter-patch fluxes are explicitly investigated. Many new demographic and evolutionary insights can be anticipated as a result of this advance.

2) Dispersal. As pointed out, interest in dispersal was almost non-existent at the beginning of this modern era. Currently, it is one of the most vigorous areas of inquiry in mammalian ecology, marking a development that is clearly one of the most dramatic of this period. Apart from some early signals (Andrzejewski et al., 1963; Howard, 1960; Kalela, 1961; Lidicker, 1962), a burgeoning interest developed in the late 1960s and 1970s (see Fenton and Thomas, 1985; Lidicker, 1975, 1985*b*; McCullough, 1985

for early reviews). In January 1992, the BIOSIS electronic data base listed 7,240 references (Zoological Record, Online, 1978 to 1991) indexed by the descriptor "dispersal."

Basically, what happened were two critical intellectual breakthroughs: 1) the realization that movements into and out of populations (immigration and emigration, respectively) are critical components, along with births and deaths, of population dynamics; and 2) the realization that if populations were not always panmictic and infinite (see previous section), subpopulations must be connected genetically, demographically, and behaviorally by dispersal. Thus, the study of dispersal became a critical ingredient in questions ranging over physiology, behavior, evolution, epidemiology, and conservation biology as well as all levels of complexity in ecology (Stenseth and Lidicker, 1992*c*).

One important factor that helped start this avalanche of research on dispersal was the extensive use of confined populations (enclosures, islands) giving meaning to the fence-effect concept. Thus it was that the study of populations in which dispersal was absent helped us realize how important it was in unconfined situations (Lidicker, 1979*a*). These studies, as well as a growing number on unenclosed populations, led to the explicit recognition that dispersal often occurred before conditions in the home habitat became economically desperate ("pre-saturation dispersal," Lidicker, 1975) and hence at least some dispersal was favored by natural selection ("adaptive," Stenseth, 1983); see Lidicker and Stenseth (1992) for summary of the factors motivating dispersal.

A second important element was the incorporation of dispersal in models of microtine rodent multi-annual cycles. Early papers (Krebs et al., 1973; Lidicker, 1973; Stenseth, 1978; Tamarin, 1978*b*) led to widespread attention to dispersal by microtine ecologists and inspired numerous investigations, empirical and theoretical, as to the role of dispersal in these cycles.

3) Coactions. I use the term "coaction" as a brief equivalent to "interspecific interaction" (Clements, 1916; Clements and Shelford, 1939; Haskell, 1949; Leary, 1985; Lidicker, 1979*b*). Such community-level processes are appropriately reviewed in another chapter (Mares and Cameron, 1994), but it is important to comment here, albeit briefly, on several paradigm shifts occurring in recent decades.

In the last section, I pointed out how the Erringtonian or benign predation view had become the prevailing one. This trend reached an extreme form in Howard's (1965) extension of the Cartright Principle to mammalian predators. He advocated the view that in management of rodent pests, predators were a hindrance rather than a help because they stimulated rodent populations to increase reproductive effort.

Two other shifts in the way predation was viewed were more generally accepted. The first was that in spite of usually lower reproductive rates (than their prey), predators could reduce prey densities through functional rather than numerical responses to prey numbers (Keith and Windberg, 1978; Weaver, 1979). The second change was the realization that predators sometimes made their greatest impact, not on increasing prey populations, but on declining ones. Thus, they have an increasing effect as density falls (anti-regulating, de-stabilizing) and can drive prey densities to extremely low levels (Lidicker, 1975, 1988*a*; MacLean et al., 1974; Maher, 1967; Newsome and Corbett, 1975; Pearson, 1966, 1971, 1985; Wagner and Stoddart, 1972). In the case of ungulates, well-documented examples of predator regulation became available (Caughley, 1970; McCullough, 1979; Peterson and Page, 1983). All of these developments reestablished predation as a potentially important influence in population regulation.

The importance of parasitism in the population biology of mammals went, as explained, from the early assumption that it was important to almost complete neglect. In recent decades a renewed interest is emerging. Partly this was fueled by theoreticians (Anderson and May, 1979; Dietz and Schenzle, 1985; May and Anderson, 1979; Mollison, 1977, 1987), who drew attention to the potential for demographic impact that parasites and disease can have. A second factor was the slowly increasing empirical evidence that parasites can regulate mammalian populations (Anderson, 1982; Anderson et al., 1981; Fenner, 1976; Gregory, 1991; Plowright, 1982; Ross, 1982; Scott, 1988). In my view, this is one area ripe for exploitation by interdisciplinary teams of investigators.

The extent to which species of mammals enter into competitive coactions with each other and with non-mammals began to be explored vigorously by the beginning of this modern period. Early leaders were Rosenzweig (Rosenzweig, 1966, 1973; Schroder and Rosenzweig, 1975), Grant (Grant, 1969, 1972, 1978; Morris and Grant, 1972) and Brown (Brown, 1971; Brown and Davidson, 1977; Brown et al., 1979; Davidson and Brown, 1980; Munger and Brown, 1981). The potentially exciting arena of cooperative coactions (mutualisms) remains to be explored in the future.

4) Social behavior. Although a topic that is discussed more fully in another chapter (Eisenberg and Wolff, 1994), it is important to mention here that studies of social behavior are an increasingly important part of mammalian population biology. Behavior has always been of interest to mammalogists, but until recently it was viewed simply as one element in the description of a species' life history. In recent years social behavior has been studied as a group process impacting in important ways and in turn being influenced by various aspects of evolutionary and ecological dynamics (Armitage, 1988; Berger, 1986, 1988; Cockburn, 1988; Krebs and Davies, 1984; Mech, 1987; Sherman et al., 1991; Slobodchikoff, 1988; Smith and Ivens, 1984; Tamarin et al., 1990). It is this view of behavior that I have included in "behavioral ecology." It began as a serious trend in mammalian ecology about 1970 (Fig. 1). Examples of a few early contributors include King (1955), Eisenberg (1967), Hamilton (1971), Trivers (1971), Kleiman and Eisenberg (1973), Alexander (1974), and Barash (1974). Wilson's (1975) influential opus on sociobiology stands as a monument to this critically important development.

Important current themes in behavioral ecology include: 1) social signaling with special emphasis on the olfactory mode; 2) mating systems; 3) kin recognition and associated cooperative behaviors; 4) plasticity versus tight genetic control of social behavior; 5) effects on demography (e.g., spacing behavior, dispersal, density dependent aggression); and 6) relationships between social structure and genetic structure of populations. Based on a 1980 conference, the ASM published an influential review of mammalian behavioral research (Eisenberg and Kleiman, 1983).

5) Density regulation. The subject of how population densities are regulated continues to be an important, exciting, and controversial area up to the present time. Past debates about "density dependent" versus "density independent" factors and intrinsic versus extrinsic regulation have abated. It is now widely appreciated that densities are influenced by a variety of factors operating in a variety of ways, but that eventually there must be a net increase in the rate at which negative forces act as density increases (regulation) or the Earth would be filled with infinite populations. Such negative forces impose either an upper limit for density or result in an equilibrium level (K) toward which densities tend. Similarly, the intrinsic-extrinsic dichotomy is now generally accepted as a non-issue. The density regulating machinery consists of the organism-environment axis, and not with either component alone (Lidicker, 1978). Properties of the organism and properties of its environment interact to result in a given density with the relative contribution of each

varying, but with both being always involved.

With these contentious issues behind us, much of importance remains. What is the actual regulating mechanism for a given population? How much does this vary spatially and temporally? Are there general patterns for certain taxonomic groups, habitat assemblages, trophic levels, and life styles? Moreover, we need to discover if one or a few factors are consistently of overriding importance for specific populations, with other forces being clearly secondary or contributing only to the variance of densities. How important are time lags and age-sex structure? Finally, can we learn to predict population trajectories accurately, and if not, why not?

A surprising development has been the emergence of sex ratios as important demographic variables. Not only can they vary greatly by microhabitat (Ostfeld et al., 1985), be biased by dispersal (Lidicker and Stenseth, 1992), and influenced by density (Clutton-Brock, 1991; Fredga et al., 1977; van Schaik and Hrdy, 1991), but in some circumstances can be influenced by litter size and maternal social status and condition (Austad and Sunquist, 1986; Clutton-Brock and Albon, 1982; Clutton-Brock and Iason, 1986; Clutton-Brock et al., 1977, 1982; Cockburn et al., 1985; Frank, 1992; Symington, 1987; Verme, 1969). I expect further significant discoveries in this area.

One important trend has been the rediscovery of multi-factorial models of population regulation. In the early part of this century, ecologists and wildlife biologists routinely accepted that populations were subject to a multiplicity of positive and negative forces. Then, as the field became more quantitative, along with the success of reductionist and experimental approaches to research, pressures became intense for finding general and simple explanations for how things worked. Complex and especially idiosyncratic explanations were viewed suspiciously as non-scientific. In recent decades, ecologists have become more comfortable with holistic views and particularly with a research protocol that balances reductionist and holistic aspects (Lidicker, 1988*b*, 1991; Macfadyen, 1975, 1978; McIntosh, 1980; Odum, 1977). This new perspective has encouraged viewing density regulation in a systems context with numerous intrinsic and extrinsic factors interacting together, a multi-factor perspective (Finerty, 1980; Lidicker, 1973, 1978, 1988*a*). Such a perspective is only the starting point, however, as the quantitative relationships among the factors remains to be determined. We need to know the temporal and spatial stability of the patterns observed, and finally we must search for generalities in pattern. This knowledge will allow us to manipulate (manage) population numbers effectively and to make predictions of future density changes, or at least to know when predictions are reliable and when they are not. It will also give us the data to look afresh at some old questions such as the extent to which carrying capacities of habitats and equilibrium densities (K) coincide.

With such a huge agenda ahead of us, it is encouraging that some mammalian ecologists are exploring effectively the realities of this complex world. Pioneering research based on multi-factorial hypotheses has been reported by Wagner and Stoddart (1972), Keith and Windberg (1978), Taitt and Krebs (1983), Sinclair (1986), Hansson and Hentonnen (1988), Desy and Batzli (1989), and others. The approach remains controversial, however (Gaines et al., 1991; Krebs, 1979*b*; Tamarin, 1978*a*); and the future is as unpredictable for this field as it is for many mammalian population densities.

6) Conservation. Conservation biology is the extension of wildlife management from concern for economically important species to the biota as a whole. As such, it was for many decades a legitimate part of biology. Then in the rush and push for "modern science" that swept through biology in the 1960s, conservation became relegated to its political and moral aspects, and was shunned

by the scientific establishment. However, with the accelerating deterioration of the Earth in the 1980s, along with the prospects for massive losses in biodiversity, and with the help of significant pressure from university students, conservation biology reemerged as an important field of scientific inquiry. Even staid academic units began to offer courses, and even major programs, in this area. Helping to legitimatize the field was the establishment of two high quality journals, *Biological Conservation* in 1968 and *Conservation Biology* in 1987. Coincident with the latter event was the initiation of the Society for Conservation Biology, which was an instant success.

Now conservation biologists are applying frontline basic research in population, community, and landscape ecology, as well as evolutionary biology and population genetics to address the mega-threats to humanity caused by losses of biodiversity and the uncontrolled growth of our own species. As they operate from an increasingly firm foundation in basic science, they can and are moving with confidence to embrace political, social, and even moral aspects of the human predicament. Thus, the realistically interdisciplinary nature of the problems are being acknowledged and addressed, but this time, hopefully, without losing a solid footing in the basic sciences. At this writing, society at large is beginning to show a glimmer of recognition for where it is headed, but support for research in the relevant areas remains a tiny fraction of that provided for activities that tend to exacerbate the problems. Whether or not human society at large recognizes its dilemma in time to deal with it humanely is the mega-question for the future.

## Future Perspectives

Even a cursory overview of how population ecology has changed during the past 75 years reveals a dramatic ontogeny. Language has changed, new concepts have appeared, and the empirical base and number of scientists have grown enormously. All these facts signal that the field has not yet reached maturity, and so should have a long future. A seedling has indeed grown into a young tree. In this development, mammalogists have played critical and constructive roles.

Setting aside this developmental metaphor, one can predict with confidence that mammalian population ecology will not fade away. Just as the structure and function of organisms and of cells is fundamental to any overview of biology, so too is the structure and function of populations. Populations, moreover, are the parts (holons) for communities and landscapes that in turn cannot be understood without knowledge of these constituents. Besides, as outlined in the six preceding vignettes about the current status of subdisciplines within population ecology, there is much to be learned at this level as well.

Trying to be as subjective as possible, I suggest that the following topics will receive increasing attention in the near future:

1. Relating genetic structure to demographic and social structure, giving new insights to all three areas, and tending to blur the traditional distinction between ecological and evolutionary time scales;
2. Focusing on landscape-level issues, both for their intrinsic interest and because community-types are being increasingly fragmented;
3. Understanding of dispersal as critical inputs and outputs to population systems and a major connector and information link within meta-populations;
4. Recognizing parasitic and cooperative coactions as important community organizers;
5. Exploring the interplay of social behavior and other aspects of population biology, with the emphasis being on mutual effects, and on a comparative approach;

6. Appreciating the local complexity and global simplicity of density regulating mechanisms, and reconciling this apparent paradox through multi-factor models; and
7. Giving all the support we can to arresting the decline in our life-support system through conservation biology and related efforts.

Where do mammals and mammalogists fit into all of this relating, focusing, understanding, recognizing, exploring, appreciating, and giving? Right at the front lines. Mammals are among the more complex inhabitants of this planet; so if we can understand them, we can provide guidelines for the rest. Also, being larger and cleverer than most creatures, they often represent keystone species (strong interactors) in their communities. As such, they often can serve as indicator species for the status and stability of intractably complex chunks of the biosphere. Finally, mammals include the species *Homo sapiens.* Thus for us, mammals are our closest kin, and no wonder many are loved, feared, admired, or reviled. When we study life, we learn about our planet and ourselves, but when we study mammals we come even closer to intimate understanding.

## Acknowledgments

History abhors any attempt to define boundaries around those who can be credited or blamed for any effort at reconstruction. All one's experiences contribute in intangible ways. Nevertheless, I gratefully acknowledge R. H. Tamarin who contributed to early discussions regarding the scope and content of this chapter, C. W. Wozencraft who kindly trusted me with seven programs of ASM annual meetings from the society's archives, E. P. Odum for helpful discussions, and the editors of this volume for choosing me for this assignment. Both Tamarin and an anonymous reviewer made many helpful suggestions for improving the manuscript. L. N. Lidicker gave logistic and other support throughout the project.

## Literature Cited

Alexander, R. D. 1974. The evolution of social behavior. Annual Review of Ecology and Systematics, 5:325–383.

Allee, W. C., A. E. Emerson, O. Park, T. Park, and K. P. Schmidt. 1949. Principles of animal ecology. W. B. Saunders, Philadelphia, Pennsylvania, 837 pp.

Allen, T. F. H., and T. B. Starr. 1982. Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago, 310 pp.

Amlaner, C. J., and D. W. MacDonald (eds.). 1980. A handbook on telemetry and radio tracking. Pergamon Press, Elmsford, New York, 804 pp.

Anderson, P. K. 1970. Ecological structure and gene flow in small mammals. Symposia of the Zoological Society of London, 26:299–325.

Anderson, R. M. 1982. Fox rabies. Pp. 242–261, *in* Population dynamics of infectious diseases: theory and applications (R. M. Anderson, ed.). Chapman and Hall, London, 368 pp.

Anderson, R. M., and R. M. May. 1979. Population biology of infectious diseases: Part I. Nature, 280: 361–367.

Anderson, R. M., H. C. Jackson, R. M. May, and A. D. M. Smith. 1981. Population dynamics of fox rabies in Europe. Nature, 289:765–61.

Andrzejewski, R., A. Kajak, and E. Pieczynska. 1963. Efecty migracji. Ekologia Polska, Seria B, 9:161–172.

Armitage, K. B. 1988. Resources and social organization of ground-dwelling squirrels. Pp. 131–155, *in* The ecology of social behavior (C. N. Slobodchikoff, ed.). Academic Press, San Diego, 429 pp.

Austad, S., and M. E. Sunquist. 1986. Sex-ratio manipulation in the common opossum. Nature, 324: 58–60.

Barash, D. P. 1974. The evolution of marmot societies: a general theory. Science, 185:415–420.

Barnett, R. J. 1982. Chinese sages and western biologists. Asianist (California State University, Chico), 7:3–13.

Bates, M. 1950. The nature of natural history. Charles Scribner, New York, 309 pp.

Bauchau, V., and E. LeBoulengé. 1991. Population biology of woodland rodents in a patchy landscape. Pp. 275–283, *in* Le rongeur et l'espace (M. LeBerre and L. Le Guelte, eds.). R. Chabaud, Paris, 362 pp.

Berger, J. 1986. Wild horses of the Great Basin: social competition and population size. University of Chicago Press, Chicago, 326 pp.

———. 1988. Social systems, resources, and phylogenetic inertia: an experimental test and its limitations. Pp. 157–186, *in* The ecology of social behavior (C. N. Slobodchikoff, ed.). Academic Press, San Diego, 429 pp.

Berry, R. J. 1987. Population studies of mammals. Symposia of the Zoological Society of London, 58: 1–5.

Bondrup-Nielsen, S., and R. A. Ims. 1988. Predicting stable and cyclic populations of *Clethrionomys.* Oikos, 52:178–185.

Bourlière, F. 1951. Vie et moeurs des mammiferes. Payot, Paris, 249 pp.

Boyce, M. S. 1977. Population growth with stochastic fluctuations in the life table. Theoretical Population Biology, 12:366–373.

Boyce, M. S. (ed.). 1988. Evolution of life histories of mammals. Yale University Press, New Haven, Connecticut, 373 pp.

Brandon, R. N., and R. M. Burian (eds.). 1984. Genes, organisms, populations: controversies over the units of selection. Massachusetts Institute of Technology Press, Cambridge, Massachusetts, 329 pp.

Brown, J. H. 1971. Mechanisms of competitive exclusion between two species of chipmunks. Ecology, 52:305–311.

Brown J. H., and D. W. Davidson. 1977. Competition between seed-eating rodents and ants in desert ecosystems. Science, 196:880–882.

Brown, J. H., and D. E. Wilson. 1994. Natural history and evolutionary ecology. Pp. 377–397, *in* Seventy-five years of mammalogy (1919–1994) (E. C. Birney and J. R. Choate, eds.). Special Publication, The American Society of Mammalogists, 11:1–433.

Brown, J. H., D. W. Davidson, and O. J. Reichman. 1979. An experimental study of competition between seed-eating desert rodents and ants. American Zoologist, 19:1129–1143.

Cabrera, A. 1922. Manual de Mastozoologia. Compania Anonima de Libreria, Madrid, 440 pp.

Calhoun, J. B. 1949. A method for self-control of population growth among mammals living in the wild. Science, 109:333–335.

———. 1962. The ecology and sociology of the Norway rat. United States Department of Health, Education, and Welfare, Public Health Service Publication, 1008, Bethesda, Maryland, 288 pp.

Caughley, G. 1970. Eruption of ungulate populations, with emphasis on Himalayan thar in New Zealand. Ecology, 51:53–72.

Chapman, R. N. 1931. Animal ecology. McGraw-Hill Book Company, New York, 464 pp.

Chitty, D. 1952. Mortality among voles (*Microtus agrestis*) at Lake Vyrnwy, Montgomeryshire in 1936-9. Philosophical Transactions of the Royal Society of London, Series B, Biological Science, 236:505–552.

———. 1955. Adverse effects of population density upon the viability of later generations. Pp. 57–67, *in* The numbers of man and animals (J. B. Cragg and N. W. Pirie, eds.). Institute of Biology Symposia, 4, Oliver and Boyd, Edinburgh, 152 pp.

———. 1958. Self-regulation of numbers through changes in viability. Cold Spring Harbor Symposia on Quantitative Biology, 22:277–280.

———. 1960. Population processes in the vole and their relevance to general theory. Canadian Journal of Zoology, 36:99–113.

———. 1967. The natural selection of self-regulatory behaviour in natural populations. Proceedings of the Ecological Society of Australia, 2:51–78.

Christian, J. J. 1950. The adreno-pituitary system and population cycles in mammals. Journal of Mammalogy, 31:247–259.

———. 1955*a*. The effect of population size on the weights of the reproductive organs of white mice. Naval Medical Research Institute Research Report, 13:81–88.

———. 1955*b*. Effect of population size on the adrenal glands and reproductive organs of male mice in populations of fixed size. American Journal of Physiology, 182:292–300.

———. 1959. The roles of endocrine and behavioral factors in the growth of mammalian populations. Pp. 71–97, *in* Comparative endocrinology (A. Gorbman, ed.). John Wiley & Sons, Incorporated, New York, 746 pp.

———. 1961. Phenomena associated with population density. Proceedings of the National Academy of Sciences, USA, 47:428–449.

Christian, J. J., and D. E. Davis. 1955. Reduction of adrenal weight in rodents by reducing population size. Transactions of the North American Wildlife Conference, 20:177–189.

Clements, F. E. 1905. Research methods in ecology. University Publishing Company, Lincoln, Nebraska, 334 pp.

———. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Institute of Washington, Publication, 242, Washington, D.C., 512 pp.

Clements, F. E., and V. E. Shelford. 1939. Bio-ecology. John Wiley & Sons, Incorporated, New York, 425 pp.

Clutton-Brock, T. H. 1991. The evolution of parental care. Princeton University Press, Princeton, 352 pp.

Clutton-Brock, T. H., and S. D. Albon. 1982. Parental investment in male and female offspring in mammals. Pp. 223–258, *in* Growing points in ethology (P. P. G. Bateson and R. A. Hinde, eds.). Cambridge University Press, Cambridge, 548 pp.

Clutton-Brock, T. H., and G. R. Iason. 1986. Sex ratio variation in mammals. The Quarterly Review of Biology, 61:339–374.

Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. Red deer: the behavior and ecology of two sexes. Chicago University Press, Chicago, 378 pp.

Clutton-Brock, T. H., P. H. Harvey, and B. Rudder. 1977. Sexual dimorphism, socionomic sex ratio and body weight in primates. Nature, 269:797–800.

Cockburn, A. 1988. Social behaviour in fluctuating populations. Croom Helm, Sydney, 239 pp.

Cockburn, A., M. P. Scott, and D. J. Scotts. 1985. Sex ratio and intra-sexual kin competition in mammals. Oecologia, 66:427–429.

Cole, L. C. 1948. Population phenomena and common knowledge. Scientific Monthly, 67:338–345.

Conley, W., and J. D. Nichols. 1978. The use of models in small mammal population studies. Pp. 14–35, *in* Populations of small mammals under natural conditions (D. P. Snyder, ed.). Pymatuning Laboratory of Ecology, Special Publication, 5, 237 pp.

Crowcroft, P. 1991. Elton's ecologists: a history of the Bureau of Animal Population. University of Chicago Press, Chicago, 177 pp.

Crowcroft, P., and F. P. Rowe. 1957. The growth of confined colonies of the wild house-mouse (*Mus msuculus* L.). Proceedings of the Zoological Society of London, 129:359–370.

Dasmann, R. F. 1964. Wildlife biology. John Wiley & Sons, Incorporated, New York, 231 pp.

Davidson, D. W., and J. H. Brown. 1980. Competition and the structure of granivore communities. BioScience, 30:233–238.

Davis, D. E. 1949. The weight of wild brown rats at sexual maturity. Journal of Mammalogy, 30:125–130.

Deevey, E. S., Jr. 1947. Life tables for natural populations of animals. The Quarterly Review of Biology, 22:283–314.

Dekker, H. 1975. A simple mathematical model of rodent population cycles. Journal of Mathematical Biology, 2:57–67.

Desy, E. A., and G. O. Batzli. 1989. Effects of food availability and predation on prairie vole demography: a field experiment. Ecology, 70:412–421.

Dietz, K., and D. Schenzle. 1985. Mathematical models for infectious disease statistics. Pp. 167–204, *in* A celebration of statistics: the ISI centenary volume (A. C. Atkinson and S. E. Fienberg, eds.). Springer-Verlag, New York, 606 pp.

Dunlap, T. R. 1981. DDT: scientists, citizens, and public policy. Princeton University Press, Princeton, 318 pp.

Eisenberg, J. F. 1967. A comparative study of rodent ethology with emphasis on evolution of social behavior, I. Proceedings of the United States National Museum, 122 (3597):1–35.

Eisenberg, J. F., and D. G. Kleiman (eds.). 1983. Advances in the study of mammalian behavior. Special Publication, The American Society of Mammalogists, 7:1–753.

Eisenberg, J. F., and J. O. Wolff. 1994. Behavior. Pp. 398–420, *in* Seventy-five years of mammalogy (1919–1994) (E. C. Birney and J. R. Choate, eds.). Special Publication, The American Society of Mammalogists, 11:1–433.

Eldridge, N. 1985. Unfinished synthesis: biological hierarchies and modern evolutionary thought. Oxford University Press, New York, 237 pp.

Elton, C. S. 1927. Animal ecology. MacMillan, New York, 207 pp.

———. 1930. Animal ecology and evolution. Oxford University Press, 96 pp.

———. 1942. Voles, mice, and lemmings: problems in population dynamics. Clarendon Press, Oxford, 496 pp.

Errington, P. L. 1946. Predation and vertebrate populations. Quarterly Review of Biology, 21:144–177, 221–245.

———. 1963. The phenomenon of predation. American Scientist, 51:180–192.

Fenner, F. 1976. Myxoma virus and *Oryctolagus cuniculus*: two colonizing species. Pp. 485–499, *in* The genetics of colonizing species (H. G. Baker and G. L. Stebbins, eds.). Academic Press, New York, 588 pp.

Fenton, M. B., and D. W. Thomas. 1985. Migrations and dispersal of bats (Chiroptera). Pp. 409–424, *in* Migration: mechanisms and adaptive significance (M. A. Rankin, ed.). Contributions in Marine Science, Supplement Volume 27, 868 pp.

Finerty, J. P. 1980. The population ecology of cycles in small mammals. Yale University Press, New Haven, Connecticut, 234 pp.

Forbes, S. A. 1880. On some interactions of organisms. Bulletin of the Illinois State Laboratory of Natural History, 1:3–17.

———. 1887. The lake as a microcosm. Bulletin of Science A (Peoria). Reprinted Illinois Natural History Survey Bulletin, 15:537–550, 1925.

Forman, R. T. T., and M. Godron. 1986. Landscape ecology. John Wiley & Sons, Incorporated, New York, 620 pp.

Frank, L. 1992. Spotted hyenas may use neonatal siblicide to bias sex ratios. Abstract of the IV International Behavioral Ecological Congress, Princeton University.

Fredga, K., A. Gropp, I. Winkling, and F. Frank, 1977. A hypothesis explaining the exceptional sex ratio of the wood lemming (*Myopus shisticolor*). Hereditas, 85:101–104.

Friederichs, K. 1927. Grundsatzliches über die Lebenseinheiten hoherer Ordnung und den ökologischen Einheitsfaktor. Naturwissenschaften, 15:153–157.

———. 1930. Die Grundfragen und Gesetzmässigkeiten der Land und Forst-wirtschaftlichen Zoölogie. Paul Parey, Berlin, 2 vols.

Gabrielson, I. N. 1951. Wildlife management. MacMillan, New York, 274 pp.

Gaines, M. S. 1981. Importance of genetics to population dynamics. Pp. 1–27, *in* Mammalian population genetics (M. H. Smith and J. Joule, eds.). University of Georgia Press, Athens, 380 pp.

Gaines, M. S., N. C. Stenseth, M. L. Johnson, R. A. Ims, and S. Bondrup-Nielsen. 1991. A response to solving the enigma of population cycles with a multifactorial perspective. Journal of Mammalogy, 72:627–631.

Gause, G. F. 1934. The struggle for existence. Williams & Wilkins, Baltimore, 163 pp.

Gill, A. E., and W. C. Wozencraft. 1994. Committees and annual meetings. Pp. 155–170, *in* Seventy-five years of mammalogy (1919–1994) (E. C. Birney and J. R. Choate, eds.). Special Publication, The American Society of Mammalogists, 11:1–433.

Grant, P. R. 1969. Experimental studies of competitive interaction in a two-species system. 1. *Microtus* and *Clethrionomys* species in enclosures. Canadian Journal of Zoology, 47:1059–1082.

———. 1972. Interspecific competition among rodents. Annual Review of Ecology and Systematics, 3:79–106.

———. 1978. Competition between species of small mammals. Pp. 38–51, *in* Populations of small mammals under natural conditions (D. P. Snyder, ed.). Pymatuning Laboratory of Ecology, Special Publication, 5, 237 pp.

Gregory, R. D. 1991. Parasite epidemiology and host population growth: *Heligmosomoides polygyrus* (Nematoda) in enclosed wood mouse populations. The Journal of Animal Ecology, 60:805–821.

Hamilton, W. D. 1971. Geometry for the selfish herd. Journal of Theoretical Biology, 31:295–311.

Hamilton, W. J., Jr. 1939. American mammals. McGraw-Hill Book Company, New York, 434 pp.

———. 1953. Migrants and emigrants. New York State Conservationist, June–July:10–11.

———. 1955. Mammalogy in North America. Pp. 661–688, *in* A century of progress in the natural sciences 1853–1953. California Academy of Science, San Francisco, 807 pp.

Hammond, P. S. 1987. Techniques for estimating the size of whale populations. Symposia of the Zoological Society of London, 58:225–245.

Hansson, L. 1977. Spatial dynamics of field voles Microtus agrestis in heterogeneous landscapes. Oikos, 29:539–544.

Hansson, L., and H. Henttonen. 1988. Rodent dynamics as community processes. Trends in Ecology & Evolution, 3:195–200.

Hansson, L., and N. C. Stenseth (eds.). 1988. Modelling small rodent population dynamics. Oikos, 52: 137–229.

Haskell, E. F. 1949. A clarification of social science. Main Currents in Modern Thought, 7:45–51.

Hestbeck, J. B. 1988. Population regulation of cyclic mammals: a model of the social fence hypothesis. Oikos, 52:156–168.

Hiby, A. R., and J. S. Jeffery. 1987. Census techniques for small populations, with special reference to the Mediterranean monk seal. Symposia of the Zoological Society of London, 58:193–210.

Hilborn, R., and S. C. Stearns. 1982. On inference in ecology and evolutionary biology: the problem of multiple causes. Acta Biotheoretica, 31:145–164.

Howard, L. O., and W. F. Fiske. 1911. The importation into the United States of the parasites of the gipsy-moth and the brown-tail moth. United States Department of Agriculture, Bureau of Entomology Bulletin, 91.

Howard, W. E. 1953. Rodent control on California ranges. Journal of Range Management, 6:423–434.

———. 1960. Innate and environmental dispersal of individual vertebrates. The American Midland Naturalist, 63:152–161.

———. 1965. Interaction of behavior, ecology, and genetics of introduced mammals. Pp. 461–480, *in* The genetics of colonizing species (H. G. Baker and G. L. Stebbins, eds.). Academic Press, New York, 588 pp.

Howell, A. B., 1923. Periodic fluctuations in the numbers of small mammals. Journal of Mammalogy, 4:149–155.

Kalela, O. 1961. Seasonal change of habitat in the Norwegian lemming, *Lemmus lemmus* (L.). Annuals of the Academy of Science Fennicae Series A, IV, Biology, 55:1–72.

Kaufman, G. A. 1989. Use of fluorescent pigments to study social interactions in a small nocturnal rodent, *Peromyscus maniculatus*. Journal of Mammalogy, 70:171–174.

Keith, L. B., and L. A. Windberg. 1978. A demographic analysis of the snowshoe hare cycle. Wildlife Monographs, 58:1–70.

King, J. A. 1955. Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota. Contributions from the Laboratory of Vertebrate Biology, University of Michigan, 67:1–123.

Kleiman, D., and J. F. Eisenberg. 1973. Comparison of canid and felid social systems from an evolutionary perspective. Animal Behaviour, 21:637–659.

Konishi M., and Y. Îto. 1973. Early entomology in East Asia. Pp. 1–20, *in* History of entomology (R. F. Smith, T. E. Mittler, and C. N. Smith, eds.). Annual Reviews Incorporated, Palo Alto, California, 517 pp.

Krebs, C. J. 1964. The lemming cycle at Baker Lake, Northwest Territories, during 1959–62. Arctic Institute of North America Technical Paper, 15, 104 pp.

———. 1971. Genetic and behavioral studies on fluctuating vole populations. Pp. 243–256 *in* Dynamics of populations (P. J. den Boer and G. R. Gradwell, eds.). Proceedings of the Advanced Study Institute on 'Dynamics of Numbers in Populations,' Oosterbeek. Centre for Agricultural Publications and Documents, Wageningen, The Netherlands, 611 pp.

———. 1979*a*. Dispersal, spacing behaviour, and genetics in relation to population fluctuations in the vole *Microtus townsendii*. Fortschrift für Zoölogie, 25:61–77.

———. 1979*b*. Small mammal ecology. Science, 203: 350–351.

Krebs, C. J., M. S. Gaines, B. L. Keller, J. H. Myers, and R. H. Tamarin. 1973. Population cycles in small rodents. Science, 179:35–41.

Krebs, J. R., and N. B. Davies (eds.). 1984. Behavioural ecology: an evolutionary approach, Second ed., Sinauer Associates, Incorporated, Sunderland, Massachusetts, 493 pp.

Lack, D. 1954. The natural regulation of animal numbers. Oxford University Press, New York, 343 pp.

———. 1966. Population studies of birds. Oxford University Press, New York, 341 pp.

Leary, R. A. 1985. Interaction theory in forest ecology and management. Junk Publishers, Boston, 219 pp.

Leopold, A. 1933. Game management. Charles Scribner, New York, 481 pp.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika, 33:183–212.

Levins, R. 1968. Evolution in changing environments: some theoretical explorations. Princeton University Press, Princeton, New Jersey, 120 pp.

Lewontin, R. C. 1970. The units of selection. Annual Review of Ecology and Systematics, 1:1–18.

Lidicker, W. Z., Jr. 1962. Emigration as a possible mechanism permitting the regulation of population density below carrying capacity. The American Naturalist, 96:29–33.

———. 1965. Comparative study of density regulation in confined populations of four species of rodents. Researches on Population Ecology, 7:57–72.

———. 1973. Regulation of numbers in an island population of the California vole, a problem in community dynamics. Ecological Monographs, 43:271–302.

———. 1975. The role of dispersal in the demography of small mammals. Pp. 103–128, *in* Small mammals: their productivity and population dynamics (F. B. Golley, K. Petrusewicz, and L. Ryszkowski, eds.). Cambridge University Press, London, 251 pp.

———. 1978. Regulation of numbers in small mammal populations—historical reflections and a synthesis. Pp. 122–141, *in* Populations of small mammals under natural conditions (D. P. Snyder, ed.). Pymatuning Laboratory of Ecology, Special Publication, 5, 237 pp.

———. 1979*a*. Analysis of two freely-growing enclosed populations of the California vole. Journal of Mammalogy, 60:447–466.

———. 1979*b*. A clarification of interactions in ecological systems. BioScience, 29:475–477.

———. 1984. Kazimierz Petrusewicz, 1906–1982. Journal of Mammalogy, 65:168–170.

———. 1985*a*. Population structuring as a factor in understanding microtine cycles. Acta Zoologica Fennica, 173:23–27.

———. 1985*b*. An overview of dispersal in non-volant small mammals. Pp. 369–385 *in* Migration: mechanisms and adaptive significance (M. A. Rankin, ed.). Contributions in Marine Science, Supplement Volume 27, University of Texas, 868 pp.

———. 1988*a*. Solving the enigma of microtine "cycles." Journal of Mammalogy, 69:225–235.

———. 1988*b*. The synergistic effects of reductionist and holistic approaches in animal ecology. Oikos, 53:278–281.

———. 1991. In defense of a multifactor perspective in population ecology. Journal of Mammalogy, 72: 631–635.

Lidicker, W. Z., Jr., and N. C. Stenseth. 1992. To disperse or not to disperse: who does it and why? Pp. 21–36, *in* Animal dispersal: small mammals as a model (N. C. Stenseth and W. Z. Lidicker, Jr., eds.). Chapman and Hall, London, 365 pp.

Lidicker, W. Z., Jr., J. O. Wolff, L. N. Lidicker, and M. H. Smith. 1991. Utilization of a habitat mosaic by cotton rats during a population decline. Landscape Ecology, 6:259–268.

Łomnicki, A. 1980. Regulation of population density due to individual differences and patchy environment. Oikos, 35:184–193.

Lotka, A. J. 1907. Relation between birth rates and death rates. Science, 26:21–22.

———. 1925. Elements of physical biology. Williams and Wilkins, Baltimore, 460 pp.

Macfadyen, A. 1975. Some thoughts on the behaviour of ecologists. The Journal of Animal Ecology, 44:351–363.

———. 1978. The ecologist's role in the international scientific community, Oikos, 31:1–2.

MacLean, S. F., Jr., B. M. Fitzgerald, and F. A. Pitelka. 1974. Population cycles in arctic lemmings: winter reproduction and predation by weasels. Arctic and Alpine Research, 6:1–12.

Maher, W. J. 1967. Predation by weasels on a winter population of lemmings, Banks Island, Northwest Territories. The Canadian Field Naturalist, 81:248–250.

Malthus, T. R. 1798. An essay on the principle of population. Johnson, London. (reprinted with introduction and bibliography. E. A. Wrigley and D. Souden [eds.]. 1988. W. Pickering, London, 139 pp.)

Mares, M. A., and G. N. Cameron. 1994. Community and ecosystem ecology. Pp. 348–376, *in* Seventy-five years of mammalogy (1919–1994) (E. C. Birney and J. R. Choate, eds.). Special Publication, The American Society of Mammalogists, 11:1–433.

Massey, D. R., and J. Joule. 1981. Spatial-temporal changes in genetic composition of deer mouse populations. Pp. 180–201, *in* Mammalian population genetics (M. H. Smith and J. Joule, eds.). University of Georgia Press, Athens, 380 pp.

May, R. M., and R. M. Anderson. 1979. Population biology of infectious diseases. II. Nature, 280:455–461.

McAtee, W. L. 1936. Malthusian principle in nature. Scientific Monthly, 42:444–456.

McCullough, D. R. 1979. The George Reserve deer herd: population ecology of a K-selected species. University of Michigan Press, Ann Arbor, 271 pp.

———. 1985. Long range movements of large terrestrial mammals. Pp. 444–465, *in* Migration: mechanisms and adaptive significance (M. A. Rankin, ed.). Contributions in Marine Science, Supplement Volume 27, 868 pp.

McIntosh, R. P. 1980. The background and some current problems in theoretical ecology. Synthese, 43:195–225.

———. 1985. The background of ecology: concept and theory. Cambridge University Press, 383 pp.

McShea, W. J., and D. M. Madison. 1992. Alternative approaches to the study of small mammal dispersal: insights from radiotelemetry. Pp. 319–332, *in* Animal dispersal: small mammals as a model (N. C. Stenseth and W. Z. Lidicker, Jr., eds.). Chapman and Hall, London, 365 pp.

Mech, L. D. 1987. Age, season, distance, direction, and social aspects of wolf dispersal from a Minnesota pack. Pp. 55–74, *in* Mammalian dispersal patterns: the effects of social structure on population genetics (B. D. Chepko–Sade and Z. T. Halpin, eds.). University of Chicago Press, Chicago, 342 pp.

Mendall, H. L. 1944. Food of hawks and owls in Maine. The Journal of Wildlife Management, 8:198–208.

Merriam, G. 1990. Ecological processes in the time and space of farmland mosaics. Pp. 121–133, *in* Changing landscapes: an ecological perspective (I. S. Zonnefeld and R. T. T. Forman, eds.). Springer-Verlag, New York, 286 pp.

———. 1991. Corridors and connectivity: animal populations in heterogeneous environments. Pp. 133–142, *in* Nature conservation 2: the role of corridors (D. A. Sauners and R. J. Hobbs, eds.). Surrey Beatty, Chipping Norton, New South Wales, 442 pp.

Miller, G. S., Jr. 1929. Mammalogy and the Smithsonian Institution. Annual Report (1928) Smithsonian Institution Publication, 2981, pp. 391–411.

Mollison, D. 1977. Spatial contact models for ecological and epidemic spread. Journal of the Royal Statistical Society, B39:283–326.

———. 1987. Population dynamics of mammalian diseases. Symposia of the Zoological Society of London, 58:329–342.

Montgomery, W. I. 1987. The application of capture-mark-recapture methods to the enumeration of small mammal populations. Symposia of the Zoological Society of London, 58:25–57.

Morris, R. D., and P. R. Grant. 1972. Experimental studies of competitive interaction in a two-species system. IV. *Microtus* and *Clethrionomys* species in

a single enclosure. The Journal of Animal Ecology, 41:275–290.
MUNGER, J. C., AND J. H. BROWN. 1981. Competition in desert rodents: an experiment with semipermeable enclosures. Science, 211:510–512.
NEWSOME, A. E., AND L. K. CORBETT. 1975. Outbreaks of rodents in semi-arid and arid Australia: causes, preventions, and evolutionary considerations. Pp. 117–153, *in* Rodents in desert environments (I. Prakash and P. K. Ghosh, eds.). Junk Publications, The Hague, 624 pp.
ODUM, E. P. 1953. Fundamentals of ecology. W. B. Saunders Company, Philadelphia, 384 pp.
———. 1977. The emergence of ecology as a new integrative discipline. Science, 195:1289–1293.
O'NEILL, R. V., D. L. DEANGELIS, J. B. WAIDE, AND T. F. H. ALLEN. 1986. A hierarchical concept of ecosystems. Princeton University Press, Princeton, 254 pp.
OSTFELD, R. S., W. Z. LIDICKER, JR., AND E. J. HESKE. 1985. The relationship between habitat heterogeneity, space use, and demography in a population of California voles. Oikos, 45:433–442.
PARK, T. 1946. Some observations on the history and scope of population ecology. Ecological Monographs, 16:313–320.
PEARL, R. 1922. The biology of death. Lippincott, Philadelphia, 275 pp.
———. 1925. The biology of population growth. Knopf, New York, 260 pp.
———. 1927. The growth of populations. The Quarterly Review of Biology, 2:532–548.
PEARSON, O. P. 1966. The prey of carnivores during one cycle of mouse abundance. The Journal of Animal Ecology, 35:217–233.
———. 1971. Additional measurements of the impact of carnivores on California voles (*Microtus californicus*). Journal of Mammalogy, 52:41–49.
———. 1985. Predation. Pp. 535–566, *in* Biology of New World *Microtus* (R. H. Tamarin, ed.). Special Publication, The American Society of Mammalogists, 8:1–893.
PETERSON, R. O., AND R. E. PAGE. 1983. Wolf-moose fluctuations at Isle Royale National Park, Michigan, U.S.A. Acta Zoologica Fennica, 174:251–253.
PETRUSEWICZ, K. 1957. Investigation of experimentally induced population growth. Ekologia Polska, Seria A, 5:281–301.
PITELKA, F. A., AND A. M. SCHULTZ. 1964. The nutrient–recovery hypothesis for Arctic microtine cycles. Pp. 55–68 *in* Grazing in terrestrial and marine environments (D. J. Crisp, ed.). British Ecological Society Symposium, 4, Blackwell Scientific Publishers, Oxford, 322 pp.
PLOWRIGHT, W. 1982. The effects of rinderpest and rinderpest control on wildlife in Africa. Symposia of the Zoological Society of London, 50:1–28.
RIBBLE, D. O., AND M. SALVIONI. 1990. Social organization and nest co-occupancy in *Peromyscus californicus*, a monogamous rodent. Behavioral Ecology and Sociobiology, 26:9–15.
ROSENZWEIG, M. L. 1966. Community structure in sympatric Carnivora. Journal of Mammalogy, 47: 602–612.
———. 1973. Habitat selection experiments with a pair of coexisting heteromyid rodent species. Ecology, 54:111–117.
ROSS, J. 1982. Myxomatosis: the natural evolution of the disease. Symposia of the Zoological Society of London, 50:77–95.
SALTHE, S. N. 1985. Evolving hierarchial systems: their structure and representation. Columbia University Press, New York, 343 pp.
SCHAFFER, W. M. 1974. Selection for optimal life histories: the effects of age structure. Ecology, 53: 291–303.
SCHNELL, G. D., AND R. K. SELANDER. 1981. Environmental and morphological correlates of genetic variation in mammals. Pp. 60–99, *in* Mammalian population genetics (M. H. Smith and J. Joule, eds.). University of Georgia Press, Athens, 380 pp.
SCHRODER, G. D., AND M. L. ROSENZWEIG. 1975. Perturbation analysis of competition and overlap in habitat utilization between *Dipodomys ordii* and *Dipodomys merriami*. Oecologia, 29:9–28.
SCHWERDTFEGER, F. 1941. Über die Ursachen des Massenwechsels der Insekten. Zeitschrift für Angewandte Entomologie, 28:254–303.
SCOTT, M. E. 1988. The impact of infection and disease on animal populations: implications for conservation biology. Conservation Biology, 2:40–56.
SEMPER, K. 1881. Animal life as affected by the natural conditions of existence. Appleton, New York, 472 pp.
SETON, E. T. 1929. Lives of game animals. 4 volumes, Doubleday, Doran & Company, New York.
SHELFORD, V. E. 1913. Animal communities in temperate America. University of Chicago Press, Chicago, 362 pp.
———. 1929. Laboratory and field ecology. Williams and Wilkins, Baltimore, 608 pp.
SHERMAN, P. W., J. U. M. JARVIS, AND R. D. ALEXANDER (EDS.). 1991. The biology of the naked mole-rat. Princeton University Press, Princeton, New Jersey, 518 pp.
SHVARTS, S. S. 1969. Evolyutsionnaya ekologiya zhivotnykh. Proceedings of the Institute of Plant and Animal Ecology, Sverdlovsk, 65:1–100.
———. 1977. The evolutionary ecology of animals (translated by A. E. Gill). Consultants Bureau, New York, 292 pp.
SINCLAIR, A. R. E. 1986. Testing multi-factor causes of population limitation: an illustration using snowshoe hares. Oikos, 47:360–364.
SLOBODCHIKOFF, C. H. (ED.). 1988. The ecology of social behavior. Academic Press, San Diego, California, 429 pp.
SMITH, A. T., AND B. L. IVENS. 1984. Spatial relationships and social organization in adult pikas: a facultatively monogamous mammal. Zeitschrift für Tierpsychologie, 66:37–47.
SMITH, F. E. 1952. Experimental methods in population dynamics: a critique. Ecology, 33:441–450.
SMITH, H. S. 1935. The role of biotic factors in the determination of population densities. Journal of Economic Entomology, 28:873–898.
SMITH, M. H., AND J. JOULE (EDS.). 1981. Mammalian population genetics. University of Georgia Press, Athens, 380 pp.
SMITH, M. H., M. N. MANLOVE, AND J. JOULE. 1975.

Spatial and temporal dynamics of the genetic organization of small mammal populations. Pp. 99–113, *in* Populations of small mammals under natural conditions (D. P. Snyder, ed.). Pymatuning Laboratory for Ecology, Special Publication, 5, 237 pp.

Smuts, J. C. 1926. Holism and evolution. MacMillan Company, New York, 362 pp.

Solomon, M. E. 1949. The natural control of animal populations. Journal of Animal Ecology, 18:1–35.

———. 1958. Meaning of density-dependence and related terms in population dynamics. Nature, 181: 1778–1780.

Southwick, C. H. 1955. The population dynamics of confined house mice supplied with unlimited food. Ecology, 36:212–225.

Stenseth, N. C. 1978. Demographic strategies in fluctuating populations of small rodents. Oecologia, 33:149–172.

———. 1981. On Chitty's theory for fluctuating populations: the importance of genetic polymorphism in the generation of regular density cycles. Journal of Theoretical Biology, 90:9–36.

———. 1983. Causes and consequences of dispersal in small mammals. Pp. 63–101, *in* The ecology of animal movement (I. R. Swingland and P. J. Greenwood, eds.). Clarendon Press, Oxford, 311 pp.

———. 1986. On the interactions between stabilizing social factors and destabilizing trophic factors in small rodent populations. Theoretical Population Biology, 29:365–385.

Stenseth, N. C., and W. Z. Lidicker, Jr. 1992*a*. The use of radioisotopes in the study of dispersal: with a case study. Pp. 333–352, *in* Animal dispersal: small mammals as a model (N. C. Stenseth and W. Z. Lidicker, Jr., eds.). Chapman and Hall, London, 365 pp.

———. 1992*b*. Presaturation and saturation dispersal 15 years later: some theoretical considerations. Pp. 201–223, *in* Animal dispersal: small mammals as a model (N. C. Stenseth and W. Z Lidicker, Jr., eds.). Chapman and Hall, London, 365 pp.

——— (eds.). 1992*c*. Animal dispersal: small mammals as a model. Chapman and Hall, London, 365 pp.

Symington, M. M. 1987. Sex ratio and maternal rank in wild spider monkeys: when daughters disperse. Behavioral Ecology and Sociobiology, 20:421–425.

Szacki, J., and A. Liro. 1991. Movements of small mammals in the heterogeneous landscape. Landscape Ecology, 5:219–224.

Taitt, M. J., and C. J. Krebs. 1983. Predation, cover and food manipulations during a spring decline of *Microtus townsendii*. Journal of Animal Ecology, 52: 837–848.

Tamarin, R. H. 1978*a*. A defense of single-factor models of population regulation. Pp. 159–162, *in* Populations of small mammals under natural conditions (D. P. Snyder, ed.). Pymatuning Laboratory of Ecology, Special Publication, 5, 237 pp.

———. 1978*b*. Dispersal, population regulation, and K-selection in field mice. The American Naturalist, 112:545–555.

Tamarin, R. H., R. S. Ostfeld, S. R. Pugh, and G. Bujalska (eds.). 1990. Social systems and population cycles in voles. Birkhäuser Verlag, Basel, 229 pp.

Taylor, J. M., and D. A. Schlitter. 1994. Awardees. Pp. 71–109, *in* Seventy-five years of mammalogy (1919–1994) (E. C. Birney and J. R. Choate, eds.). Special Publication, The American Society of Mammalogists, 11:1–433.

Thienemann, A. 1939. Grundzüge einer allgemeinen Oekologie. Archives of Hydrobiology, 35:267–285.

Thompson, W. R. 1939. Biological control and the theories of the interactions of populations. Parasitology, 31:299–388.

Trippensee, R. E. 1948. Wildlife management. McGraw-Hill Book Company, New York, 479 pp.

Trivers, R. L. 1971. The evolution of reciprocal altruism. The Quarterly Review of Biology, 46:35–57.

Turner, N. 1960. The effect of inbreeding and crossbreeding on numbers of insects. Annals of the Entomological Society of America, 53:686–688.

Uvarov, B. P. 1931. Insects and climate. Transactions of the Entomological Society of London, 79: 1–247.

van Schaik, C. P., and S. B. Hrdy. 1991. Intensity of local mate competition shapes the relationship between maternal rank and sex ratios at birth in cercopithecine primates. The American Naturalist, 138:1556–1562.

Verme, L. H. J. 1969. Reproductive patterns of white-tailed deer related to nutritional plane. The Journal of Wildlife Management, 33:881–887.

Volterra, V. 1926. Fluctuations in the abundance of a species considered mathematically. Nature, 118: 558–560.

———. 1931. Lecons sur la theorie mathematique que de la lutte pour la vie. Gauthiers-Villars, Paris, 214 pp.

Vrba, E. S., and N. Eldredge. 1984. Individuals, hierarchies and processes: towards a more complete evolutionary theory. Paleobiology, 10:146–171.

Wagner, F. H., and L. C. Stoddart. 1972. Influence of coyote predation on black-tailed jackrabbit populations in Utah. The Journal of Wildlife Management, 36:329–342.

Ward, A. J., D. Thompson, and A. R. Hiby. 1987. Census techniques for grey seal populations. Symposia of the Zoological Society of London, 58:181–191.

Weaver, J. L. 1979. Wolf predation upon elk in the Rocky Mountain parks of North America: a review. Pp. 29–33, *in* North American elk: ecology, behavior and management (M. S. Boyce and L. D. Hayden-Wing, eds.). University of Wyoming Press, Laramie, 294 pp.

Wegner, J., and G. Merriam. 1990. Use of spatial elements in a farmland mosaic by a woodland rodent. Biological Conservation, 54:236–276.

Wellington, W. G. 1960. Qualitative changes in natural populations during changes in abundance. Canadian Journal of Zoology, 38:289–314.

Wilbert, H. 1963. Können Insekten populationen durch Selektionprozesse reguliert werden? Zietschrift für Angewandte Entomologie, 52:185–204.

Wilson, E. O. 1975. Sociobiology, the new synthesis. Harvard University Press, Cambridge, 697 pp.

Wolff, J. O. 1980. The role of habitat patchiness in the population dynamics of snowshoe hares. Ecological Monographs, 50:111–130.

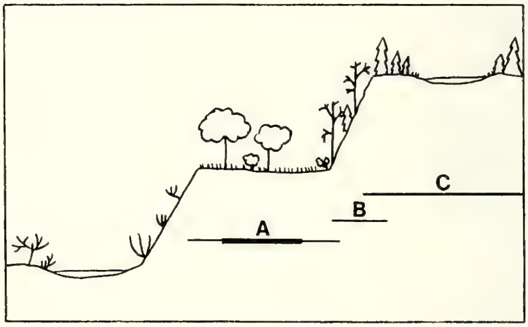
Wynne-Edwards, V. C. 1962. Animal dispersal in relation to social behaviour. Hafner Publishing Company, New York, 653 pp.

———. 1965. Self-regulating systems in populations of animals. Science, 147:1543–1548.

———. 1986. Evolution through group selection. Blackwell Scientific Publishers, Oxford, 386 pp.

# *COMMUNITY AND ECOSYSTEM ECOLOGY*

Michael A. Mares and Guy N. Cameron




### *Introduction*

A biotic community is defined by Odum (1971:140) as "... any assemblage of populations living in a prescribed area or physical habitat; it is an organized unit to the extent that it has characteristics additional to its individual and population components." Organisms forming a community interact in some manner with one another, whether through coevolutionary adaptations, as links in food chains, or any of innumerable other potential biotic nexuses. Thus, a community may include all of the tree species in a particular forest, or all of the trees plus their associated plant and animal species, including detritus-feeding organisms. Ecosystems, on the other hand, include all of the organisms composing a community plus the abiotic components of the environment. Organization and interaction among trophic levels, in addition to energy flow or nutrient cycling between the living and non-living parts of the system, is implied in this definition.

While inclusion of several trophic levels within a single community is common, research on mammals seldom deals with an entire community. It is important to understand these terms as they were classically employed because they are frequently misused. For example, Jaksic (1981) cited several studies of mammals that ostensibly dealt with communities, but actually dealt either with a partial guild [e.g., a guild being (Root, 1967:335) " a group of species that exploit the same class of environmental resources in a similar way ... without regard to taxonomic positions"] or with simple taxonomic assemblages. An example of the former might be the seed-eating rodents in a desert, which are a part of the granivore guild—the complete guild would include birds, ants, and other consumers of seeds. An example of the latter is research conducted on a "rodent community," when in fact a study may have been done at the population level—the community would include all of the mammals and other organisms that interact in some important manner within a particular habitat or defined region (see, for example, the discussion of Slobodkin, 1987). As May (1984:15) stated: "... any attempt to elucidate patterns of community structure must deal with the question of how to delimit the community. Much academic research restricts itself to a particular taxonomic group ... instead of first consciously deciding which groups of species comprise a coherent and irreducible community." In this context, however, it is important to emphasize that entire communities do not have to be studied in a community ecology study as long as investigations are undertaken within a community-based framework.

Our goal in this chapter is to examine how research on mammals has influenced, or has been influenced by, ideas of community and ecosystem organization. Mammals perform important functions at and above the community level, whether through pathways of energy flow (e.g., mammals are trophically diverse and may be primary, secondary, or tertiary consumers), through widespread coevolutionary adaptations with plants and other organisms (e.g., pollination activities of tropical bats or dispersal of seeds by tropical rodents and ungulates), by affecting standing biomass and production, or by dramatic impacts on a particular habitat, such as elephants and ungulates in the African savanna community. The effects of mammals on each other and on other organisms, as well as on the abiotic portions of the ecosystem, are extensive. A good deal of effort has been dedicated to understanding interactions at levels of biological organization above the individual and the population. It is this area of investigation—research examining the place and the importance of mammals in biological communities and ecosystems—that will be reviewed in this chapter.

When the ASM was founded in 1919, information on community and ecosystem relationships of mammals was negligible. Research at this time focused on questions dealing with individual and population ecology, championed by such giants as Joseph Grinnell; however, many of the guiding principles in community and ecosystem ecology were being formed (see below for work by Merriam, Shelford, and Elton) and were rapidly incorporated into studies dealing with mammals.

## Historical Overview

*Background research on communities and ecosystems.*—Odum (1971:Chapters 1–2) and Kendeigh (1974) reviewed the history of the conceptualization of the terms "ecosystem" and "community," and McIntosh (1985) provided an overview of the history of ecology. The idea that plants and animals occur together in some type of non-random pattern is quite old. Kendeigh (1974), for example, mentioned a reference to species assemblages by Theophrastus at the time of Aristotle in the 4th century BC (see McIntosh, 1985; Ramalay, 1940). As early as 1807, Humboldt and Bonpland referred to plant associations which could be identified by physiognomy and which were related to both latitudinal and vertical zonation. In 1815, Humboldt devised a grid system for recording presence or absence of plant species between different landscapes (McIntosh, 1985). The German botanist, A. Grisebach, in 1838, described animals and plants occurring together in interrelated associations. Seventy years after Humboldt's ground-breaking work, in 1877, another German, Karl Möbius, discussed oyster communities on a coral reef; Möbius used the term biocoenosis, which subsequently became the European term for biotic communities. When Möbius' work was translated into English in 1883, biocoenosis became community (e.g., Allee et al., 1949). C. Schröter, a Swiss botanist, working in the late 1800s and early 1900s, was one of the first biologists to use the concept of plant community consistently for describing vegetation (Gigon et al., 1981).

S. A. Forbes (1887) also used the term community in his classic work on lake ecology, and it became the term generally used in North America to describe interrelated biotic associations. Forbes, who has been called the complete ecologist (e.g., McIntosh, 1985), was curator of the Illinois Natural History Museum and director of the State Laboratory of Natural History (=Illinois Biological Survey). As McIntosh (1985) noted, Forbes' influence on ecology was enormous, with his 1887 paper founding the science of limnology and other papers anticipating such modern ecological concepts as competitive exclusion. Curiously, competitive exclusion was first more specifically defined, if in a qualitative manner, by two mammalogists, Joseph Grinnell (1904, 1908), the father of academic mammalogy in North America (Jones, 1991), a charter member of ASM and president of the society in 1937, and Angel Cabrera (1932), a Spaniard, who was named an honorary member of the ASM (see Hutchinson, 1978).

One of the first animal ecologists, Victor Shelford, wrote that ecology was the science of communities (Shelford, 1913). Community theory primarily developed by plant ecologists (e.g., A. G. Tansley, F. E. Clements, H. C. Cowles) in the early part of this century initially was exemplified by the organismic dynamic theory of Clements that predicted a stable, climax stage. This early view, widely accepted by plant ecologists and more or less by animal ecologists, was challenged from the 1930s to the 1950s by plant ecologists espousing an individualistic theory (Gleason, 1917, 1939; McIntosh, 1975, 1980; Whittaker, 1951). Whereas these studies challenged the idea of the plant community, animal ecologists adopted the concept of the community as an entity composed of species at equilibrium. Such an idea, associated with the work of Robert MacArthur, derived largely from the belief that many patterns in nature were a consequence of competition to promote niche separation (Cody and Diamond, 1975; Connell, 1980; Diamond, 1978). Mammalogists contributed substantially to uncovering the role of competition in structuring natural communities (see below). However, another mammalogist (Brown, 1981) argued that theoretical population ecology largely failed to produce a quantitative theory applicable to community ecology. The largest oversight, he argued, was a failure to emphasize energy flow as a coalescing pattern (see also Hall et al., 1992).

The idea of the ecosystem is more recent than that of the community. A botanist, A. G. Tansley (1935), in a review of botanical concepts, coined the term ecosystem, which expanded the concept of the biotic community to include the interactions of the organisms comprising the community with the abiotic parts of the environment. The term biocoenosis was enlarged to geobiocoenosis by a Russian, V. N. Sukachev (Odum, 1971; see Sukachev, 1958), thus becoming the equivalent of ecosystem. Although the terminology used in the New and Old World differed, and different underlying ecological philosophies influenced research within these two regions (e.g., Gigon et al., 1981), there was a general appreciation of supra-individual and supra-population effects in ecology, especially in contributing to community stability and system cohesiveness.

Inherent in the work of some ecologists was the idea that communities, and later, ecosystems, were superorganisms, responding as unified units to experimental and evolutionary perturbations (e.g., Clements, 1905, 1916; Semper, 1881). Tansley (1935), however, argued strongly that neither the community nor the ecosystem should be viewed as some type of superorganism. The concept of the ecosystem as a super entity largely has been discounted by most ecologists. However, the idea has arisen again in recent years under the guise of a biospheric entity called Gaia (see Barlow, 1991). This mystical super life form is almost sentiently responsive to deviations from "normal" environmental parameters that are conducive to maintaining the life to which it (Gaia) is presently adapted.

*Mammalogists, communities, and ecosystems.*—Despite the long history of European botanists and invertebrate biologists who developed community-based studies, a number of North American biologists, who also conducted important research on mammals, were intimately involved with the foundations of community and ecosystem ecology. As early as the late nineteenth century, C. Hart Merriam, the father of modern mammalogy (e.g., Osgood, 1943; Sterling, 1977), was the first North American to develop research interests relating to communities and ecosystems. Merriam developed the team method of conducting survey research in particular regions. This involved sending groups of researchers into the field to study botany, geology, and most aspects of vertebrate biology (systematics, distribution, natural history, and ecology of both birds and mammals), either for specific localities or for broader regions (e.g., Merriam, 1890, 1892, 1894, 1898).

Merriam was among the earliest proponents in North America of a unified view of natural communities. The biological surveys that were conducted in a broad-based manner across taxa, and that included extensive geological investigations and data on climate, amassed a great deal of information on how the biota of a region reflected abiotic factors in the environment. In examining such data for the San Francisco Mountains region of northern Arizona, Merriam formulated the concept of life zones (Merriam, 1894, 1898). The life zone concept was the first attempt to include dominant animals in a community classification scheme. This concept warrants additional discussion because it led to early consideration of the interactions among taxonomically diverse organisms (i.e., community interactions) and with their abiotic environment (i.e., ecosystems).

Merriam attempted to explain the distribution of animals in relation to life zones that were themselves defined by temperature laws that he formulated. The resultant zones formed altitudinal and latitudinal bands that stretched across the North American continent. The life zone concept worked effectively in the mountainous areas of the western United States where it was derived, partially because the temperature limits defining the faunal zones coincided with vegetation regions. There was a good deal of criticism of Merriam's life zones (see Odum, 1945, for a review), and the suggestion that there were definable life zones was replaced by the biome concept (see below) which is still widely used today.

Merriam's revolutionary techniques of field research and broadly based field surveys assisted in the development of a holistic view of entire biotas as organized and interrelated units responding to abiotic influences. Subsequently, several other mammalogists helped lay the foundations of modern community and ecosystem ecology. Charles C. Adams, for example, who initially worked for S. A. Forbes in the Illinois Natural History Survey, published some of the earliest work in community ecology when he described a number of animal communities while conducting a biological survey of Michigan (Adams, 1905, 1909; see Kendeigh, 1974; and McIntosh, 1985). Adams was a charter member of ASM, was nominated by president Merriam to chair the ASM Committee on Life Histories of Mammals (Hollister, 1920), and published the first manual on animal ecology (Adams, 1913).

Another landmark in the development of community ecology was also produced by a mammalian ecologist in North America. The first book ever published on animal or plant communities was by Victor Shelford (1913), who was the first president of the Ecological Society of America (in 1915) and who joined ASM in 1923. Some of his work had a physiological orientation and led to initial ideas about how environmental extremes limited species (and community) ranges. Although he did not formalize the concept, Shelford's work outlined food chains and made initial conceptual linkages between communities and ecosystems, describing them as dynamic units responding to changing environmental parameters. [Ideas concerning food chains and the concept of the pyramid of numbers were first set forth by K. Semper, a North American zoologist, who published a book on animals and their relationship to their natural environments (Semper, 1881, see McIntosh, 1985). Semper's work was an early zoology text that applied Darwin's ideas of natural selection to a wide array of organisms and included discussion of such topics as crypsis, warning coloration, and competition between similar species.] Shelford realized the importance of biological surveys (e.g., Shelford, 1926) and conducted detailed research on lemming populations (e.g., Shelford and

Twomey, 1941). Shelford's landmark work was the development of the biome concept in conjunction with the plant ecologist, F. Clements (Clements and Shelford, 1939).

Shortly after these contributions of North American ecologists were published, seminal research on how organisms functioned was conducted in Great Britain. Perhaps the preeminent work contributing to the development of community and ecosystem theory (and to the development of ecology in general) was that of the mammalian ecologist, Charles Elton (Elton joined the ASM in 1931), who formulated or developed in detail four important ecological concepts: the niche; differences in food particle size as a mechanism to reduce competition; the food web; and the pyramid of numbers (Duff and Lowe, 1981; Elton, 1927, 1933). These ideas became paradigms of ecological theory and contributed greatly to an appreciation of the functional relationships of organisms in communities and ecosystems.

Elton's work, which built directly upon the research of Adams and Shelford, was fundamental to understanding the complexities of nature. With the pyramid of numbers, Elton showed that there was a structure to nature—organisms in a community were not randomly organized so far as their abundance was concerned; rather, different trophic levels showed specific numerical relationships to one another (e.g., herbivores were more abundant than carnivores). Similarly, pyramids of biomass and energy illustrated non-random organizations with both biomass and energy content decreasing in a pyramidal fashion toward higher trophic levels. Even though we now know that only the pyramid of energy cannot be inverted, these descriptions of natural communities were pivotal to the development of the modern underpinnings of ecosystem research. With the description of food chains and webs, Elton clearly showed how energy linked component species in an ecosystem in often unexpectedly complex pathways. This was a profound description of nature that continues to impact current ideas of community structure (e.g., Pimm et al., 1991). Elton was also responsible for quantitative research on mammal population ecology, particularly with his benchmark publication on 10-year population cycles of the lynx (Elton and Nicholson, 1942), his classic book on population ecology of mice, lemmings, and voles (Elton, 1942), and other contributions (e.g., Elton, 1958, 1966).

Although the original concept of niche was not necessarily associated with community studies, it has had an important impact on modern ecological theory (e.g., Ehrlich and Roughgarden, 1987). It is worth noting that Grinnell (1914, 1917*a,* 1917*b*) was among the earliest individuals to develop the idea of the niche. Indeed, until Gaffney (1973) reviewed the history of the niche concept and found that it was coined by Robert Johnson in 1910, the origin of the term had been attributed to Grinnell (Cox, 1980).

Clearly, Adams, Shelford, Grinnell, and Elton utilized their ecological expertise, especially that developed from working on mammals, to influence the foundations of ecology, particularly at the higher levels of biological organization. By the early 20th Century, mammalogists were among the leading ecologists in conducting studies and developing theories bearing on the development of community and ecosystem ecology. Their work, along with the burgeoning disciplines of limnology and plant community ecology, helped drive the field into the modern age. Mammalogists have continued to play a role in the development of community and ecosystem studies, not only in the field and the laboratory but, at least in the case of modern ecosystem research, in the biopolitical arena as well.

## *Approaches to Community and Ecosystem Ecology*

Early studies in mammalian ecology mirrored the natural history approach exemplified by Grinnell's work. This descriptive approach was reflected in biotic surveys that encompassed a variety of techniques to sample both plants and animals through the 1940s in the United States (i.e., Fautin, 1946). The 1940s and 1950s were a period during which studies were designed to describe community processes, in particular trophic dynamics and energy flow (Lindeman, 1942; Odum, 1957; Teal, 1957). Initial emphasis was on aquatic habitats, but subsequent studies in terrestrial ecosystems included small mammals as major consumers (e.g., Golley, 1960).

The International Biological Program (1969–1974; IBP) was an important factor in the development of community and ecosystem ecology because it bridged the earlier descriptive approach and the current emphasis on empiricism. One thrust of IBP was to organize groups of specialists to study major terrestrial biomes and to integrate the findings with models used as predictive tools. This international effort at understanding the structure and function of ecosystems on a global scale was in large part developed and administered by another mammalogist, W. Frank Blair. Many mammalogists active today participated in IBP (IBP will be discussed in detail below).

One of the criticisms about IBP was the lack of hypothesis testing. Ecological studies since the mid-1970s have become increasingly grounded in the scientific method, thus completing the transition from the descriptive approach that was begun at the turn of the century. To facilitate experimental studies at appropriate ecological scales (both spatial and temporal), a variety of ecological research areas have been established, including Biosphere Reserves, Experimental Ecological Reserves, and Long-term Experimental Research areas (Franklin et al., 1990). Ecological experiments are conducted in the laboratory and field, use natural or experimentally controlled perturbations, and consider factors that influence organisms over the short- or long-term (Diamond, 1986). Mammalogists have been at the forefront of development of empirical studies conducted in the field (see citations below) and have argued for the development of facilities where long-term experimental research could be undertaken. Mammalogists also have argued that natural history should continue to play a critical role in empirical studies by providing the crucial knowledge to design appropriate experiments (Bartholomew, 1986; Brown, 1986; Mares and Braun, 1986). Finally, mammalogists have played a role in developing methods to conduct and analyze field experiments, such as taking into account the effect of scale, both spatial (J. S. Brown, 1989; Morris, 1987, 1989; Price and Kramer, 1984) and temporal (Brown and Heske, 1990; Brown and Kurzius, 1989).

## Community Ecology

*The concept of niche.*—The development of the concept of the niche began with several mammalogists. Joseph Grinnell wrote that "As with zones and faunas, associations are often capable of subdivision; in fact such splitting may be carried logically to the point where but one species occupies each its own niche" (Grinnell and Swarth, 1913:218), and "A concurrent axiom is that if associational analysis is carried far enough, no two species of birds or mammals will be found to occupy precisely the same ecologic niche, although they may apparently do so where their respective associations are represented fragmentarily and in intermixture" (Grinnell, 1914:91). Grinnell defined the niche as "the concept of the ultimate distributional unit, within which each species is held by its structural and instinctive limitations . . ." (Grinnell, 1928/1943:192–194). This view of the niche as a distributional entity was complemented by Charles Elton's (1927:64) idea that the "niche of an animal means its place in the biotic environment, its relations to food and enemies"—the so-called functional niche. Dice (1952) suggested that the niche represented a coalescence of both functional and distributional attributes of a species.

The current concept of the niche was formalized mathematically as an $n$-dimensional hyperspace by an aquatic biologist, G. Evelyn Hutchinson (1957). Mammalogists have contributed to refining the niche concept. For example, MacMahon et al. (1981) discussed how the niche reflects the actual or potential state of an organism at an instant in time. They concluded that an organism's niche is bounded by tolerance limits set by heredity, maturity, and acclimatization, and that changes in tolerances during an organism's life cycle create ontogenetic bottlenecks in the niche.

Mammalogists have contributed to our knowledge of the niche concept with research measuring niche parameters (Carnes and Slade, 1982; Churchfield, 1991; Dueser and Shugart, 1979, 1982; Montgomery, 1989; Slobodchikoff and Schultz, 1980; Smartt, 1978; Van Horne and Ford, 1982). In addition, mammalogists have conducted empirical studies that illustrated increases in niche breadth with intraspecific competition (Smartt and Lemen, 1980; Van Horne and Ford, 1982), variation in genetic and morphological measurements with niche breadth (i.e., the niche variation hypothesis; Smith, 1981), a correlation of niche breadth with species abundance (Brown, 1984; Seagle and McCraken, 1986), body size (Barclay and Brigham, 1991; Willig and Moulton, 1989), and partitioning of resources (Brown, 1973, 1975; Cameron, 1971; Emmons, 1980; Mares and Williams, 1977; McKenzie and Start, 1989; M'Closkey, 1980; Meserve, 1981; Owen-Smith, 1989; Price et al., 1991; Willig et al., 1993).

*Interspecific interactions.*—In addition to the niche concept, mammalogists have contributed substantially to another basic concept of community and ecosystem ecology, that of interspecific interactions, including competition, predation, and mutualism. Again, Joseph Grinnell laid the framework for this concept when he wrote "these various circumstances, which emphasize dependence upon cover, and adaptation in physical structure and temperament thereto, go to demonstrate the nature of the ultimate associational niche occupied by the California thrasher. . . . It is, of course, axiomatic that no two species regularly established in a single fauna have precisely the same niche relationships" (Grinnell, 1917*a*: 433), and that "no two species in the same general territory can occupy for long identically the same ecological niche . . . competitive displacement of one of the species by the other is bound to take place" (Grinnell, 1928/1943:192–194). The great Spanish mammalogist, A. Cabrera, who spent most of his professional life in Argentina and was the preeminent force in the history of South American mammalogy, also published an important paper on competitive exclusion that described the concept as a biological law (Cabrera, 1932).

Interspecific competition was first described mathematically by Lotka and Volterra (see Slobodkin, 1961). Over the years, mammalogists have contributed to the modification of these models to overcome some of the limiting assumptions (Fryxell et al., 1991). Mammalogists have also devised statistical methods to measure competition in the field (Hallett and Pimm, 1970; Rosenzweig et al., 1984). Other mammalogists were instrumental in beginning the classification of this process into what is now known as interference and exploitation competition (Elton and Miller, 1954; Miller, 1967) and in describing the relative importance of these processes (King and Moors, 1979). Mammalogists have completed numerous other studies on the process of interspecific competition (e.g., Brown, 1971; Brown et al., 1979; Dickman, 1989; Fox, 1989; Holbrook, 1979; Kirkland, 1991; Pulliam and Brand, 1975; Rosenzweig, 1966; Smith and Balda, 1979; Willig and Moulton, 1989; see below for role of competition in community structure), but data gathered across entire mammal faunas to clarify competitive or other mechanisms that are important in structuring temperate and tropical faunas are still rudimentary (Lacher and Mares, 1986; Willig, 1986).

The niche overlap hypothesis states that maximum tolerable niche overlap decreases as the intensity of competition increases

(Pianka, 1974). Studies on several mammalian systems offer support for this hypothesis (Fox, 1981; Lacher and Alho, 1989; M'Closkey, 1978; Porter and Dueser, 1981; but the multivariate technique used by Porter and Dueser has been questioned by Carnes and Slade, 1982). However, Brown (1975) found that niche overlap increased when number of species increased for North American desert rodents. He attributed this response to the fact that the Mohave desert communities he studied may be composed of more generalist species than those examined in the other studies.

A second interspecific interaction to which mammalogists have contributed is the process of predation. As with competition, basic models for this process were developed by Lotka and Volterra. Mammalogists were instrumental in refining these models (Rosenzweig, 1969, 1973; Rosenzweig and MacArthur, 1963). Much of the subsequent development of this aspect of community ecology relied on studies of mammals; for example, functional and numerical responses were described with responses between *Sorex, Blarina,* and *Peromyscus* and their sawfly larva prey (Holling, 1959), and differences in susceptibility of age groups to predation were described in the moose-wolf system (Mech, 1966).

Mammalogists have conducted many studies on the basic nature of predator-prey relations (e.g., Hornocker, 1970; Pearson, 1971; Schnell, 1968; Wagner and Stoddart, 1972). Two views on the role of predators arose earlier in this century. One, championed by the mammalogist Paul Errington (1946), held that predators only took surplus prey above the carrying capacity, a view without current support. The other view arose in the entomological literature and concluded that predators regulated their prey. Demonstration of this phenomenon has been elusive largely because of the myriad of definitions given to this process (Varley, 1975); population regulation, however, is a density-dependent feedback of either increasing mortality or decreasing fecundity proportional with increasing predation. Erlinge and his colleagues (Erlinge et al., 1983, 1984) analyzed population density of field voles and rabbits, as well as food habits of their major avian and mammalian predators, in Sweden. They recorded both functional and numerical responses by predators to changes in prey numbers and concluded that the functional response, combined with switching by predators from voles to rabbits and vice versa when numbers of prey became low, produced a density-dependent effect during the period of highest vole density (autumn). These findings were challenged by Kidd and Lewis (1987), who argued that Erlinge and his colleagues had not demonstrated density-dependent predation; Erlinge et al. (1988) responded that predator switching among alternative prey affected regulation. Korpimäki (1993), however, presented evidence that *Microtus* sp. in Finland are regulated by density-dependent avian predation and delayed density-dependent mammalian predation. Sinclair et al. (1990) concluded that house mice in Australia were regulated by delayed density-dependent predation at low-moderate mouse densities, but by inverse density-dependence at high mouse densities. Trostel et al. (1987) found that avian and mammalian predators may affect the 10-year cycle of snowshoe hares in a delayed density-dependent fashion.

Mutualism has been studied much less intensively than either competition or predation, but research on mammals has again provided perspectives on the mechanics and pervasiveness of this process. Mutualism can be a direct or indirect process. Mammal-plant interactions, such as seed dispersal (Carpenter, 1978; Sazima and Sazima, 1978; Simpson and Neff, 1981; Sussman and Raven, 1978) or pollination (Fleming, 1981; Howe, 1980; Smith, 1970; Stapanian and Smith, 1978) are direct processes. In indirect mutualism, a positive interaction is achieved even though there is no direct contact between the species. For example, although Thompson gazelles, zebras, and wildebeests eat different foods on the Serengeti, the gazelles prefer to feed in areas where wildebeests have grazed a month earlier, since such areas contain greater plant biomass (McNaughton, 1976). Brown et al. (1986), building upon an evolutionary hypothesis developed by Mares and Rosenzweig (1978), demonstrated that rodents in the Mohave desert eat large seeds, whereas ants prefer smaller seeds. When rodents were removed, large-seeded plants increased in abundance, reduced the abundance of small-seeded plants and, consequently, the small seed resources of ants. Thus, rodents acted as indirect mutualists on ants (Davidson et al., 1984).

Other examples of indirect mutualism include the observation that the progress of plant succession may be positively affected when pocket gophers alter soil characteristics and thereby affect the resultant plant species composition (Andersen and MacMahon, 1985; Huntly and Inouye, 1988; Tilman, 1983). In a similar fashion, food availability for granivorous birds is affected positively by desert rodents that forage preferentially upon those plant species that compete with plant species eaten by the birds and that maintain areas of bare soil which serve as germination sites for those plants eaten by the birds (Mitchell et al., 1990). Coppock et al. (1983*b*) also discovered that bison preferentially grazed in areas where prairie dogs had reduced the occurrence of less preferred plants, thereby allowing growth of more preferred plants. Finally, dispersal of seeds from parent plants reduced seed predation by desert rodents and thereby enhanced seed germination (O'Dowd and Hay, 1980).

*Community structure.*—Structure within a community is determined by both composition and relative abundance of species. Many studies have addressed Elton's (1927) concept of limited membership: Why is it that what does occur together constitutes a limited subset of what might occur together? One avenue of research has been to investigate whether structure exists for subsets of a community [i.e., within community structure, termed guild structure by Root (1967) to refer to groups of species exploiting resources in a similar way; the multiple meanings of guild, however, have been discussed by Hawkins and MacMahon (1989) and Simberloff and Dayan (1991)]. Most of this work has centered on insects and lower vertebrates. In one of the few studies with mammals, MacMahon (1976) concluded that similarities in guild structure of small mammals among sites in the deserts of the western United States resulted from interactions of evolutionary events and site characteristics. Fox (1989) and others (e.g., Findley, 1989; Humphrey et al., 1983; McKenzie and Start, 1989; Rosenzweig, 1989; Smythe, 1986; Willig and Moulton, 1989) have also examined the mechanisms affecting community (or guild) assembly in mammals. Fox (1989) used a taxonomically-based rule for species assembly of small mammals in Australian heathlands that stipulated there was a higher probability that species comprising a community will have been drawn from a genus, guild, or taxonomically-related group of species with similar diets. Fox and Brown (1993) applied an assembly rule based upon functional groups to suggest that interspecific competition was an important mechanism structuring desert rodent communities in North America. Willig and Moulton (1989), on the other hand, found that ecomorphology in bat communities was not different from that expected by a stochastic model; Willig et al. (1993) reported that dietary differences among Brazilian bats did not order community structure, but suggested that competition for some other resource could be more important.

Other research has centered on the role of competition in determining community structure. This research can be divided into observational and empirical evidence. Here again, mammalogists have played prominent roles. Several sorts of observational evidence have been used to conclude that interspecific competition has been important in determining community structure. Resource partitioning, comparative species distributions, and character displacement will be considered.

Resource partitioning, the subdivision of resources by two or more species, is one outcome of the Lotka-Volterra model of competition, whereby niche dimensions of competing species are modified such that niche overlap decreases (see reviews by Schoener, 1974, 1986*a*). Numerous studies have demonstrated resource partitioning in mammals (e.g., Belk et al., 1989; Brown, 1989; Dueser and Hallett, 1980; Fleming et al., 1972; Hallett et al., 1983; Heithaus et al., 1975; McNab, 1971; McNaughton and Georgiadis, 1986; Meserve, 1981).

The negative correlation between spatial distributions of species is another way that the effect of competition on community structure has been inferred. There are many examples of this effect from the literature on mammals. For example, mammalogists have noted such spatial partitioning between *Sigmodon hispidus, S. fulviventer,* and *S. ochrognathus* in Durango, Mexico (Petersen, 1970, 1973); *Sigmodon leucotis* and *Microtus mexicanus* in Durango, Mexico (Baker, 1969); among seven species of *Microtus* in western North America (Anderson, 1959); and among desert rodents in the southwestern United States (Whitford and Steinberger, 1989). Similarly, the northward withdrawal of *Microtus* coincident with a gradual northward advance of *S. hispidus* is also viewed as an indication of competition (Baker, 1969). Other mammalogists have devised methods of detecting the effects of competition by analysis of captures at trap stations (Hallett and Pimm, 1970; Rosenzweig et al., 1984).

Character displacement is the change under natural selection of morphological, physiological, or behavioral characteristics in one or more ecologically similar species whose ranges overlap in sympatry. Such evolved differences reduce competition. Malmquist (1985) demonstrated that *Sorex minutus* had significantly smaller jaws when it occurred in sympatry with *S. araneus* (Sweden) than when it occurred allopatrically (Ireland). Similarly, Dayan et al. (1989, 1990) analyzed cranial characteristics of weasels in North America and Israel, and feline carnivores in Israel, and concluded that past competition for food led to present-day cranial differences.

Although these studies suggest an important role for competition in community structure, they are not conclusive. Empirical evidence demonstrating a change in niche breadth in response to a change in abundance of a potential competitor is necessary. Such evidence can be gathered from natural experiments or from perturbation experiments. Natural experiments involve comparing an area where a species is allopatric with a similar area where it occurs sympatrically with a potential competitor; differences in niche dimensions between the two areas are taken to indicate the effect of competition. For example, Glass and Slade (1980) reported that when *S. hispidus* declined locally in Kansas, *Microtus ochrogaster* expanded its spacial use of habitats; there was spatial separation when both species were present. The greatest problem with such natural experiments is that the sites compared may differ in ways other than the presence or absence of the species under consideration.

A perturbation experiment is arguably the best way to demonstrate whether competition affects community structure. This type of experiment, where one species is removed or reduced in density by the investigator, and the effect upon the remaining species is documented, avoids problems of possible differences between study sites. Such field experiments have demonstrated that interspecific competition affects community structure in a wide variety of systems (Busch and Kravetz, 1992; Connell, 1983; Schoener, 1983, 1985; Underwood, 1986). The inclusion in these general reviews of certain field experiments on mammals in which experimental flaws had been detected were criticized (i.e., enclosures smaller than home ranges; Galindo and Krebs, 1986; Schoener, 1986*b*). However, Dueser et al. (1989) reaffirmed the role of competition in structuring rodent communities. Details of these effects can be found in the numerous studies cited in the above reviews, such as Grant (1972), Crowell and Pimm (1976), and Dickman (1988).

One of the major criticisms to the conclusion that competition affects community structure was that many empirical studies were biased and that null models (i.e., models assuming no biological effects) could explain observed patterns of community structure (see Harvey et al., 1983; Strong et al., 1984). Community patterns of neotropical bats seem to be affected by factors other than simple competitive interactions (e.g., Willig and Mares, 1989). While problems certainly existed with empirical studies, analyses and reanalyses of data with null models have reconfirmed the importance of competition in general, and among mammals in particular, in structuring some communities (Bowers and Brown, 1982; Brown and Bowers, 1984; Dayan et al., 1990; Findley, 1989). However, Owen-Smith (1989), studying African ungulates in savanna grasslands, concluded that competition had little effect on community structure. Similarly, Findley (1993), in a comprehensive analysis of data on bat communities from throughout the world, concluded that competitive interactions had little or no part in structuring the communities; rather, their structure had a great deal to do with stochastic processes.

Predation also has been shown to be an important determinant of community structure (Sih et al., 1985). Removal of sea otters from nearshore communities along the coast of the western United States increased abundance of a major prey item (sea urchins). Abundant sea urchins decimated nearshore kelp communities, both in terms of abundance and diversity; simplification of the kelp community caused loss of many associated marine organisms. Thus, the sea otter can be classified as a keystone species in this system (Duggins, 1980; Estes and Palmisano, 1974; Estes et al., 1978; Simenstad et al., 1978). Similarly, Brown and Heske (1990) classified a guild of three species of kangaroo rats in the Mohave Desert as keystone species because their removal decreased the abundance of bare areas (germination sites for plants), changed the species composition of the plants, and favored invasion of the desert area by grassland species of mammals. Such effects were noted also in areas where species were introduced. Case and Bolger (1991) observed that introduction of mongoose, domestic dogs and cats, and *Rattus* on islands in various parts of the world constrains the distribution, colonization, and abundance of reptiles. Predators also affect microhabitat distribution of small mammals (Brown et al., 1988; Longland and Price, 1991). Kotler demonstrated that desert rodents forage in microhabitats offering shelter from predators and that the effects of predation risk, in combination with resource availability, influence structure of desert rodent assemblages (Kotler, 1984, 1989; Kotler and Holt, 1989; Kotler et al., 1988).

*Community patterns.*—Community pattern was defined by Elton (1966:22) as "the repetition of certain component shapes to form a connected or interspersed design." Here we consider patterns in species richness, abundance, and diversity. The number of species (species richness) of mammals increases with area (the well-known species area curve; Brown, 1971; Brown and Nicoletto, 1991; Connor and McCoy, 1979; Dritschilo et al., 1975), although Lomolino (1989) warned of statistical considerations when interpreting the slope of the species-area curve (see Coleman et al., 1982). The distributional extent and density of mammals are also related (Brown, 1984).

Several taxa of mammals exhibit hyperdiversity (Dial and Marzluff, 1989), that is, their biodiversity is greater than what would be expected by chance alone. Latitudinal patterns in species diversity of mammals are well known (Fleming, 1973; Heaney, 1991; Harrison et al., 1992; McCoy and Connor, 1980; Owen, 1990*a,* 1990*b,* Pagel et al., 1991; Rosenzweig, 1993; Schum, 1984; Simpson, 1964; Willig and Sandlin, 1991; Willig and Selcer, 1989), but not all groups of mammals respond to latitude in the same way. Indeed, quadrupedal mammals (as opposed to bats) do not fit the classic pattern of increasing the diversity of species as one moves toward the equator (Lacher and Mares, 1986; Mares, 1992; Mares and Ojeda, 1982). Many reasons for this gradient in species diversity have been advanced, including the supposition of a longer, uninterrupted time for evolution in the tropics [although Dritschilo et al. (1975) showed that rodent species introduced to North America within the past 2,000 years do not have fewer mite species than species that arose in the Pleistocene as predicted by the time hypothesis], spatial heterogeneity (Hafner, 1977; Kotler and Brown, 1988; M'Closkey, 1978), primary productivity (Abramsky, 1989; Abramsky and Rosenzweig, 1984; Brown, 1973; Brown and Davidson, 1977; Owen, 1988), potential evapotranspiration (Currie, 1991; Rosenzweig, 1968), and disturbances (Fuentes and Jaksic, 1988). Bowers (1993) demonstrated that plant communities with high and low intensity of herbivory have lower diversity than when herbivory was at an intermediate intensity. Rosenzweig (1993) reviewed evidence from mammals and other taxa that reveals a productivity-diversity pattern with highest diversity at intermediate productivities and suggests hypotheses to explain it, particularly the decline at high productivities.

Control of species diversity has been linked to the theory of limiting similarity, whereby the number of species in a community may be limited by their niche overlap (often measured as size ratios; Hutchinson, 1959). Most data on size ratios, including that from mammals, do not support limiting similarity (Brown and Lieberman, 1973; Willig, 1986). In fact, the presence of vacant niches in mammalian communities may facilitate invasions (Davis and Ward, 1988).

Finally, the study of several other patterns provides insight into mammalian community dynamics. Differences in patterns of body mass of North American land mammals seen at different measurement scales have been attributed to diverse ecological and evolutionary processes operating at those scales (i.e., competition, extinction, and allometric energetic constraints; Brown and Nicoletto, 1991). Stage of succession affects mammalian diversity (Buckner and Shure, 1985; Foster and Gaines, 1991; Fox, 1982; Sly, 1976) and, in turn, mammals have a profound effect on patterns of plant succession by the processes of herbivory and disturbance; mammals usually facilitate the entrance of later successional (plant) species into a successional sere (Anderson et al., 1980; Huntly and Inouye, 1987, 1988; Pearst, 1989; Platt, 1975; Tilman, 1983). Most recently, mammalian ecologists have begun to focus attention on patterns at the landscape scale. In particular, current work is revealing the effect of sizes of habitat patches (particularly resulting from habitat fragmentation) and corridors on dynamics of small mammal populations (Foster and Gaines, 1991; Henderson et al., 1985; Henein and Merriam, 1990; Laurance, 1991; Merriam and Lanoue, 1990).

*Community function.* — Community function involves relationships among constituent species whereby energy and nutrients are exchanged among these species. However, other sorts of interactions among species affect the community. For example, the study of mammalian communities has contributed to our knowledge of ecological stability. McNaughton (1977, 1985) considered how grazing mammals affected the relation among stability, diversity, and functional properties in grasslands of the Serengeti, concluding that the effect on grassland plant diversity may be different from the effect on grassland function (measured as primary production).

Trophic interactions among species are discussed in the section on Ecosystem Ecology below. Here we consider the impact of such trophic interactions and address the question as to the effects mammalian consumers might have on ecological communities. Hairston et al. (1960; hereafter HSS) concluded that herbivores were seldom food-limited and unlikely to compete for resources, whereas producers, carnivores, and decomposers competed in a density-dependent fashion for resources. This landmark study stimulated much research into consumer effects in various taxa, including mammals. Mammals usually consume 2–8% of available net production, but may eat as much as 30% under some conditions (Pimentel, 1988), tending to support HSS. However, the addition of food results in increased population density, growth rate, and survival, and smaller home ranges, countering predictions of HSS (Boutin, 1990; Desy et al., 1990; Dobson and Kjelgaard, 1985; Klenner and Krebs, 1991; Mares et al., 1976, 1982; Sullivan et al., 1983; Taitt and Krebs, 1983). The conclusion that not all plants are edible and that food is limiting has been strengthened by studies demonstrating that dietary intake by mammalian consumers is restricted by the nutrient and secondary plant compound content of their food (Batzli, 1986; Batzli et al., 1980; Bergeron and Jodoin, 1987; Bryant et al., 1991; Bucyanayandi and Bergeron, 1990; Eshelman and Jenkins, 1989; Hanley, 1982; Jonasson et al., 1986; Jung and Batzli, 1981; Kerley and Erasmus, 1991; Kuropat and Bryant, 1983; Marquis and Batzli, 1989; Randolph et al., 1991; Schultz, 1964; Seagle and McNaughton, 1992; Sinclair et al., 1982, 1988; Snyder, 1992; Willig and Lacher, 1991).

Mammalian consumers have a variety of other effects on community function (Huntly, 1991; Huntly and Inouye, 1988; Paige, 1992; Whicker and Detling, 1988). In summary, mammals affect plant production (Detling et al., 1980; Grant and French, 1980; Reichman and Smith, 1991), fitness (Belsky, 1986; Edwards, 1985; Maschinski and Whitham, 1989; McNaughton, 1986; Paige and Whitham, 1987), pollination and seed dispersal (Borchert and Jain, 1978; Fleming, 1982; Golley et al., 1975; Howell and Roth, 1981), vegetative diversity (Archer et al., 1987; Batzli and Pitelka, 1970; Borchert and Jain, 1978; Bryant, 1987; Coffin and Lauenroth, 1988; Fox and Bryant, 1984; Fuentes et al., 1983; Grant et al., 1982; Lidicker, 1989; Reichman and Smith, 1985; Reichman et al., 1993; Spatz and Mueller-Dombois, 1973; Stapanian and Smith, 1986; Truszkowski, 1982), and nutrient content (Coppock et al., 1983*a*). The complexity of biotic and abiotic interactions can be pronounced. For example, Grant et al. (1977) demonstrated that addition of nitrogen and water affected composition and density of a short-grass prairie and, concomitantly, affected structure of the mammalian community (see also Grant et al., 1980, for the effects of burrowing by fossorial mammals on plant production).

*Convergent evolution and the development of communities.*—Community ecologists have paid a good deal of attention to determining if communities develop over evolutionary time in a predictable manner. Because all species within a community respond to complex stimuli in an evolutionary manner, it might appear that populations evolving under broadly similar climatic regimes would develop suites of similar adaptations. Certainly it has long been known that several mammals are remarkably convergent, and this general morphological similarity is particularly prevalent among desert rodents, perhaps because they inhabit areas that are especially challenging to the physiology and ecology of small mammals (Eisenberg, 1975; Hatt, 1932; Schmidt-Nielsen, 1964).

Pianka (1969, 1973, 1975, 1985, 1986) and Cody (1970, 1973, 1974, 1975) were among the first evolutionary ecologists to examine community convergence. Pianka conducted research on lizard communities in the United States, Australia, and Africa. Cody studied birds occurring on different continents in similar habitats (Mediterranean chaparral-scrubland birds of California and Chile). Both examined various aspects of ecology and community structure, and devised quantitative methods for comparing niche parameters of faunas. Broadly speaking, birds were more convergent than lizards, although in each area there were striking examples of ecologically and morphologically convergent pairs, as well as remarkably different species. Karr and James (1975) studied the bird faunas of forested habitats of North and Central America and of Africa. Utilizing multivariate techniques, they concluded that convergence was pronounced among some species that differed phylogenetically, whereas divergence was evident among some species with similar phylogenetic backgrounds.

At about this same time, Mares (1975, 1976), for desert rodents, and Findley (1976), for bats, used multivariate analyses of morphoecological data to assess similarities and differences between faunas occurring on different continents. Both concluded that convergence was pronounced; morphology (and ecology) had evolved in many members of each fauna in a similar manner. Nevo (1979) demonstrated that fossorial rodents on many continents converged in ecological, morphological, behavioral, physiological, genetic, and many other characteristics in response to the subterranean environment.

Mares (1980, 1993*a*, 1993*b*) later extended his original analysis, which had been limited to an examination of desert and nondesert rodents in North and South America, to small mammals inhabiting all of the world's deserts. His results showed that community-wide convergence of morphology and ecology generally was detectable when species with widely different phylogenies were compared. Similar results were found by Berman (1985) in a rigorous morphological analysis of the evolution of bipedality among small mammals in deserts. Mares (1983:37–38) noted: "If one were to go into an unknown desert region, there are many predictions that could be made concerning the small mammal fauna . . . of the area . . . [A]t least some rodents . . . would exhibit the following adaptations: specialized kidneys . . . a counter-current heat exchange system in the nasal region; modified brain cells responsible for ADH secretion; lowered metabolic rate; facultative torpor; ability to exist without free water; minimization of water loss through respiratory, excretory, and defecatory pathways; inflated tympanic bullae or elongate pinnae; bipedality . . . [which] . . . could occur in all trophic categories except the completely fossorial niche . . . [and] coexisting species might exhibit regular patterns of body size differences." These comments about the pervasiveness of convergent evolution on the biology of organisms were in broad agreement with Nevo (1979).

The International Biological Program dedicated a great deal of effort to assess the pervasiveness and predictability of convergent evolution between communities (Mabry et al., 1977; Orians and Solbrig, 1977; Simpson, 1977). The results of these extensive studies indicated that, differences in history, phylogeny, and climate notwithstanding, ecosystematic convergence can be quite pronounced, especially for some of the components of the ecosystem.

Recent research on convergent evolution indicated that similar evolutionary adaptations to similar physical environments may not only be striking, but may extend beyond morphological traits to complex behavioral and ecological attributes. For example, Mares and Lacher (1987) showed that mammals that are specialized for life on isolated piles of boulders in different parts of the world can develop strongly convergent suites of characteristics that are associated with life in this rocky environment. These similarities will override phylogenetic similarities to such an extent that, for the traits examined, animals in different orders that inhabited very similar microenvironments (e.g., hyraxes, *Cavia* and *Procavia* of Africa, and the rock cavy, *Kerodon,* of the Brazilian Caatinga), were more similar to one another than they were to their own confamilials.

Curiously, when the entire mammal fauna of the Brazilian Caatinga was examined, there was little or no faunal convergence evidence between the Caatinga's fauna and those of other semiarid areas in the world (Mares et al., 1985). The Caatinga, although an extensive tropical dry area, has had a special history of isolation from grasslands where pre-adaptations for aridity might have developed over time, as they did for the other deserts and semideserts of the world. Rather, the Caatinga is a tropical dryland surrounded by moist forests, an unusual zone that undergoes periodic and catastrophic droughts (perhaps every two decades). Mares et al. (1985) showed that the largely tropically adapted fauna of the Caatinga was unable to adapt to aridity because droughts likely functioned as a frequent bottleneck that regularly eliminated most small mammals from the region. This research made clear the role of history, climate, and surrounding habitats on the evolution of convergent assemblages of mammals.

Research on convergent evolution is continuing for many groups of organisms (e.g., Luke, 1986; Schluter, 1986, 1990). Many questions remain to be answered. What is the influence of history on the evolution of similar species in similar areas? How challenging must an environment be to limit the evolutionary responses of organisms and thus make convergence likely? To what extent can phylogeny be overridden by natural selection? At the higher levels of organization (e.g., alpha and beta diversity, coexistence, competitive interactions, predation effects), what are the factors that cause convergence to be manifested, and *can* convergence be measured in some meaningful manner when entire faunas are compared (see Mares, 1993*a*)?

## Ecosystem Ecology

*Energetics.* —With the publication of Tansley's (1935) classic paper on plant ecology, it was possible to begin formulating experiments that would describe the functional relationships of organisms in a defined area. Perhaps because it is difficult to define the boundaries of an ecosystem [Colinvaux (1973:296) noted: "Ecosystems are in the eye of the beholder . . ."], it follows that the breakthrough in ecosystem ecology was made by an investigator studying lakes, which by their nature have distinct boundaries. The landmark paper on ecosystem ecology was Lindeman's (1942) report on the energetics of organisms in Cedar Bog Lake in Minnesota. Lindeman determined the standing crop of the various trophic levels in the lake and then assigned caloric values to the productivity at each level. Thus, the currency of systems ecology (energy) was defined, quantified, and applied. Additionally, it subsequently became possible to have at least a frame of comparison for parameters of standing crop, turnover, productivity, and so forth.

After Lindeman, ecosystems were considered a basic unit of ecology (e.g., Evans, 1956; Odum, 1953), and many ecologists, particularly those working in aquatic systems, began conducting research on either natural systems or systems constructed in the laboratory (e.g., Slobodkin, 1962). If lakes have relatively well-defined boundaries, and test tube communities even more so, terrestrial communities are notoriously difficult to control or even to obtain measurements of their component species. As Engelmann (1966) observed, it is a daunting task to apply a systems approach to a terrestrial ecosystem. It was almost surely this difficulty in capturing, observing, and quantifying population sizes (standing crop), determining the energetics of respiration and of daily activities, estimating turnover rates, and obtaining the myriad of other data required to understand how the system functioned, that delayed the application of Lindeman's ideas (and those that had expanded systems theory in the intervening period) to a terrestrial system. It would be 18 years before a trophic dynamic study of a terrestrial community would be conducted. That classic paper would be provided by a mammalogist, Frank Golley (1960).

Golley, who joined ASM in 1955 and would later publish an important text in mammalogy with David E. Davis (Davis and Golley, 1963) and field guides to the mammals of Georgia and South Carolina (Golley 1962, 1966), began a study of an old field terrestrial ecosystem whose vegetation consisted largely of grasses and herbs. The main herbivore was a vole (*Microtus pennsylvanicus*) and the major predator was the least weasel (*Mustela nivalis*). As might be expected, Golley had to census plants, determine their energy content and the proportion of energy that the plants devoted to respiration, and estimate their productivity. Similar measurements (e.g., standing crop biomass and energy content, population dynamics, growth, reproduction, assimilation efficiency, energy consumption) had to be made for *Microtus* and *Mustela*. Clearly, Golley's study required a prodigious effort, yet it remains one of the few examples of energy flow through a simple terrestrial system (e.g., "Even the work of Golley . . . is not very comprehensive," Collier et al., 1973:420). This criticism notwithstanding, Golley's work established the field of terrestrial energetics in vertebrate populations (see also Golley, 1961, 1967, 1968, 1983; Golley and Golley, 1972; Golley et al., 1975).

Shortly after Golley published his paper, Odum et al. (1962) expanded the scope of research on energy flow in another old field ecosystem. They examined energy flow through more components of the food chain than Golley did, including grasshoppers, a cricket, a sparrow, and the old field mouse, *Peromyscus polionotus*. Their research allowed them to tease apart differences in energy flow between vertebrates and invertebrates, as well as between herbivores and granivores.

Much research into the energetics of mammals was devoted to determining the energy costs associated with various daily activities for mammals. This was generally carried out in the laboratory on resting animals, or utilized physiological instrumentation to compare resting and active rates of metabolism. These investigations centered on single species and the results often were compared to energetic assumptions and determinations made by Golley (e.g., Chew et al., 1965; Gessaman, 1973; Golley et al., 1965; Górecki, 1965; Grodzinski and Górecki, 1967; McNab, 1963, 1991; McNab and Morrison, 1963; Pearson, 1960).

Terrestrial ecosystems were as difficult to study after Golley's research had been published as they were before, but the publication of his study on energy flow showed that, in principle, terrestrial systems, albeit extremely complex, were amenable to field research. Investigators thus began the difficult task of examining energy flow through other systems. One of the first to publish on this topic was a mammalogist, Oliver Pearson, who examined populations of several species of rodents and various carnivores (including feral house cats) in a large park in California (Pearson, 1964). Pearson censused rodent populations to determine density, then deduced the impact of carnivores on rodents by intensively collecting feces of predators. He also measured plant standing crop and estimated energetics of the organisms involved in energy flow through the system. This study was important because it dealt with a system which was more complex than that studied by Golley, although it was done over a much shorter time, necessitating more assumptions than did Golley's work.

Several studies dealing with one or another aspect of secondary productivity in ecosystems were published by Petrusewicz (1967), but it was another mammalogist who directed the research that would provide the next major energy flow study in a complex field situation. Robert Chew and his wife, Alice Eastlake Chew (Chew and Chew, 1965, 1970), conducted an extensive study on the energetics of a desert scrub community, including its mammals. Working in a creosote bush (*Larrea tridentata*) scrubland, the Chews determined bioenergetics of plants, including density, productivity, and standing crop, and gathered the same information on 13 species of small- and medium-sized mammals that occurred on the area. Their work remains one of the finest studies of energy flow in mammals ever conducted and provided important data to understand the pathways of energy flow through a desert system, ecological efficiencies of herbivores and granivores, and the net energy flow through various links in the food chain. Their research described the minor role played by small mammals (herbivores, granivores) in energy transfer in a community, converting only 0.016% of the primary above-ground production to mammal tissue that was then available as a food resource to carnivores in higher trophic levels. This work provided dramatic quantitative data on the shape of the pyramids of energy and biomass.

Following these early seminal studies, other investigators began to refine our understanding of energy flow through mammal species and communities (e.g., Collier et al., 1975; Collins and Smith, 1976; Fleharty and Choate, 1973; French et al., 1976; Gebczynska, 1970; Gebczynski et al., 1972; Grodzinski, 1971; Grodzinski and French, 1983; Kenagy, 1973; McNaughton, 1976; Merritt and Merritt, 1978; Montgomery and Sunquist, 1975; Myrcha, 1975; Soholt, 1973). These studies were conducted in temperate and tropical areas, and on both small and large mammals.

*The International Biological Program (IBP).*—Undoubtedly, the major research stimulus to work on bioenergetics, and a continuing factor throughout the world on current interest in community dynamics, was the establishment of the IBP in the 1960s. Because of its importance to research on ecosystems, some background on IBP is provided.

In 1962 Ledyard Stebbins, a plant geneticist at the University of California, Davis, published a paper on the activities of the International Union of Biological Sciences, of which he was Secretary-General (Stebbins, 1962; see Blair, 1977). In that report, he outlined the International Biological Program, a program of global ecological research. W. Frank Blair, who was then President of the Ecological Society of America, and who had been one of the leading mammalian ecologists in ASM before dedicating his research program to the evolutionary ecology of amphibians and reptiles (cf., Blair, 1939, 1941, 1953, 1955), became intimately involved in the complex planning that ultimately resulted in the establishment of an internationally organized and funded program of comparative ecosystem research in 1967. The initial program had limited funding; broad-based financial support provided by congressional action did not become available until Blair, in his role as Chairman of the US/IBP, led the fight to push funding bills through committees of both the House and Senate between 1967 and 1970.

IBP was dedicated to elucidating the structure and function of the earth's major ecosystems. The methodologies employed were those of population ecology, energetics, community structure, mathematical modeling, and elemental cycling, among others. At the heart of this multi-country research effort were the biome programs. These included programs focusing on the major terrestrial biomes (Tundra Biome, Grassland Biome, Desert Biome, Coniferous Forest Biome, Deciduous Forest Biome, Tropical Forest Biome), as well as programs dealing with the Conservation of Ecosystems, Man in the Andes, Circumpolar Peoples, Upwelling Areas, and Origin and Structure of Ecosystems, which examined the role of convergent evolution in structuring communities of organisms in North and South America.

IBP was big science in all of its glory, and with all of its problems (Blair, 1977). Because it cut across disciplines and countries, IBP was an extremely difficult undertaking and was widely criticized by scientists who were not involved in the programs or who felt that this type of coordinated research was not the way to do science (Michell et al., 1976). It was viewed negatively by some (e.g., Boffey, 1976), but time has provided a more balanced historical perspective. As McIntosh (1985:215) noted, "the status of ecology and ecologists at the inception of IBP was clearly 'minor'," but IBP changed "the way ecology was done and the way ecologists thought about ecology" (McIntosh, 1985:219). IBP was a maturing force in the development of ecosystem ecology; it pushed this type of investigation into the forefront of organismal biology, giving it a high public profile and underscoring the importance of developing an understanding of how the natural environment functions. Attempts to devise mathematical models of ecosystems were clearly less than successful (e.g., Berlinski, 1976), but ecosystem ecology has continued to develop, both conceptually and methodologically (McIntosh, 1985).

The effect of IBP on world ecology was pronounced (Kormondy and McCormick, 1981). In reviewing country after country, it is clear that field research flourished where IBP sites had been located. The program functioned as a training ground for students in the various fields of ecology, including mammalian community structure, energetics, population dynamics, and evolution. Literally thousands of papers on mammals have been published from work that was funded by, or related to, the IBP's many foci. In Poland, for example, Kajak and Pieczynska (1981:287–288) reported: "Four major periods can be distinguished in the development of Polish ecology after 1945: . . . [f]rom 1969 to 1975 was a period of intense studies on ecological productivity and of ecosystem studies connected with . . . IBP . . . [including especially s]tudies on small mammals." For Sweden, Sjörs (1981: 305–306) noted, "The . . . (IBP) meant increased contacts among ecologists all over the world. . . . Thanks to the IBP [production and biomass studies] became highlighted in basic research." In most countries where IBP research was conducted, mammal investigations were extensive.

The results of the efforts of the IBP are still being witnessed today in mammalogical research. There are ecosystem-oriented studies and research based in energetics that are currently providing important information on the ecology of populations and communities of mammals. Research stimulated by the projects or scientists who participated in IBP is still being conducted in a wide array of habitats throughout the world. Even as we approach two decades since the termination of IBP, there has probably been insufficient time to assess objectively the impacts and contributions of the entire program on a global basis. However, scientists involved with IBP not only conducted research on ecosystem function, community evolution, and ecosystem development, but were also instrumental in carrying on empirical research on the effects of abiotic factors on the structure of mammalian communities. The Structure of Ecosystems Program was dedicated to this goal. IBP and ecosystem studies will be intimately associated in the future.

## *Conclusions*

Mammalogists have contributed greatly to the development of community and ecosystem ecology. Their influence has been pervasive and continuous, and extends from the very foundations of these fields of research. Present trends indicate that important empirical and theoretical contributions to elucidating patterns of community and ecosystem structure and function will continue to be made by mammalogists. There is no doubt that members of the ASM have been, and will continue to be, at the forefront of this research.

## *Acknowledgments*

We thank O. J. Reichman and M. R. Willig for critical reviews of the manuscript. We also thank J. K. Braun, R. B. Channell, and R. Humphrey for assistance in preparing the manuscript.

## *Literature Cited*

ABRAMSKY, Z. 1989. Communities of gerbilline rodents in sand dunes of Israel. Pp. 205–217, *in* Patterns in the structure of mammalian communities (D. W. Morris, Z. Abramsky, B. J. Fox, and M. R. Willig, eds.). Texas Tech University Press, Lubbock, 266 pp.

ABRAMSKY, Z., AND M. L. ROSENZWEIG. 1984. Tilman's predicted productivity-diversity relationship shown by desert rodents. Nature, 309:150–151.

ADAMS, C. C. 1905. The postglacial dispersal of the North American biota. The Biological Bulletin, 9:53–71.

———. 1909. An ecological survey of Isle Royal, Lake Superior. Report of the Board of the Geological Survey of 1908, Lansing, Michigan, 468 pp.

———. 1913. Guide to the study of animal ecology. Macmillan, New York, 183 pp.

ALLEE, W. C., A. E. EMERSON, O. PARK, T. PARK, AND K. P. SCHMIDT. 1949. Principles of animal ecology. W. B. Saunders Company, Philadelphia, Pennsylvania, 837 pp.

ANDERSEN, D. C., AND J. A. MACMAHON. 1985. Plant succession following the Mount St. Helens volcanic eruption: facilitation by a burrowing rodent, Thomomys talpoides. The American Midland Naturalist, 114:62–69.

ANDERSEN, D. C., J. A. MACMAHON, AND M. L. WOLFE. 1980. Herbivorous mammals along a montane sere: community structure and energetics. Journal of Mammalogy, 61:500–519.

ANDERSON, S. 1959. Mammals of the Grand Mesa, Colorado. University of Kansas Publications, Museum of Natural History, 9:405–414.

ARCHER, S., M. G. GARRETT, AND J. K. DETLING. 1987. Rates of vegetation change associated with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie. Vegetatio, 72:159–166.

BAKER, R. H. 1969. Cotton rats of the Sigmodon fulviventer group. Pp. 177–232, *in* Contributions in Mammalogy (J. K. Jones, ed.). Miscellaneous Publications, Museum of Natural History, University of Kansas, 51:1–428.

BARCLAY, R. M. R., AND R. M. BRIGHAM. 1991. Prey detection, dietary niche breadth, and body size in bats: why are aerial insectivorous bats so small? The American Naturalist, 137:693–703.

BARLOW, C. 1991. From Gaia to selfish genes. MIT Press, Cambridge, Massachusetts, 273 pp.

BARTHOLOMEW, G. A. 1986. The role of natural history in contemporary biology. BioScience, 36:324–329.

BATZLI, G. O. 1986. Nutritional ecology of the California vole: effects of food quality on reproduction. Ecology, 67:406–412.

BATZLI, G. O., AND F. A. PITELKA. 1970. Influence of meadow mouse populations on California grassland. Ecology, 51:1027–1039.

BATZLI, G. O., R. G. WHITE, S. F. MACLEAN, F. A. PITELKA, AND B. D. COLLIER. 1980. The herbivore-based trophic system. Pp. 335–410, *in* An Arctic ecosystem: the coastal tundra at Barrow, Alaska (J. Brown, P. C. Miller, L. L. Tieszen, and F. L. Bunnell, eds.). Dowden, Hutchinson & Ross, Incorporated, Stroudsburg, Pennsylvania, 571 pp.

BELK, M. C., H. D. SMITH, AND J. LAWSON. 1989. Use and partitioning of montane habitat by small mammals. Journal of Mammalogy, 69:688–695.

BELSKY, A. J. 1986. Does herbivory benefit plants? A review of the evidence. The American Naturalist, 127:870–892.

BERGERON, J. M., AND L. JODOIN. 1987. Defining "high quality" food resources of herbivores: the case for meadow voles (*Microtus pennsylvanicus*). Oecologia, 71:510–517.

BERLINSKI, D. 1976. On systems analysis: an essay concerning the limitations of some mathematical methods in the social, political, and biological sciences. MIT Press, Cambridge, Massachusetts. pp.

BERMAN, S. L. 1985. Convergent evolution in the hindlimb of bipedal rodents. Zeischrift für Zoologische Systematik und Evolutionsforschung, 23:59–77.

BLAIR, W. F. 1939. Faunal relationships and geographic distribution of mammals in Oklahoma. The American Midland Naturalist, 22:85–133.

———. 1941. Techniques for the study of small mammal populations. Journal of Mammalogy, 22: 148–157.

———. 1953. Population dynamics of rodents and other small mammals. Advances in Genetics, 5:1–41.

———. 1955. Size differences as a possible isolation mechanism in *Microhyla*. The American Naturalist, 89:297–302.

———. 1977. Big biology. Dowden, Hutchinson and Ross, Incorporated, Stroudsburg, Pennsylvania, 261 pp.

BOFFEY, P. M. 1976. International Biological Program: was it worth the cost and effort? Science, 193: 866–868.

BORCHERT, J. I., AND S. K. JAIN. 1978. The effect of rodent seed predation on four species of California annual grasses. Oecologia, 33:101–113.

BOUTIN, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. Canadian Journal of Zoology, 68:203–220.

BOWERS, M. A. 1993. Influence of herbivorous mammals on an old-field plant community: years 1–4 after disturbance. Oikos, 67:129–141.

BOWERS, M., AND J. H. BROWN. 1982. Body size and coexistence in desert rodents: chance or community structure? Ecology, 63:391–400.

BROWN, J. H. 1971. Species richness of boreal mammals living on the montane islands of the Great Basin. The American Naturalist, 105:467–478.

———. 1973. Species diversity of seed-eating desert rodents in sand dune habitats. Ecology, 54:775–787.

———. 1975. Geographical ecology of desert rodents. Pp. 315–341, *in* Ecology and evolution of communities (M. L. Cody and J. M. Diamond, eds.). Harvard University Press, Cambridge, Massachusetts, 543 pp.

———. 1981. Two decades of homage to Santa Rosalia: toward a general theory of diversity. The American Zoologist, 21:877–888.

———. 1984. On the relationship between abundance and distribution of species. The American Naturalist, 124:255–279.

———. 1986. Two decades of interaction between the MacArthur-Wilson model and the complexities of mammalian distributions. Biological Journal of the Linnean Society, 28:231–251.

Brown, J. H., and M. A. Bowers. 1984. Patterns and processes in three guilds of terrestrial vertebrates. Pp. 282–296, *in* Ecological communities. Conceptual issues and the evidence (D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle, eds.). Princeton University Press, Princeton, New Jersey, 613 pp.

Brown, J. H., and D. W. Davidson. 1977. Competition between seed-eating rodents and ants in desert ecosystems. Science, 196:880–882.

Brown, J. H., and E. J. Heske. 1990. Control of a desert-grassland transition by a keystone rodent guild. Science, 250:1705–1707.

Brown, J. H., and M. Kurzius. 1989. Spatial and temporal variation in guilds of North American granivorous desert rodents. Pp. 71–90, *in* Patterns in the structure of mammalian communities (D. W. Morris, Z. Abramsky, B. J. Fox, and M. R. Willig, eds.). Texas Tech University Press, Lubbock, 266 pp.

Brown, J. H., and G. A. Lieberman. 1973. Resource utilization and coexistence of seed-eating desert rodents in sand dune habitats. Ecology, 54:788–797.

Brown, J. H., and P. F. Nicoletto. 1991. Spatial scaling of species composition: body masses of North American land mammals. The American Naturalist, 138:1478–1512.

Brown, J. H., D. W. Davidson, and O. J. Reichman. 1979. An experimental study of competition between seed-eating rodents and ants. The American Zoologist, 19:1129–1143.

Brown, J. H., D. W. Davidson, J. C. Munger, and R. S. Inouye. 1986. Experimental community ecology: the desert granivore system. Pp. 41–62, *in* Community ecology (J. Diamond and T. Case, eds.). Harper and Row, New York, 665 pp.

Brown, J. S. 1989. The role of resource variability in structuring desert rodent communities. Pp. 141–154, *in* Patterns in the structure of mammalian communities (D. W. Morris, Z. Abramsky, B. J. Fox, and M. R. Willig, eds.). Texas Tech University Press, Lubbock, 266 pp.

Brown, J. S., B. P. Kotler, R. J. Smith, and W. O. Wirtz, II. 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. Oecologia, 76:408–415.

Bryant, J. P. 1987. Feltleaf willow-snowshoe hare interactions: plant carbon/nutrient balance and floodplain succession. Ecology, 68:1319–1327.

Bryant, J. P., F. D. Provenza, J. Pastor, P. B. Reichardt, T. P. Clausen, and J. T. duToit. 1991. Interactions between woody plants and browsing mammals mediated by secondary metabolites. Annual Review of Ecology and Systematics, 22:431–446.

Buckner, C. Z., and D. J. Shure. 1985. The response of *Peromyscus* to forest opening size in the southern Appalachian Mountains. Journal of Mammalogy, 66: 299–307.

Bucyanayandi, J. F., and J. M. Bergeron. 1990. Effects of food quality on feeding patterns of meadow voles (*Microtus pennsylvanicus*) along a community gradient. Journal of Mammalogy, 71:390–396.

Busch, M., and F. O. Kravetz. 1992. Competitive interactions among rodents (*Akodon azarae, Calomys laucha, Calomys musculinus* and *Oligoryzomys flavescens*) in a two-habitat system. II. Effect of species removal. Mammalia, 56:540–554.

Cabrera, A. 1932. La incompatabilidad ecológica: una ley biológica interesante. Anales Sociedad Científica de Argentina, 114:243–260.

Cameron, G. N. 1971. Niche overlap and competition in woodrats. Journal of Mammalogy, 52:288–296.

Carnes, B. A., and N. A. Slade. 1982. Some comments on niche analysis in canonical space. Ecology, 63:888–893.

Carpenter, F. L. 1978. Hooks for mammal pollination. Oecologia, 35:123–132.

Case, T. J., and D. T. Bolger. 1991. The role of interspecific competition in the biogeography of island lizards. Trends in Ecology and Evolution, 6:135–139.

Chew, R. M., and A. E. Chew. 1965. The primary productivity of a desert scrub (*Larrea tridentata*) community. Ecological Monographs, 35:355–375.

———. 1970. Energy relationships of the mammals of a desert scrub (*Larrea tridentata*) community. Ecological Monographs, 40:1–21.

Chew, R. M., R. G. Lindberg, and P. Hayden. 1965. Circadian rhythm of metabolic rate in pocket mice. Journal of Mammalogy, 46:477–494.

Churchfield, S. 1991. Niche dynamics, food resources, and feeding strategies in multispecies communities of shrews. Pp. 23–34, *in* The biology of the Soricidae (J. S. Findley and T. L. Yates, eds.). Special Publication, The Museum of Southwestern Biology, 1:1–91.

Clements, F. E. 1905. Research methods in ecology. University Publishing Company, Lincoln, Nebraska.

———. 1916. Plant succession. An analysis of the development of vegetation. Carnegie Institute of Washington Publication, 242:1–512.

Clements, F. E. and V. E. Shelford. 1939. Bioecology. John Wiley & Sons, Incorporated, New York, 425 pp.

Cody, M. L. 1970. Chilean bird distributions. Ecology, 51:455–464.

———. 1973. Parallel evolution and bird niches. Pp. 307–338, *in* Mediterranean-type ecosystems: origin and structure (F. di Castri and H. A. Mooney, eds.). Springer-Verlag, New York, 405 pp.

———. 1974. Competition and the structure of bird communities. Princeton University Press, Princeton, New Jersey, 318 pp.

———. 1975. Towards a theory of continental species diversity: bird distributions over Mediterranean habitat gradients. Pp. 214–257, *in* Ecology and evolution of communities (M. Cody and J. Diamond, eds.). Harvard University Press, Cambridge, Massachusetts, 543 pp.

Cody, M. L., and J. M. Diamond (eds.). 1975. Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts, 543 pp.

COFFIN, D. P., AND W. K. LAUENROTH. 1988. The effects of disturbance size and frequency on a short-grass plant community. Ecology, 69:1609–1617.

COLEMAN, B. D., M. A. MARES, M. R. WILLIG, AND Y. H. HSIEH. 1982. Randomness, area, and species richness. Ecology, 63:1121–1133.

COLINVAUX, P. 1973. Introduction to ecology. John Wiley & Sons, Incorporated, New York, 621 pp.

COLLIER, B. D., G. W. COX, A. W. JOHNSON, AND P. C. MILLER. 1973. Dynamic ecology. Prentice-Hall, Incorporated, Englewood Cliffs, New Jersey, 563 pp.

COLLIER, B. D., N. C. STENSETH, S. BARKLEY, AND R. OSBORN. 1975. A simulation model of energy acquisition and utilization by the brown lemming *Lemmus trimucronatus* at Barrow, Alaska. Oikos, 26:276–294.

COLLINS, V. R., AND M. H. SMITH. 1976. Field determination of energy flow in a small nocturnal mammal. Journal of Mammalogy, 57:149–158.

CONNELL, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos, 35:131–138.

———. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. The American Naturalist, 122:661–696.

CONNOR, E. F., AND E. D. MCCOY. 1979. The statistics and biology of the species-area relationship. The American Naturalist, 113:791–833.

COPPOCK, D. L., J. K. DETLING, J. E. ELLIS, AND M. I. DYER. 1983*a*. Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. Oecologia, 56:1–9.

COPPOCK, D. L., J. E. ELLIS, J. K. DETLING, AND M. I. DYER. 1983*b*. Plant-herbivore interactions in a North American mixed-grass prairie. II. Responses of bison to modification of vegetation by prairie dogs. Oecologia, 56:10–15.

COX, D. 1980. A note on the queer history of "niche." Bulletin of the Ecological Society of America, 64: 201–202.

CROWELL, K. L., AND S. L. PIMM. 1976. Competition and niche shifts of mice introduced onto small islands. Oikos, 27:251–258.

CURRIE, D. J. 1991. Energy and large-scale patterns of animal- and plant-species richness. The American Naturalist, 137:27–49.

DAVIDSON, D. W., R. S. INOUYE, AND J. H. BROWN. 1984. Granivory in a desert ecosystem: experimental evidence for indirect facilitation of ants by rodents. Ecology, 65:1780–1786.

DAVIS, D. E., AND F. B. GOLLEY. 1963. Principles in mammalogy. Reinhold Publishing Company, New York, 335 pp.

DAVIS, R., AND O. G. WARD. 1988. A vacant "Microtus niche" now occupied by the yellow-nosed cotton rat (*Sigmodon ochrognathus*) on an isolated mountain in southeastern Arizona. Journal of Mammalogy, 69:362–365.

DAYAN, T., D. SIMBERLOFF, E. TCHERNOV, AND Y. YOM-TOV. 1989. Inter- and intraspecific character displacement in mustelids. Ecology, 70:1526–1539.

———. 1990. Feline canines: community-wide character displacement among the small cats of Israel. The American Naturalist, 136:39–60.

DESY, E. A., G. O. BATZLI, AND J. LIU. 1990. Effects of food and predation on behaviour of prairie voles. Oikos, 58:159–168.

DETLING, J. K., M. I. DYER, C. PROCTER-GREGG, AND D. T. WINN. 1980. Plant-herbivore interactions: examination of potential effects of bison saliva on regrowth of *Bouteloua gracilis*. Oecologia, 45:26–31.

DIAL, K. P., AND J. M. MARZLUFF. 1989. Nonrandom diversification within taxonomic assemblages. Systematic Zoology, 38:26–37.

DIAMOND, J. M. 1978. Niche shifts and the rediscovery of interspecific competition. American Scientist, 66:322–331.

———. 1986. Overview: laboratory experiments, field experiments, and natural experiments. Pp. 3–22, *in* Community ecology (J. M. Diamond and T. Case, eds.). Harper and Row, New York, 665 pp.

DICE, L. 1952. Natural communities. University of Michigan Press, Ann Arbor, 547 pp.

DICKMAN, C. R. 1988. Body size, prey size, and community structure in insectivorous mammals. Ecology, 69:569–580.

———. 1989. Patterns in the structure and diversity of marsupial carnivore communities. Pp. 241–251, *in* Patterns in the structure of mammalian communities (D. W. Morris, Z. Abramsky, B. J. Fox, and M. R. Willig, eds.). Texas Tech University Press, Lubbock, 266 pp.

DOBSON, F. S., AND J. D. KJELGAARD. 1985. The influence of food resources on life history in Columbian ground squirrels. Canadian Journal of Zoology, 63:2105–2109.

DRITSCHILO, W., H. CORNELL, D. NAFUS, AND B. O'CONNOR. 1975. Insular biogeography of mice and mites. Science, 190:467–469.

DUESER, R. D., AND J. G. HALLETT. 1980. Competition and habitat selection in a forest-floor small mammal fauna. Oikos, 35:293–297.

DUESER, R. D., AND H. H. SHUGART. 1979. Niche pattern in a forest-floor small-mammal fauna. Ecology, 60:108–118.

——. 1982. Reply to comments by Van Horne and Ford and by Carnes and Slade. Ecology, 63:1174–1175.

DUESER, R. D., J. H. PORTER, AND J. L. J. DOOLEY. 1989. Direct tests for competition in North American rodent communities: synthesis and prognosis. Pp. 105–126, *in* Patterns in the structure of mammalian communities (D. W. Morris, Z. Abramsky, B. J. Fox, and M. R. Willig, eds.). Texas Tech University Press, Lubbock, 266 pp.

DUFF, A. G., AND P. D. LOWE. 1981. Great Britain. Pp. 141–156, *in* Handbook of contemporary developments in world ecology (E. J. Kormondy and J. F. McCormick, eds.). Greenwood Press, Westport, Connecticut, 776 pp.

DUGGINS, D. O. 1980. Kelp beds and sea otters: an experimental approach. Ecology, 61:447–453.

EDWARDS, J. 1985. Effects of herbivory by moose on flower and fruit production of *Aralia nudicaulis*. The Journal of Ecology, 73:861–868.

EHRLICH, P. R., AND J. ROUGHGARDEN. 1987. The science of ecology. Macmillan, New York, 710 pp.

EISENBERG, J. F. 1975. The behavior patterns of desert rodents. Pp. 189–224, *in* Rodents in desert environments (I. Prakash and P. K. Ghosh, eds.). Junk, b.v., The Hague, The Netherlands, 624 pp.

ELTON, C. 1927. Animal ecology. Sidgwick & Jackson, London, 207 pp.

———. 1933. The ecology of animals. Methuen and Company Limited, London, 97 pp.

———. 1942. Voles, mice, and lemmings: problems in population dynamics. Clarendon Press, Oxford, 496 pp.

———. 1958. The ecology of invasions by animals and plants. Methuen & Company Limited, London, 181 pp.

———. 1966. The pattern of animal communities. Methuen & Company Limited, London, 432 pp.

ELTON, C., AND R. S. MILLER. 1954. The ecological survey of animal communities with a practical system of classifying habitats by structural characters. The Journal of Ecology, 42:460–496.

ELTON, C., AND M. NICHOLSON. 1942. The ten-year cycle in numbers of the lynx in Canada. The Journal of Animal Ecology, 11:215–244.

EMMONS, L. H. 1980. Ecology and resource partitioning among nine species of African rain forest squirrels. Ecological Monographs, 50:31–54.

ENGELMANN, M. D. 1966. Energetics, terrestrial field studies, and animal productivity. Advances in Ecological Research, 3:73–115.

ERLINGE, S., ET AL. 1983. Predation as a regulation factor on small rodent populations in southern Sweden. Oikos, 40:36–52.

———. 1984. Can vertebrate predators regulate their prey? The American Naturalist, 123:125–133.

———. 1988. More thoughts on vertebrate predator regulation of prey. The American Naturalist, 132: 148–154.

ERRINGTON, P. L. 1946. Predation and vertebrate populations. The Quarterly Review of Biology, 21: 144–177.

ESHELMAN, R. D., AND S. H. JENKINS. 1989. Food selection by Belding's ground squirrels in relation to plant nutritional features. Journal of Mammalogy, 70:846–851.

ESTES, J. A., AND J. F. PALMISANO. 1974. Sea otters: their role in structuring nearshore communities. Science, 185:1058–1060.

ESTES, J. A., N. S. SMITH, AND J. F. PALMISANO. 1978. Sea otter predation and community structure. Ecology, 59:822–833.

EVANS, F. C. 1956. Ecosystems as the basic unit in ecology. Science, 123:1127–1128.

FAUTIN, R. 1946. Biotic communities of the northern desert shrub biome in western Utah. Ecological Monographs, 16:251–310.

FINDLEY, J. S. 1976. The structure of bat communities. The American Naturalist, 110:129–139.

———. 1989. Morphological patterns in rodent communities of southwestern North America. Pp. 253–263, *in* Patterns in the structure of mammalian communities (D. W. Morris, Z. Abramsky, B. J. Fox, and M. R. Willig, eds.). Texas Tech University Press, Lubbock, 266 pp.

———. 1993. Bats. A community perspective. Cambridge University Press, New York, 200 pp.

FLEHARTY, E. D., AND J. R. CHOATE. 1973. Bioenergetic strategies of the cotton rat, *Sigmodon hispidus*. Journal of Mammalogy, 54:680–692.

FLEMING, T. H. 1973. Numbers of mammal species in North and Central American forest communities. Ecology 54:555–563.

———. 1981. Fecundity, fruiting pattern, and seed dispersal in *Piper amalago* (Piperaceae), a bat-dispersed tropical shrub. Oecologia, 51:42–46.

———. 1982. Foraging strategies of plant visiting bats. Pp. 287–326, *in* Ecology of bats (T. H. Kunz, ed.). Plenum Press, New York, 425 pp.

FLEMING, T. H., E. T. HOOPER, AND D. E. WILSON. 1972. Three Central American bat communities: structure, reproductive cycles, and movement patterns. Ecology, 53:555–569.

FORBES, S. A. 1887. The lake as a microcosm. Bulletin Science Association of Peoria, Illinois, 1887:77–87.

FOSTER, J., AND M. S. GAINES. 1991. The effects of a successional habitat mosaic on a small mammal community. Ecology, 72:1358–1373.

FOX, B. J. 1981. Niche parameters and species richness. Ecology, 62:1415–1425.

———. 1982. Fire and mammalian secondary succession in an Australian coastal heath. Ecology, 63: 1332–1341.

———. 1989. Small-mammal community pattern in Australian heathland: a taxonomically-based rule for species assembly. Pp. 91–103, *in* Patterns in the structure of mammalian communities (D. W. Morris, Z. Abramsky, B. J. Fox, and M. R. Willig, eds.). Texas Tech University Press, Lubbock, 266 pp.

FOX, B. J., AND J. H. BROWN. 1993. Assembly rules for functional groups in North American desert rodent communities. Oikos, 67:358–370.

FOX, J. F., AND J. P. BRYANT. 1984. Instability of the snowshoe hare and woody plant interaction. Oecologia, 63:128–135.

FRANKLIN, J. F., C. S. BLEDSOE, AND J. T. CALLAHAN. 1990. Contributions of the long-term ecological research program. BioScience, 40:509–523.

FRENCH, N. R., W. E. GRANT, W. GRODZINSKI, AND D. M. SWIFT. 1976. Small mammal energetics in grassland ecosystems. Ecological Monographs, 46: 201–220.

FRYXELL, J. M., D. J. T. HUSSELL, A. B. LAMBERT, AND P. C. SMITH. 1991. Time lags and population fluctuations in white-tailed deer. The Journal of Wildlife Management, 55:377–385.

FUENTES, E. R., AND F. M. JAKSIC. 1988. The humpbacked species diversity curve: why has it not been found among land animals? Oikos, 53:139–143.

FUENTES, E. R., F. M. JAKSIC, AND J. A. SIMONETTI. 1983. European rabbits versus native rodents in central Chile: effects on shrub seedlings. Oecologia, 58:411–414.

GAFFNEY, P. M. 1973. Roots of the niche concept. The American Naturalist, 109:490.

GALINDO, C., AND C. J. KREBS. 1986. Evidence for competition in small rodents. Oikos, 46:116–118.

GEBCZYNSKA, Z. 1970. Bioenergetics of a root vole population. Acta Theriologica, 15:33–66.

GEBCZYNSKI, M., A. GÓRECKI, AND A. DROZDZ. 1972. Metabolism, food assimilation and bioenergetics of three species of dormice (Gliridae). Acta Theriologica, 17:271–294.

Gessaman, J. A. (ed.). 1973. Ecological energetics of homeotherms. A view compatible with ecological modeling. Monograph Series, Utah State University Press, Logan, 20:1–155.

Gigon, A., F. Klötzli, and U. Rahm. 1981. Switzerland. Pp. 313–329, *in* Handbook of contemporary developments in world ecology (E. J. Kormondy and J. F. McCormick, eds.). Greenwood Press, Westport, Connecticut, 776 pp.

Glass, G. E., and N. A. Slade. 1980. The effect of *Sigmodon hispidus* on spatial and temporal activity of *Microtus ochrogaster*: evidence for competition. Ecology, 61:358–370.

Gleason, H. A. 1917. The structure and development of the plant association. Bulletin of the Torrey Botanical Club, 43:463–481.

———. 1939. The individualistic concept of the plant association. The American Midland Naturalist, 21: 92–110.

Golley, F. B. 1960. Energy dynamics of a food chain of an old-field community. Ecological Monographs, 30:187–206.

———. 1961. The energy value of ecological materials. Ecology, 42:581–584.

———. 1962. The mammals of Georgia: a study of their distribution and functional role in the ecosystem. University of Georgia Press, Athens, Georgia, 218 pp.

———. 1966. South Carolina mammals. Contributions of the Charleston Museum, No. 15. 181 pp.

———. 1967. Methods of measuring secondary productivity in terrestrial vertebrate populations. Pp. 99–124, *in* Secondary productivity of terrestrial ecosystems (K. Petrusewicz, ed.). 2 vol. Panstwowe Wydawnictwo Naukowe, Warsaw, Poland, 879 pp.

———. 1968. Secondary productivity in terrestrial ecosystems. American Zoologist, 8:53–59.

——— (ed.). 1983. Tropical rainforest ecosystems: structure and function. Ecosystems of the world, 14A, Elsevier Scientific Publishing Company, Amsterdam, 381 pp.

Golley, F. B., K. Petrusewicz, and L. Ryszkowski (eds.). 1975. Small mammals: their productivity and population dynamics. Cambridge University Press, Cambridge, 451 pp.

Golley, F. B., G. A. Petrides, E. L. Rauber, and J. H. Jenkins. 1965. Food intake and assimilation by bobcats under laboratory conditions. The Journal of Wildlife Management, 29:442–447.

Golley, F. B., J. T. McGinnis, R. G. Clements, G. I. Child, and M. J. Duever. 1975. Mineral cycling in a tropical moist ecosystem. University of Georgia, Athens, 248 pp.

Golley, P. M., and F. B. Golley (eds.). 1972. Tropical ecology with an emphasis on organic production. University of Georgia, Athens.

Górecki, A. 1965. Energy values of body in small mammals. Acta Theriologica, 10:333–352.

Grant, P. R. 1972. Interspecific competition among rodents. Annual Review of Ecology and Systematics, 3:79–196.

Grant, W. E., and N. R. French. 1980. Evaluation of the role of small mammals in grassland ecosystems: a modelling approach. Ecological Modelling, 8:15–37.

Grant, W. E., N. R. French, and L. J. Folse, Jr. 1980. Effects of pocket gopher mounds on plant production in shortgrass prairie ecosystems. The Southwestern Naturalist, 25:215–224.

Grant, W. E., N. R. French, and D. M. Swift. 1977. Response of a small mammal community to water and nitrogen treatments in a short-grass prairie ecosystem. Journal of Mammalogy, 58:637–652.

Grant, W. E., E. C. Birney, N. R. French, and D. M. Swift. 1982. Structure and productivity of grassland small mammal communities related to grazing-induced changes in vegetative cover. Journal of Mammalogy, 63:248–260.

Grinnell, J. 1904. The origin and distribution of the chestnut-backed chickadee. The Auk, 21:364–382.

———. 1908. The biota of the San Bernardino Mountains. University of California Publications in Zoology, 5:1–170.

———. 1914. An account of the mammals and birds of the lower Colorado Valley. University of California Publications in Zoology, 12:51–294.

———. 1917*a*. The niche-relationships of the California thrasher. The Auk, 34:427–433.

———. 1917*b*. Field test of theories concerning distributional control. The American Naturalist, 51:115–128.

———. 1928. The presence and absence of animals. University of California Chronicle, 30:429–450 (Reprinted in: Joseph Grinnell's Philosophy of Nature, Berkeley, 1943. Pp. 187–208).

Grinnell, J., and H. S. Swarth. 1913. An account of the birds and mammals of the San Jacinto area of southern California, with remarks upon the behavior of geographic races on the margins of their habitats. University of California Publications in Zoology, 10:197–406.

Grodzinski, W. 1971. Energy flow through populations of small mammals in the Alaska taiga forest. Acta Theriologica, 16:231–276.

Grodzinski, W., and N. R. French. 1983. Production efficiency in small mammal populations. Oecologia, 56:41–49.

Grodzinski, W., and A. Górecki. 1967. Daily energy budgets of small rodents. Pp. 295–314, *in* Secondary productivity of terestrial ecosystems (K. Petrusewicz, ed.). 2 vol. Panstwowe Wydawnictwo Naukowe, Warsaw, Poland, 879 pp.

Hafner, M. S. 1977. Density and diversity in Mojave Desert rodent and shrub communities. The Journal of Animal Ecology, 46:925–938.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control and competition. The American Naturalist, 94:421–425.

Hall, A. S., J. A. Stanford, and F. R. Hauer. 1992. The distribution and abundance of organisms as a consequence of energy balances along multiple environmental gradients. Oikos, 65:377–390.

Hallett, J. G., and S. L. Pimm. 1970. Direct estimation of competition. The American Naturalist, 113:593–600.

Hallett, J. G., M. A. O'Connell, and R. L. Honeycutt. 1983. Competition and habitat selection: test of a theory using small mammals. Oikos, 40:175–181.

Hanley, T. A. 1982. The nutritional basis for food selection by ungulates. Journal of Range Management, 35:146–151.

Harrison, S., S. J. Ross, and J. H. Lawton. 1992. Beta diversity on geographic gradients in Britain. The Journal of Animal Ecology, 61:151–158.

Harvey, P. H., R. K. Colwell, J. W. Silverton, and R. M. May. 1983. Null models in ecology. Annual Review of Ecology and Systematics, 14:189–212.

Hatt, R. T. 1932. The vertebral column of ricochetal rodents. Bulletin American Museum of Natural History, 63:599–738.

Hawkins, C. P., and J. A. MacMahon. 1989. Guilds: the multiple meanings of a concept. Annual Review of Entomology, 34:423–451.

Heaney, L. R. 1991. An analysis of patterns of distribution and species richness among Philippine fruit bats (Pteropodidae). Bulletin American Museum of Natural History, 206:145–167.

Heithaus, E. R., T. H. Fleming, and P. A. Opler. 1975. Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. Ecology, 56:841–854.

Henderson, M. T., G. Merriam, and J. Wegner. 1985. Patchy environments and species survival: chipmunks in an agricultural mosaic. Biological Conservation, 31:95–105.

Henein, K., and G. Merriam. 1990. The elements of connectivity where corridor quality is variable. Landscape Ecology, 4:157–170.

Holbrook, S. J. 1979. Habitat utilization, competitive interactions and coexistence of three species of cricetine rodents in east-central Arizona. Ecology, 60:758–769.

Holling, C. S. 1959. The components of predation as revealed by a study of small mammal predation in the European pine sawfly. Canadian Entomologist, 91:293–320.

Hollister, N. 1920. Editorial comment. Journal of Mammalogy, 1:108–110.

Hornocker, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. Wildlife Monographs, 21:1–39.

Howe, H. F. 1980. Monkey dispersal and waste of a neotropical fruit. Ecology, 61:944–959.

Howell, D. J., and B. S. Roth. 1981. Sexual reproduction in agaves: the benefits of bats; the cost of semelparous advertising. Ecology, 62:1–7.

Humphrey, S. R., F. J. Bonaccorso, and T. L. Zinn. 1983. Guild structure of surface-gleaning bats in Panama. Ecology, 64:284–294.

Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. Annual Review of Ecology and Systematics, 22:477–504.

Huntly, N., and R. S. Inouye. 1987. Small mammal populations of an old-field chronosequence: successional patterns and association with vegetation. Journal of Mammalogy, 68:739–745.

———. 1988. Pocket gophers in ecosystems: patterns and mechanisms. BioScience, 38:786–793.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposium on Quantitative Biology, 22:415–427.

———. 1959. Homage to Snata Rosalia or why are there so many kinds of animals? The American Naturalist, 93:145–159.

———. 1978. An introduction to population ecology. Yale University Press, New Haven, Connecticut, 260 pp.

Jaksic, F. M. 1981. Abuse and misuse of the term "guild" in ecological studies. Oikos, 37:397–400.

Jonasson, S., J. P. Bryant, F. S. I. Chapin, and M. Andersson. 1986. Plant phenols and nutrients in relation to variations in climate and rodent grazing. The American Naturalist, 128:379–408.

Jones, J. K., Jr. 1991. Genealogy of twentieth-century systematic mammalogists in North America: the descendants of Joseph Grinnell. Pp. 48–56, *in* Latin American mammalogy: history, biodiversity, and conservation (M. A. Mares and D. J. Schmidly, eds.). University of Oklahoma Press, Norman, 468 pp.

Jung, H. J. G., and G. O. Batzli. 1981. Nutritional ecology of microtine rodents: effects of plant extracts on the growth of Arctic microtines. Journal of Mammalogy, 62:286–292.

Kajak, Z., and E. Pieczynska. 1981. Poland. Pp. 287–302, *in* Handbook of contemporary developments in world ecology (E. J. Kormondy and J. F. McCormick, eds.). Greenwood Press, Westport, Connecticut, 776 pp.

Karr, J. R., and F. C. James. 1975. Eco-morphological configurations and convergent evolution in species and communities. Pp. 258–291, *in* Ecology and evolution of communities (M. Cody and J. Diamond, eds.). Harvard University Press, Cambridge, Massachusetts, 543 pp.

Kenagy, G. J. 1973. Daily and seasonal patterns of activity and energetics in a heteromyid rodent community. Ecology, 54:1201–1219.

Kendeigh, S. C. 1974. Ecology, with special reference to animals and man. Prentice-Hall, Inc., Englewood Cliffs, New Jersey, 474 pp.

Kerley, G. I. H., and T. Erasmus. 1991. What do mice select for in seeds? Oecologia, 86:261–267.

Kidd, N. A. C., and G. B. Lewis. 1987. Can vertebrate predators regulate their prey? A reply. The American Naturalist, 130:448–453.

King, C. M., and P. J. Moors. 1979. On co-existence, foraging strategy and the biogeography of weasels and stoats (*Mustela nivalis* and *M. erminea*) in Britain. Oecologia, 39:131–150.

Kirkland, G. L., Jr. 1991. Competition and coexistence in shrews (Insectivora: Soricidae). Pp. 15–22, *in* The biology of the Soricidae (J. S. Findley and T. L. Yates, eds.). Special Publication, The Museum of Southwestern Biology, 1:1–91.

Klenner, W., and C. J. Krebs. 1991. Red squirrel population dynamics. I. The effect of supplemental food on demography. The Journal of Animal Ecology, 60:961–978.

Kormondy, E. J., and J. F. McCormick (eds.). 1981. Handbook of contemporary developments in world ecology. Greenwood Press, Westport, Connecticut, 776 pp.

Korpimäki, E. 1993. Regulation of multiannual vole cycles by density-dependent avian and mammalian predation? Oikos, 66:359–363.

Kotler, B. P. 1984. Risk of predation and the structure of desert rodent communities. Ecology, 65:689–701.

———. 1989. Temporal variation in the structure of a desert rodent community. Pp. 127–139, *in* Patterns in the structure of mammalian communities (D. W. Morris, Z. Abramsky, B. J. Fox, and M. R. Willig, eds.). Texas Tech University Press, Lubbock, 266 pp.

Kotler, B. P., and J. S. Brown. 1988. Environmental heterogeneity and the coexistence of desert rodents. Annual Review of Ecology and Systematics, 19:281–308.

Kotler, B. P., and R. D. Holt. 1989. Predation and competition: the interaction of two types of species interactions. Oikos, 54:256–260.

Kotler, B. P., J. S. Brown, R. J. Smith, and W. O. Wirtz, II. 1988. The effects of morphology and body size on rates of owl predation on desert rodents. Oikos, 53:145–152.

Kuropat, P., and J. P. Bryant. 1983. Digestibility of caribou summer forage in Arctic Alaska in relation to nutrient, fiber, and phenolic constituents. Acta Zoologica Fennica, 175:51–52.

Lacher, T. E., Jr., and C. J. R. Alho. 1989. The structure of a small mammal community in a central Brazilian savanna. Pp. 137–162, *in* Advances in neotropical mammalogy (K. H. Redford and J. F. Eisenberg, eds.). Sandhill Crane Press, Gainesville, Florida, 614 pp.

Lacher, T. E., Jr., and M. A. Mares. 1986. Neotropical mammal communities: an appraisal. Revista Chilena de Historia Natural, 59:121–134.

Laurance, W. F. 1991. Edge effects in tropical forest fragments: application of a model for the design of nature reserves. Biological Conservation, 57:205–219.

Lidicker, W. Z., Jr. 1989. Impacts of non-domesticated vertebrates on California grasslands. Pp. 135–150, *in* Grassland structure and function: California annual grassland (L. F. Huenneke and H. Mooney, eds.). Kluwer Academic Publishers, Dordrecht, Netherlands.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology, 23:399–418.

Lomolino, M. V. 1989. Interpretations and comparisons of constants in the species-area relationship: an additional caution. The American Naturalist, 133: 277–280.

Longland, W. S., and M. V. Price. 1991. Direct observations of owls and heteromyid rodents: can predation risk explain microhabitat use? Ecology, 72:2261–2273.

Luke, C. 1986. Convergent evolution of lizard toe fringes. Biological Journal of the Linnean Society, 27:1–16.

Mabry, T., J. Hunziker, and D. R. DiFeo, Jr. (eds.). 1977. Creosote bush: biology and chemistry of *Larrea* in New World deserts. Dowden, Hutchinson and Ross, East Stroudsburg, Pennsylvania, 284 pp.

MacMahon, J. A. 1976. Species and guild similarity of North American desert mammal faunas: a functional analysis of communities. Pp. 133–148, *in* Evolution of desert biota (D. W. Goddall, ed.). University of Texas, Austin, 250 pp.

MacMahon, J. A., D. J. Schimpf, D. C. Anderson, K. G. Smith, and R. L. Bayn, Jr. 1981. An organism-centered approach to some community and ecosystem concepts. Journal of Theoretical Biology, 88:287–307.

Malmquist, M. G. 1985. Character displacement and biogeography of the pygmy shrew in Northern Europe. Ecology, 66:372–377.

Mares, M. A. 1975. South American mammal zoogeography: evidence from convergent evolution in desert rodents. Proceedings of the National Academy of Science, USA, 72:1702–1706.

———. 1976. Convergent evolution of desert rodents: multivariate analysis and zoogeographic implications. Paleobiology, 2:39–64.

———. 1980. Convergent evolution among desert rodents: a global perspective. Bulletin of Carnegie Museum of Natural History, 16:1–51.

———. 1983. Desert rodent adaptation and community structure. Great Basin Naturalist Memoirs, 7:30–43.

———. 1992. Neotropical mammals and the myth of Amazonian biodiversity. Science, 255:976–979.

———. 1993*a*. Desert rodents, seed consumption, and convergence: the evolutionary shuffling of adaptations. BioScience, 43:372–379.

———. 1993*b*. Heteromyids and their ecological counterparts: a pandesertic view of rodent ecology and evolution. Pp. 652–714, *in* Biology of the Heteromyidae (H. H. Genoways and J. H. Brown, eds.). Special Publication, The American Society of Mammalogists, 10:1–719.

Mares, M. A., and J. K. Braun. 1986. An international survey of the popular and technical literature of mammalogy. Annals of Carnegie Museum, 55:149–209.

Mares, M. A., and T. E. Lacher, Jr. 1987. Ecological, morphological and behavioral convergence in rock-dwelling mammals. Current Mammalogy, 1:307–348.

Mares, M. A., and R. A. Ojeda. 1982. Patterns of diversity and adaptation in South American hystricognath rodents. Pp. 393–432, *in* Mammalian biology in South America (M. A. Mares and H. H. Genoways, eds.). Pymatuning Laboratory of Ecology, Special Publication 6, Linesville, Pennsylvania, 539 pp.

Mares, M. A., and M. L. Rosenzweig. 1978. Granivory in North and South American deserts: rodents, birds and ants. Ecology, 59:235–241.

Mares, M. A., and D. F. Williams. 1977. Experimental support for food particle size resource allocation in heteromyid rodents. Ecology, 58:1186–1190.

Mares, M. A., M. Watson, and T. E. Lacher, Jr. 1976. Home range perturbations in *Tamias striatus*: food supply as a determinant of home range and density. Oecologia, 25:1–12.

Mares, M. A., M. R. Willig, and T. E. Lacher, Jr. 1985. The Brazilian Caatinga in South American zoogeography: tropical mammals in a dry region. Journal of Biogeography, 12:57–69.

Mares, M. A., T. E. Lacher, Jr., M. R. Willig, N. A. Bitar, R. Adams, A. Klinger, and D. Tazik. 1982. An experimental analysis of social spacing in *Tamias striatus*. Ecology, 63:267–273.

Marquis, R. J., and G. O. Batzli. 1989. Influence of chemical factors on palatability of forage to voles. Journal of Mammalogy, 70:503–511.

Maschinski, J., and T. G. Whitham. 1989. The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. The American Naturalist, 134:1–19.

MAY, R. M. 1984. An overview: real and apparent patterns in community structure. Pp. 3–16, *in* Ecological communities: conceptual issues and the evidence (D. R. Strong, Jr., et al., eds.). Princeton University Press, Princeton, New Jersey, 613 pp.

McCOY, E. D., AND E. F. CONNOR. 1980. Latitudinal gradients in the species diversity of North American mammals. Evolution, 34:193–203.

McINTOSH, R. P. 1975. H. A. Gleason, "individualistic ecologist," 1882–1975: his contributions to ecological theory. Bulletin of the Torrey Botanical Club, 102:263–273.

———. 1980. The background and some current problems of theoretical ecology. Synthese, 43:195–255.

———. 1985. The background of ecology: concept and theory. Cambridge University Press, Cambridge. 383 pp.

McKENZIE, N. L., AND A. N. START. 1989. Structure of bat guilds in mangroves: environmental disturbance and determinism. Pp. 167–178, *in* Patterns in the structure of mammalian communities (D. W. Morris, Z. Abramsky, B. J. Fox, and M. R. Willig, eds.). Texas Tech University Press, Lubbock, 266 pp.

M'CLOSKEY, R. T. 1978. Niche separation and assembly in four species of Sonoran desert rodents. The American Naturalist, 112:683–694.

———. 1980. Spatial patterns in sizes of seeds collected by four species of heteromyid rodents. Ecology, 61:486–489.

McNAB, B. K. 1963. A model of the energy budget of a wild mouse. Ecology, 44:521–532.

———. 1971. The structure of tropical bat faunas. Ecology, 52:352–358.

———. 1991. The energy expenditure of shrews. Pp. 35–45, *in* The biology of the Soricidae (J. S. Findley and T. L. Yates, eds.). Special Publication, The Museum of Southwestern Biology, 1:1–91.

McNAB, B. K., AND P. MORRISON. 1963. Body temperature and metabolism in subspecies of *Peromyscus* from arid and mesic environments. Ecological Monographs, 33:63–82.

McNAUGHTON, S. J. 1976. Serengeti migratory wildebeest: facilitation of energy flow by grazing. Science, 191:92–94.

———. 1977. Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. The American Naturalist, 111:515–525.

———. 1985. Ecology of a grazing ecosystem: the Serengeti. Ecological Monographs, 55:259–294.

———. 1986. On plants and herbivores. The American Naturalist, 128:765–770.

McNAUGHTON, S. J., AND N. J. GEORGIADIS. 1986. Ecology of African grazing and browsing mammals. Annual Review of Ecology and Systematics, 17:39–65.

MECH, L. D. 1966. The wolves of Isle Royale. Fauna of the National Parks of the United States. Fauna Series, 7:1–210.

MERRIAM, C. H. 1890. Results of a biological survey of the San Francisco Mountain region and the desert of the Little Colorado, Arizona. North American Fauna, 3:1–136.

———. 1892. The geographic distribution of life in North America. Proceedings of the Biological Society of Washington, 7:1–64.

———. 1894. Laws of temperature control of the geographical distribution of terrestrial animals and plants. National Geographic Magazine, 6:229–238.

———. 1898. Life zones and crop zones. United States Department of Agriculture Bulletin 10, 79 pp.

MERRIAM, G., AND A. LANOUE. 1990. Corridor use by small mammals: field measurement for three experimental types of *Peromyscus leucopus*. Landscape Ecology, 4:123–131.

MERRITT, J. F., AND J. M. MERRITT. 1978. Population ecology and energy relationships of *Clethrionomys gapperi* in a Colorado subalpine forest. Journal of Mammalogy, 59:576–598.

MESERVE, P. L. 1981. Resource partitioning in a Chilean semi-arid small mammal community. The Journal of Animal Ecology, 50:745–758.

MICHELL, R., R. A. MAYER, AND J. DOWNHOWER. 1976. An evaluation of three biome programs. Science, 192: 859–865.

MILLER, R. S. 1967. Pattern and process in competition. Advances in Ecological Research, 4:1–74.

MITCHELL, W. A., Z. ABRAMSKY, B. P. KOTLER, B. PINSHOW, AND J. S. BROWN. 1990. The effect of competition on foraging activity in desert rodents: theory and experiments. Ecology, 71:844–854.

MONTGOMERY, G. G. 1989. Population parameters, spatial division, and niche breadth in two *Apodemus* species sharing a woodland habitat. Pp. 45–58, *in* Patterns in the structure of mammalian communities (D. W. Morris, Z. Abramsky, B. J. Fox, and M. R. Willig, eds.). Texas Tech University Press, Lubbock, 266 pp.

MONTGOMERY, G. G., AND M. E. SUNQUIST. 1975. Impact of sloths on neotropical forest energy flow and nutrient cycling. Pp. 69–98, *in* Tropical ecological systems (F. B. Golley and E. Medina, eds.). Springer-Verlag, New York, 398 pp.

MORRIS, D. W. 1987. Spatial scale and the cost of density-dependent habitat selection. Evolutionary Ecology, 1:379–388.

———. 1989. The effect of spatial scale on patterns of habitat use: red-backed voles as an empirical model of local abundance for northern mammals. Pp. 23–34, *in* Patterns in the structure of mammalian communities (D. W. Morris, Z. Abramsky, B. J. Fox, and M. R. Willig, eds.). Texas Tech University Press, Lubbock, 266 pp.

MYRCHA, A. 1975. Bioenergetics of an experimental population and individual laboratory mice. Acta Theriologica, 20:175–226.

NEVO, E. 1979. Adaptive convergence and divergence of subterranean mammals. Annual Review Ecology and Systematics, 10:269–308.

O'DOWD, D. J., AND M. E. HAY. 1980. Mutualism between harvester ants and a desert ephemeral: seed escape from rodents. Ecology, 61:531–540.

ODUM, E. P. 1945. The concept of the biome as applied to the distribution of North American birds. The Wilson Bulletin, 57:191–201.

———. 1953. Fundamentals of ecology. W. B. Saunders Company, Philadelphia. 384 pp.

———. 1971. Fundamentals of ecology. Third ed. W. B. Saunders Company, Philadelphia, 574 pp.

ODUM, E. P., C. E. CONNELL, AND L. B. DAVENPORT. 1962. Population energy flow of three primary consumer components of old-field ecosystems. Ecology, 43:88–96.

ODUM, H. T. 1957. Trophic structure and productivity of Silver Springs, Florida. Ecological Monographs, 27:55–115.

ORIANS, G. H., AND O. T. SOLBRIG. 1977. Convergent evolution in warm deserts. Dowden, Hutchinson and Ross, East Stroudsburg, Pennsylvania, 333 pp.

OSGOOD, W. H. 1943. Clinton Hart Merriam—1855–1942. Journal of Mammalogy, 24:421–436.

OWEN, J. G. 1988. On productivity as a predictor of rodent and carnivore diversity. Ecology, 69:1161–1165.

———. 1990*a*. An analysis of the spatial structure of mammalian distribution patterns in Texas. Ecology, 71:1823–1832.

———. 1990*b*. Patterns of mammalian species richness in relation to temperature, productivity, and variance in elevation. Journal of Mammalogy, 71:1–13.

OWEN-SMITH, N. 1989. Morphological factors and their consequences for resource partitioning among African savanna ungulates: a simulation modelling approach. Pp. 155–165, *in* Patterns in the structure of mammalian communites (D. W. Morris, Z. Abramsky, B. J. Fox, and M. R. Willig, eds.). Texas Tech University Press, Lubbock, 266 pp.

PAGEL, M. D., R. M. MAY, AND A. R. COLLIE. 1991. Ecological aspects of the geographic distribution and diversity of mammalian species. The American Naturalist, 137:791–815.

PAIGE, K. N. 1992. Overcompensation in response to mammalian herbivory: from mutualistic to antagonistic interactions. Ecology, 73:2076–2085.

PAIGE, K. N., AND T. G. WHITHAM. 1987. Overcompensation in response to mammalian herbivory: the advantage of being eaten. The American Naturalist, 129:407–416.

PEARSON, O. P. 1960. The oxygen consumption and bioenergetics of harvest mice. Physiological Zoology, 33:152–160.

———. 1964. Carnivore-mouse predation: an example of its intensity and bioenergetics. Journal of Mammalogy, 45:177–188.

———. 1971. Additional measurements of the impact of carnivores on California voles (*Microtus californicus*). Journal of Mammalogy, 52:41–49.

PEARST, D. R. 1989. Species interactions in a successional grassland. III. Effect of canopy gaps, gopher mounds, and grazing on colonization. Journal of Ecology, 77:267–289.

PETERSEN, M. K. 1970. Competition between the cotton rats, *Sigmodon fulviventer* and *S. hispidus*. Ph.D. dissert., Michigan State University, East Lansing, 110 pp.

———. 1973. Interactions between the cotton rats, *Sigmodon fulviventer* and *S. hispidus*. The American Midland Naturalist, 90:319–333.

PETRUSEWICZ, K. (ED.). 1967. Secondary productivity of terrestrial ecosystems, 2 vol. Panstwowe Wydawnictwo Naukowe, Warsaw, Poland, 879 pp.

PIANKA, E. R. 1969. Habitat specificity, speciation, and species density in Australian desert lizards. Ecology, 50:498–502.

———. 1973. The structure of lizard communities. Annual Review of Ecology and Systematics, 4:53–74.

———. 1974. Niche overlap and diffuse competition. Proceedings of the National Academy of Sciences, USA, 71:2141–2145.

———. 1975. Niche relations of desert lizards. Pp. 292–314, *in* Ecology and evolution of communities (M. Cody and J. Diamond, eds.). Harvard University Press, Cambridge, Massachusetts, 543 pp.

———. 1985. Some intercontinental comparisons of desert lizards. National Geographic Research, 1:490–504.

———. 1986. Ecology and natural history of desert lizards. Princeton University Press, Princeton, New Jersey, 208 pp.

PIMENTEL, D. 1988. Herbivore population feeding pressure on plant hosts: feedback evolution and host conservation. Oikos, 53:289–302.

PIMM, S. L., J. H. LAWTON, AND J. E. COHEN. 1991. Food web patterns and their consequences. Nature, 350:669–674.

PLATT, W. J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. Ecological Monographs, 45:285–305.

PORTER, J. H., AND R. D. DUESER. 1981. Niche overlap and competition in an insular small mammal fauna: a test of the niche overlap hypothesis. Oikos, 39:228–236.

PRICE, M. V., AND K. A. KRAMER. 1984. On measuring microhabitat affinities with special reference to small mammals. Oikos, 42:349–354.

PRICE, M. V., W. S. LONGLAND, AND R. L. GOLDINGAY. 1991. Niche relationship of *Dipodomys agilis* and *D. stephensi*: two sympatric kangaroo rats of similar size. The American Midland Naturalist, 126:172–186.

PULLIAM, H. R., AND M. R. BRAND. 1975. The production and utilization of seeds in plains grassland of southeastern Arizona. Ecology, 56:1158–1166.

RAMALAY, R. 1940. The growth of a science. University of Colorado Studies, General Series A, 26:3–14.

RANDOLPH, J. C., G. N. CAMERON, AND J. A. WRAZEN. 1991. Dietary choice of generalist grassland herbivore, *Sigmodon hispidus*. Journal of Mammalogy, 72:300–313.

REICHMAN, O. J., AND S. C. SMITH. 1985. Impact of pocket gopher burrows on overlying vegetation. Journal of Mammalogy, 66:720–725.

REICHMAN, O. J., AND S. C. SMITH. 1991. Responses to simulated leaf and root herbivory by a biennial, *Tragopogon dubius*. Ecology, 72:116–124.

REICHMAN, O. J., J. H. BENEDIX, JR., AND T. R. SEASTEDT. 1993. Distinct animal-generated edge effects in a tallgrass prairie community. Ecology, 74:1281–1284.

ROOT, R. B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. Ecological Monographs, 37:317–350.

ROSENZWEIG, M. L. 1966. Community structure in sympatric Carnivora. Journal of Mammalogy, 47:602–612.

———. 1968. Net primary productivity of terrestrial

communities: prediction from climatological data. The American Naturalist, 102:67–74.
———. 1969. Why the prey curve has a hump. The American Naturalist, 103:81–87.
———. 1973. Evolution of the predator isocline. Evolution, 27:84–94.
———. 1989. Habitat selection, community organization, and small mammal studies. Pp. 5–21, *in* Patterns in the structure of mammalian communities (D. W. Morris, Z. Abramsky, B. J. Fox, and M. R. Willig, eds.). Texas Tech University Press, Lubbock, 266 pp.
———. 1993. Species diversity gradients: we know more and less than we thought. Journal of Mammalogy, 73:715–730.
Rosenzweig, M. L., and R. H. MacArthur. 1963. Graphical representation and stability conditions of predator-prey interactions. The American Naturalist, 97:209–223.
Rosenzweig, M. L., Z. Abramsky, and S. Brand. 1984. Estimating species interactions in heterogeneous environments. Oikos, 43:329–340.
Sazima, M., and I. Sazima. 1978. Bat pollination of the passion flower, *Passiflora mucronata,* in southeastern Brazil. Biotropica, 10:100–109.
Schluter, D. 1986. Tests for similarity and convergence of finch communities. Ecology, 67:1073–1083.
———. 1990. Species-for-species marching. The American Naturalist, 136:560–568.
Schmidt-Nielsen, K. 1964. Desert animals. Clarendon Press, Oxford, England, 277 pp.
Schnell, J. H. 1968. The limiting effects of natural predation on experimental cotton rat populations. The Journal of Wildlife Management, 32:698–711.
Schoener, T. W. 1974. Competition and the form of habitat shift. Theoretical Population Biology, 6:265–307.
———. 1983. Field experiments on interspecific competition. The American Naturalist, 122:240–285.
———. 1985. Some comments on Connell's and my reviews of field experiments on interspecific competition. The American Naturalist, 125:730–740.
———. 1986*a*. Mechanistic approaches to community ecology: a new reductionism? American Zoologist, 26:81–106.
———. 1986*b*. When should a field experiment be counted? A reply to Galindo and Krebs. Oikos, 46: 119–121.
Schultz, A. M. 1964. The nutrient-recovery hypothesis for Arctic microtine cycles. Pp. 57–68, *in* Grazing in terrestrial and marine environments (D. Crisp, ed.). British Ecological Society Symposium 4. Blackwell Scientific Publishers, Oxford, 322 pp.
Schum, M. 1984. Phenetic structure and species richness in North and Central American bat faunas. Ecology, 65:1315–1324.
Seagle, S. W., and G. F. McCraken. 1986. Species abundance, niche position, and niche breadth for five terrestrial animal assemblages. Ecology, 67:816–818.
Seagle, S. W., and S. J. McNaughton. 1992. Spatial variation in forage nutrient concentrations and the distribution of Serengeti grazing ungulates. Landscape Ecology, 7:229–241.
Semper, K. 1881. Animal life as affected by the natural conditions of existence. Appleton, New York.
Shelford, V. E. 1913. Animal communities in temperate North America. University of Chicago Press, Chicago, 368 pp.
———. 1926. Naturalists' guide to the Americas. Williams & Wilkins Company, Baltimore, Maryland, 761 pp.
Shelford, V. E., and A. C. Twomey. 1941. Tundra animal communities in the vicinity of Churchill, Manitoba. Ecology, 22:47–69.
Sih, A., P. Crowley, M. McPeek, J. Petranka, and K. Strohmeier. 1985. Predation, competition, and prey communities: a review of field experiments. Annual Review of Ecology and Systematics, 16:269–312.
Simberloff, D., and T. Dayan. 1991. The guild concept and the structure of ecological communities. Annual Review of Ecology and Systematics, 22:115–144.
Simenstad, C. A., J. A. Estes, and K. W. Kenyon. 1978. Aleuts, sea otters, and alternate stable-state communities. Science, 200:403–411.
Simpson, B. B. 1977. Mesquite: its biology in two desert ecosystems. Dowden, Hutchinson and Ross, East Stroudsburg, Pennsylvania, 250 pp.
Simpson, B. B., and J. L. Neff. 1981. Floral rewards: alternatives to pollen and nectar. Annals of the Missouri Botanical Garden, 68:301–322.
Simpson, G. G. 1964. Species density of North American recent mammals. Systematic Zoology, 13:57–73.
Sinclair, A. R. E., C. J. Krebs, and M. Smith. 1982. Diet quality and food limitation in herbivores: the case of the snowshoe hare. Canadian Journal of Zoology, 60:889–897.
Sinclair, A. R. E., P. D. Olsen, and T. D. Redhead. 1990. Can predators regulate small mammal populations? Evidence from house mouse outbreaks in Australia. Oikos, 59:382–392.
Sinclair, A. R. E., C. J. Krebs, J. N. M. Smith, and S. Boutin. 1988. Population biology of snowshoe hares. III. Nutrition, plant secondary compounds and food limitation. The Journal of Animal Ecology, 57: 787–806.
Sjörs, H. 1981. Sweden. Pp. 303–312, *in* Handbook of contemporary developments in world ecology (E. J. Kormondy and J. F. McCormick, eds.). Greenwood Press, Westpoprt, Connecticut, 776 pp.
Slobodchikoff, C. N., and W. C. Schultz. 1980. Measures of niche overlap. Ecology, 61:1051–1055.
Slobodkin, L. B. 1961. Growth and regulation of animal populations. Holt, Rinehart, and Winston, New York, 184 pp.
———. 1962. Energy in animal ecology. Advances in Ecological Research, 4:69–101.
———. 1987. How to be objective in community studies. Pp. 93–108, *in* Neutral models in biology (M. H. Nitecki and A. Hoffman, eds.). Oxford University Press, Oxford, 166 pp.
Sly, G. R. 1976. Small mammal succession on strip-mined land in Vigo County, Indiana. The American Midland Naturalist, 95:257–267.
Smartt, R. A. 1978. A comparison of ecological and morphological overlap in a *Peromyscus* community. Ecology, 59:216–220.
Smartt, R. A., and C. Lemen. 1980. Intrapopulation morphological variation as a predictor of feeding

behavior in deermice. The American Naturalist, 116: 891–894.

Smith, C. C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecological Monographs, 40:349–371.

Smith, C. C., and R. P. Balda. 1979. Competition among insects, birds and mammals for conifer seeds. The American Zoologist, 19:1965–1083.

Smith, M. F. 1981. Relationships between genetic variability and niche dimensions among coexisting species of *Peromyscus*. Journal of Mammalogy, 62: 273–285.

Smythe, N. 1986. Competition and resource partitioning in the guild of neotropical terrestrial frugivorous mammals. Annual Review of Ecology and Systematics, 17:169–188.

Snyder, M. A. 1992. Selective herbivory by Abert's squirrel mediated by chemical variability in ponderosa pine. Ecology, 73:1730–1741.

Soholt, L. 1973. Consumption of primary production by a population of kangaroo rats (*Dipodomys merriami*) in the Mojave Desert. Ecological Monographs, 43:357–376.

Spatz, G., and D. Mueller-Dombois. 1973. The influence of feral goats on Koa tree reproduction in Hawaii Volcanoes National Park. Ecology, 54:870–877.

Stapanian, M. A., and C. C. Smith. 1978. A model for seed scatter-hoarding: coevolution of fox squirrels and black walnuts. Ecology, 59:884–896.

———. 1986. How fox squirrels influence the invasion of prairies by nut-bearing tress. Journal of Mammalogy, 67:326–332.

Stebbins, G. L. 1962. Toward better international cooperation in the life sciences. Plant Science Bulletin, 8:1–10.

Sterling, K. B. 1977. Last of the naturalists: the career of C. Hart Merriam. Arno Press, New York, 472 pp.

Strong, D. R., D. Simberloff, L. G. Abele, and A. B. Thistle. 1984. Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, New Jersey, 613 pp.

Sukachev, V. N. 1958. On the principles of genetic classification in biocenology. Ecology, 39:364–367.

Sullivan, T. P., D. S. Sullivan, and C. J. Krebs. 1983. Demographic responses of a chipmunk (*Eutamias townsendi*) population with supplemental food. The Journal of Animal Ecology, 52:743–756.

Sussman, R. W., and P. H. Raven. 1978. Pollination by lemurs and marsupials: an archaic coevolutionary system. Science, 200:731–736.

Taitt, M. J., and C. J. Krebs. 1983. Predation, cover, and food manipulations during a spring decline of *Microtus townsendi*. Journal of Animal Ecology, 52:837–848.

Tansley, A. G. 1935. The use and abuse of vegetational concepts and terms. Ecology, 16:284–307.

Teal, J. M. 1957. Community metabolism in a temperate cold spring. Ecological Monographs, 27:283–302.

Tilman, D. 1983. Plant succession and gopher disturbance along an experimental gradient. Oecologia, 60:285–292.

Trostel, K., A. Sinclair, C. Walters, and C. Krebs. 1987. Can predation cause the 10-yr hare cycle? Oecologia, 74:185–192.

Truszkowski, J. 1982. The impact of the common vole on the vegetation of agroecosystems. Acta Theriologica, 27:305–345.

Underwood, T. 1986. The analysis of competition by field experiments. Pp. 240–268, *in* Community ecology: pattern and process (J. Kikkawa and D. Anderson, ed.). Blackwell Scientific Publishers, Oxford, England, 432 pp.

Varley, G. C. 1975. Should we control the use of the word control? Bulletin of the British Ecological Society, 6:7.

Van Horne, B., and R. G. Ford. 1982. Niche breadth calculation based on discriminant analysis. Ecology, 63:1172–1174.

Wagner, F. H., and L. C. Stoddart. 1972. Influence of coyote predation on black-tailed jackrabbit populations in Utah. The Journal of Wildlife Management, 36:329–342.

Whicker, A. D., and J. K. Detling. 1988. Ecological consequences of prairie dog disturbances. BioScience, 38:778–785.

Whitford, W. G., and Y. Steinberger. 1989. The long-term effects of habitat modification on a desert rodent community. Pp. 33–43, *in* Patterns in the structure of mammalian communities (D. W. Morris, Z. Abramsky, B. J. Fox, and M. R. Willig, eds.). Texas Tech University Press, Lubbock, 266 pp.

Whittaker, R. H. 1951. A criticism of the plant association and climatic climax concepts. Northwest Science, 26:17–31.

Willig, M. R. 1986. Bat community structure in South America: a tenacious chimera. Revista Chilena de Historia Natural, 59:151–168.

Willig, M. R., and T. E. Lacher, Jr. 1991. Food selection of a tropical folivore in relation to leaf-nutrient content. Journal of Mammalogy, 72:314–321.

Willig, M. R., and M. A. Mares. 1989. A comparison of bat assemblages from phytogeographic zones of Venezuela. Pp. 59–67, *in* Patterns in the structure of mammalian communities (D. W. Morris, Z. Abramsky, B. J. Fox, and M. R. Willig, eds.). Texas Tech University Press, Lubbock, 266 pp.

Willig, M. R., and M. P. Moulton. 1989. The role of stochastic and deterministic processes in structuring Neotropical bat communities. Journal of Mammalogy, 70:323–329.

Willig, M. R., and E. A. Sandlin. 1991. Gradients of species density and turnover in New World bats: a comparison of quadrat and band methodologies. Pp. 81–96, *in* Latin American mammalogy: history, biodiversity, and conservation (M. A. Mares and D. J. Schmidly, eds.). University of Oklahoma Press, Norman, 468 pp.

Willig, M. R., and K. W. Selcer. 1989. Bat species density gradients in the New World: a statistical assessment. Journal of Biogeography, 16:189–195.

Willig, M. R., G. R. Camilo, and S. J. Noble. 1993. Dietary overlap in frugivorous and insectivorous bats from edaphic cerrado habitats of Brazil. Journal of Mammalogy, 74:117–128.

# *NATURAL HISTORY AND EVOLUTIONARY ECOLOGY*

James H. Brown and Don E. Wilson

## *Introduction*

The last 75 years have seen dramatic changes in both the theoretical concepts of ecology and evolution, and in the field and laboratory studies that provide the empirical basis for theoretical advances. On the one hand, there has been a trend toward increasing conceptual specialization as the broad field of natural history has been supplanted by the specialized study of life histories, population dynamics, community organization, and morphological, physiological, and behavioral adaptation. On the other hand, there has been a corresponding trend toward decreasing taxonomic specialization as the practitioners of these disciplines have chosen to study organisms on the basis of their suitability for testing ecological theory.

This chapter attempts to describe how these trends have influenced the development of North American mammalogy, as well as how studies of mammals have contributed to the theory and data of modern ecology and evolutionary biology. When the ASM was founded in 1919, many of its charter members and earliest recruits included the leading natural historians of the early 20th Century (Merriam, Bailey, Jackson, Allen, Osgood, Nelson, Goldman). Over the 75-year history of the society, studies of mammals have continued to play key roles as classical natural history has evolved into modern evolutionary ecology.

The history of changes in ecological and evolutionary studies of mammals reflect more fundamental changes in the development of modern science. As we shall see, many of the questions posed by early natural historians have not yet been completely answered and are still the subject of major research programs today. This is not to say that there has been no progress. A great deal has been learned about how wild mammals survive, reproduce, and coexist in diverse habitats, and this knowledge frequently raises more questions than it answers. The questions have become more focused and the standards for acceptable answers have become more rigorous. New tools, such as mathematical models, field experiments, and statistical analyses, have been developed to facilitate the interplay of theory and data. Broad syntheses have been attempted. In all of these developments, studies of mammals have played major roles.

For convenience, this history can be divided into several phases. The first, the discovery phase, began with the earliest studies of mammals in the Americas; the last, the evolutionary ecology phase, is a major theme of contemporary research.

## *Discovery Phase*

Humans have always been curious about the plants and animals that share their world, and they have always had a special interest in their nearest relatives, other mammals. The earliest humans studied the ecology and behavior of mammals out of necessity, because different mammal species were important food sources, deadly predators, serious competitors, helpful mutualists, and objects of admiration and worship. As modern human civilizations developed, they retained their fascination with the natural world and with the lives of their wild mammalian relatives. Mammals figure prominently in the art and writing of ancient Oriental, Mediterranean, African, European, and American civilizations. As western civilization emerged from the middle ages, European naturalists such as Linneaus, Cuvier, and Buffon began to describe, classify, and study the lives of their native mammals. These studies received added impetus when the voyages of discovery returned from around the world bearing specimens of amazing new kinds of mammals and other living things.

North American mammalogy began in earnest when the newly arrived European colonists began to explore the continent and assess its natural resources. As with so many other human endeavors, the initial impetus for this exploration was economic. Beaver and other furbearers were among the earliest of North America's vast natural resources to be exploited by Europeans. Demand for beaver pelts drove fur trappers and mountain men into parts of the continent that previously had been accessible only to indigenous tribes (Chittenden, 1954). The Hudson Bay Company and the Pacific Fur Company kept meticulous records of their annual trade in pelts that provided long-term records of population fluctuations and predator-prey dynamics. These data have been analyzed by several generations of ecologists, beginning with Elton (1942). Although the immediate influence of the fur trade on studies of natural history was limited, one major contribution was a landmark study of beaver by Lewis H. Morgan (1868), one of America's first ethologists. The fur trappers did much to stimulate interest in wildlife and exploration when they returned to the outposts of civilization with tales of a vast continent inhabited by animals unknown to Europeans.

The early part of the 19th Century saw several exploring expeditions that contributed importantly to our knowledge of mammals. When the newly independent United States had acquired the immense Louisiana Purchase from France in 1803, President Thomas Jefferson dispatched an expedition under command of Captains Merriweather Lewis and William Clark to survey and map the Missouri and Columbia rivers, to study the natural history and natural resources of the area, and to provide a detailed report of all Indian tribes and how to deal with them peacefully (Thwaites, 1904). Lewis and Clark's journals provided the first descriptions of many North American mammals, and specimens were also brought back. Unfortunately, the United States had no national museum at the time, and all of the specimens ultimately were lost. Lewis and Clark's collection was deposited in Peale's Museum in Philadelphia; subsequently, most of it was purchased by P.T. Barnum and destroyed by fire in 1865 (Gunderson, 1976). Other notable early expeditions that obtained valuable information and specimens of mammals were those of J. J. Audubon and J. Bachman, and of T. Say.

Mammalian natural history also benefited from expeditions directed towards the discovery of a Northwest Passage that would provide access between the Atlantic and Pacific. Beginning in 1819, several expeditions to northern Canada were led by Sir John Franklin and Sir William Edward Parry. Sir John Richardson was surgeon-naturalist on the earlier Franklin expeditions and he also described birds and mammals collected on the Parry expeditions. Richardson's (1829) *Fauna Boreali-Americana* contains a complete volume on mammals. All three of these early explorers have been honored with patronyms proposed for ground squirrels: *Spermophilus franklinii, S. parryii,* and *S. richardsonii.*

North American mammalogy, like other branches of natural history, is indebted to another set of explorations, begun in the 1850s to seek routes for a transcontinental railroad (Miller, 1929). After passage of the Railroad Surveys Bill in 1853, the Federal Government set out surveying parties that were accompanied by physician-naturalists from the U.S. Army Medical Corps. They made mammal collections of enormous breadth and value that were deposited in the newly founded (1846) Smithsonian Institution. These were first studied and described by Professor Spencer Fullerton Baird, whose *Mammals of North America* (1859, which appeared as Volume VIII of the Pacific Railway Survey Reports) provided a state-of-the-art synopsis of the then 758 known species of North American mammals.

Another physician-naturalist of the U.S. Army Medical Corps, Dr. Edgar Alexander Mearns, accompanied the survey of the U.S.–Mexican International Boundary. From his field work in 1892–1894, Mearns contributed over 30,000 specimens of plants and animals, including over 7,000 mammals, to the National Museum (Mearns, 1907). Earlier, Mearns had contributed to the specimens that established the vertebrate collections of the American Museum of Natural History in New York. Later, during two tours of duty in the Philippines, then accompanying President Theodore Roosevelt's African expedition, and finally as a collaborator with Childs Frick on two additional African expeditions, Mearns continued his field studies and collected many additional specimens.

The discovery phase of American mammalogy owes much to the physician-naturalists of the U.S. Army Medical Corps. In addition to Mearns and others associated with the Pacific Railroad and Mexican Boundary Surveys, a major contributor was Dr. Elliot Coues. Coues published his first scientific paper at 19 and received his M.D. 2 years later. In 1864 he joined the Army Medical Corps and spent the next 20 years doing field work, collecting specimens, and publishing extensively on mammals, birds, and other vertebrates. He served as the first curator of mammals after Baird had organized the National Museum in 1879. He also served as secretary and naturalist to the Geological and Geographical Survey of the Territories under F. V. Hayden. Among other contributions, Coues wrote five monographs on rodents, which form Volume 4 of the Hayden Survey Monographs (Coues, 1877*a*), and a classic revision of the family Mustelidae (Coues, 1877*b*).

Owing largely to the contributions of these explorer-physician-naturalists, most of the North American continent had been surveyed, and most, but by no means all, of the native mammals had been collected and classified, by the beginning of the 20th Century. Increasingly, naturalists were concerned, not with describing new species, but with understanding what determines the distribution and abundance of the species that they now knew about. They began to study the lives of wild mammals directly by observation and indirectly by trapping and tracking. The study of North American mammals had begun to pass from the discovery phase to a natural history phase.

## *Natural History Phase*

When the ASM was founded in 1919, its charter members included some of the most prominent North American biologists. The majority of these, including Hartley H. T.

Jackson, C. Hart Merriam, Edward W. Nelson, Wilfred H. Osgood, Marcus Ward Lyon, Jr., T. S. Palmer, Edward A. Preble, Glover M. Allen, Joseph Grinnell, Gerrit S. Miller, Jr., Angel Cabrera, A. H. Howell, Ned Hollister, Harold E. Anthony, Vernon Bailey, Edgar Alonzo Goldman, Laurance M. Huey, Remington Kellogg, Nagamichi Kuroda, Austin Roberts, Waldo L. Schmitt, Arthur deC. Sowerby, Witmer Stone, Oldfield Thomas, Alexander Wetmore, A. H. Winge, and Joel Asaph Allen (the first Honorary Member), were primarily taxonomists, still actively engaged in classifying species and documenting their distributions over the continent. Even though their systematic work represented the culmination of the discovery phase, their studies were becoming increasingly synthetic, analytical, and conceptual. It is no accident that these taxonomists also made some of the most important contributions to natural history.

Perhaps the most seminal of these early contributions that bridged the gap between taxonomy and natural history were those of C. Hart Merriam. Gerrit S. Miller, Jr., himself a talented taxonomist, argued that while the writings of Darwin had aroused initial interest in mammalian natural history, it was Merriam who developed the techniques for the systematic study of mammals (Miller, 1929). Merriam, yet another medical doctor influenced by Baird, had an early interest in ornithology and an impressive combination of intellect, energy, and foresight that enabled him to establish in 1885 an organization that began as the Section of Ornithology in the Division of Entomology under the Commissioner of Agriculture. Within a year the Division of Ornithology had attained independence, and by 1888 it had expanded to the Division of Economic Ornithology and Mammalogy. Merriam's later predilection for mammals was illustrated by his staff's reference to the "Division of Economic Ornithology and *Extravagant* Mammalogy" (Osgood, 1943). This unit, which became the Bureau of Biological Survey in 1905, and the cadre of distinguished field and museum personnel assembled by Merriam between 1885 and 1910, were the major reasons for the rapid advance in our knowledge of North American mammals early in this century.

Merriam's efforts were facilitated by the otherwise unremarkable decision by a manufacturing company to turn its attention from making clothes wringers to producing and marketing a truly better mousetrap, the "Cyclone" trap, which made its appearance in the 1880s. Merriam knew from his studies of birds that a key to advancing the systematics of mammals was to accumulate and study large series of uniformly prepared specimens from throughout the range. The new cyclone trap made this possible for small mammals (Miller, 1929).

Merriam's monumental contributions to mammalogy were made possible by a combination of personal science, inspired leadership, and ability to recruit outstanding scientists (Osgood, 1943). Merriam personally described 660 new species of mammals and published more than 600 papers (Grinnell, 1943). Perhaps his most important paper was the one that used the observed elevational and latitudinal zonation of flora and fauna to develop the life zone concept (Merriam, 1890). In addition, Merriam emphasized the use of cranial characters in classification, and he perfected field and museum methods that are still in use today. He initiated a new publication series, *North American Fauna,* and wrote the first 11 volumes himself. From its first volume in 1889 to its 75th and most recent one (Timm et al., 1989), this series has been extremely influential; several volumes represent milestones in the transition from the discovery to the natural history phase of North American mammalogy. Under Merriam's leadership the Biological Survey became the primary center of mammalogical research. Much of this was owing to his genius for picking exceptional colleagues.

The group assembled at the Biological

Survey comprised an extraordinary group of field and museum biologists. Beginning about 1883, Merriam had communicated with a Minnesota farm boy named Vernon Bailey, who had supplied him with difficult to obtain specimens, such as shrews. Soon after accepting the position in Washington, Merriam hired Bailey, thus beginning a close and productive friendship between two giants of American mammalogy. Bailey and his wife, Florence, who was Merriam's sister, crisscrossed the continent collecting mammals and birds and described their studies in a series of volumes on the fauna of various states and geographic regions.

Two other remarkable members of the Biological Survey were Edward W. Nelson and Edward Alphonso Goldman. Beginning in 1892, Nelson, who later became Chief of the Survey, undertook a 14-year biological survey of Mexico. He hired Goldman, then an 18-year-old California youth, to accompany him. The results of their collaborative study are undoubtedly the most important ever achieved by two individuals for a single country. They obtained 12,400 specimens of birds and 17,400 specimens (including 354 new species and subspecies) of mammals. In addition, they collected reptiles, amphibians, and plants, and their field reports contained a wealth of information on the vegetation and climate of Mexico (Goldman, 1951).

If Merriam's life zone concept was the first important ecological principle that signaled the shift from the discovery phase to the natural history phase, Joseph Grinnell's (1917*a*, 1917*b*) niche concept was the second. Grinnell's concept, which emphasized the role of environmental conditions in limiting the distribution of a species, was later redefined and formalized by Hutchinson (1957). Although Grinnell used a bird species, the California thrasher, to illustrate his idea of the niche, he made enormous contributions to both mammalogy and ornithology. Grinnell not only published 554 papers between 1893 and 1939, he also started a mammalogical dynasty by training an exceptional cadre of students at the University of California at Berkeley (Jones, 1991; Whitaker, 1994).

Although the majority of the classic descriptive studies that marked the transition from the discovery phase to the natural history phase were done on rodents, many were performed on other groups that have more unusual or conspicuous lifestyles, such as bats, ungulates, carnivores, and marine mammals. Pioneering studies on bats included Glover Merrill Allen's (1939) classic treatise and two important papers by A. B. Howell (1920*a*, 1920*b*) in the first volume of the *Journal of Mammalogy.* A subsequent volume by Griffin (1958) emphasized behavioral and physiological studies of echolocation, but also summarized much of the information on natural history. These early studies were limited to insights that could be obtained from studies at roosts, direct observations of flying bats, and laboratory experiments, until the use of Japanese mist nets around the middle of the century.

Carnivores and ungulates were the subjects of important early studies, especially those of E. T. Seton (e.g., 1909, 1923), which included a multivolume work on the lives of game animals (1929). More recent classic studies were Murie's (1944) and Young and Goldman's (1944) on wolves, Hall's (1951; which included taxonomy as well as natural history) on weasels, Taylor's (1956) on deer, and Altmann's (1952) on elk. Important early studies of marine mammals included papers by Evermann (1921) and Kellogg (1921), both in the second volume of the *Journal of Mammalogy.* The more recent tradition of natural history studies is illustrated by Bartholomew and Peterson's (1967; the first Special Publication of the American Society of Mammalogists) monograph on the California sea lion and Le Boeuf and colleagues' studies of the northern elephant seal (e.g., Le Boeuf and Reiter, 1988).

Natural history studies gathered momentum in the 1920s and 1930s, and they continued to dominate ecological mammalogy until the 1960s. Some of these, such as those by Grinnell and his students on different areas in California (Grinnell and Storer, 1924; Grinnell et al., 1930, 1937), focused on particular geographic regions. Others were restricted to single species or a few related species. Natural history investigations reached their epitome in monographic studies of various kinds of rodents. These included major works on woodrats (Finley, 1958; Linsdale and Tevis, 1951; Vorhies and Taylor, 1940), ground squirrels (Linsdale, 1946), deer mice (McCabe and Blanchard, 1950), microtines (Elton, 1942; Errington, 1963), and heteromyid rodents (Eisenberg, 1963; Reynolds, 1958, 1960). In contrast to these large, integrated studies of particular species or genera, the contributions of two of the most influential mammalian natural historians, W. J. Hamilton, Jr., and W. H. Burt, consisted primarily of a combination of books on all mammals and shorter papers on particular kinds (e.g., Burt, 1940, 1946; Hamilton, 1939; Layne and Whitaker, 1992; Muul, 1990).

The natural history phase of research in mammalogy also saw the beginnings of the conservation movement. W. T. Hornaday (1899) detailed the life history and near extinction of the North American bison, and Volume 2 of the *Journal of Mammalogy* contained a paper on the status of the European bison (Ahrens, 1921). The works of Seton (1909, 1923, 1929) are filled with accounts of the relentless killing, declining abundances, and contracting ranges of carnivores and ungulates. The Biological Survey monitored the status of furbearers and the fur trade (Ashbrook, 1922). Lang (1923) called attention to the plight of the white rhinoceros in Volume 4 of the *Journal of Mammalogy.* Aldo Leopold (e.g., 1933) emerged as an eloquent advocate for conservation and developed wildlife management as an applied science based on the principles of natural history and ecology. E. P. Walker worked diligently to stimulate interest in mammalian conservation during his years at the National Zoological Park, and culminated his career with his opus on mammals of the world (Walker, 1964).

Natural history is still a significant component of contemporary American mammalogy. This is apparent from the success of the ASM's *Mammalian Species* series of publications and from the large number of "descriptive" papers appearing in the *Journal of Mammalogy* and other journals.

## Mammalogy and the New Synthesis

By the 1930s the study of ecology and evolution was already beginning to enter a new phase. The new synthesis was laying a theoretical and genetical foundation for the study of evolution. Fisher, Wright, and Haldane introduced mathematical models to characterize the genetic mechanisms of evolutionary change, as well as experimental and statistical techniques to test rigorously the predictions of these models. Simpson, Dobzhansky, and Mayr developed a broad view of evolution that incorporated not only genetic mechanisms, but also systematics, biogeography, paleontology, and ecology.

In North American mammalogy, the influence of the new synthesis is seen most clearly in two research programs. One is the work on the genetics of *Peromyscus* by F. B. Sumner and L. R. Dice. These studies rivaled those of *Drosophila,* if not for their elucidation of genetic mechanisms per se, then for their insights into the adaptive context of genetic variation. Sumner (e.g., 1932) showed that coat color and other traits of *Peromyscus* were heritable, and Dice and his students at Michigan, P. M. Blossom, W. F. Blair, and B. E. Horner, went on to explain geographic variation in coat color and morphology in terms of natural selection by predators in environments that differ in background coloration and vegetation structure (e.g., Dice, 1947; Dice and Blossom, 1937; see also Benson, 1933). This research program is notable for its use of

*Peromyscus* as an empirical "model system" for addressing general conceptual questions, for its combination of controlled experiments in the laboratory to test mechanisms and comparative field observations to place the experimental results in a realistic natural context, and for its use of rigorous experimental designs and statistical analyses.

The other major contribution of North American mammalogy to the new synthesis was G. G. Simpson's interpretation of the historical record of evolution, based on his studies of fossil and Recent mammals. Simpson (1940, 1943, 1944, 1947*a*, 1947*b*, 1950, 1953) focused on the evolution of the North and South American faunas, and on the effects of the interchange of species across the Interamerican and Bering land bridges. He also brought new quantitative approaches to paleontology and comparative biology by developing mathematical techniques for assessing similarity among faunas, quantifying diversity, and measuring rates of evolutionary change. Simpson can be credited with primary responsibility for giving the new synthesis an historical and biogeographic dimension.

With a few conspicuous exceptions, such as Dice and Simpson, descriptive natural history studies predominated in North American mammalogy until after World War II.

## Evolutionary Ecology Phase

In the late 1950s and 1960s, a major emphasis on science in the U.S. and Canada was stimulated by military and scientific competition with the U.S.S.R. This period saw the emergence of modern evolutionary ecology. The seminal event was the Cold Spring Harbor Symposium in Quantitative Biology in 1957. This symposium is noteworthy for three things. First, it had several papers on the dynamics of small mammal populations (Chitty, 1957; Pitelka, 1957). These signaled a shift to North America of the research on the dramatic fluctuations in rodent populations that had been pioneered in Europe by Elton (1927, 1942). Second, the mix of genetics, ecology, and evolution indicated an effort to expand the new synthesis to include ecology. Here and in the symposium on the genetics of colonizing species held in Syracuse in the mid-1960s (Lewontin, 1968), the foundations of evolutionary ecology were laid. Finally, Hutchinson (1957) in his "concluding remarks," capped the symposium by presenting his theory of the multidimensional niche. This was by no means the first use of mathematical models in ecology, but it took theoretical ecology beyond the problems of population growth and regulation that had preoccupied ecologists prior to that time. It provided a new conceptual framework to address questions about limiting factors, interspecific interactions, species diversity, and adaptation.

*Population dynamics.*—Mammalian ecologists were well represented at the Cold Spring Harbor Symposium. Attendees included Frank Pitelka, Dennis Chitty, Paul Errington, John B. Calhoun, John J. Christian, and David E. Davis. Charles Elton, perhaps the most eminent of all British ecologists, had attracted much interest to the population fluctuations of microtines. Elton had begun field work in the Scandinavian arctic in the 1920s, and had summarized much of this work in his *Voles, Mice and Lemmings* (1942). Errington (1946, 1963) had been working in Iowa since the 1930s on the role of predation, disease, and other factors in limiting muskrat populations. Influential papers in the Cold Spring Harbor Symposium by Pitelka (1957) on lemming cycles at Point Barrow, Alaska, and by Chitty (1957) on the genetics and behavioral components of microtine population regulation signaled the seminal roles that these two newcomers would play in North American mammalian ecology.

The challenge that microtines pose to ecologists is to explain the dramatic multiannual fluctuations in populations.

Whether microtine populations "cycle" and what causes the fluctuations are the two questions that have preoccupied microtine ecologists since Elton (1942) and Errington (1946, 1963). The chapter by Lidicker (1994) documents the history and accomplishments of the enormous research program that developed in both North America and Europe to address these questions (see also Gaines et al., in press; Henttonen et al., 1984; Krebs and Myers, 1974; Krohne, 1982; Lidicker, 1988, in press; Taitt and Krebs, 1985; Tamarin, 1985).

Although much attention has been devoted to microtines, important investigations of population dynamics have been performed on other mammals. Many studies have focused on other rodents, because of their small size, ease of trapping, and occurrence in a wide variety of habitats (e.g., Adler and Tamarin, 1984; Brown and Heske, 1990; Brown and Zeng, 1989; Petticrew and Sadler, 1974; Stickel and Warbach, 1960; Whitford, 1976). These have often implicated temporal variation in climate and food supply as the primary cause of population fluctuations. Yet another perspective is offered by large mammals, whose population dynamics often appear to be controlled by complex relationships between food supply and susceptibility to predation (e.g., Fowler and Smith, 1981; McCullough, 1979). Thus, mammals continue to offer a wealth of different patterns of population fluctuations, of different mechanisms of population regulation, and of different kinds of populations for study.

*Species diversity and community structure.*—After formulating the multidimensional ecological niche in his "Concluding remarks" at the Cold Spring Harbor Symposium, Hutchinson (1959) gave a presidental address to the American Society of Naturalists entitled "Homage to Santa Rosalia, or Why are there so many kinds of animals?" By explicitly focusing on patterns of species diversity, resource utilization, and coexistence, and on processes of population regulation, interspecific interaction, and adaptation, these two papers laid much of the foundation for modern community ecology. Although David Lack had addressed some of these problems in his *Darwin's Finches* in 1947, they were not pursued vigorously until the late 1950s. Other important contributions at this time included Brown and Wilson's (1956) treatise on character displacement and MacArthur's (1958, 1960, 1965, 1970, 1972) empirical and theoretical studies.

Data from mammals figured prominently in these studies in community ecology. Hutchinson (1959) used weasels as examples of the regular ratios in the body sizes or trophic appendages that can be observed among coexisting species and that were hypothesized to reflect the influence of interspecific competition on community structure. Hutchinson and MacArthur (1959) used the frequency distribution of body sizes among all species of North American mammals to develop models of niche relationships and coexistence.

Others were quick to exploit the advantages of mammals for studies in evolutionary ecology. In 1959, Hall and Kelson published a major taxonomic treatise, *The Mammals of North America,* which contained, among other information, detailed range maps of every species. Simpson (1964) used this data base to quantify patterns of species diversity across the continent. Thus began a long tradition of using these range maps to address Hutchinson's question about the ecological processes causing geographic variation in species diversity (Brown, 1981; Hagmeir and Stults, 1964; MacArthur, 1972; Owen, 1990; Rapoport, 1982; Wilson, 1974; see also Fleming, 1973). Unfortunately, despite a great deal of research, the question remains largely unanswered. The major geographic gradients in species richness, including the dramatic increase in diversity from poles to equator, have been increasingly well documented in mammals and other organisms, but investigators have had only limited success in evaluating the contributions of several, and not necessarily exclusive, mechanisms that may have caused these patterns (e.g., Brown, 1988; MacArthur, 1972).

One ecological legacy of Dice's genetic research on *Peromyscus* was two elegant experimental studies of habitat selection. Harris (1952) showed that forest and grassland races of *P. maniculatus* preferred artificial habitats of different structure in the laboratory. Wecker (1963, 1964) took this approach to the field, where he showed not only that young mice exhibited a strong preference for appropriate habitat, but also that there were both inherited and learned components of this behavior. Rosenzweig, Dueser, M'Closkey, Price, and Morris (see references below) continued to investigate habitat selection, using it as a vehicle to understand population dynamics and community structure.

MacArthur's student, Rosenzweig, having analyzed geographic variation in body size in North American mammals for his doctoral dissertation (Rosenzweig, 1966, 1968), began to study habitat selection, resource utilization, and coexistence in desert rodents. Rosenzweig's studies (e.g., Rosenzweig, 1973; Rosenzweig and Sterner, 1970; Rosenzweig and Winakur, 1969; Rosenzweig et al., 1975; Schroder and Rosenzweig, 1975) were the first of many (see Brown and Harney, 1993) that used the desert rodent system to address fundamental questions in community ecology. From these and other studies we have learned that species diversity and composition vary on geographic scales with precipitation and productivity (Brown, 1973, 1975), and on local to regional scales with soil and vegetation type (M'Closkey, 1976, 1978; Rosenzweig and Winakur, 1969; Rosenzweig et al., 1975). Coexisting species tend to be more different in body size, body shape, and other attributes than expected by random community assembly (Bowers and Brown, 1982; Brown, 1973; Dayan and Simberloff, in press; Findley, 1989; Hopf and Brown, 1986), and they tend to use different microhabitats (Brown and Liebermen, 1973; Lemen and Rosenzweig, 1978; M'Closkey, 1981; Price, 1978; Rosenzweig, 1973; Rosenzweig and Winakur, 1969). These observations suggest that interspecific competition plays a major role in the organization of these communities. Field experiments in which some species increased in abundance or shifted their microhabitat use in response to removal of other species have provided additional direct evidence for interspecific competition (Bowers et al., 1987; Brown and Munger, 1985; Freeman and Lemen, 1983; Munger and Brown, 1981; Price, 1978; see also Larsen, 1986). Clever experiments that have altered the risk of predation have shown that it influences foraging behavior and microhabitat use and probably interacts with competition to affect community structure (Brown et al., 1987; Kotler, 1984*a,* 1984*b,* 1985; Thompson, 1982*a,* 1982*b*).

Although studies of desert rodents rival those of Darwin's finches and *Anolis* lizards for their contributions to community ecology, many questions remain unanswered and several research programs are pursuing them. Populations appear to be limited largely by food supplies and to fluctuate with climatic conditions that determine the availability of seeds, insects, and foliage (e.g., Beatley, 1976), but the coupling between the abiotic environment and population dynamics varies among species and is poorly understood (Brown and Heske, 1990). There has been widespread agreement that differences in microhabitat use promote coexistence, but the extent and significance of food resource partitioning has been much more controversial (Brown, 1975; Brown and Lieberman, 1973; Dayan and Simberloff, in press; Lemen, 1978; Mares and Williams, 1977; Rosenzweig and Sterner, 1970; Smigel and Rosenzweig, 1974). Although the importance of predation and interspecific competition no longer seems to be in doubt, the way that these processes separately and jointly affect population dynamics and community structure requires further study. Finally, the importance of character displacement and other kinds of coevolutionary responses to biotic interactions is receiving considerable study, but remains largely unresolved.

By no means were all of the important community-level studies were of desert rodents. Miller (1967), Dueser and Shugart (1978), Dueser and Hallett (1980), Morris (1984), Kirkland (1985), and others investigated habitat selection and interspecific interactions of rodents and shrews in forest and grassland habitats. Competitive interactions among chipmunk species were studied in coniferous forest habitats in several places in western North America (Brown, 1971; Chappell, 1978; Heller, 1971; Sheppard, 1971). Findley (1973, 1976, 1993) used bats for pioneering studies of ecomorphology, the relationships between patterns of morphological variation among species and the composition of ecological communities. Moors (1984), Ralls and Harvey (1985), and Dayan et al. (1989) performed more detailed morphological and field studies to reexamine Hutchinson's and Rosenzweig's inferences about sexual dimorphism, resource partitioning, and character displacement in mustelids. Fleming (1971, 1973, 1988; Fleming et al., 1972) and Wilson (1971, 1973; Wilson and Findley, 1970) pioneered studies of tropical communities of both terrestrial mammals and bats, and these were followed by others (August, 1983; Heithaus et al., 1975; Sanchez-Cordero and Fleming, 1993).

*Life history studies.*—In terms of their use of direct observations in the field to learn about important events in the lives of individual free-living mammals, the most direct descendants of the classical natural history studies of the early 1900s were the life history studies of the latter half of the century. Because of their high densities and diurnal habits, colonial sciurid rodents were frequently chosen for longitudinal studies of life histories. J. A. King's (1955) work on black-tailed prairie dogs (*Cynomys ludovicianus*) was probably the most influential, if not the first, of the detailed field studies of a single population of marked individuals. This was followed by Armitage's (1962) work on marmots, and then by many other studies using different species of ground squirrels (reviewed in Murie and Michener, 1984).

These studies have been much more than descriptive natural history; they have been instrumental in gathering data to build and test theories of social behavior and life history tactics. Together with studies of the wolf by Mech (1966, 1970), of Scottish red deer (*Cervus elaphus*) by Clutton-Brock et al. (1982), of African carnivores (e.g., Kruuk, 1972; Packer, 1986; Packer et al., 1988), and of primates (e.g., Altmann and Altmann, 1970; Cheney et al., 1988), the body of work on North American sciurids has been instrumental in the development of our ideas about the roles of environmental conditions and social interactions in determination of individual reproductive success and in evolution of social systems. Perhaps the two most extreme and spectacular mammalian life histories—and ones that have far-reaching theoretical implications—are the eusocial systems of naked mole rats and the semelparous life histories of some dasyurid marsupials. Mole-rats (*Heterocephalus glaber*) resemble social bees and ants, living in large colonies in which a single dominant female effectively castrates and enslaves her relatives (Jarvis, 1981). Marsupial mice (Genus *Antechinus*) resemble salmon and certain plants in that the males of several species are semelparous; they put all of their resources into a single reproductive effort and then die after just one breeding season (Lee and Cockburn, 1985).

Another approach to studying the evolution of life histories and social systems that was pioneered by North American mammalogists involved allometric relationships—patterns of variation with respect to body size. In 1963, McNab published an influential paper on the correlation between home range size and body size (see also Schoener, 1968). This was followed by several studies of the allometry of life history traits, such as litter size, gestation length, and maternal investment in offspring (e.g., Calder, 1984; Clutton-Brock and Harvey, 1983; Eisenberg, 1981; Eisenberg and Wilson, 1979; Peters, 1983). These studies have not only demonstrated correlates of body size that are expressed in allometric relationships across large samples of mammal species, they have also pointed out deviations from these relationships that can be attributed to evolutionary constraints or to adaptations to special ecological conditions, or both. For other evolutionary and ecological approaches to the study of mammalian life histories see Millar (1977) and Millar and Zammuto (1983).

*Coevolution.*—Several early naturalists noted that mammals play potentially important roles as dispersers, as well as consumers, of seeds. Smith (1970) put these kinds of interactions in a modern perspective with a classic study of coevolution between red squirrels (*Tamiasciurus hudsonius* and *T. douglasii*) and conifers. He showed that the two squirrel species have different morphological and behavioral traits that reflect adaptations to the different kinds of conifers that predominate in their geographic ranges, and the trees also exhibit adaptations to promote dispersal and to limit consumption by the squirrels. Small forest-dwelling mammals, such as deer mice and voles, have been shown to play a major role in dispering the mutualistic mycorrhizal fungi that are obligately associated with the roots of many tree species (e.g., Maser et al., 1978). Howell (1979) found that a bat, *Leptonycteris sanbornii,* is the principal pollinator of several century plant and cactus species in the Sonoran and Chihuahuan deserts.

Subsequently, much of the attention turned to the tropics, where both rodents and bats were shown to be important dispersers of seeds of fleshy-fruited trees (e.g., Fleming, 1988; Janzen, 1983; Smythe, 1970). These studies have for the most part supported Janzen's (1970) suggestion that animals, especially frugivorous and granivorous mammals and birds, play a major role in the structure and dynamics of tropical forests. Rodents and bats are particularly important in carrying seeds away from the parent tree, where they are subject to heavy predation from insect consumers and microbial pathogens, to distant sites that may be more favorable for survival and germination. Janzen's (1981) discovery that introduced horses are important agents of seed dispersal for some tropical tree species led to the suggestion that the extinction of the Pleistocene megafauna and the extirpation of modern species of large mammals, such as tapirs and peccaries, may be causing substantial changes in tropical forests (Janzen and Martin, 1982).

Recently, evolutionary ecologists have speculated about coevolutionary relationships between parasitic or symbiotic organisms and their hosts (e.g., Holmes and Price, 1986; Price, 1980). Studies of mammals have supported suggestions that "parasites" may not always have significant negative effects on their hosts; in fact, some apparent parasites might even benefit their hosts (Munger and Holmes, 1988). Other fascinating symbiotic relationships have been discovered. Several tropical mammals have symbiotic insects that live in their fur, their nests, or both, and prey on lice, fleas, and other ectoparasites (e.g., Ashe and Timm, 1987; Timm and Ashe, 1988). In desert and arid grassland habitats bannertailed kangaroo rats (*Dipodomys spectabilis*) and woodrats (*Neotoma* sp.) construct large dens that provide refuges for many kinds of invertebrates and small vertebrates (Monson and Kessler, 1940). In addition, the seed stores of the bannertailed kangaroo rats are inhabited by many kinds of fungi that have been suggested to have beneficial effects on their rodent hosts by enhancing the nutritional value of infested seeds (e.g., Hawkins, 1992; Reichman et al., 1985).

### *The Transition from Natural History to Evolutionary Ecology*

*The transition.*—The period of active research in mammalogy in North America, from about 1850 to the present, marked the transition from studies that emphasized descriptive taxonomy, morphology, distribution, paleontology, and natural history to investigations that were motivated by the theoretical questions of modern disciplines such as biomechanics, physiology, behavior, genetics, evolution, systematics, ecology, and biogeography. The 19th-Century naturalists were generalists. The greatest of them, such as Cuvier, Darwin, Wallace, Bates, von Humboldt, and Prinz Maximilian zu Wied, were knowledgeable about plants, invertebrates, and vertebrates, studied geology and paleontology as well as biology, and developed concepts and theories to explain their empirical observations. Even the early 20th-Century mammalogists were amazingly diverse scientists. For example, Merriam published in geography and anthropology as well as mammalogy (Grinnell, 1943; Osgood, 1943), and Grinnell wrote influential papers on the behavior, ecology, biogeography, and systematics of both birds and mammals (Miller, 1943).

The natural historians of the first half of the 20th Century represented a transition from the 19th-Century naturalists to modern evolutionary ecologists. These natural historians, best represented by individuals such as Linsdale, Murie, Vorhies, and Hamilton, made detailed, descriptive studies of particular species that emphasized behavior, reproductive biology, and distribution with respect to habitat. Today their work may seem quaint, descriptive, and lacking theoretical motivation. It is important however, to recognize the extent to which the natural historians laid the foundations for the more conceptual approach of contemporary mammalogy. Taxonomic mammalogists were still describing new species and mapping their geographic ranges well into the present century. It was necessary to document the basic biology of these mammals before it was apparent which ones were well suited for addressing ecological and evolutionary questions of theoretical interest.

The dependence of modern evolutionary ecologists on the work of their more descriptive antecedents is illustrated by two observations. First, many of the evolutionary ecologists were trained either by natural historians or by taxonomists. Note, for example, the academic histories of Findley, Krebs, Lidicker, Eisenberg, Wilson, Brown, Fleming, and other mammalian evolutionary ecologists (Jones, 1991; Whitaker, 1994). Second, the influence of the natural historians is illustrated by the frequency with which the studies of Linsdale, Grinnell, Hall, Vorhies and Taylor, Findley, and others are cited in recent publications. The descriptive observations of the natural historians often provide the inspiration for the modern experimental studies of evolutionary ecologists.

*The role of theory.*—The transition from natural history to evolutionary ecology can be attributed largely to the influence of mathematical theory and the seminal contributions of Hutchinson, MacArthur, and others. The foundations of the new synthesis were laid by the mathematical models of genetic evolutionary change of Fisher, Wright, and Haldane. Although this work was largely completed before World War II, the consolidation of the new synthesis did not come until the major works of Dobzhansky (1937), Simpson (1944, 1953) and Mayr (1942, 1963). These major advances in understanding the evolutionary process demonstrated the power of mathematical models to motivate important experimental and synthetic empirical studies.

The incorporation of an evolutionary perspective into studies of ecology and life history can be attributed largely to the influence of Hutchinson and his student, MacArthur. As mentioned above, Hutchinson (1957, 1959) set much of the agenda for the next several decades with his papers on the niche and the diversity of species. MacArthur (e.g., 1960, 1970, 1972) followed with mathematical treatments of species abundance and diversity, competition and resource utilization, coexistence and coevolution, life history theory, optimal foraging, and island biogeography. There was hardly a topic in modern evolutionary ecology that MacArthur did not address. He was almost certainly the most influential ecologist who ever lived, an assessment that is borne out by the total number of times his papers have been cited (see Science Citation Index).

The specific mathematical models developed by Hutchinson, MacArthur, and others have had mixed success. Some, such as the broken stick distribution of niches and the idea that complexity promotes stability, were misguided or just plain wrong, and have been abandoned. Others, such as $r$ and $K$ reproductive strategies and the limiting similarity of species were too simplistic; they represented important advances, but were eventually replaced by more complex and realistic theory. Still others, such as resource-based competition equations and the theory of island biogeography are still widely used to motivate both theoretical and empirical studies. Despite the mixed success of these models, their influence on the development of modern evolutionary ecology is enormous. Almost every influential empirical paper since 1960 cites theoretical literature and attempts to evaluate predictions of mathematical theory.

Even more important than its success in explaining evolutionary and ecological phenomena, however, was the way that mathematical theory revolutionized the science. It led to more conceptual, question-asking, quantitative, analytical, experimental, and statistical approaches to both theoretical and empirical studies. To produce mathematical theory requires conceptual innovation, quantitative skills, and analytical rigor. To test empirically the predictions of theory requires understanding the theory, choice of an appropriate system for study, design and execution of appropriate experiments or comparative observations, and rigorous statistical analysis and inference.

*Mammalian systems for testing theory.*—The appearance of compelling mathematical models called for empirical tests of their assumptions and predictions in appropriate natural systems. Beginning with Hutchinson and MacArthur's (1959) paper on the distribution of body sizes among species, North American mammals have played a major role in the interaction between theory and data. Some of this was largely serendipitous. Thanks to the efforts of the natural historians, mammals had already been relatively well studied and young scientists trained in more descriptive mammalogy soon became interested in testing the exciting new theories.

Furthermore, certain kinds of mammals possess combinations of characteristics that have made them excellent systems for quantitative and experimental field studies. The influential roles of sciurid rodents, primates, and ungulates in life history studies, of microtine rodents in studies of population dynamics, and of desert rodents in investigations of coexistence and interactions of species are no accident. Each of these groups has specific traits that facilitate observation, quantification, and experimental manipulation to obtain definitive tests of hypotheses and theoretical predictions. No organism is ideal for all kinds of studies, and some groups of birds, lizards, insects, plants, and intertidal organisms, have rivaled mammals as empirical systems for studies in evolutionary ecology. Nevertheless, mammals have played and will continue to play an influential role in the development of evolutionary ecology (see citations in the previous section).

*Increasing scientific rigor.*—As mentioned above, the development of mathematical theory had a profound effect on the way that empirical studies of mammals were conducted. The emphasis shifted from qualitative description motivated by economic concerns or investigator fancy, to statistically rigorous, experimental hypothesis-testing motivated by theoretical issues.

Once empirical studies shifted from describing the natural history of mammal species to evaluating the assumptions and predictions of particular theories they then needed to provide more definitive answers. This required formulating and testing hypotheses. Usually the goals of natural history studies were essentially similar to Linsdale's (1946:vii): "The need for an extensive study of the life of the California Ground Squirrel has grown with increasing rapidity as more and more questions have been raised about this animal, its habitat, distribution, and characteristics." There is no way to frame this objective in the form of a single hypothesis, or to satisfy this need except by doing the kind of broad, descriptive study that Linsdale did. This changed when the goal became to learn whether habitat heterogeneity affects the dynamics of a microtine population or whether two desert rodent species are competing. Each of these questions can be cast as a specific hypothesis, and answered definitively with a single set of observations or experimental manipulations.

Another impact of theory, then, was that it led to an increased emphasis on the design and execution of controlled experiments to give definitive tests of hypotheses. Connell (1961) brought to modern evolutionary ecology the approach, long practiced by British plant ecologists, of doing replicated manipulative experiments in the field. It did not take long for field experiments to be applied to mammalian ecology, first and most notable in manipulations of microtine populations by Krebs and colleagues (Krebs et al., 1969) and in Rosenzweig's (1973) "habitat tailoring" experiments on desert rodents. Now a large proportion of field studies in mammalian ecology are well-designed experiments, with appropriate controls, adequate replication, and standardized data collection. Of course, a number of conceptually or practically important questions simply cannot be answered by manipulative experiments. It is either impractical to experiment on the spatial or temporal scale required to test the hypothesis (e.g., to address biogeographic questions), or it is illegal or unethical to perturb the natural system (e.g., in the case of endangered species). This does not diminish the need to adopt a rigorous, hypothesis-testing approach, but it requires that carefully designed comparative observations be substituted for artificial manipulations (e.g., Brooks and McLennan, 1991; Harvey and Pagel, 1991).

Finally, the emphasis on evaluating theory, testing hypotheses, and doing experiments has led to the development of an increasingly powerful battery of statistical techniques. In fact, many of the analyses were developed by theoreticians, including Fisher and Wright, for testing empirically the predictions of their models. Statistical analyses are virtually absent from most of the natural history literature before World War II, although means and occasionally some measure of variance were sometimes reported. Now ecological papers contain such sophisticated experimental designs and statistical analyses that constant updating of biometric skills is required to interpret the results, let alone to do state-of-the-art research (e.g., see Dueser et al., 1989).

It is hard to overestimate how much our science has changed since World War II. In just a few decades traditional descriptive natural history has fallen into disfavor in the classroom and the journals. It has been eclipsed by an evolutionary approach to ecology that asks theoretical questions, and uses sophisticated experimental and statistical techniques to answer them. Mammalogists have not simply responded to this revolution, they have often been in the forefront, using the special advantages of mammals to make important conceptual and empirical advances.

## Summary

The history of North American mammalogy began with the exploration of the continent by Europeans. There was added incentive to study mammals, because one of the resources most valuable to the early colonists was fur, especially beaver pelts. After the fur trade slackened, official voyages to explore and survey the remote parts of the continent were usually accompanied by scientists, many of them physician-naturalists with particular interests in mammals. During this discovery phase, the early naturalists were concerned with describing and classifying the different kinds of mammals and beginning to accumulate information on their distributions and habits.

By the beginning of the 20th Century, most of the species of North American mammals had been described and mammalogists were beginning to specialize. One of the specialties was natural history, which encompassed all aspects of ecology and behavior. In contrast to modern disciplines, natural history was a descriptive science. Its goal was to describe the environmental relationships and lives of particular species, groups of related species, or entire assemblages of coexisting species.

The new evolutionary synthesis began the transformation of the field sciences into modern theory-testing, experimental disciplines. Early studies of mammalian genetics, adaptations, paleontology, and biogeography contributed importantly to the data and concepts of the new synthesis.

After World War II, the interjection of evolutionary concepts and mathematical modeling was instrumental in the transformation of traditional, descriptive natural history into the modern discipline of evolutionary ecology. Mammals were used to make important empirical and theoretical contributions to our understanding of population dynamics, community organization, foraging, habitat selection, life history traits, and coevolution.

## *Acknowledgments*

We thank W. L. Gannon, L. Hawkins, E. J. Heske, B. D. Patterson, and R. M. Timm for their comments on this manuscript. Brown's research has been supported by the National Science Foundation, most recently by Grant BSR-8718139.

## *Literature Cited*

Adler, G. H., and R. H. Tamarin. 1984. Demography and reproduction in island and mainland white-footed mice (*Peromyscus leucopus*) in southeastern Massachusetts. Canadian Journal of Zoology, 62:58–64.

Ahrens, T. G. 1921. The present status of the European bison or wisent. Journal of Mammalogy, 2:58–62.

Allen, G. M. 1939. Bats. Harvard University Press, Cambridge, 368 pp.

Altmann, M. 1952. Social behavior of elk, *Cervus canadensis nelsoni*, in the Jackson Hole area of Wyoming. Behaviour, 4:116–143.

Altmann, S. A., and J. Altmann. 1970. Baboon ecology: African field research. University of Chicago Press, Chicago, 220 pp.

Armitage, K. B. 1962. Social behavior of a colony of the yellow-bellied marmot (*Marmota flaviventris*). Animal Behaviour, 10:319–331.

Ashbrook, F. G. 1922. The fur trade and the fur supply. Journal of Mammalogy, 3:1–7.

Ashe, J. S., and R. M. Timm. 1987. Predation by and activity patterns of 'parasitic' beetles of the genus *Amblyopinus* (*Coleoptera*: *Staphylinidae*). Journal of Zoology (London), 212:429–437.

August, P. V. 1983. The role of habitat complexity and heterogeneity in structuring tropical mammal communities. Ecology, 64:1495–1507.

Baird, S. F. 1859. Mammals: general report upon the zoology of the several Pacific railroads routes. Reports, explorations and surveys for railroad route from Mississippi River to Pacific Ocean. Volume 8 (part 1), Washington, D.C., 757 pp.

Bartholomew, G. A., and R. S. Peterson. 1967. The natural history and behavior of the California sea lion. Special Publications, The American Society of Mammalogists, 1:1–79.

Beatley, J. C. 1976. Environments of kangaroo rats (*Dipodomys*) and effects of environmental change on populations in southern Nevada. Journal of Mammalogy, 57:67–93.

Benson, S. B. 1933. Concealing coloration among some desert rodents of the southwestern United States. University of California Publication of Zoology, 40:1–70.

Bowers, M. A., and J. H. Brown. 1982. Body size and coexistence in desert rodents: chance or community structure. Ecology, 63:391–400.

Bowers, M. A., D. B. Thompson, and J. H. Brown. 1987. Foraging and microhabitat use in desert rodents: the role of a dominant competitor. Oecologia, 72:77–82.

Brooks, D. L., and D. A. McLennan. 1991. Phylogeny, ecology, and behavior. University of Chicago Press, Chicago, 434 pp.

Brown, J. H. 1971. Mechanisms of competitive ex-

clusion between two species of chipmunks. Ecology, 52:305–311.
———. 1973. Species diversity of seed-eating desert rodents in sand dune habitats. Ecology, 54:775–787.
———. 1975. Geographical ecology of desert rodents. Pp. 315–341, *in* Ecology and evolution of communities (M. L. Cody and J. M. Diamond, eds.). Belknap Press, Cambridge, Massachusetts, 545 pp.
———. 1981. Two decades of homage to Santa Rosalia: toward a general theory of diversity. American Zoologist, 21:877–888.
———. 1988. Species diversity. Pp. 57–90, *in* Analytical biogeography (A. A. Myers and P. S. Giller, eds.). Chapman and Hall, London, 578 pp.
Brown, J. H., and B. A. Harney. 1993. Population and community ecology of heteromyid rodents in temperate habitats. Pp. 618–651, *in* Biology of the Heteromyidae (H. H. Genoways and J. H. Brown, eds.). Special Publications, The American Society of Mammalogists, 10:1–719.
Brown, J. H., and E. J. Heske. 1990. Temporal changes in a Chihuahuan Desert rodent community. Oikos, 59:290–302.
Brown, J. H., and G. A. Lieberman. 1973. Resource utilization and coexistence of seed-eating desert rodents in sand dune habitats. Ecology, 54:788–797.
Brown, J. H., and J. C. Munger. 1985. Experimental manipulation of a desert rodent community: food addition and species removal. Ecology, 66:1545–1563.
Brown, J. H., and Z. Zeng. 1989. Comparative life population ecology of eleven species of rodents in the Chihuahuan Desert. Ecology, 70:1507–1525.
Brown, J. S., B. P. Kotler, R. J. Smith, and W. O. Wirtz, II. 1987. The effects of owl predation on the foraging of heteromyid rodents. Oecologia, 76: 408–415.
Brown, W. L., Jr., and E. O. Wilson. 1956. Character displacement. Systematic Zoology, 5:49–64.
Burt, W. F. 1940. Territorial behavior and populations of some small mammals in southern Michigan. Miscellaneous Publication of the Museum of Zoology, University of Michigan, 45:1–58.
———. 1946. The mammals of Michigan. University of Michigan Press, Ann Arbor, 288 pp.
Calder, W. A., III. 1984. Size, function, and life history. Harvard University Press, Cambridge, Massachusetts, 431 pp.
Chappell, M. A. 1978. Behavioral factors in the altitudinal zonation of chipmunks (*Eutamias*). Ecology, 59:565–579.
Cheney, D. L., R. M. Seyfarth, S. J. Andelman, and P. C. Lee. 1988. Reproductive success in vervet monkeys. Pp. 384–402, *in* Reproductive success (T. H. Clutton-Brock, ed.). University of Chicago Press, Chicago, 538 pp.
Chittenden, H. 1954. The American fur trade. Stanford University Press, Stanford, California, 2 volumes, 1,029 pp.
Chitty, D. 1957. Self-regulation of numbers through changes in viability. Cold Spring Harbor Symposium in Quantitative Biology, 22:277–280.
Clutton-Brock, T. H., and P. H. Harvey. 1983. The functional significance of variation in body size in mammals. Pp. 632–663, *in* Advances in the study of mammalian behavior (J. F. Eisenberg and D. G. Kleiman, eds.). Special Publications, The American Society of Mammalogists, 7:1–753.
Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. Red deer: behavior and ecology of two sexes. University of Chicago Press, Chicago, 378 pp.
Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle, *Chthamalus stellatus*. Ecology, 42:710–723.
Coues, E. 1877*a*. Monographs of North American rodents. United States Geological Survey of the Territories, Washington, D.C., 1,091 pp.
———. 1877*b*. Fur-bearing animals. Miscellaneous Publication No. 8, United States Geological Survey of the Territories, Washington, 349 pp.
Dayan, T., and D. Simberloff. In press. Morphological relationships among coexisting heteromyids: an incisive dental character. The American Naturalist.
Dayan, T., D. Simberloff, E. Tchernov, and Y. Yom-Tov. 1989. Inter- and intraspecific character displacement in mustelids. Ecology, 70:1526–1539.
Dice, L. R. 1947. Effectiveness of selection by owls of deer mice (*Peromyscus maniculatus*) which contrast in color with their background. Contributions from the Laboratory of Vertebrate Biology, University of Michigan, 50:1–15.
Dice, L. R., and P. M. Blossom. 1937. Studies of mammalian ecology in southwestern North America with special attention to the colors of desert mammals. Carnegie Institution of Washington, Publication, 485:1–129.
Dobzshansky, T. 1937. Genetics and the origin of species. Columbia University Press, New York, 364 pp.
Dueser, R. D., and J. G. Hallett. 1980. Competition and habitat selection in a forest-floor small mammal fauna. Oikos, 35:293–297.
Dueser, R. D., J. H. Porter, and J. L. Dooley, Jr. 1989. Direct tests for competition in North American rodent communities: synthesis and prognosis. Pp. 105–125, *in* Patterns in the structure of mammalian communities (D. W. Morris, Z. Abramsky, B. J. Fox, and M. R. Willig, eds.). Special Publications, The Museum, Texas Tech University, 28:1–xxx.
Dueser, R. D., and H. H. Shugart. 1978. Microhabitats in a forest-floor small mammal fauna. Ecology, 59:89–98.
Eisenberg, J. F. 1963. The behavior of heteromyid rodents. University of California Publications in Zoology, 69:1–114.
———. 1981. The mammalian radiations. University of Chicago Press, Chicago, 610 pp.
Eisenberg, J. F., and D. E. Wilson. 1979. Relative brain size and feeding strategies in the Chiroptera. Evolution, 32:740–751.
———. 1981. Relative brain size and demographic strategies in didelphid marsupials. The American Naturalist, 118:1–15.
Elton, C. 1927. Animal ecology. The Macmillan Company, New York, 207 pp.

———. 1942. Voles, mice and lemmings. Clarendon Press, Oxford, 496 pp.
ERRINGTON, P. L. 1946. Predation and vertebrate populations. The Quarterly Review of Biology, 21: 144–177, 221–245.
———. 1963. Muskrat populations. Iowa State University Press, Ames, 665 pp.
EVERMANN, B. W. 1921. The Año Nuevo Steller sea lion rookery. Journal of Mammalogy, 2:16–19.
FINDLEY, J. S. 1973. Phenetic packing as a measure of faunal diversity. The American Naturalist, 107: 580–584.
———. 1976. The structure of bat communities. The American Naturalist, 110:129–139.
———. 1989. Morphological patterns in rodent communities of southwestern North America. Pp. 253–264, *in* Patterns in the structure of mammalian communities (D. W. Morris, Z. Abramsky, B. J. Fox, and M. R. Willig, eds.). Special Publications, The Museum, Texas Tech University, 28:1–xxx.
———. 1993. Bats: a community perspective. Cambridge University Press, 167 pp.
FINLEY, R. B., JR. 1958. The wood rats of Colorado: distribution and ecology. University of Kansas Publications, Museum of Natural History, 10:213–552.
FLEMING, T. H. 1971. Population ecology of three species of neotropical rodents. Miscellaneous Publications of the Museum of Zoology, University of Michigan, 143:1–77.
———. 1973. Numbers of mammal species in North and Central American forest communities. Ecology, 54:555–563.
———. 1988. The short-tailed fruit bat. University of Chicago Press, Chicago, 363 pp.
FLEMING, T. H., E. T. HOOPER, AND D. E. WILSON. 1972. Three Central American bat communities: structure, reproductive cycles and movement patterns. Ecology, 53:555–569.
FOWLER, C. W., AND T. D. SMITH (EDS.). 1981. Dynamics of large mammal populations. Wiley, New York, 477 pp.
FREEMAN, P. W., AND C. LEMEN. 1983. Quantification of competition among coexisting heteromyids in the Southwest. The Southwestern Naturalist, 28:41–46.
GAINES, M. S., N. C. STENSETH, M. L. JOHNSON, R. A. IMS, AND S. BONDRUP-NIELSEN. In press. A response to solving the enigma of population cycles with a multifactorial perspective. Journal of Mammalogy.
GOLDMAN, E. A. 1951. Biological investigations in Mexico. Smithsonian Miscellaneous Collections, 115: 1–476.
GRIFFIN, D. R. 1958. Listening in the dark. Yale University Press, New Haven, 413 pp.
GRINNELL, H. W. 1943. Bibliography of Clinton Hart Merriam. Journal of Mammalogy, 24:436–457.
GRINNELL, J. 1917*a*. Field tests of theories concerning distributional controls. The American Naturalist, 51:115–128.
———. 1917*b*. The niche-relationship of the California thrasher. Auk, 34:427–433.
GRINNELL, J., J. DIXON, AND J. M. LINSDALE. 1930. Vertebrate natural history of Lassen Peak. University of California Publications in Zoology, 35:1–594.
———. 1937. Fur-bearing mammals of California. University of California Press, Berkeley, 2 volumes.
GRINNELL, J., AND T. I. STORER. 1924. Animal life in the Yosemite. University of California Press, Berkeley, California, 752 pp.
GUNDERSON, H. L. 1976. Mammalogy. McGraw-Hill Book Company, New York, 483 pp.
HAGMEIER, E. M., AND C. D. STULTS. 1964. A numerical analysis of the distributional patterns of North American mammals. Systematic Zoology, 13:125–155.
HALL, E. R. 1951. American weasels. University of Kansas Publications, Museum of Natural History, 4:1–466.
HALL, E. R., AND K. R. KELSON. 1959. The mammals of North America. The Ronald Press Company, New York, 2 volumes, 1,083 pp.
HAMILTON, W. J. 1939. American mammals. McGraw-Hill Book Company, New York, 434 pp.
HARRIS, V. T. 1952. An experimental study of habitat selection by prairie and forest races of the deer mouse, *Peromyscus maniculatus*. University of Michigan Contributions from the Laboratory of Vertebrate Biology, 56:1–53.
HARVEY, P. H., AND M. D. PAGEL. 1991. The comparative method in evolutionary biology. Oxford University Press, Oxford, 239 pp.
HAWKINS, L. K. 1992. Banner-tailed kangaroo rats and molds: a possible vertebrate-fungus mutualism. Ph.D. dissert., University of New Mexico, Albuquerque, xxx pp.
HEITHAUS, E. R., T. H. FLEMING, AND P. A. OPLER. 1975. Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. Ecology, 56:841–854.
HELLER, H. C. 1971. Altitudinal zonation of chipmunks (*Eutamias*): interspecific aggression. Ecology, 52:312–319.
HENTTONEN, H., J. TAST, J. VIITALA, AND A. KAIKUSALO. 1984. Ecology of cyclic rodents in northern Finland. Society Flora Fauna Fennici, Memoirs, 60: 84–92.
HOLMES, J. C., AND P. W. PRICE. 1986. Communities of parasites. Pp. 187–213, *in* Community ecology: patterns and process (D. J. Anderson and J. Kikkawa, eds.). Blackwell Scientific Publications, Oxford, xxx pp.
HOPF, F. A., AND J. H. BROWN. 1986. The bull's-eye method for testing randomness in ecological communities. Ecology, 67:1139–1155.
HORNADAY, W. T. 1899. The extermination of the American bison with a sketch of its discovery and life history. Smithsonian Institution Annual Report, 1887, Washington, D.C., pp. 367–548.
HOWELL, A. B. 1920*a*. Contribution to the life-history of the California mastiff bat. Journal of Mammalogy, 1:111–117.
———. 1920*b*. Some Californian experiences with bat roosts. Journal of Mammalogy, 1:169–177.
HOWELL, D. J. 1979. Flock foraging in nectar-feeding bats: advantages to the bats and to the host plants. The American Naturalist, 113:23–49.
HUTCHINSON, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposium in Quantitative Biology, 22:415–427.

———. 1959. Homage to Santa Rosalia *or* why are there so many kinds of animals? The American Naturalist, 93:145–159.

Hutchinson, G. E., and R. H. MacArthur. 1959. A theoretical ecological model of size distributions among species of animals. The American Naturalist, 93:117–126.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. The American Naturalist, 104:501–528.

———. 1981. Guanacaste tree seed-swallowing by Costa Rican range horses. Ecology, 62:587–592.

———. 1983. Dispersal of seeds by vertebrate guts. Pp. 232–262, *in* Coevolution (D. J. Futuyma and M. Slatkin, eds.). Sinaur, Sunderland, Massachusetts, xxx pp.

Janzen, D. H., and P. S. Martin. 1982. Neotropical anachronisms: the fruits the gomphotheres ate. Science, 215:19–27.

Jarvis, J. M. 1981. Eusociality in a mammal: cooperative breeding in naked mole-rat colonies. Science, 212:571–573.

Jones, J. K., Jr. 1991. Genealogy of Twentieth-century systematic mammalogists in North America: the descendants of Joseph Grinnell. Pp. 48–56, *in* Latin American mammalogy: history, biodiversity, and conservation (M. A. Mares and D. J. Schmidly, eds.). University of Oklahoma Press, Norman, 468 pp.

Kellogg, R. 1921. A new pinniped from the Upper Pliocene of California. Journal of Mammalogy, 2:221–226.

King, J. A. 1955. Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota. University of Michigan Contributions from the Laboratory of Vertebrate Zoology, 67:1–123.

Kirkland, G. L., Jr. 1985. Small mammal communities in temperate North American forests. Australian Mammalogy, 8:137–144.

Kotler, B. P. 1984*a*. Predation risk and the structure of desert rodent communities. Ecology, 65:689–701.

———. 1984*b*. Harvesting rates and predatory risk in desert rodents: a comparison of two communities on different continents. Journal of Mammalogy, 65: 91–96.

———. 1985. Owl predation on desert rodents which differ in morphology and behavior. Journal of Mammalogy, 66:824–828.

Krebs, C. J., B. L. Keller, and R. H. Tamarin. 1969. *Microtus* population biology: demographic changes in fluctuating populations of *Microtus ochrogaster* and *M. pennsylvanicus* in southern Indiana. Ecology, 50:587–607.

Krebs, C. J., and J. H. Myers. 1974. Population cycles in small mammals. Advances in Ecological Research, 8:267–399.

Krohne, D. T. 1982. Demography of low-litter-size populations of *Microtus californicus.* Canadian Journal of Zoology, 60:368–374.

Kruuk, H. 1972. The spotted hyena. University of Chicago Press, Chicago, 335 pp.

Lack, D. 1947. Darwin's finches. Cambridge University Press, Cambridge, 204 pp.

Lang, H. 1923. Recent and historical notes on the square-lipped rhinoceros (*Ceratotherium simum*). Journal of Mammalogy, 4:155–163.

Larsen, E. C. 1986. Competitive release in microhabitat use among coexisting desert rodents: a natural experiment. Oecologia, 69:231–237.

Layne, J. N., and J. O. Whitaker, Jr. 1992. William J. Hamilton. Jr. 1902–1990. Journal of Mammalogy, 73:693–706.

Le Boeuf, B. J., and J. Reiter. 1988. Lifetime reproductive success in northern elephant seals. Pp. 344–362, *in* Reproductive success (T. H. Clutton-Brock, ed.). University of Chicago Press, Chicago, 538 pp.

Lee, A. K., and A. Cockburn. 1985. The evolutionary ecology of marsupials. Cambridge University Press, Cambridge, 274 pp.

Lemen, C. A. 1978. Seed size selection in heteromyids. Oecologia, 35:13–19.

Lemen, C. A., and M. L. Rosenzweig. 1978. Microhabitat selection in two species of heteromyid rodents. Oecologia, 33:127–135.

Leopold, A. 1933. Game management. Scribners, New York, 481 pp.

Lewontin, R. C. 1968. Population biology and evolution. Syracuse University Press, Syracuse, New York, 205 pp.

Lidicker, W. Z., Jr. 1988. Solving the enigma of microtine "cycles." Journal of Mammalogy, 69:693–704.

———. 1994. Population Ecology. Pp 323–347, *in* seventy-five years of mammalogy (1919–1994) (E. C. Birney and J. R. Choate, eds.). Special Publication, American Society of Mammalogists, 11:1–433.

———. In press. In defense of a multifactor perspective in population ecology: a response to Gaines, Stenseth, Johnson, Ims, and Bondrup-Nielsen. Journal of Mammalogy.

Linsdale, J. M. 1946. The California ground squirrel. University of California Press, Berkeley, 475 pp.

Linsdale, J. M., and L. P. Tevis. 1951. The dusky-footed wood rat. University of California Press, Berkeley, 664 pp.

M'Closkey, R. T. 1976. Community structure in sympatric rodents. Ecology, 57:728–739.

———. 1978. Niche separation and assembly in four species of Sonoran Desert rodents. The American Naturalist, 112:683–694.

———. 1981. Microhabitat use in coexisting desert rodents—the role of population density. Oecologia, 50:310–315.

MacArthur, R. H. 1958. Population ecology of some warblers in northeastern coniferous forests. Ecology, 39:599–619.

———. 1960. On the relative abundance of species. The American Naturalist, 94:25–36.

———. 1965. Patterns of species diversity. Biological Reviews, 40:510–533.

———. 1970. Species packing and competitive equilibrium for many species. Theoretical Population Biology, 1:1–11.

———. 1972. Geographical ecology. Patterns in the distribution of species. Harper and Row, New York, 269 pp.

MARES, M. A., AND D. F. WILLIAMS. 1977. Experimental support for food particle size resource allocation in heteromyid rodents. Ecology, 58:1186–1190.

MASER, C., J. M. TRAPPE, AND R. A. NUSSBAUM. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology, 59: 799–809.

MAYR, E. 1942. Systematics and the origin of species. Columbia University Press, New York, 334 pp.

———. 1963. Animal species and evolution. Harvard University Press, Cambridge, Massachusetts, 813 pp.

MCCABE, T. T., AND B. D. BLANCHARD. 1950. Three species of Peromyscus. Rood Associates, Santa Barbara, California, 136 pp.

MCCULLOUGH, D. R. 1979. The George Reserve deer herd. University of Michigan Press, Ann Arbor, 271 pp.

MCNAB, B. K. 1963. Bioenergetics and the determination of home range size. The American Naturalist, 97:133–140.

MEARNS, E. A. 1907. The mammals of the Mexican boundary of the United States. Bulletin of the United States National Museum, 56:1–530.

MECH, L. D. 1966. The wolves of Isle Royale. U.S. National Park Service, Fauna ser. 7, 210 pp.

———. 1970. The wolf: the ecology and behavior of an endangered species. American Museum of Natural History, Natural History Press, Garden City, New York, 384 pp.

MERRIAM, C. H. 1890. Results of a biological survey of the San Francisco Mountain Region and desert of the Little Colorado, Arizona. North American Fauna, 3:1–136.

MILLAR, J. S. 1977. Adaptive features of mammalian reproduction. Evolution, 31:370–386.

MILLAR, J. S., AND R. M. ZAMMUTO. 1983. Life histories of mammals: an analysis of life tables. Ecology, 64:631–635.

MILLER, A. H. 1943. Joseph Grinnell's philosophy of nature. University of California Press, Berkeley, California, 237 pp.

MILLER, G. S. 1929. Mammalogy and the Smithsonian Institution. Smithsonian Report for 1928, Publication 2995, United States Government Printing Office, pp. 391–411.

MILLER, R. S. 1967. Pattern and process in competition. Advanced Ecology Research, 4:1–74.

MONSON, G., AND W. KESSLER. 1940. Life history notes on the banner-tailed kangaroo rat, Merriam's kangaroo rat, and the white-footed wood rat in Arizona and New Mexico. The Journal of Wildlife Management, 4:37–43.

MOORS, P. J. 1984. Coexistence and interspecific competition in the carnivore genus *Mustela.* Acta Zoologica Fennica, 172:37–40.

MORGAN, L. H. 1868. The American beaver and his works. J. B. Lippincott, Philadelphia, 330 pp.

MORRIS, D. W. 1984. Patterns and scale of habitat use in two temperate-zone small mammal faunas. Canadian Journal of Zoology, 62:1517–1523.

MUNGER, J. C., AND J. H. BROWN. 1981. Competition in desert rodents: an experiment with semipermeable exclosures. Science, 211:510–512.

MUNGER, J. C., AND J. C. HOLMES. 1988. Benefits of parasitic infection: a test using a ground squirrel system. Canadian Journal of Zoology, 66:222–227.

MURIE, A. 1944. The wolves of Mt. McKinley. United States Department of the Interior, National Park Service Fauna series, 5:1–238.

MURIE, J. O., AND G. R. MICHENER (EDS.). 1984. The biology of ground-dwelling squirrels. University of Nebraska Press, Lincoln, 464 pp.

MUUL, I. 1990. William Henry Burt: 1903–1987. Journal of Mammalogy, 71:113–116.

OSGOOD, W. H. 1943. Clinton Hart Merriam—1855–1942. Journal of Mammalogy, 24:421–436.

OWEN, J. G. 1990. An analysis of the spatial structure of mammalian distribution patterns in Texas. Ecology, 71:1823–1832.

PACKER, C. 1986. The ecology of sociality in felids. Pp. 429–451, *in* Ecological aspects of social evolution: birds and mammals (D. I. Rubenstein and R. W. Wrangham, eds.). Princeton University Press, Princeton, New Jersey, xxx pp.

PACKER, C., ET AL. 1988. Reproductive success of lions. Pp. 363–383, *in* Reproductive success (T. H. Clutton-Brock, ed.). University of Chicago Press, Chicago, 538 pp.

PETERS, R. H. 1983. Ecological implications of body size. Cambridge University Press, Cambridge, 329 pp.

PETERSON, R. S., AND G. A. BARTHOLOMEW. 1967. The natural history and behavior of the California sea lion. Special Publications, The American Society of Mammalogists, 1:1–79.

PETTICREW, B. G., AND R. M. F. S. SADLER. 1974. The ecology of the deer mouse *Peromyscus manicurist* in a coastal coniferous forest. I. Population dynamics. Canadian Journal of Zoology, 52:107–118.

PITELKA, F. A. 1957. Some aspects of population structure in the short-term cycles of the brown lemming in northern Alaska. Cold Spring Harbor Symposium in Quantitative Biology, 22:237–251.

PRICE, M. V. 1978. The role of microhabitat in structuring desert rodent communities. Ecology, 59:910–921.

PRICE, P. W. 1980. Evolutionary biology of parasites. Princeton University Press, Princeton, New Jersey, 237 pp.

RALLS, K., AND P. H. HARVEY. 1985. Geographic variation in size and sexual dimorphism of North American weasels. Biological Journal of the Linnean Society, 25:119–167.

RAPOPORT, E. H. 1982. Areography. Pergamon Press, New York, 269 pp.

REICHMAN, O. J., D. T. WICKLOW, AND C. REBAR. 1985. Ecological and mycological characteristics of the caches in the mounds of *Dipodomys spectabilis.* Journal of Mammalogy, 66:643–651.

REYNOLDS, H. G. 1958. Ecology of Merriam's kangaroo rat on the grazing lands of southern Arizona. Ecological Monographs, 28:111–127.

———. 1960. Life history notes on Merriam's kangaroo rat in southern Arizona. Journal of Mammalogy, 41:48–58.

RICHARDSON, J. 1829. Fauna boreali-Americana; or the zoology of the northern parts of British America: containing descriptions of the objects of natural history collected on the late northern land expedition under command of Captain Sir John Franklin. J. Murray, London, 4 volumes.

ROSENZWEIG, M. L. 1966. Community structure in sympatric Carnivora. Journal of Mammalogy, 47: 602–612.

———. 1968. The strategy of body size in mammalian carnivores. The American Midland Naturalist, 80:299–315.

———. 1973. Habitat selection experiments with a pair of coexisting heteromyid rodent species. Ecology, 54:111–117.

ROSENZWEIG, M. L., B. SMIGEL, AND A. KRAFT. 1975. Patterns of food, space and diversity. Pp. 241–268, *in* Rodents in desert environments (I. Prakash and P. Gosh, eds.). W. Junk, The Hague, The Netherlands.

ROSENZWEIG, M. L., AND P. W. STERNER. 1970. Population ecology of desert rodent communities: body size and seed husking as bases for heteromyid coexistence. Ecology, 51:217–224.

ROSENZWEIG, M. L., AND J. WINAKUR. 1969. Population ecology of desert rodent communities: habitats and environmental complexity. Ecology, 50:558–572.

SANCHEZ-CORDERO, V., AND T. H. FLEMING. 1993. Ecology of tropical heteromyids. Pp. 596–617, *in* Biology of heteromyid rodents (H. H. Genoways and J. H. Brown, eds.). Special Publications, The American Society of Mammalogists, 10:1–719.

SCHOENER, T. W. 1968. Sizes of feeding territories among birds. Ecology, 49:123–131.

SCHRODER, G. D., AND M. L. ROSENZWEIG. 1975. Perturbation analysis of competition and overlap in habitat utilization between *Dipodomys ordii* and *Dipodomys merriami*. Oecologia, 19:9–28.

SETON, E. T. 1909. Life histories of northern animals. Charles Scribner's Sons, New York, 2 volumes, 299 pp.

———. 1923. The arctic prairies. Charles Scribner's Sons, New York, 308 pp.

———. 1929. Lives of game animals. Doubleday, Doran and Company, Inc., Garden City, New York, 4 volumes.

SHEPPARD, D. H. 1971. Competition between two chipmunk species. Ecology, 52:320–329.

SIMPSON, G. G. 1940. Mammals and land bridges. Journal of the Washington Academy of Sciences, 30: 137–163.

———. 1943. Mammals and the nature of continents. American Journal of Science, 241:1–31.

———. 1944. Tempo and mode in evolution. Columbia University Press, New York, 237 pp.

———. 1947*a*. Evolution, interchange and resemblance of the North American and Eurasian Cenozoic mammalian fauna. Evolution, 1:218–220.

———. 1947*b*. Holarctic mammalian faunas and continental relationships during the Cenozoic. Bulletin of the Geological Society of America, 58:613–688.

———. 1950. History of the fauna of Latin America. American Scientist, 38:361–389.

———. 1953. The major features of evolution. Columbia University Press, New York, 424 pp.

———. 1964. Species density of North American Recent mammals. Systematic Zoology, 13:57–73.

SMIGEL, B. W., AND M. L. ROSENZWEIG. 1974. Seed selection in *Dipodomys merriami* and *Perognathus penicillatus*. Ecology, 55:329–339.

SMITH, C. C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecological Monographs, 40:349–371.

SMYTHE, N. 1970. Relationships between fruiting seasons and seed dispersal methods in a Neotropical forest. The American Naturalist, 104:25–35.

STICKEL, L. F., AND O. WARBACH. 1960. Small-mammal populations of a Maryland woodlot, 1949–1954. Ecology, 41:269–286.

SUMNER, F. B. 1932. Genetic, distributional, and evolutionary studies of the subspecies of deer mice (*Peromyscus maniculatus*). Bibliography of Genetics, 9:1–106.

TAITT, M. J., AND C. J. KREBS. 1985. Population dynamics and cycles. Pp. 567–620, *in* Biology of New World *Microtus* (R. H. Tamarin, ed.). Special Publications, The American Society of Mammalogists, 8:1–893.

TAMARIN, R. H. (ED.). 1985. Biology of New World *Microtus*. Special Publications, The American Society of Mammalogists, 8:1–893.

TAYLOR, W. P. (ED.). 1956. The deer of North America. The Stackpole Company, Harrisburg, Pennsylvania, and the Wildlife Management Institute, Washington, D.C., 668 pp.

THOMPSON, S. D. 1982*a*. Microhabitat utilization and foraging behavior of bipedal and quadrupedal heteromyid rodents. Ecology, 63:1303–1312.

———. 1982*b*. Structure and species composition of desert heteromyid rodent species assemblages: effects of a simple habitat manipulation. Ecology, 63: 1313–1321.

THWAITES, R. G. 1904. The original journals of the Lewis and Clark expeditions. Dodd, Mead and Company, Inc., New York, 8 volumes.

TIMM, R. M., AND J. S. ASHE. 1988. The mystery of the gracious hosts. Natural History, 9:6–9.

TIMM, R. M., D. E. WILSON, B. L. CLAUSON, R. K. LAVAL, AND C. S. VAUGHAN. 1989. Mammals of the La Selva-Braulio Carrillo Complex, Costa Rica. North American Fauna, 75:1–162.

VORHIES, C. T., AND W. P. TAYLOR. 1940. Life history and ecology of the white-throated wood rat, *Neotoma albigula* Hartley, in relation to grazing in Arizona. University of Arizona College of Agriculture, Agricultural Experiment Station Technical Bulletin, 86:453–529.

WALKER, E. P. 1964. Mammals of the world. The Johns Hopkins University Press, Baltimore, Maryland, 3 volumes.

WECKER, S. C. 1963. The role of early experience in habitat selection by the prairie deer mouse, *Peromyscus maniculatus bairdii*. Ecological Monographs, 33:307–325.

———. 1964. Habitat selection. Scientific American, 211:109–116.

WHITAKER, J. O., JR. 1994. Academic propinquity, Pp. 121–138, *in* Seventy-five years of mammalogy

(1919–1994). Special Publications, The American Society of Mammalogists, 11:1–433.

WHITFORD, W. G. 1976. Temporal fluctuations in density and diversity of desert rodent populations. Journal of Mammalogy, 57:351–369.

WILSON, D. E. 1971. Ecology of *Myotis nigricans* (Mammalia: Chiroptera) on Barro Colorado Island, Panama Canal Zone. Journal of Zoology, 163:1–13.

———. 1973. Bat faunas: a trophic comparison. Systematic Zoology, 22:14–29.

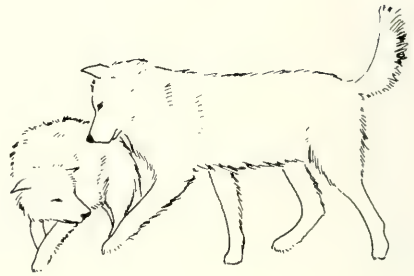
WILSON, D. E., AND J. S. FINDLEY. 1970. Reproductive cycle of a Neotropical insectivorous bat, *Myotis nigricans*. Nature, 225:1155.

WILSON, J. W., III. 1974. Analytical zoogeography of North American mammals. Evolution, 28:124–140.

YOUNG, S. P., AND E. A. GOLDMAN. 1944. The wolves of North America. American Wildlife Institute, Washington, D.C., 636 pp.

# *BEHAVIOR*

John F. Eisenberg and Jerry O. Wolff



## *Introduction*

Humankind is a product of organic evolution, as are all living organisms on the planet Earth. Although anthropologists may disagree as to the date of transition from *Homo erectus* to *H. sapiens,* the cultural transition of some 100 to 70 × $10^3$ years B.P. by *H. sapiens* was profound. Modern humans developed the capacity for rapid cultural evolution and, in conjunction with a very large brain, began to set about taming the environment in ways we can scarcely comprehend except through the minds and evidence of archaeologists. Our early ancestors were gifted naturalists and keen observers of nature. The manner of life styles exhibited by organisms of concern to the early economic systems were well known and communicated by direct participation in hunting, gathering, and also presumably by an oral tradition. Thus, a knowledge of the behavior and life history of animals and plants has been part and parcel to our cultural heritage as human beings (Count, 1973).

By the middle of the 19th Century, European naturalists were beginning to move away from the naming and describing of floras and faunas and attempting to grapple with the more intangible aspects of biology. One aspect that preoccupied attention was animal behavior. The behavior of organisms has always held a special fascination. Consider the admonition of King Solomon "Behold the ant, thy sluggard and consider her ways" (Proverbs 6:6, King James version of the Bible). By the middle of the 19th Century two major schools of thought had developed. On the one hand, the empiricists, following René Descartes, tried to analyze the behavior of non-human mammals in terms of a mechanistic model. Questions were posed concerning what an animal could perceive and thus respond to. Elaborate experiments were designed to determine the limits of human and non-human animal perceptions (Mach, 1959). On the other hand, a determined group of naturalists persisted in attempting to describe (in writing) what animals actually did in their natural habitat. Charles Darwin, arguably the finest 19th-Century English speaking, objective observer and recorder of nature, who wrote and communicated his thoughts in the 1800s, was also concerned with animal behavior (Darwin, 1859, 1872). His influence was profound because he not only offered an explanation for morphological change through natural selection, but also suggested avenues for the study of behavioral change, ultimately controlled by natural selection.

## *A Brief History of Ethology: its Origins, Reception, and Modification in America*

In 1973, Niko Tinbgergen, Konrad Lorenz, and Karl von Frisch received the Nobel Prize in Physiology and Medicine. These three men exemplified the early 20th-Century fruit of the Darwinian revolution in terms of the analysis of animal behavior (see Lorenz, 1981 for a review). Lorenz emphasized the close observation of behavior involving animals kept at semi-liberty, but habituated to human observers. The comparative method was stressed. Tinbergen championed the observation of wild creatures and was ingenious in developing experimental techniques applied to free-living populations. von Frisch was the consummate experimentalist and studied the perceptual capacities of fish and bees (von Frisch, 1950). The general theory that these three men developed was first consolidated in Tinbergen's book, *The Study of Instinct,* published in English in 1951. The book outlined a theoretical framework for the analysis of behavior, but the analysis rested firmly on the correct description of an animal's repertoire—the ethogram. It was noted that an animal's behavior consisted at least of two major types of actions: 1) seeking an appropriate goal (appetitive behavior); and 2) satisfying a need (consummatory behavior). With this publication the framework was set for the next 20 years of research in North America and Europe.

The theoretical framework built in Europe on Darwinian foundations was resisted by many 20th-Century students of animal behavior in North America. This situation derived mainly from the fact that the North Americans were often associated with psychology departments that were strongly tied to the experimental method and Cartesian reductionism. Experimental design was paramount and as a result two American schools developed: 1) those devoted to the physiological mechanisms underlying discrete behaviors—a reductionist position; and 2) those devoted to the analysis of how animals learn. Both approaches (with a view toward public funding) were justified before the general public and elected officials on the grounds that animal "surrogates" could lead to a better understanding of human behavior. Thus, the study of non-human animals in and of themselves was sublimated to utilitarian needs in terms of human welfare. A possible third North American tradition was grounded in an attempt to understand cognitive processes. While experimental designs were important, the concept of higher mental processes and how to study the phenomenon has remained elusive (Dewsbury, 1989*a*; Schusterman et al., 1986).

Strangely enough, in Europe and North America, many of the earlier studies of mammalian behavior were undertaken by naturalists and wildlife managers who justified their activities in terms of understanding the life history of organisms that were of economic importance in terms of "harvesting" or "control" by humans (Leopold, 1933). In fact, the applied researchers investigating vertebrate behavior were often considered outside the boundaries of "pure science" by many academics and such a dreary dichotomy was to persist for some time (Wilson and Eisenberg, 1990). Nevertheless, regardless of the motivation, animal behavior has held a great fascination for all observers across all cultures.

The social behavior of animals has long preoccupied mankind. Aside from the wonders of individualistic behaviors, the variety of patterns displayed during mating, parental care, and seemingly altruistic behaviors were of special concern after the Darwinian revolution. Darwin (1859), Kropotkin (1902), and Deegener (1918) grappled with the problem. Tinbergen (1951) pointed out that a social system is basically a communication system and thus opened a new arena of research. A paper by W. D. Hamilton (1964) was revolutionary because it laid the groundwork for a rational analysis of how societies could evolve through natural selection. Eisenberg (1966) outlined the evolutionary trends of social behavior within the class Mammalia. Trivers (1971, 1972, 1974) amplified and clarified some intricate problems raised by Hamilton (1964), and E. O. Wilson (1975) brought the most recent, comprehensive synthesis to the forefront. Darwinian selection, Mendelian genetics, ecology, and behavior had been wedded into a system of testable hypotheses. This revolution in thought will be treated in a later section.

## *A Record of the Beginnings of Animal Behavior Studies in North America*

Given that the basis of ethology is anchored in the systematic observation of an animal's behavior, who can we identify as the first North American mammalian ethologist? With all due respect, we must overlook the preliterate but viable cultures of hunter-gatherers that preceded European occupation of the continent. We suggest (among others) L. H. Morgan as a candidate. Not only did he write a classic work on the beaver (*Castor canadensis*) (Morgan, 1868), but he also wrote a magnificent ethnography of the Iroquois Indians in New York and Ontario (Morgan, 1851). While not an ethologist in the 20th-Century sense, he nevertheless was an objective observer and dutiful recorder of his observations. While such naturalists as Audubon and Bachman (1846–1854) recorded facts concerning the habits of their subjects, L. H. Morgan concentrated on a single species or a human culture and described their behavior and social structure in astonishing detail.

Through the late 19th and early 20th centuries, mammalian behavior patterns continued to be described often in a fragmented fashion or as a series of anecdotes. Ernest Thompson Seton (1953) made a fine contribution in the compilation of anecdotes by organizing descriptions of behavior within species accounts in the form of a functional classification, e.g., mating behavior, parental care, feeding and foraging, and the like (Note: Seton did not apply these exact subheadings, but the sense was there.)

The beginning of a theoretical framework for behavior studies grounded in Darwinian theory started within North America during the late 19th and early 20th centuries with the work of C. O. Whitman, who observed that the courtship of pigeons was composed of numerous stereotypic components. The behavioral units and their sequencing were often characteristic of each domestic breed. Could some types of behavior be compared among breeds or species in the manner of a comparative anatomist? Were the units of behavior as expressions of nerve-muscle relationships subject to the laws of heredity (Whitman, 1899, 1919)?

Whitman's student, Wallace Craig, chose bird song for comparative study and soon discovered that while some songs were species specific and relatively fixed, other species show plasticity and a good deal of learning in song development (Craig, 1918). Craig and Whitman were pioneers in their studies. Parallel efforts in Europe by Oskar Heinroth and Konrad Lorenz led to the founding of European ethology, but in North America, behavior studies developed on many different fronts with little intellectual cross fertilization (Dewsbury, 1989*b*). Application of these concepts to mammalian behavior was to occur much later (see the next section).

## *Mammalian Behavior Studies Prior to 1965*

*Threads in the loom—behavior studies.*—Ethology as a discipline did not become consolidated in the U.S. until the mid-1950s. Although a knowledge of "species-typical behavior" was a working tool for all great naturalists, to presume that behavior studies represent something new is to oversimplify a very complex situation. Our predecessors and seniors of the last 70 years were involved with behavior studies, whether or not their labors were organized into a formal system. For example, Vernon Bailey, who worked with the U.S. Biological Survey, was intrigued by the behavior of his subjects (Bailey, 1931). Ned Hollister, before he took command of the U.S. National Zoological Park, wrote a classic paper concerning the effects of captivity and captive diets on the skull morphology of African lions (Hollister, 1917). Joseph Grinnell, the spirit of the Museum of Vertebrate Zoology at Berkeley during its most formative years, was one of the most astute observers of vertebrate behavior ever to document his observations (Grinnell, 1914). A. Brazier-Howell was deeply concerned with the problems of form and function, a true behaviorist by anyone's definition (Howell, 1944). Shadle (1946) with his delightful, yet incisive, observations on the sexual life of porcupines is also a case in point. While on the subject of mammalian reproduction, the efforts of R. K. Enders (1935, 1952) and O. P. Pearson (1944) in mammalian behavior studies stand out, not to diminish their other considerable contributions. Many others could be cited (Bronson, 1989 for review).

One area of the discipline of behavior that has not received much attention from the standpoint of the "behaviorist" is that vague area of energetics and behavior, or "ecophysiology," which not only has had a long history, but also a profound influence on the types of questions that behaviorists ask. The beginnings may go back to Claude Bernard in the 19th Century but the fact of the matter remains that in the 1940s mammalogists began asking hard questions concerning how mammals were able to withstand the rigors of adverse environments. Morrison and B. K. McNab began to ask the questions and seek the answers (Morrison and McNab, 1962), as did Bartholomew (Bartholomew and Cade, 1957). Feedback between the so-called behaviorists and the physiologists continued (McNab, 1983).

Another area of research with a long history of mammals as subjects includes behavioral genetics. Sumner (1932) and subsequently Lee Dice literally pioneered the research on the genetics of non-domesticated mammals (Dice, 1933). *Peromyscus* was their genus of choice and it was a sound one. With the Michigan stocks, Howard (1948), Harris (1952), and King (1961) were to shape the thinking of younger biologists concerning the genetics of behavior in the 1950s (see also King, 1968).

Population dynamics and the behavior of mammalian species at different densities has become a focus of interest since the synthesis published by Elton (Crowcroft, 1991 for review). The pioneers on this frontier of the 1950s included D. E. Davis, D. Chitty, J. B. Calhoun, and J. Christian (Anderson, 1989; Cockburn, 1988 for reviews). The role of density-dependent and density-independent factors on the regulation of population size was a "hot topic" at that time, and the discovery that endocrine changes could mediate and be mediated by behavioral changes only added fuel to the fires of controversy (Calhoun, 1963*a*, 1963*b*; Christian, 1963). That behavior could be linked to the genetic background of an individual led to a flurry of productive research and once again behavioral studies were an integral part of the effort (Calhoun, 1963*a*; Harris, 1952).

The unique sensory abilities of mammals had long been recognized, but D. R. Griffin's publication on the echolocation of bats in 1958 was truly a watershed. Kellogg (1961) synthesized similar data for dolphins. Bioacoustics became a field unto its own.

At Cornell, W. J. Hamilton, Jr. and his colleagues initiated important studies on mammalian food habits. Although many other aspects of mammalian behavior were studied at Cornell, perhaps one of the most notable single-species monographs was James Layne's contribution on the behavior and ecology of the red squirrel (*Tamiasiurus hudsonicus*) (Layne, 1954).

The use of livetraps for the purpose of

trap, mark, and release studies opened a new era in the studies of how mammals use space. H. B. Sherman invented a successful metal livetrap in the late 1930s that is marketed to this day. Sherman and his students at the University of Florida developed a series of studies aimed at clarifying microhabitat use and the spacing behavior of small mammals utilizing the trap, mark, and release scheme. William Burt, utilizing a livetrap modification of his own at Michigan, wrote an influential paper in 1940 proposing that some species of small mammals appeared to show territorial behavior (Burt, 1940). The study of nocturnal, cryptic mammals and their movements received an enormous assist with the introduction of radiotelemetric techniques in the 1960s. Perhaps the most pioneering group was associated with the University of Minnesota with their magnificent setup at the Cedar Creek Natural History Area (Tester et al., 1964).

As an aside, immobilization of mammals with a reliable series of drugs and instruments for projection was revolutionary (Harthoorn, 1976). Younger students will not appreciate fully the revolution introduced by reliable telemetry and pharmaceutical systems.

Given the advanced techniques of trap, mark, and release, monographic treatises involving these methods began to supplement direct observation. The focus was often ecological, but behavior became more and more a concern regardless of technique: Linsdale and Tevis (1951) on the dusky-footed woodrat, *Neotoma fuscipes*; Linsdale (1946) on the California ground squirrel; Linsdale and Tomich (1953) on *Odocoileus hemionus*; Moore (1957) on *Sciurus niger*; and Layne (1954) on *Tamiasciurus hudsconicus* all appeared in the 1940s and 1950s. One of the benchmark field studies of mammalian social behavior was John King's monograph on the black-tailed prairie dog, *Cynomys ludovicianus* (King, 1955). This classic study demonstrated that careful observations of marked individuals could yield insight into the use of space, mode of communication, and relations among kin. King's effort paved the way for field experiments and ever more sophisticated studies of diurnal sciurids (Murie and Michener, 1984, 1989 for review).

Nocturnal small mammals still presented problems because direct observation was not possible. Eisenberg, following the techniques developed by Eibl-Eibesfeldt (1958) in Germany, developed the strategy of combining field studies with captive studies. With the aid of the electronic flash camera, behavior patterns of small, nocturnal mammals could be recorded on film for analysis (Eisenberg, 1962, 1963).

Kaufmann in the late 1950s and early 1960s carried out a classic field study on a diurnal carnivore, the coati (*Nasua narica*) in Panama (Kaufmann, 1962). His creative analysis of the social use of space by female bands has stood the test of time. Shortly thereafter, Valerius Geist produced his classic study of *Ovis dalli* and *O. canadensis* in British Columbia (Geist, 1971). Ungulate behavior studies had come of age. Kleiman (1967) stimulated interest in the comparative social behavior of the Canidae. McKay (1973), based upon his studies in the 1960s, brought the Asiatic elephant to the forefront of attention.

DeVore, in his studies of the baboon (*Papio cynocephalus*) in Kenya, ushered in the new era of primate studies; Schaller's study of free-ranging mountain gorillas (*Gorilla gorilla beringei*) was a true milestone in the art of field work (DeVore, 1965; Schaller, 1963). They demonstrated that a field worker could habituate the subjects to the presence of an intruder. Eisenberg and Kuehn (1966) attempted a synthesis for neotropical primates.

The pure ethological approach based on efforts as applied to mammals (Hediger, 1942) was summarized in R. F. Ewer's (1969) classic, *The Ethology of Mammals.* New disciplines were already forming around the interface between ecology and behavior. Suitably inspired, Smythe and Wemmer working in the 1960s provided important contributions (Smythe, 1970; Wemmer, 1977). With the inclusion of population genetics the stage was set for the development of sociobiology as a synthetic discipline by Wilson in 1975 (see section From ethology to sociobiology).

*The watershed of the late 1960s.*—In 1969, the Smithsonian Institution convened its public symposium under the broad title of *Man and Beast*, the results of which were published in 1971 (Eisenberg and Dillon, 1971). The symposium and its published results were an attempt to focus public attention on the relevance of animal behavior studies to understanding human behavior. To this end, the participants in the symposium included biologists, philosophers, psychologists, anthropologists and sociologists. In part, the public symposium was in response to the recently published work of Konrad Lorenz titled in English translation, *On Aggression*. The notion that some aspects of human behavior could have a genetic basis was anathema to some of the North American social scientists. As Watson (1914) had proclaimed some years before, the human mind could be considered at birth as a *tabula rasa*, where environmental conditioning reigns supreme in forming the life of the infant, juvenile, and subadult.

One member of the conference, E. O. Wilson, who delivered a provocative paper on the evolution of territoriality, was deeply moved by the conference. By his own admission, it inspired him to produce his classic *Sociobiology*. The raging controversy that accompanied the publication of Wilson's synthesis remains a remarkable quirk in the development of the behavioral sciences. Many of us regarded, with dismay, the vitriolic attacks, often personal, to which Wilson was subjected. However, wounds heal, and those aspects of philosophical confrontation that seemed so desperately important in the early 1970s diminished, and by the time a sequel to the volume was prepared via the mechanism of a conference at the Smithsonian in 1986, barely a flicker occurred within the halls of academe. The results of this conference were published in 1991 under the title: *Man and Beast Revisited* (Robinson and Tiger, 1991).

A certain amount of emotional maturity must have occurred in the intervening 16 to 20 years, and one might hope that the healing process will continue. It should be noted that there were no philosophical villains leading to the first major confrontation, following *Man and Beast* (1969). To the contrary, the philosophical confrontation of the mid-1970s was long overdue and, sadly, somewhat protracted in the manner in which the participants registered their viewpoints. One felt at the conclusion of the 1986 symposium in Washington, D.C., that the burning issues of the relevance of animal behavior studies to the interpretation of human behavior had somewhat declined. This is not to say that the cross-fertilization during the intervening 20 years had not been useful. It simply says that rapid and facile generalizations forthcoming from popularists did not necessarily solve any of the current problems of the human race. Clearly the social scientists contributing to the 1986 symposium, such as Helen Fisher and Lionel Tiger, had gleaned a great deal from the earlier ruminations in 1969.

## The Influence of Some Seminal Institutions

*The American Museum of Natural History and relations with the New York Zoological Society.*—The American Museum of Natural History (AMNH) was one of the earliest museums in the United States to create a separate Department of Animal Behavior. The origin of the behavior group was established under G. Kingsley Noble (See Koestler, 1971, for an account of the midwife toad scandal and Noble's role.). Although best known for his work with the Amphibia, Noble was a pioneer in the analysis of the relationship between hormones and behavior (Noble, 1931). Thus, he founded an experimentally based discipline that was basically reductionist. After Noble's premature death, Frank A. Beach was appointed to head the group and created the Department of Animal Behavior while pursuing the role of hormones and behavior (Beach, 1948). He recruited T. C. Schneirla in the late 1940s to join him. After World War II, the department began in earnest to assemble a graduate student group. Beach championed the hormone and behavior tradition, but also brought some of his own interests. Beach had been a student of Lashley, who had pioneered brain and behavior studies, and thus a second reductionist tradition was added. Beach left AMNH for Yale, and Schneirla succeeded him as chair. E. Tobach, L. Aronson, and D. Lehrman became the key players as former students. D. Lehrman, a contemporary, would later found the Institute of Animal Behavior at Rutgers. Aronson, pursuing brain-behavior relationships, would continue with fish, but also turned to cat behavior. Aronson became chair on the occasion of Schneirla's retirement.

Given the ties of the AMNH with the local New York universities and subsequently with Rutgers, its influence was considerable. The research efforts were often grounded in attempting to understand physiological mechanisms underlying behavior and were often allied with colleagues in human medicine. The application of the results of animal-based research to human problems became for some a guiding ideal (Rosenblatt and Komisaruk, 1977).

The New York Zoological Society (NYZS) maintained relations with the AMNH primarily through curators in various departments of vertebrate zoology. Early in the Century, the NYZS sponsored field research with an aim to improve knowledge applicable to the proper captive maintenance of exotics. William Beebe was supported and his attempts to found field stations in the Neotropics are renowned. In the early 1900s Beebe had assembled groups of researchers in what is now Guayana. Beebe (1925) published the first behavioral ecology study of the three-toed sloth, an effort not to be equalled until research by Montgomery and Sunquist (1975). In the late 1960s, the NYZS established the unit that was to become "Wildlife Conservation International," thereby supporting a core group of mammalogists concerned with the interface between ecology and behavior including R. Payne, T. Struhsaker, and G. Schaller in the original assemblage.

*The University of Chicago.*—The University of Chicago established connections with the Field Museum of Natural History at an early stage. These close ties contributed greatly to the study of zoogeography and ecology. Many students of the first author's generation studied the classic *Principles of Ecology* by Allee, Park, Park, Emerson and Schmidt. The ecologists of the Chicago group also had a deep concern with the behavior of animals. Emerson concentrated on social insects and the problem of the evolution of social behavior. Allee shared many of Emerson's interests, but his concerns were more wide ranging. Although neither Emerson nor Allee may be considered mammalogists, their contribution to the theoretical links between behavior and ecology is incalculable. Indeed the highest student award conferred at the annual meetings of the U. S. Animal Behavior Society is the W. C. Allee Award. Upon leaving Chicago, Allee joined the University of Florida where he had an influence on the direction of behavioral research at that institution.

*Yale and the primatologists.*—Robert Yerkes of Yale University pioneered the study of primate behavior. A psychologist by training, he founded what was to become the Yerkes Primate Institute at Orange Park, Florida (now at Atlanta, Georgia under Emory University). Although Yerkes' efforts were directed at captive, nonhuman primates, he actively sponsored field research with a genuine concern for objective descriptions of naturalistic behavior (Yerkes and Yerkes, 1929). Bingham and Nissen were dispatched to Africa (Bingham, 1932; Nissen, 1931); while C. R. Carpenter was sent to Panama. Carpenter's studies of *Ateles* and *Alouatta* stand today as classics (Carpenter, 1934, 1935). He went on to study *Hylobates* and *Macaca* in Asia (Carpenter, 1964, for a summary). Sherwood Washburn, a graduate student during the gibbon project, subsequently promoted primate studies after World War II. His students (including I. DeVore) created a nexus of active research, first at Chicago, and then at Berkeley, during the late 1950s and 1960s.

*The history of the Smithsonian in the promotion of animal behavior studies.*—The beginnings of animal behavior studies at the Smithsonian were rooted in the traditions of natural history. The collections at the National Zoological Park (NZP) were studied and sketched by artists, most notably by Ernest Thompson Seton, to illustrate, in part, his *Lives of Game Animals.* Although Ned Hollister and William Mann made numerous contributions to mammalian natural history, behavior studies and documentation were not systematically approached until E. P. Walker became Assistant Director of the NZP in 1930. Walker was interested in photography and pioneered the techniques of the use of synchronized flash bulbs, allowing bats and flying squirrels to be photographed in mid-flight. He recorded primate sounds with an early version of the sound spectrograph, and attempted to describe the vocal repertoire of the night monkey (*Aotus*). His arduous pursuit of photography eventually led to the publication of *Mammals of the World* after his retirement (Walker, 1964).

The creation of a unit at the NZP with the mandate of studying the ethology of higher vertebrates was not to occur until 1965. For the last 28 years, the NZP has provided leadership in the study of animal behavior and in the interface between behavior and ecology. The full maturity of the Smithsonian's role in behavioral studies came at two important points: 1969 when the symposium *Man and Beast* was convened; and in 1973 when a consortium among the University of Maryland, George Washington University, and the Smithsonian Institution hosted the XIth International Ethology Conference, marking the first time that this international body had convened in the USA.

*The University of California, Berkeley.*—Zoologists at Berkeley had an early interest in animal behavior. Samuel J. Holmes published his *Animal Intelligence* in 1910, and W. E. Ritter published *The California Woodpecker and I* in 1938. Thereafter the animal behavior studies, particularly of higher vertebrates, mainly derived from the Museum of Vertebrate Zoology (MVZ). The emphasis at the museum was often behavior and ecology, or behavior and evolution, both approaches firmly anchored in the Darwinian tradition, and the guiding force in the museum was Joseph Grinnell. A student of David Starr Jordan, Grinnell was to found one of the great dynasties in American mammalogy (see Jones, 1991; Whitaker, 1994).

Mammalian behavior studies were not the sole domain of the MVZ. The Department of Psychology also had some giants in the field of learning studies, including E. C. Tolman (1932). Tolman's influence was profound, because he did not pursue a reductionist approach, but rather championed the more holistic approach of cognition and "higher mental processes." A. Kroeber, in the Department of Anthropology, stimulated the study of human cultures on a comparative basis (Kroeber, 1925) and Karl Sauer, in the Department of Geography, championed the analysis of the role of *H. sapiens* in altering the contemporary environments (1969). All the elements were in place for the synthesis at Berkeley that would commence in the mid-fifties.

*A case study of synergism: Berkeley, California—1955–1965.*—To illustrate the interdependency of behavior studies with respect to related disciplines, allow us to pursue a case study—Berkeley, California (UC), from 1955 to 1965. At the beginning of the period, the great museum legacy of Grinnell was in place and viable. If we confine ourselves to senior staff who worked with mammals, F. A. Pitelka, A. Starker Leopold, O. P. Pearson, and S. B. Benson were powerful influences on the cadre of aspiring young mammalogists. The specialties of ecology, wildlife management, physiological ecology, and systematics were well represented. In addition, the MVZ had close ties with the Department of Paleontology. Between 1957 and 1959, four new faculty were added to the biological sciences who had a significant impact on the "mammal group": W. Z. Lidicker, Jr., in the MVZ, P. V. Marler in Zoology, S. A. Washburn in Anthropology, and F. A. Beach in Psychology.

Leopold, Beach, Washburn, and Marler were instrumental in developing the behavioral research station in the Berkeley hills, during the 1960s, but more importantly they actively encouraged interdisciplinary studies at a significant crossroads in the maturation of behavioral research at the graduate level at UC. In addition, the long standing field station, "The Hastings Reserve," was emphasized as a place to do research. Lidicker became a catalyst in promoting an interface between systematics and mammalian ecology. Those were indeed "heady" times. Washburn introduced primates as suitable subjects for field studies, Beach extolled the virtues of the controlled experiment and a modified view of the reductionists' vision of behavior, and Marler presented us with the philosophy of the ethologists.

The original, senior faculty gave all of us an anchor associated with the MVZ and those virtues as set out by Grinnell. We may miss some names, but the younger mammalogists who completed their Ph.D. degrees in Anthropology, Psychology, Zoology, and Paleontology during that period included: W. J. Hamilton III, P. K. Anderson, J. Mary Taylor, G. Heinsohn, M. Murie, D. Isaac, J. Kaufmann, C. Thaler, T. Struhsaker, S. David Webb, B. LeBoeuf, T. Grand, S. R. Ripley, P. Jay, D. D. Thiessen, L. Clemens, and one of us (J. F. Eisenberg)—J. O. Wolff was of the next generation. In addition, we had many close associations with other vertebrate zoologists (pre- and postdoctoral) who went on to earn their "spurs" as behaviorists and systematists including: R. B. Root, D. Wilhoft, R. Behnke, Jerram Brown, D. Dewsbury, M. Konishi, J. Mulligan, K. Nelson, E. Neil, F. Notebaum, G. Orians, J. Nelson, and G. Hirsch (see also Marler, 1985).

If we consider only the cadre of post-baccalaureate "mammalogists" within the period of that "magic" decade, 12 well-acclaimed books have been produced as of 1993, one member became the President of the ASM, two members became President of the Animal Behavior Society (ABS), one member won the C. Hart Merriam Award at the ASM, one member was President of the American Society of Paleontologists (ASP), one member became the director of a major US metropolitan museum, and all taught and mentored graduate students and produced numerous publications. In their efforts, all had influence to the far corners of the Earth including (exclusive of the USA) Australia, Canada, Botswana, Namibia, Panama, Mexico, Uganda, Kenya, India, Sri Lanka, Madagascar, Venezuela, Honduras, Chilé, Argentina, and Brazil.

## *The Years of Consolidation and Subsequent Fractionation*

The Second World War interrupted all aspects of pure biological research. Communication with European colleagues was almost non-existent. Some of the ideas from European ethologists had begun to be accepted by American mammalogists, often paradoxically via the ornithological or ichthyological literature. Visits by N. Tinbergen and G. Baerends to North America during the 1950s helped disseminate some of these concepts, and the hiring of European ethologists at North American universities facilitated the process (Dewsbury, 1989*a*, 1992). Notable among these early "immigrants" were Peter Marler at Berkeley, Franz Sauer at Florida, Erik Klinghammer at Purdue, and Fritz Walther at Missouri and subsequently at Texas A&M. Whether called ethology or animal behavior, the study of the behavior of mammals rapidly became a part of the curriculum at every major university in North America. There were parallel developments in Australia, South Africa, New Zealand, Israel, Japan, Kenya, and India. Thus a European tradition had taken root in many new locations.

Literally hundreds of students in the United States during the 1960s and 1970s became involved in animal behavior studies. The short period of consolidation was followed by the creation of new subdisciplines and new societies. The Animal Behavior section of the Ecological Society of America became a full society in 1964. Through an arrangement with the British Society for the Study of Animal Behavior, a newly organized journal of *Animal Behaviour* served as a publication outlet for the fledgling effort. Subsequently, new societies were formed with their own journals based on taxonomic lines: Chiroptera, Primates, Cetaceans, or a "wedding" between ecology and behavior.

One of us (J. F. Eisenberg) remembers at our meeting of the ASM in 1964 in Mexico City when papers dealing with behavior were a rarity. By 1983, at our meetings in Gainesville, Florida, the behavior section was well represented (231 presentations). In 1983, the ASM also published Special Publication No. 7, *Advances in the Study of Mammalian Behavior* (Eisenberg and Kleiman, 1983). This volume marks a point of recognition, namely that behavioral studies had "come of age." There were 27 participants contributing to the volume drawn not only from the United States, but also from Canada, Australia, England, Germany, Israel, and France. In order to illustrate how behavioral studies span many disciplines, we will briefly outline the organization of this volume.

Part one deals with the interwoven themes of structure, development, and function; obviously, the underpinnings of behavior. The second part of the volume deals with mechanisms of communication. Communication is still the touchstone of behavioral studies. That is to say, whether an animal be solitary or social, it must have information concerning its conspecific neighbors, or for that matter, its competitors and potential predators. The third section deals with case studies of mammalian behavior. In this time when testable hypotheses seem to dominate as a reason for practicing science, we wish to remind everyone that good, solid descriptions are still the matrix and the foundation for all subsequent research. Part four was entitled, *The adaptiveness of behavior: constraints, population mechanisms and evolution.* Obviously, the recent developments and fragmentation of the ethological group are reflected in the eclectic nature of the subtitle. Clearly, behavioral studies have relevance to students of physiology, population ecology, genetics, and evolution.

## *From Ethology to Sociobiology and Socioecology—the Last 25 Years*

*The level of selection—the 1970s.*—The last 25 years of research in mammalian behavior still have been strongly influenced by Darwin's theory of evolution by natural selection. Descriptions of ethograms and mechanistic aspects of specific behaviors that predominated throughout the 1960s were largely replaced by observational and empirical studies concerning the adaptive or evolutionary significance of behavioral patterns. Behavior was still looked upon as an adaptive strategy, but within a more refined context. Research became more experimental and was conducted more often in natural environments. The "group selection" arguments for behavior, such as alarm calls and other apparent altruistic behavior

(Wynne-Edwards, 1962), were largely, but not entirely, explained away by kin selection (Hamilton, 1964), individualistic selection (Williams, 1966), or selfish gene (Dawkins, 1976) theories. Hamilton's kin selection, or inclusive fitness theory, presented conceptual and mathematical reasoning to explain cooperative and nepotistic behavior among related individuals, and antagonistic or selfish behavior exhibited toward nonrelatives. Also during this period an emphasis was placed on concepts, theory, and hypothesis testing, rather than studying a species per se. The state-of-the-art of animal behavior in the early 1970s was reviewed by Richard Alexander (1974) and further summarized by Alexander and Tinkle (1981), and of course E. O. Wilson's (1975) treatise, *Sociobiology—the New Synthesis.*

*Parental investment and the influence of Robert L. Trivers.*—Associated with kin selection and selfish gene theory, several pivotal papers were published in the early 1970s that strongly influenced our understanding of mammalian behavior. Perhaps the most influential paper published during this time was Robert L. Trivers' (1972) theory on parental investment and sexual selection. Trivers proposed that when one gender provided greater parental investment than the other, competition occurred among the latter for the former. When applied to mammals, this theory explained the intense competition observed among males, the significance of social organs and secondary sex characteristics associated with sexual dimorphism, and the predominance of polygynous mating systems (Geist, 1974; Ralls, 1977). Two other contributions by Trivers were his theories of reciprocal altruism (Trivers, 1971) and parent-offspring conflict (Trivers, 1974). Reciprocal altruism was used to explain communal nesting in bats (Trune and Slobodchikoff, 1978), helping among dolphins (Connor and Norris, 1982), and cooperative coalition behavior among male baboons (*Papio anubis,* Packer, 1977). Reciprocal altruism became an alternative explanation for apparent altruistic behavior that did not have an inclusive fitness payoff. Supportive evidence for the parent-offspring conflict theory was provided in weaning studies on bighorn sheep (*Ovis canadensis,* Berger, 1979), red deer (*Cervus elephas,* Clutton-Brock et al., 1984), and Rhesus macaques (*Macaca mulatta,* Gomendio, 1991).

*Facultative sex ratio adjustment.*—In 1973, Trivers published a provocative theory on facultative sex ratio adjustment (Trivers and Willard, 1973). The theory states that females should provide more parental investment in the sex offspring that exhibits the greater variance in reproductive success. In mammals, this is usually considered to be males. Trivers argued that by providing more maternal investment in male offspring, sons would be healthier and better competitors as adults and thus pass on more genes than if their mothers provided less investment, even though the male cohort could be reduced in numbers at adulthood. Likewise, dominant or high ranking females or those females in "good" condition should produce sons, or at least provide more investment in them, than they do in daughters. Conversely, lower ranking and less healthy females should produce daughters, or at least provide more investment in them, than in sons. Support for this theory was found in such diverse mammals as Galapagoes fur seals (*Arctocephalus galapagoensis,* Trillmich, 1986), red deer (Clutton-Brock et al., 1968), opossums (*Didelphis virginiana,* Austad and Sunquist, 1988; Sunquist and Eisenberg, 1993), toque macaques, (*Macaca sinical,* Dittus, 1977), and domestic swine (*Sus scrofa,* Meikle et al., 1993). In 1983, Joan Silk provided an alternative hypothesis, which stated that in social systems where females compete locally for resources (referred to as the local-resource competition hypothesis), mothers should provide more investment in daughters than in sons. Supportive evidence was provided for this theory in white-tailed deer (*Odocoileus virginianus,* Caley and Nudds, 1987) and several primate species (Clark, 1978; Silk, 1983). The relationship between social systems and male and female reproductive strategies with respect to facultative sex ratio adjustment remains an active area of research in mammal behavior in the 1990s.

*Evolutionarily stable strategies (ESSs).*—Another significant development in animal behavior that came out of the 1970s was John Maynard Smith's concept of an evolutionarily stable strategy or ESS (Maynard Smith, 1974, 1982). An ESS is *a strategy which when adopted by most members of the population cannot be beaten by any other strategy in the game.* The theory attempts to explain the "best" or optimal behavioral strategy for an individual to exhibit. This behavior is often dependent on what other members of the population are doing and therefore is subject to frequency-dependent selection (Dawkins, 1980). ESS theory was used to explain hawk-dove strategies in animal contests (Clutton-Brock et al., 1979), parental investment (Maynard Smith, 1977), balanced sex ratios (Maynard Smith, 1981), cooperative mating (Packer and Pusey, 1982), sex-biased natal dispersal (Krebs and Davies, 1987), and optimal foraging behavior (Belovsky, 1984). The theory was very helpful in demonstrating why altruism and group-benefit traits are not evolutionarily stable (Dawkins, 1976, 1980) unless they benefit the inclusive fitness of kin (Hamilton, 1964). ESS or optimality theory also contended that individuals would sometimes be prevented from behaving optimally due to risk of predation or interference from better competitors and therefore would have to "make the best of a bad job" (Dawkins, 1980; Maynard Smith, 1982). These "conditional" ESSs (Dawkins, 1980) were used to explain "sneaky" mating tactics in subordinate red deer (Clutton-Brock et al., 1982) and reproductively-suppressed helpers in communal or cooperatively breeding mongooses (*Helogale parvula*), black-backed jackals (*Canis mesomelas*), and hunting dogs (*Lycaon pictus*), reviewed in Gittleman (1989). Since its inception in 1974, ESS theory has been a central theme in developing arguments for the adaptive significance of behavioral patterns.

*Optimization.*—Optimization models began achieving prominence in animal behavior in the 1970s when they were applied to "decision-making" rules associated with foraging efficiency, risk sensitivity, and life histories (R. M. Alexander, 1982; Maynard Smith, 1974). Optimality theory was first applied to foraging behavior in birds (MacArthur and Pianka, 1966) and later to mammals, such as forage selection in moose (*Alces alces,* Belovsky, 1978) and hoarding behavior in chipmunks (Elliot, 1978). In general, herbivores exhibit a trade-off between maximizing energy intake and some external constraint such as obtaining an adequate mix of nutrients (Owen-Smith and Novellie, 1982) or avoiding plant secondary compounds (Freeland and Janzen, 1974). Belovsky (1978) demonstrated that moose tended to optimize energy intake subject to a sodium constraint. Habitat choice for white-tailed deer during winter is a trade-off between maximizing energy intake within a thermal constraint (Schmitz, 1991). Caraco and Wolf (1975) calculated that the mean size of African lion prides was not optimal for foraging efficiency, but was probably evolutionarily stable with respect to defense of carcasses, feeding territories, or offspring (Packer et al., 1990). Optimality theory has also been applied to nursing behavior and reproductive success in female house mice (Fuchs, 1982), territorial defense (Schoener, 1987), managing rangelands of the western United States (Painter and Belsky, 1993), foraging behavior of primates (Robinson, 1986), and harvesting management for whales (Horwood, 1990) and white-tailed deer (Leberg et al., 1987).

Optimality theory, evolutionarily stable strategies, and game theory have been used extensively by bird and insect behavioral ecologists, more so by British and European biologists than by North American mammalogists. These three behavioral concepts have contributed considerably to behavioral theory and should be used more by mammal behaviorists. Beware, however, that although these concepts provide a powerful set of tools, truly long-term studies may raise many more questions (Clutton-Brock, 1988).

*Sex-biased natal dispersal.*—Historically, dispersal was examined from ecological or population-level perspectives (e.g., Lidicker, 1975; Stenseth and Lidicker, 1992; see also Chepko-Sade and Halpin, 1987). Behaviorists, on the other hand, were interested in the proximate mechanisms and ultimate consequences of dispersal to the individual. During the 1960s and 1970s, the general consensus regarding dispersal of juveniles away from their natal home range or social group was that adults forced the dispersal of their offspring to reduce resource or reproductive competition or both in the natal home range (reviewed in Anderson, 1989; Shields, 1982). During the late 1970s and continuing to the present, an emphasis has been placed on natal dispersal as being an adaptive mechanism for juveniles to separate from opposite-sex relatives to prevent inbreeding (Crockett, 1984; Harvey and Ralls, 1986; Pusey, 1987; Wolff, 1993). Packer (1979) was the first to propose that juvenile male baboons dispersed "voluntarily" from their natal social group to avoid inbreeding with female relatives. This idea was criticized by Moore and Ali (1984), but later substantiated by Packer (1985). Since then, theoretical (Clutton-Brock, 1989*a*, 1989*b*) and empirical (Wolff, 1993) arguments have been made to demonstrate that juvenile dispersal is correlated with the presence of opposite-sex parents in the natal home range and does not result from parental aggression. Several experimental studies conducted in the mid-1980s and early 1990s confirmed that juvenile dispersal functions to avoid inbreeding (e.g., marmots, *Marmota flaviventris,* Brody and Armitage, 1985; white-tailed deer, *Odocoileus virginianus,* Holzenbein and Marchinton, 1992; and white-footed mice, *Peromyscus leucopus,* Wolff, 1992). The current trend is to consider juvenile dispersal as an adaptive, evolved behavior that benefits the inclusive fitness interests of both the dispersing juvenile and the relatives it left behind—in short, a possible long-term compromise.

*Mating systems and certainty of paternity.*—An important component of mammalian behavior has been male and female mating strategies, especially as they pertain to mate guarding, pair bonding, and paternal care. Early classifications of mammalian mating systems included the basic monogamy, polygyny, polyandry, and promiscuity. This classification system proved to be too simplistic and was later divided to include, for instance: serial and permanent monogamy, harem-defense and territorial polygyny, and broadcast and arena promiscuity (Wittenberger, 1981). In the late 1980s and 1990s, mating systems were further classified based on male and female mating bonds and defense systems that were ultimately based on ecological and social conditions (Clutton-Brock, 1989*b*; Eisenberg, 1981). Although as many as 20 different male and female bonding and defense systems have been described, mating systems of over 95% of all mammal species reportedly are polygynous or promiscuous, with less than 5% being monogamous (Kleiman, 1977). Paternal care is extensive in monogamous species or even in some unimale polygynous systems in which males are confident of paternity. As altruism is rarely described for mating systems in mammals, any type of paternal care must be associated with confidence of paternity.

The use of molecular techniques such as electrophoresis and DNA fingerprinting that employ polymorphic blood proteins as genetic markers have revolutionized our thinking about male and female reproductive strategies (Amos and Pemberton, 1992). Foltz (1981) was the first to use electrophoretic techniques to demonstrate that the oldfield mouse, *Peromyscus polionotus,* was truly monogamous with males and females forming long-term pair bonds and all the young of a given female were sired by her mate. Conversely, Birdsall and Nash (1973) had earlier demonstrated that *Peromyscus maniculatus* was promiscuous. Ribble (1992) used DNA fingerprinting to corroborate the monogamous mating system of *Peromyscus californicus.* Similarly, in unimale polygynous black-tailed prairie dogs, *Cynomys ludovicianus,* and yellow-bellied marmots, *Marmota flaviventris,* paternity analyses confirmed that all offspring within a territory were sired by the resident male (Foltz and Hoogland, 1981; Schwartz and Armitage, 1980). Pope (1991) demonstrated that the dominant male in multi-male troops of *Alouatta seniculus* sired most offspring.

In species where males do not defend females and competition for estrous females is intense, several males may mate with the same female, possibly resulting in sperm competition and multiple paternity (see Elliot, 1978, for a review). Female Belding's ground squirrels, *Spermophilus beldingi,* and thirteen-lined ground squirrels, *Spermophilus tridecemlineatus,* mate promiscuously with three to five different males and litters are often sired by up to three different males. In both species, first males sire 60–75% of the offspring (Foltz and Schwagmeyer, 1988; Hanken and Sherman, 1981), and consequently, males do not guard females, but leave to search for more mates as soon as copulation is over. In some species, however, first males do not have a reproductive advantage (Dewsbury, 1984), and in those species males are more apt to guard females after copulation (Sherman, 1989). An interesting correlation of species in which females are promiscuous and sperm competition occurs is that males have larger testes than in species in which females mate with only one male (Harcourt et al., 1981; Heske and Ostfeld, 1990).

Electrophoretic paternity analyses have also revealed that many species that were once thought to be polygynous were in fact promiscuous, with a relatively large portion of the offspring sired by nonresident males (*Peromyscus leucopus,* Xia and Millar, 1991; *Microtus pennsylvanicus,* Boonstra et al., 1993). DNA fingerprinting has been used to relate reproductive success to harem membership in red deer, *Cervus elephas* (Pemberton et al., 1992); parentage, kinship, and cooperation in African lions, *Panthera leo* (Gilbert et al., 1991; Packer et al., 1991); demonstrate that high-ranking males sire most of the offspring in a troop of long-tailed macaques, *Macaca fascicularis* (DeRuiter et al., 1992); confirm that wolf (*Canis lupus*) packs consist of an unrelated pair and their related offspring (Lehman et al., 1992); and describe the unique mating systems in pilot whales (*Globicephala melas*), in which pods consist of adult females and related males, but all mating occurs with nonpod members (Amos et al., 1991).

*Infanticide as a reproductive strategy.*—John Calhoun was one of the first behaviorists to document the killing of pups by adults while studying crowding behavior in Norway rats (*Rattus norvegicus*) in a seminatural environment (Calhoun, 1963*a*). This early account considered infanticide an aberrant pathological behavior associated with crowded or unnatural conditions. Infanticide was first observed in the wild in the early 1970s. Rudran, working with primates in both Sri Lanka and Venezuela, pioneered in the observations of infanticide and suggested a density dependent model as an explanation (Rudran, 1973). Hrdy (1977), while studying a naturally occurring population of langurs (*Presbytis entellus*) in Abu, expounded on the phenomenon. The initial reports of infanticide in wild populations of primates precipitated a series of often hasty observational and empirical studies on infanticide in a variety of mammal species (Hausfater and Hrdy, 1984). In 1979, Hrdy presented five hypotheses to explain the functional significance of infanticidal behavior that had been observed in a variety of species in a variety of situations: 1) offspring were killed to be eaten for food; 2) sexual selection—where males would kill pups to remove genetic competitors and terminate lactation to stimulate the onset of estrus in the victim female; 3) competition for resources—where females would kill offspring of other females as a mechanism of competing for burrows or nest sites; 4) parental manipulation of offspring numbers or sex ratio; and 5) social pathology. Eisenberg (1981) opposed a simplistic explanation and advocated that several mechanisms could possibly be operative under natural selection.

Observational and experimental field and laboratory studies tested these hypotheses and provided support primarily, but not exclusively, for the sexual selection and resource competition hypotheses. Killing of offspring by strange males to terminate lactation and stimulate the onset of estrus was reported in several taxa of mammals including lions (*Panthera leo,* Packer and Pusey, 1983), horses (*Equus caballus,* Berger, 1983), several primate species (reviewed in Pusey and Packer, 1987), sciurids (e.g., McLean, 1983), and murids (Labov et al., 1985; Wolff and Cicirello, 1989). Resource-competition infanticide committed by females was reported in Belding's ground squirrels (*Spermophilus beldingi,* Sherman, 1981), prairie dogs (*Cynomys ludovicianus,* Hoogland, 1985), *Peromyscus* sp. (Wolff and Cicirello, 1991), and wild rabbits (*Oryctolagus cuniculus,* Kunkele, 1992). The current perspective on infanticide in mammals is that killing of offspring by nonrelated adults is an adaptive and evolutionarily stable reproductive strategy. Killing of offspring as a social pathology, as originally proposed by Calhoun, seems to be not often recorded and certainly is not evolutionarily stable; however, long-term studies of long-lived mammals are sparse. Younger students must maintain an open mind (Clutton-Brock, 1988).

*Socioecology—the contemporary synthesis.*—In the last 10 years, animal behavior has become behavioral ecology or socioecology. Behavior now includes an animal's entire behavioral repertoire, which is shaped largely by the distributions and abundance of resources, risk of predation, and competition from conspecifics. Following E. O. Wilson's introduction to this synthesis in 1975, several major contributions have been made to this field in the form of texts, and long-term case studies, and two new journals have been produced: *Behavioral Ecology,* and *Behavioral Ecology and Sociobiology.*

A major influence in this field in the 1980s has been the texts and edited volumes of John Krebs and Nicholas Davies (1984, with subsequent revisions). The editors and contributors to these books have used an evolutionary approach to synthesize published works derived from a variety of taxa into major concepts in animal behavioral ecology. In the most recent volume (Krebs and Davies, 1993), mammals have been used to address dispersal theory, sexual selection, parental investment, optimal foraging, territoriality, and many other evolutionary principles. All of these concepts should promote future research. Other excellent and synthetic books include: Eisenberg and Kleiman's *Advances in the Study of Mammalian Behavior* (1983), *Ecological Aspects of Social Evolution* (Rubenstein and Wrangham, 1987), *Social Evolution* (Trivers, 1983), *Sociobiology and Behavior* (Barash, 1982), and *The Ecology of Social Behavior* (Slobodchikoff, 1988). Comprehensive case studies that have made major contributions to the field of mammal behavioral ecology include *Red Deer* (*Cervus elaphus*)*: the Behaviour and Ecology of Two Sexes* (Clutton-Brock et al. 1982), *Wild Horse* (Equus callabus) *of the Great Basin* (Berger, 1986), as well as several summary texts such as *Primates in Nature* (Richard, 1985), and *Primate Societies* (Smuts et al., 1987), *Primate Social Systems* (Dunbar, 1988), *Carnivore Behavior, Ecology, and Evolution* (Gittleman, 1989), *Behavioral Ecology of Ground Squirrels* (Michener and Murie, 1989), *Marmots: Social Behavior and Ecology* (Barash, 1989), and *Social Systems and Population Cycles of Voles* (Tamarin et al., 1990).

*Applying behavioral theory to humans.*—Comparisons of human behavior and societies with those of nonhuman animals dates back to pre-Darwinian times and has always shadowed studies on mammals and behavior through time. We presented an historical aspect for the implications of applying sociobiological theory to humans earlier in this chapter and illustrate here that human behavior is still a main concern of mammalogists as well as anthropologists and psychologists in the 1990s. Several prominent texts that have deservedly received attention in the last 20 years include Ortner (1983), Eibl-Eibesfeldt (1989), and Dissayanake (1992), as well as the volumes edited by Napoleon Chagnon and William Irons, *Evolutionary Biology and Human Social Behavior* (1979), and George Barlow and James Silverberg's *Sociobiology: Beyond Nature/Nurture* (1980). Martin Daly and Margo Wilson (1983) keep providing updated editions of their well-used undergraduate text *Sex, Evolution, and Behavior.* Donald Symons' publication of *The Evolution of Human Sexuality* in 1979 sparked considerable controversy, primarily from the feminist movement, which countered with Hrdy's *The Woman that Never Evolved* in 1981. The journal *Ethology and Sociobiology* was started in 1979 and is strongly oriented toward humans. A new interdisciplinary society was organized in the late 1980s, the Human Behavior and Evolution Society, which held its fifth annual meeting in 1993. The popular writing style of Richard Dawkins' *The Selfish Gene* and David Barash's *The Whisperings Within* helped these books reach much of the general public—a laudable but perhaps futile effort. Although an integration of evolutionary theory into the social sciences has been a task with much resistance, mammal behaviorists continue to promote the universal theme of evolution by natural selection applicable to the social systems of *all* mammals. Yet, some caution is necessary, and a reading of Pepper (1958) could be of help.

## Some Advances in Sister Disciplines

*Form and function—paleontology.*—The evolution of mammals and the behavior of early mammals has been an area of active research. Outstanding contributions have derived from the efforts of Crompton and his associates and students. Lillegraven and the Wyoming group have broadened our horizons with new perspectives on the eutherian-marsupial dichotomy. Guthrie, in Alaska, has brought paleontology, behavior, and ecology to a grand synthetic treatment (1990; see Haynes, 1991). Paleocommunities and their relevance for understanding community form and extinction events in contemporary times has been pioneered also by Webb (1983), Valkenburgh (1990), and Behrensmeyer et al. (1992). A little-appreciated area of research is the use by humans of animal resources as revealed by archaeologists (Sigler-Eisenberg, 1988).

*Behavior and conservation.*—The New York Zoological Society and the Smithsonian Institution deserve special note in this arena of research. In both institutions an emphasis on field studies with an aim to apply results to conservation issues has been overwhelming. From NYZS have come seminal studies on the behavior of the humpbacked whale (*Megaptera*), African lion (*Panthera leo*), African forest primates (Cercopithecidae), the giant panda (*Ailuropoda*), and the ungulates of the Tibetan plateau (Payne, 1983; Schaller, 1972, 1993; Struhsaker, 1975). From the Smithsonian-NZP came such studies as the behavior and ecology of the golden lion tamarin (*Leontopithecus*), the ecology of the tiger (*Panthera tigris*) in Nepal, the behavior and ecology of the Asiatic elephant (*Elephas maximus*), and the behavior and conservation of Pere David's deer (*Elaphurus davidianus*), as well as ecosystem issues (Beck and Wemmer, 1983; Kleiman et al., 1986; Seidensticker and Lumpkin, 1991; Sunquist, 1981).

The US Fish and Wildlife Service and the US National Park Service, often in conjunction with the NZP and the US National Museum of Natural History, have taken a new turn in research emphasis by encouraging important work on cetaceans, pinnipeds, manatees, and sea lions. Leadership in conservation biology is also noted (Schonewald-Cox et al., 1983). This effort is often under-appreciated by those outside the service. Meanwhile, there have been widespread efforts to cope with human-animal conflicts as the march of human population growth proceeds (Redford and Padoch, 1992; Robinson and Redford, 1991; Smythe, 1991).

## *Quo Vadis?*

Some readers may consider this document a rather personal account, and in many ways this is true, because John F. Eisenberg was deeply involved in the processes that led to the acceptance of mammalian behavior as a legitimate discipline of study in North America. Despite the fractionation following the synthesis, we firmly believe that, when necessary, the disparate students of behavior will come together for a new round of synthetic activity. In short, what comes around, will come around again.

Let us point out that we trust some of us have not lost our primary mission as biologists, which is to say that if given a tract of land and custodianship, then inventory, monitoring, and long-term population studies are the rule. This is especially true as some of us begin to expand and train students in third world countries for roles in conservation. In such a situation, the infrastructure often does not exist without going back to basics, and the study of animal behavior touches everything. If we choose to be a bit foolish, then please indulge us. We think of the discipline of behavior as embodied by "Tinker Bell," who will appear again and again, when necessary, to keep our view of nature forever young.

## *Literature Cited*


Alexander, R. D. 1974. The evolution of social behavior. Annual Review of Ecology and Systematics, 5:325–383.

Alexander, R. D., and D. W. Tinkle. 1981. Natural selection and social behavior: recent research and new theory. Chiron Press, New York, 532 pp.

Alexander, R. M. 1982. Optima for animals. Edward Arnold, London, 112 pp.

Amos, B., J. Barrett, and G. A. Dover. 1991. Breeding behaviour of pilot whales revealed by DNA fingerprinting. Heredity, 67:49–55.

Amos, B., and J. Pemberton. 1992. DNA fingerprinting in non-human populations. Current Opinion in Genetics and Development, 2:857–860.

Anderson, P. K. 1989. Dispersal in rodents: a resident fitness hypothesis. Special Publications, The American Society of Mammalogists, 9:1–141.

Audubon, J. J., and J. Bachman. 1846–1854. The viviparous quadrupeds of North America, 3 vols. V. G. Audubon, New York. Reprint 1989, Wellfleet Press, Seacaucus, New Jersey, 440 pp.

Austad, S. N., and M. E. Sunquist. 1988. Sex-ratio manipulation in the common opossum. Nature, 324: 58–60.

Bailey, V. 1931. Mammals of New Mexico. North American Fauna, 53:1–412.

Barash, D. 1979. The whisperings within. Harper and Row, New York, 274 pp.

———. 1982. Sociobiology and behavior. Elsevier, Amsterdam, 426 pp.

———. 1989. Marmots: social behavior and ecology. Stanford University Press, Stanford, 360 pp.

Barlow, G. W., and J. Silverberg. 1980. Sociobiology: beyond nature/nurture? AAAS Selected Symposia Series, Westview Press, Boulder, 627 pp.

Bartholomew, G. A., and T. J. Cade. 1957. Temperature regulation, hibernation and aestivation in the little pocket mouse. Journal of Mammalogy, 38: 60–72.

Beach, F. A. 1948. Hormones and behavior. Harper Brothers, New York, 368 pp.

Beck, B., and C. Wemmer. 1983. Pere David's deer: conservation of an extinct species. Garland Press, New York, 193 pp.

Beebe, W. 1925. The three-toed sloth. Zoologica, 7:1–67.

Behrensmeyer, A., J. D. Damuth, W. A. DeMichele, R. Potts, H. D. Sues, and S. L. Wing. 1992. Terrestrial ecosystems through time. The University of Chicago Press, Chicago, 568 pp.

Belovsky, G. E. 1978. Diet optimization in a generalist herbivore; the moose. Theoretical Population Biology, 14:105–134.

———. 1984. Herbivore optimal foraging: a comparative test of three models. The American Naturalist, 124:97–115.
Berger, J. 1979. Weaning conflict in desert and mountain bighorn sheep (Ovis canadensis): an ecological interpretation. Zeitschrist für Tierpsychologie, 50:188–200.
———. 1983. Induced abortion and social factors in wild horses. Nature, 303:59–61.
———. 1986. Wild horses of the Great Basin: social competition and group size. The University of Chicago Press, Chicago, 325 pp.
Bingham, H. C. 1932. Gorillas in native habitat. Publications of Carnegie Institute (Carnegie Institute of Washington, Washington, D. C.), 426:1–66.
Birdsall, D. A., and D. Nash. 1973. Occurrence of successful multiple insemination of females in natural populations of deer mice (*Peromyscus maniculatus*). Evolution, 27:106–110.
Boonstra, R., X. Xia, and L. Pavone. 1993. Mating system of the meadow vole, *Microtus pennsylvanicus*. Behavioral Ecology, 4:83–89.
Brody, A. K., and K. B. Armitage. 1985. The effects of adult removal on dispersal of yearling yellow-bellied marmots. Canadian Journal of Zoology, 63: 2560–2564.
Bronson, F. H. 1989. Mammalian reproductive biology. The University of Chicago Press, Chicago, 325 pp.
Burt, W. H. 1940. Territorial behavior and populations of some small mammals in southern Michigan. Miscellaneous Publication of the Museum of Zoology, The University of Michigan, 45:1–58.
Caley, M. J., and T. D. Nudds. 1987. Sex-ratio adjustment in *Odocoileus virginianus*: does local resource competition play a role? The American Naturalist, 129:452–457.
Calhoun, J. B. 1963*a*. The ecology and sociology of the Norway rat. U.S. Department of Health, Education, and Welfare, Public Health Service, Bethesda, Maryland, 288 pp.
———. 1963*b*. The social use of space. Pp. 2–187, *in* Physiological mammalogy (Van Gelder and Maier, eds.). Academic Press, New York, 1:1–380.
Caraco, T., and L. L. Wolf. 1975. Ecological determinants of group sizes of foraging lions. The American Naturalist, 109:343–352.
Carpenter, C. R. 1934. A field study of the behavior and social relations of howler monkeys (*Alouatta palliata*). Comparative Psychology Monographs, 10: 1–168.
———. 1935. Behavior of red spider monkeys in Panama. Journal of Mammalogy, 16:171–180.
———. 1964. Naturalistic behavior of non-human primates. Pennsylvania State University Press, University Park, 454 pp.
Chagnon, N. A., and W. Irons. 1979. Evolutionary biology and human social behavior: an anthropological perspective. Duxbury Press, North Scituate, Massachusetts, 623 pp.
Chepko-Sade, B. D., and Z. T. Halpin. 1987. Mammalian dispersal patterns. The University of Chicago Press, Chicago, 342 pp.
Christian, J. J. 1963. Endocrine adaptive mechanisms and the physiological regulation of population growth. Physiological Mammalogy, 1:189–353.
Clark, A. B. 1978. Sex ratio and local resource competition in a prosimian primate. Science, 201:163–165.
Clutton-Brock, T. H. (ed.). 1988. Reproductive success. The University of Chicago Press, Chicago, 538 pp.
———. 1989*a*. Female transfer and inbreeding avoidance in social mammals. Nature, 337:70–72.
———. 1989*b*. Mammalian mating systems. Proceedings of the Royal Society of London, 236:339–372.
Clutton-Brock, T. H., S. D. Albon, and F. E. Guiness. 1984. Maternal dominance, breeding success, and birth sex ratios in red deer. Nature, 308: 358–360.
———. 1986. Great expectations: dominance, breeding success and offspring sex ratios in red deer. Animal Behaviour, 34:460–471.
Clutton-Brock, T. H., F. E. Guiness, and S. D. Albon. 1982. Red deer: the behaviour and ecology of two sexes. The University of Chicago Press, Chicago, 378 pp.
Clutton-Brock, T. H., S. D. Albon, R. M. Gibson, and F. E. Guiness. 1979. The logical stag: adaptive aspects of fighting in red deer (*Cervus elephas* L.). Animal Behaviour, 27:211–225.
Cockburn, A. 1988. Social behavior in fluctuating populations. Croom Helm Ltd., North Ryde, New South Wales, 239 pp.
Connor, R. C., and K. S. Norris. 1982. Are dolphins reciprocal altruists? The American Naturalist, 119:358–374.
Count, E. 1973. Being and becoming human. Van Nostrand, New York, 349 pp.
Craig, W. 1918. Appetites and aversions as constituents of instincts. Biological Bulletin of Woods Hole, 34:91–107.
Crockett, C. 1984. Emigration by female red howler monkeys. Pp. 159–173, *in* Female primates (M. F. Small, ed.). Liss, New York, 272 pp.
Crowcroft, P. 1991. Elton's ecologists. The University of Chicago Press, Chicago, 177 pp.
Daly, M., and M. Wilson. 1983. Sex, evolution, and behavior. Wadsworth Publishing Company, Belmont, California, 402 pp.
Darwin, C. 1859. The origin of species. John Murray, London (and many reprints), 816 pp.
———. 1872. The expression of the emotions in man and animals. Appleton, New York, London, 372 pp.
Dawkins, R. D. 1976. The selfish gene. Oxford University Press, Oxford, 224 pp.
———. 1980. Good strategy or evolutionarily stable strategy. Pp. 331–367, *in* Sociobiology: beyond nature/nurture? (G. W. Barlow and J. Silverberg, eds.). AAAS Selected Symposia Series. Westview Press, Boulder, Colorado, 627 pp.
Deegener, P. 1918. Die Formen der Vergesellschaftung im Tierriche. Verlag von Vict, Leipzig, 420 pp.
DeRuiter, S. W., Jr., G. J. J. M. Trommelen, A. G. S. W. Utterlinden, R. D. Martin, and J. Van Hooff. 1992. Male social rank and reproductive success in wild long-tailed macaques. Paternity ex-

clusions by blood analysis and DNA fingerprinting. Pp. xx–xx, *in* Paternity in primates: genetic tests and theories, implications of human DNA fingerprinting (R. D. Martin, A. F. Dixson, and E. J. Wickings, eds.). S. Karger, Basel.

DeVore, B. I. (ed.). 1965. Primate behavior: field studies of monkeys and apes. Holt, Rinehart and Winston, New York, 654 pp.

Dewsbury, D. A. 1984. Sperm competition in muroid rodents. Pp. 547–571, *in* Sperm competition and the evolution of animal mating systems (R. L. Smith, ed.). Academic Press, New York, 687 pp.

———. 1989*a*. A brief history of animal behavior in North America. Perspectives in Ethology, 8:85–122.

———. 1989*b*. Comparative psychology, ethology and animal behavior. Annual Review of Psychology, 40: 581–602.

———. 1992. Comparative psychology and ethology: a reassessment. American Psychology, February:208–215.

Dice, L. R. 1933. Fertility relationships between some of the species and subspecies of mice in the genus *Peromyscus*. Journal of Mammalogy, 14:298–305.

Dissanayake, E. 1992. *Homo aestheticus*. Free Press, New York, 297 pp.

Dittus, W. 1977. The social regulation of population density and age-specific distribution in the toque monkey. Behaviour, 63:281–322.

Dunbar, R. I. M. 1988. Primate social systems. Cornell University Press, Ithaca, 378 pp.

Eibl-Eibesfeldt, I. 1958. Das Verhalten der Nayetiere. Handbuch der Zoologie, Band 8, Lieferung, 12, 10:1–88.

———. 1989. Human ethology. Aldine de Gruyter, New York, 848 pp.

Eisenberg, J. F. 1962. Studies on the behavior of *Peromyscus maniculatus gambelii* and *Peromyscus californicus parasiticus*. Behaviour, 19:177–207.

———. 1963. The behavior of heteromyid rodents. University of California Publication in Zoology, 69: 1–100.

———. 1966. The social organizations of mammals. Handbuch der Zoologie, Band 8, Lieferung, 39, 10: 1–92.

———. 1981. The mammalian radiations. The University of Chicago Press, Chicago, 610 pp.

Eisenberg, J. F., and W. S. Dillon (eds.). 1971. Man and beast. Smithsonian Press, Washington, D.C., 401 pp.

Eisenberg, J. F., and D. G. Kleiman (eds.). 1983. Advances in the study of mammalian behavior. Special Publication, The American Society of Mammalogists, 7:1–753.

Eisenberg, J. F., and R. E. Kuehn. 1966. Behavior of *Ateles geoffroyi* and related species. Smithsonian Miscellaneous Collection, 151:63 pp.

Elliot, L. 1978. Social behavior and foraging ecology of the chipmunk (*Tamias striatis*). Smithsonian Contributions to Zoology, 265:1–107.

Enders, R. K. 1935. Mammalian life histories from Barro Colorado Island, Panama. Bulletin of the Museum of Comparative Zoology, Harvard, 78:385–502.

———. 1952. Reproduction in the mink. Proceedings of the American Philosophical Society, 96:691–755.

Ewer, R. 1969. The ethology of mammals. Logos, London, 418 pp.

Foltz, D. W. 1981. Genetic evidence for long-term monogamy in a small rodent *Peromyscus polionotus*. The American Naturalist, 117:665–675.

Foltz, D. W., and J. L. Hoogland. 1981. Analysis of the mating system in the black-tailed prairie dog (*Cynomys ludovicianus*) by likelihood of paternity. Journal of Mammalogy, 62:706–712.

Foltz, D. W., and P. L. Schwagmeyer. 1988. Sperm competition in the thirteen-lined ground squirrel: differential fertilization success under field conditions. The American Naturalist, 133:257–265.

Freeland, W. J., and D. H. Janzen. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. The American Naturalist, 108:269–284.

Frisch, K. von. 1950. Bees, their vision, chemical senses and language. Cornell University Press, Ithaca, 157 pp.

Fuchs, S. 1982. Optimality of parental investment: the influence of nursing on reproductive success of mother and female young house mice. Behavioral Ecology and Sociobiology, 10:39–51.

Geist, V. 1971. Mountain sheep. The University of Chicago Press, Chicago, 383 pp.

———. 1974. On the relationship of social evolution and ecology in ungulates. American Zoologist 14: 205–220.

Gilbert, D. A., C. Packer, A. E. Pusey, J. C. Stephens, and S. J. O'Brien. 1991. Analytical DNA fingerprinting in lions: parentage, genetic diversity, and kinship. Journal of Heredity, 82:378–386.

Gittleman, J. L. (ed.). 1989. Carnivore behavior, ecology, and evolution. Cornell University Press, Ithaca, 620 pp.

Gomendio, M. 1991. Parent/offspring conflict during the weaning process in rhesus macaques. Animal Behaviour, 42:993–1005.

Griffin, D. 1958. Listening in the dark. Yale University Press, New Haven, 356 pp.

Grinnell, J. 1914. An account of the mammals and birds of the lower Colorado Valley with special reference to the distributional problems presented. University of California Publications in Zoology, 12: 51–294.

Guthrie, R. D. 1990. Frozen fauna of the mammoth steppe. The University of Chicago Press, Chicago, 323 pp.

Hamilton, W. D. 1964. The genetical theory of social behavior. Journal of Theoretical Biology, 7:1–52.

Hanken, J., and P. W. Sherman. 1981. Multiple paternity in Belding's ground squirrel litters. Science, 212:351–353.

Harcourt, A. H., P. H. Harvey, S. G. Larson, and R. V. Short. 1981. Testis weight and breeding system in primates. Nature, 293:55–57.

Harris, V. T. 1952. An experimental study of habitat selection by prairie and forest races of the deermouse, *Peromyscus maniculatus*. Contributions from the Laboratory of Vertebrate Biology, University of Michigan, 56:1–53.

Harthoorn, A. M. 1976. The chemical capture of animals. Baillare, Tyndale, London, 416 pp.
Harvey, P. H., and K. Ralls. 1986. Do animals avoid incest? Nature, 320:575–576.
Hausfater, G., and S. B. Hrdy (eds.). 1984. Infanticide: comparative and evolutionary perspectives. Aldine, New York, 598 pp.
Haynes, G. 1991. Mammoths, mastodonts, and elephants. Cambridge University Press, 413 pp.
Hediger, H. 1942. Wildetiere in Gafangenschaft. Benno Schwabe, Basel, 205 pp.
Heske, E. J., and R. S. Ostfeld. 1990. Sexual dimorphism in size, relative size of testes, and mating systems in North American voles. Journal of Mammalogy, 71:510–519.
Hollister, N. 1917. Some effects of environment and habitat on captive lions. Proceedings of the United States National Museum, 53:177–193.
Holzenbein, S., and R. L. Marchinton. 1992. Spatial integration of maturing-male white-tailed deer in the adult population. Journal of Mammalogy, 73: 326–334.
Hoogland, J. L. 1985. Infanticide in prairie dogs: lactating females kill offspring of close kin. Science, 230:1037–1040.
Horwood, J. W. 1990. Whale management: an optimality approach. Report of the International Whaling Commission, 40:493–497.
Howard, W. E. 1948. Dispersal, amount of inbreeding and longevity in a local population of deer mice. Contributions from the Laboratory of Vertebrate Biology, University of Michigan, 43:1–50.
Howell, A. B. 1944. Speed in animals. The University of Chicago Press, Chicago, 270 pp.
Hrdy, S. B. 1977. The langurs of Abu: female and male strategies of reproduction. Harvard University Press, Cambridge, 361 pp.
———. 1979. Infanticide among animals: a review, classification, and examination of the implications for reproductive strategies of females. Ethology and Sociobiology, 1:13–40.
———. 1981. The woman that never evolved. Harvard University Press, Cambridge, 256 pp.
Jones, J. K., Jr. 1991. Geneology of 20th century mammalogists in North America. Pp. 33–47, *in* Latin American mammalogy (M. Mares and D. Schmidly, eds.). University of Oklahoma Press, Norman, 468 pp.
Kaufmann, J. H. 1962. Ecology and social behavior of the coati, *Nasua narica* on Barro Colorado Island, Panama. University of California Publications in Zoology, 60:95–222.
Kellogg, W. N. 1961. Porpoises and sonar. The University of Chicago Press, Chicago, 177 pp.
King, J. A. 1955. Social behavior, social organization, and population dynamics in a black-tailed prairiedog town in the Black Hills of South Dakota. Contributions from the Laboratory of Vertebrate Biology, University of Michigan, 67:1–123.
———. 1961. Development and behavioral evolution in *Peromyscus.* Pp. 122–147, *in* Vertebrate speciation (W. F. Blair, ed.). University of Texas Press, Austin, Texas, 642 pp.
———. (ed.). 1968. Biology of Peromyscus (Rodentia). Special Publications, The American Society of Mammalogists, 2:1–593.
Kleiman, D. G. 1967. Some aspects of social behavior in the Canidae. American Zoologist, 7:365–372.
———. 1977. Monogamy in mammals. Quarterly Review of Biology, 52:39–69.
Kleiman, D. G., B. B. Beck, J. M. Dietz, L. A. Dietz, J. D. Ballou, and A. J. Coimbra-Filho. 1986. Conservation program for the golden lion tamarin: captive research and management, ecological studies, educational strategies, and reintroduction. Pp. 959–979, *in* Primates: the road to self-sustaining populations (K. Benirschke, ed.). Springer-Verlag, New York, 1,044 pp.
Koestler, A. 1971. The case of the midwife toad. Random House, New York, 187 pp.
Krebs, J. R., and N. B. Davies. 1984. Behavioural ecology. Blackwell Scientific Publications, Oxford, 493 pp.
———. 1987. An introduction to behavioural ecology. Blackwell Scientific Publications, Oxford, (Second ed.) 389 pp.
——— (eds). 1991. Behavioural ecology: an evolutionary approach. Blackwell Scientific Publications, Oxford, (Third ed.) 482 pp.
———. 1993. An introduction to behavioral ecology. Blackwell Scientific Publications, Oxford, (Third ed.) 420 pp.
Kroeber, A. 1925. Yana and Yani. Handbook of the Indians of California. Bulletin of American Ethnology, 78. Smithsonian Institution, Washington, D.C.
Kropotkin, P. 1902. Mutual aid: a factor in evolution. A. Knopf, New York, 362 pp. (Republished in 1914.)
Kunkele, J. 1992. Infanticide in wild rabbits (*Oryctolagus cuniculus*). Journal of Mammalogy, 73:317–320.
Labov, J. B., U. W. Huck, R. W. Elwood, and R. J. Brooks. 1985. Current problems in the study of infanticidal behavior of rodents. The Quarterly Review of Biology, 60:1–20.
Layne, J. N. 1954. The biology of the red squirrel, *Tamiasciurus hudsonicus lognax,* in central New York. Ecology Monographs, 24:227–267.
Leberg, P. L., M. H. Smith, and K. T. Scribner. 1987. Optimization strategies in a white-tailed deer harvest program. Transaction of Congress of the International Union of Game Biologists, 18:102–103.
Lehman, N., P. Clarkson, L. D. Mech, T. J. Meier, R. K. Wayne, and S. W. Zack. 1992. A study of the genetic relationships within and among wolf packs using DNA fingerprinting and mitochondrial DNA. Behavioral Ecology and Sociobiology, 30:83–94.
Leopold, A. 1933. Game management. Scribners, New York, 481 pp.
Lidicker, W. Z., Jr. 1975. The role of dispersal in the demography of small mammals. Pp. 203–233, *in* Small mammals: their productivity and population dynamics (F. B. Golley, F. Petrusewicz, and L. Ryskowski, eds.). International Biological Program, Cambridge University Press, Cambridge, 5:1–451.
Linsdale, J. M. 1946. The California ground squirrel. University of California Press, Berkeley, 475 pp.
Linsdale, J. M., and L. P. Tevis. 1951. The dusky-

footed wood rat. University of California Press, Berkeley, 664 pp.

Linsdale, J. M., and P. Q. Tomich. 1953. A herd of mule deer. University of California Press, Berkeley, 567 pp.

Lorenz, K. Z. 1981. The foundations of ethology. Springer-Verlag, New York, 380 pp.

MacArthur, R. H., and E. R. Pianka. 1966. On the optimal use of a patchy environment. The American Naturalist, 100:603–609.

Mach, E. 1959. Analysis of sensations. Dover, New York, 310 pp. (reprint.)

Marler, P. 1985. Hark ye to the birds. Pp. 315–346, *in* Studying animal behavior (D. A. Dewsbury, ed.). The University of Chicago Press, Chicago, 512 pp.

Maynard Smith, J. 1974. The theory of games and the evolution of animal conflicts. Journal of Theoretical Biology, 47:209–221.

———. 1977. Parental investment—a prospective analysis. Animal Behaviour, 25:1–9.

———. 1981. Will a sexual population evolve to an ESS? The American Naturalist, 117:1015–1018.

———. 1982. Evolution and theory of games. Cambridge University Press, Cambridge, 224 pp.

McKay, G. 1973. Behavior and ecology of the Asiatic elephant in southeastern Ceylon. Smithsonian Contributions to Zoology, 125:113 pp.

McLean, I. G. 1983. Paternal behaviour and killing of young Arctic ground squirrels. Animal Behaviour, 31:32–44.

McNab, B. K. 1983. Would-be ecological and behavioral consequences of adaptation to various food resources. Pp. 664–697, *in* Advances in the study of mammalian behavior (J. F. Eisenberg and D. G. Kleiman, eds.). Special Publications, The American Society of Mammalogists, 7:1–753.

Meikle, D. B., L. C. Drickamer, S. H. Vessey, T. L. Rosenthal, and K. S. Fitzgerald. 1993. Maternal dominance rank and secondary sex ratio in domestic swine. Animal Behaviour, 46:79–85.

Montgomery, G. G., and M. E. Sunquist. 1975. Impact of sloths on Neotropical forest energy flow. Pp. 69–98, *in* Tropical ecological systems (F. B. Golley and E. Medina, eds.). Springer-Verlag, New York, 398 pp.

Moore, J., and R. Ali. 1984. Are dispersal and inbreeding avoidance related? Animal Behaviour, 32: 94–112.

Moore, J. C. 1957. Natural history of Shermann's fox squirrel. Bulletin of the American Museum of Natural History, 113:71 pp.

Morgan, L. H. 1851. League of the Ho-De-No-Sau-Nee. Rochester, New York.

———. 1868. The American beaver and his works. Burt Franklin, New York, 330 pp. (reprint 1970.)

Morrison, P., and B. K. McNab. 1962. Daily torpor in a Brazilian murine oppossum (*Marmosa*). Comparative Biochemical Physiology, A. Comparative Physiology, 6:57–68.

Murie, J., and G. Michener. 1984. The biology of ground-dwelling squirrels. University of Nebraska Press, Lincoln, 459 pp.

Nissen, H. W. 1931. A field study of the chimpanzee. Comparative Psychology Monographs, 8:1–121.

Noble, J. K. 1931. The biology of the Amphibia. McGraw-Hill Book Company, Ltd. Inc., New York, 577 pp.

Ortner, D. J. (ed.). 1983. How humans adapt: a biocultural odyssey. Smithsonian Institution, Washington, D.C., 560 pp.

Owen-Smith, N., and P. Novellie. 1982. What should a clever ungulate eat? The American Naturalist, 119:151–178.

Packer, C. 1977. Reciprocal altruism in olive baboons. Nature, 265:441–443.

———. 1979. Inter-group transfer and inbreeding avoidance in *Papio anubis*. Animal Behaviour, 27: 1–36.

———. 1985. Dispersal and inbreeding avoidance. Animal Behaviour, 33:676–678.

Packer, C., and A. E. Pusey. 1982. Cooperation and competition within a coalition of male lions: kin selection of game theory? Nature, 296:740–742.

———. 1983. Adaptations of female lions to infanticide by incoming males. The American Naturalist, 121:716–728.

Packer, C., D. Scheel, and A. E. Pusey. 1990. Why lions form groups: food is not enough. The American Naturalist, 136:1–19.

Packer, C., D. A. Gilbert, A. E. Pusey, and S. J. O'Brien. 1991. Kinship and cooperation in African lions: a molecular genetic analysis. Nature, 351: 562–565.

Painter, E. L., and A. J. Belsky. 1993. Application of herbivore optimization theory to rangelands of the western United States. Ecological Applications, 3:2–9.

Payne, R. (ed.). 1983. Communication and behavior of whales. Westview Press, Boulder, 643 pp.

Pearson, O. P. 1944. Reproduction in the shrew (*Blarina brevicauda* Say). The American Journal of Anatomy, 75:39–93.

Pemberton, J. M., S. D. Albon, F. E. Guiness, T. H. Clutton-Brock, and G. A. Dover. 1992. Behavioral estimates of male mating success tested by DNA fingerprinting in a polygynous mammal. Behavioural Ecology, 3:66–75.

Pepper, S. C. 1958. The sources of value. University of California Press, Berkeley, 732 pp.

Pope, T. 1991. The reproductive consequences of male cooperation in red howler monkeys. Behavioral Ecology and Sociobiology, 27:439–446.

Pusey, A. E. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. Trends in Ecology and Evolution, 2:295–299.

Pusey, A. E., and C. Packer. 1987. Dispersal and philopatry. Pp. 250–266, *in* Primate societies (B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker, eds.). The University of Chicago Press, Chicago, 578 pp.

Ralls, K. 1977. Sexual dimorsphism in mammals: avian models and unanswered questions. The American Naturalist, 111:917–938.

Redford, K., and C. Padoch (eds.). 1992. Conservation of Neotropical forests. Columbia University Press, New York, 475 pp.

Ribble, D. O. 1992. The monogamous mating system of *Peromyscus californicus* as revealed by DNA fingerprinting. Behavioral Ecology and Sociobiology, 29:161–166.

Richard, A. 1985. Primates in nature. W. H. Freeman, New York, 558 pp.

Robinson, J. G. 1986. Seasonal variation in use of time and space by the wedge capped capuchin monkey. Smithsonian Contributions to Zoology, 431:1–60.

Robinson, J. G., and K. H. Redford (eds.). 1991. Neotropical use and conservation. The University of Chicago Press, Chicago, 520 pp.

Robinson, M., and L. Tiger. 1991. Man and beast revisited. Smithsonian Press, Washington, D.C., 386 pp.

Rosenblatt, J., and B. Komisaruk. 1977. Reproductive behavior and evolution. Plenum Press, New York, 169 pp.

Rubenstein, D. I., and R. W. Wrangham (eds.). 1987. Ecological aspects of social evolution. Princeton University Press, Princeton, New Jersey, 551 pp.

Rudran, R. 1973. Adult male replacement in troops of purple faced langurs. Folia Primatologica, 19:41–60.

Sauer, K. 1969. Seed, spades, hearths and herbs. MIT Press, Cambridge, Massachusetts, 194 pp. (reprint.)

Schaller, G. B. 1963. The mountain gorilla: ecology and behavior. The University of Chicago Press, Chicago, 431 pp.

———. 1972. The Serengeti lion. The University of Chicago Press, Chicago, 480 pp.

———. 1993. The last panda at the zoo. The University of Chicago Press, Chicago, 292 pp.

Schmitz, O. J. 1991. Thermal constraints and optimization of winter feeding and habitat choice in white-tailed deer. Holarctic Ecology, 14:104–111.

Schoener, T. 1987. Time budgets and territory size: some simultaneous optimization models for energy maximizers. American Zoologist, 27:259–291.

Schonewald-Cox, C. M., S. M. Chambers, B. MacBryde, and W. L. Thomas (eds.). 1983. Genetics and conservation. Benjamin Cummings, London, 174 pp.

Schusterman, R., J. Thomas, and F. Wood (eds.). 1986. Dolphin cognition and behavior: a comparative approach. Laurence Erlbaum Associates, Hillsdale, New Jersey, 393 pp.

Schwartz, O. A., and K. B. Armitage. 1980. Genetic variation in social mammals: the marmot model. Science, 207:665–667.

Seidensticker, J., and S. Lumpkin (eds.). 1991. Asian elephants. Friends of the National Zoo in the Zoological National Park, Washington D.C., 271 pp.

Seton, E. T. 1953. Lives of game animals, vols. 1–4. Charles T. Brandford, Boston, Originally published in 1909 and 1925, 949 pp. (reprint.)

Shadle, A. R. 1946. Copulation in the porcupine. The Journal of Wildlife Management 10:159–162.

Sherman, P. W. 1981. Reproductive competition and infanticide in Belding ground squirrels and other animals. Pp. 311–331, *in* Natural selection and social behavior: recent research and new theory (R. D. Alexander and D. W. Tinkle, eds.). Chiron Press, New York, 532 pp.

———. 1989. Mate guarding as paternity assurance in Idaho ground squirrels. Nature, 338:418–420.

Shields, W. M. 1982. Philopatry, inbreeding and the evolution of sex. State University New York Press, Albany, 245 pp.

Sigler-Eisenberg, B. J. 1988. Settlement, subsistence and environment. Pp. 291–306, *in* Wetlands site archaeology (B. Purdy, ed.). Telford Press, Caldwell, New Jersey, 338 pp.

Silk, J. B. 1983. Local resource competition and facultative adjustment of sex ratios in relation to competitive ability. The American Naturalist, 121:56–66.

Slobodchikoff, C. N. 1988. The ecology of social behavior. Academic Press, San Diego, 429 pp.

Smuts, B. B., D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Strusaker (eds.). 1987. Primate societies. The University of Chicago Press, Chicago, 578 pp.

Smythe, N. 1970. Relationships between fruiting seasons and seed dispersal methods. The American Naturalist, 104:25–35.

———. 1991. Steps toward the domestication of the paca. Pp. 202–216, *in* Neotropical use and conservation (J. G. Robinson and K. Redford, eds.). University of Chicago Press, Chicago, 520 pp.

Stenseth, N. C., and W. Z. Lidicker, Jr. 1992. Animal dispersal: small mammals as a model. Chapman and Hall, London, 365 pp.

Struhsaker, T. 1975. The red colobus monkey. The University of Chicago Press, Chicago, 311 pp.

Sumner, F. B. 1932. Genetic, distributional, and evolutionary studies of the subspecies of deer mice (*Peromyscus*). Bibliographica Genetica, 9:1–106.

Sunquist, M. E. 1981. The social organization of tigers (*Panthera tigris*). Pp. xx–xxx, *in* Royal Chitawan National Park. Smithsonian Contributions to Zoology, 336:1–98.

Sunquist, M. E., and J. F. Eisenberg. 1993. Reproductive strategies in female *Didelphis*. Bulletin of the Florida Museum of Natural History, Biological Sciences, 36:109–140.

Symons, D. 1979. The evolution of human sexuality. Oxford University Press, New York, 358 pp.

Tamarin, R. H., R. S. Ostfeld, S. R. Pugh, and G. Bujalska. 1990. Social systems and population cycles of voles. Birkhauser, Basel, Switzerland, 229 pp.

Tester, J. R., D. W. Warner, and W. W. Cochran. 1964. A radio tracking system for studying movements of deer. The Journal of Wildlife Management, 28:42–45.

Tinbergen, N. 1951. The study of instinct. Oxford University Press, London, 228 pp.

Tolman, E. 1932. Purposive behavior in animals and men. University of California Press, Berkeley, 463 pp.

Trillmich, F. 1986. Maternal investment and sex allocation in the Galapagoes fur seal, *Arctocephalus galapagoensis*. Behavioral Ecology and Sociobiology, 19:157–164.

Trivers, R. L. 1971. The evolution of reciprocal altruism. The Quarterly Review of Biology, 46:35–57.

———. 1972. Parental investment and sexual selection. Pp. 136–179, *in* Sexual selection and the descent of man 1871–1971 (B. Campbell, ed.). Aldine, Chicago, 378 pp.

———. 1974. Parent-offspring conflict. American Zoologist, 14:249–264.

———. 1983. Social evolution. Benjamin Cummings, Menlo Park, 462 pp.

Trivers, R. L., and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science, 179:90–92.

Trune, D. R., and C. N. Slobodchikoff. 1978. Position of immatures in pallid bat clusters: a case of reciprocal altruism? Journal of Mammalogy, 59:193–195.

Valkenburgh, B. Van. 1990. Skeletal and dental predictors of body mass in carnivores. Pp. 181–205, *in* Body size in mammalian paleobiology (J. Damuth and B. MacFadden, eds.). Cambridge University Press, Cambridge, 397 pp.

Walker, E. P. 1964. Mammals of the world, 3 vols. Johns Hopkins University Press, Baltimore, 2:1–268.

Watson, J. B. 1914. Behavior: an introduction to comparative psychology. Holt, New York, 439 pp.

Webb, S. D. 1983. The rise and fall of the ungulate fauna in the Miocene. Pp. 267–306, *in* Coevolution (M. H. Nitecki, ed.). The University of Chicago Press, Chicago, 392 pp.

Wemmer, C. 1977. Comparative ethology of the large spotted genet. Smithsonian Contributions to Zoology, 239:1–93.

Whitaker, J. O., Jr. 1994. Academic propinquity. Pp. 121–138, *in* Seventy-five years of mammalogy (1919–1994) (E. C. Birney and J. R. Choate, eds.). Special Publication, The American Society of Mammalogists, 11:1–433.

Whitman, C. O. 1899. Animal behavior. Biological Lectures of the Marine Biological Laboratory (Wood's Hole), 6:285–338.

———. 1919. The behavior of pigeons. Publications of Carnegie Institute, Carnegie Institute of Washington, Washington, D.C., 257:1–161.

Williams, G. G. 1966. Adaptation and natural selection. Princeton, New Jersey, 307 pp.

Wilson, D. E., and J. F. Eisenberg. 1990. Origin and applications of mammalogy in North America. Current mammalogy (H. H. Genoways, ed.). 2:1–35.

Wilson, E. O. 1975. Sociobiology—the New Synthesis. Harvard University Press, Cambridge, Massachusetts, 697 pp.

Wittenberger, J. F. 1981. Animal social behavior. Duxbury Press, Boston, 722 pp.

Wolff, J. O. 1992. Parents suppress reproduction and stimulate dispersal in opposite-sex juvenile white-footed mice. Nature, 359:409–410.

———. 1993. What is the role of adults in mammalian juvenile dispersal? Oikos, 68:173–176.

Wolff, J. O., and D. M. Cicirello. 1989. Field evidence for sexual selection and resource competition infanticide in white-footed mice. Animal Behaviour, 36:456–465.

———. 1991. Comparative paternal and infanticidal behavior of white-footed mice and deermice. Behavioural Ecology, 2:38–45.

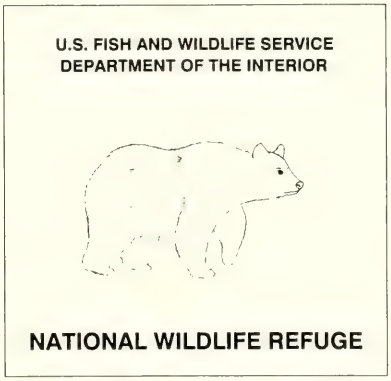
Wynne-Edwards, V. C. 1962. Animal dispersion in relation to social behaviour. Oliver and Boyd, Edinburgh, 653 pp.

Yerkes, R. M., and A. W. Yerkes. 1929. The great apes. Yale University Press, New Haven, Connecticut, 652 pp.

Xia, X., and J. S. Millar. 1991. Genetic evidence of promiscuity in *Peromyscus leucopus*. Behavioral Ecology and Sociobiology, 28:171–178.

# *CONSERVATION AND MANAGEMENT*

James H. Shaw and David J. Schmidly




## *Introduction*

If the space allocated them in zoos throughout the world is an accurate gauge, the public considers mammals to be the most popular class of vertebrates. This popularity is confirmed by the history of conservation, in which wild species of mammals, from American bison (*Bison bison*) in the 19th Century to the giant panda (*Ailuropoda melanoleuca*) in the late 20th Century have been prominently featured.

Yet popularity alone is not enough to ensure survival. Some characteristics of mammals, including thick, luxurious coats of hair, have prompted commercial exploitation, depletion and, in some cases extinction, within historical times. Higher energy demands imposed by homeothermy require larger areas of natural habitat to sustain populations of mammals, as compared with reptiles of similar body size and food habits. The large brains of mammals, together with lengthy periods of lactation and parental protection, generally correlate with relatively low reproductive rates. Animals with low reproductive rates are slow to recover from population reductions and fare poorly in unstable environments.

Wild mammals are thus esthetically popular, commercially valuable, and biologically vulnerable. In a world increasingly dominated by human activities, political clashes over the fate of wild mammals will increase. The early successes of North American conservation stemmed more from shifts in public attitudes than from the science of mammalogy. Indeed, direct legal protection, popularly supported and rigorously enforced, remains a cornerstone of conservation.

But the problems faced by mammalian species worldwide are now far more complex and subtle than direct overharvesting. These include habitat destruction, isolation through fragmentation, assorted effects of scale, genetic depletion, introduced organisms, and the prospects of global climatic changes. Since its inception, the ASM has actively promoted the conservation of wild mammals, but today's more pervasive and complicated threats require greater involvement by mammalogists and other scientists. Thus, a major theme featured here is the increasing role of science in the formulation and evaluation of conservation.

## *Before 1919*

From the establishment of the first colonies through the 19th Century, Americans of European descent viewed wild animals as obstacles to progress that would, like the American Indian, vanish before the advance of civilization. Wild mammals were, at best, perceived as temporary resources for uses ranging from subsistence by early settlers to a means of enriching speculators through the fur trade.

Given such attitudes and conditions, game abundance around settlements declined. The Massachusetts Bay Colony, for example, first closed the season on deer in 1694 (Matthiessen, 1987).

Subsistence hunting by settlers and market hunting by native Americans for trade with whites had begun to take its toll by the time of American independence. Principally through analysis of early trade records, McCabe and McCabe (1984) estimated that white-tailed deer (*Odocoileus virginianus*) numbered between 24 and 34 million in pristine North America. By 1800, the population had declined by an estimated 50–65%. Deer rebounded slightly during the first half of the 19th Century, owing to the displacement of many native Americans from the East, but a resurgence of market hunting, this time by Americans of European descent, forced the number of white-tailed deer to a low of between 300,000 and 500,000 by 1900 (McCabe and McCabe, 1984).

*Market hunting.*—Market hunting flourished after the Civil War. Firearms improved, first with breech-loaders and then with repeating rifles and shotguns. During the same period, railroad transportation greatly expanded wild game markets to burgeoning eastern populations.

The white-tailed deer, of course, was not the only species to decline in the face of more efficient market hunting. American bison were slaughtered first for subsistence and later for the market value of their tongues and hides. Naturalist and anthropologist George Bird Grinnell, hunting bison along the Republican River in 1872, found the species even then in such serious decline that he thought extinction likely (Reiger, 1972). In 1874, Congress passed legislation to prohibit the killing of female bison by Americans of European descent, but President Grant gave the bill a pocket veto (McHugh, 1972). Further interest in protecting bison dissipated two years later with news that Custer and five companies of the 7th Cavalry had died at the Little Bighorn. Thereafter, European Americans accepted Phil Sheridan's praise for bison hunters who were busily destroying the "Indians' commissary" (McHugh, 1972).

*The early conservation movement in North America.*—The near extinction of the bison provided a rallying point for America's first movement for wildlife preservation. This movement, beginning in the 1880s, resulted from pressure by sportsmen's groups that flourished during that period, and from nature enthusiasts, who took much of their sentiment from 19th Century romanticism (Dunlap, 1988). Prompted by the American Ornithologists' Union, Congress established the Office of Economic Ornithology and Mammalogy within the U.S. Department of Agriculture in 1885. Forerunner of the Bureau of Biological Survey and U.S. Fish and Wildlife Service, this new Office had Clinton Hart Merriam as its first chief.

The early preservation movement gathered momentum in the 1890s with development of "realistic" nature stories, by Ernest Thompson Seton and others. These stories attempted to use the science of that time (including the now discredited "science" of animal psychology) as a vehicle to deliver a moral message, and gained wide readership through popular magazines (Dunlap, 1988).

Despite growing sentiment in favor of wildlife preservation, market hunting continued. By 1900, most states had laws regulating hunting, but inconsistencies between neighboring states, together with ease of transporting wild animal products from one state to another, allowed de facto market hunting to continue. Growing sentiment in favor of wildlife protection led Congress to pass the Lacey Act in 1900. The Lacey

Act, drawing on Congressional authority to regulate interstate commerce, made interstate shipment of game taken in violation of state laws a federal offense. In addition, the Lacey Act imposed federal restrictions on importation of exotic wildlife.

Sentiment toward predators was an entirely different matter. Neither hunters nor nature lovers of the early 20th Century appreciated the value of carnivores. The same sentimental view that advocated protection for "noble" species like the elk (*Cervus elaphus*) depicted predators such as the gray wolf (*Canis lupus*) as cruel, cunning, destructive, and even dangerous. Lacking a lobby, predators of the time did not lack opponents; stockmen looked to the federal government for support in their war on predators.

Responding to the stockmen's wishes, Congress authorized the expenditure of the first federal funds for predator control in 1914. The following year, the Bureau of Biological Survey hired professional trappers and began implementing its Congressional mandate.

*Direct legal protection.*—Through the early years of the 20th Century, efforts to aid wild mammals focused almost entirely upon direct legal protection. Motives stemmed from the desire of sportsmen to increase their hunting opportunities and from nature enthusiasts whose interest in wildlife was sentimental and aesthetic. Zoologists (the term "mammalogist" was not then in general use) had little direct involvement with efforts to improve the status of wildlife. Those who specialized in mammals studied taxonomy and made inferences concerning phylogeny. Moreover, many early mammal specialists lacked formal academic preparation, having learned mammalogy through apprenticeships.

In the absence of science, wildlife conservationists developed measures based on cultural tradition, sentiment, and dogma, and used the law as the main vehicle for implementation. Given the rudimentary state of ecology at the time, such an approach may have been unavoidable. The drawback of such a non-scientific basis was that its effectiveness and progress could not be objectively measured and evaluated. A program's success, aside from a few obvious cases in which wild populations greatly expanded or declined, simply could not be determined. Ineffective or misguided programs, such as the "buck laws" that protected female cervids, were sustained for decades.

## *After 1919*

By the time that the ASM was founded in 1919, the term "conservation" had come into general use. Gifford Pinchot first used the word in its modern context, feeling the need for a term that included the taking of a sustainable yield from a managed resource (Trefethen, 1975). To sport hunters, of course, Pinchot's goal of sustainable yield, developed initially for commercial timber, applied equally well to game.

Application of Pinchot's principles to wild mammals required information obtainable only through field studies. Given the limited development of ecological principles at the time, almost nonexistent funding for research, and the shortage of qualified field workers, field data would be long in coming. Wildlife conservation as applied to game would continue to be based on tradition and implemented through arbitrary seasons and bag limits that may have had little to do with biological reality.

*Controversy over policy on mammalian predators.*—Popular sentiment in the years between the World Wars still favored the destruction of medium-to-large carnivores, both to protect livestock and to protect popular game animals. Gradually, however, many of the naturalists and biologists with the Bureau of Biological Survey became concerned over the decline of large mammalian predators and the accidental killings of other wild animals. Others accepted more traditional views of predators and embarked enthusiastically on their agency's mission to eradicate them. Neither side could seek answers in science, as not even the most basic field studies of food habits, behavior, and population ecology of wild predatory mammals existed. Given that many of the ASM's founders, including its first president, C. Hart Merriam, were past or present employees of the Bureau, that controversy was bound to divide the new society as well.

Open opposition to government predator control flared at the society's 1924 meeting, where two Survey biologists, Edward A. Goldman and W. B. Bell, were called upon to defend their agency's policy (Dunlap, 1988). Thus began a protracted and often bitter controversy that would erupt from time to time for nearly half a century. The controversy was propelled not only by a lack of field data, but also by a fundamental question concerning the mission of the Survey and of its successor, the U.S. Fish and Wildlife Service. Critics of predator control contended that the agency should work on behalf of publicly-owned wildlife, as it did in most other programs. Predator control was another matter. With cooperative funding from states and livestock growers, it was becoming a service for the benefit of the livestock industry.

As the predator control controversy continued, gradual progress was made on the conservation and management of game species. Game recovery turned out to require more than mere legal protection. Changes in the land, brought about through agriculture, grazing, mining, and the clearing of forests took place at about the same time as excessive commercial hunting. Thus, without some type of habitat restoration, game protection often could not succeed.

*Science-based conservation programs in universities.*—Early in the 20th Century, Frederick Clements (1916) gave the world his theory of plant succession and Victor Shelford (1913) described the concept of natural animal communities. These pioneering treatises laid the theoretical foundations for the study of natural communities by describing the process of plant succession and by presenting criteria for defining the original biomes or major habitat associations of North America. Wildlife conservation could now take advantage of these discoveries and did so, albeit slowly at first. What was needed was a formal textbook and academic programs in wildlife conservation and management.

The unifying textbook (Leopold, 1933) appeared and, shortly thereafter, its author accepted a professorship in game management at the University of Wisconsin, the first of its kind in the United States. Leopold and his students provided some of the first ecological studies on wild animals that could be applied directly to conservation and management.

Academic programs in wildlife management received another important boost through one of the many ideas of J. N. "Ding" Darling. Darling helped set up a special research unit at Iowa State University, paying some of the initial costs himself. The U.S. Fish and Wildlife Service expanded Darling's prototype into a series of Wildlife Cooperative Research Units at major universities to bolster graduate programs in wildlife conservation and management.

*Public funding for conservation.*—Through the mid-1930s, state wildlife conservation agencies received virtually all of their funds from the sale of hunting and fishing licenses. These funds were generally insufficient for wildlife research and, more importantly, the money from license sales was controlled by state legislatures, who often transferred funds to state projects unrelated to wildlife.

The solution to the problems of inadequate funding, and the allocation of fish and game monies to other state projects, came in the form of the Federal Aid to Wildlife Restoration Act in 1937. Often called simply the Pittman-Robertson (P-R) Act, it was arguably the most important federal legislation affecting American wildlife. The Act placed a federal excise tax on the manufacture of sporting arms and ammunition, and redistributed the revenue, via federal authorities, to state wildlife conservation agencies on a matching basis.

To qualify for this federal aid, each state had to pass enabling legislation ensuring that all funds collected through license sales would be used only for fish and wildlife purposes. State wildlife agencies now had a broader, more sustainable source of funding, and one that was virtually immune to policial manipulation. Within a year, 43 of the then 48 states complied, and the other five followed soon thereafter (Williamson, 1987). In 1939, P-R apportioned $890,000 to the states. By 1986, that figure had grown to over $107 million (Kallman, 1987).

Federal aid funds were earmarked for wildlife restoration, not for law enforcement. These monies made possible much of the desperately needed research on wildlife habitat problems and on the implementation of solutions. Finally, legal regulations of harvests were being supplemented by habitat improvement.

*Progress after World War II.*—The prosperity after World War II prompted many changes in wildlife conservation. Returning servicemen exchanged uniforms for hunting garb and state license sales boomed. Correspondingly, P-R reapportionment soared from $817,500 in 1945 to nearly $11 million in 1949 (Kallman, 1987). Increased revenue led to more wildlife research and management.

The postwar years brought about increases in international cooperation and trade. As international concerns in general grew, so did interest in wildlife management and conservation on a global scale. The International Union for Conservation of Nature and Natural Resources (IUCN) was formed in 1948 as an independent international organization to promote wise and sustainable use of the world's natural resources. Membership in the IUCN consisted of national government, governmental agencies concerned with conservation, and private or non-governmental organizations (NGOs). Leadership from the IUCN has helped develop international treaties on behalf of wildlife.

In 1961, another important NGO, the World Wildlife Fund, came into being. The World Wildlife Fund's primary mission was to raise money on behalf of vanishing species throughout the Earth. Both the IUCN and the World Wildlife Fund were based in Switzerland.

The first postwar international convention affecting wild mammals was the International Convention for the Regulation of Whaling, which met in Washington, D.C., late in 1946. Superceding the earlier 1931 Convention, this one established the International Whaling Commission (IWC), charged with reviewing harvests and establishing quotas. The Commission issued few restrictions until the early 1960s when, faced with clear evidence of depleted stocks and an international lobby opposed to whaling, it gradually shifted toward more protection. In 1982, the IWC agreed to set commercial whaling quotas at zero by 1986 and to review the effects of this protection on whale stocks by 1990 (Lyster, 1985).

*Sustainable harvests.*—Detailed understanding of the effects of harvest on wild mammals has been slow in coming because the species most likely to be affected by harvest are large, have low rates of increase, and long generation times. These traits make conclusive field investigations lengthy and expensive. Furthermore, large mammals fall under the jurisdiction of established wildlife agencies, subject to their own priorities and pressures exerted by various interest groups. Such agencies are often reluctant to approve the sort of long-term, high-visibility field investigations that would be required to improve the predictability of the effects of game harvests.

Game harvests have remained imprecise and unrefined since the turn of the century. About the best that can be said about traditional seasons and bag limits is that, with rare exception, they avoid overharvests. Even into the 1980s, a leading specialist in the harvest of large mammals concluded that the principle change in hunting regulations in the United States over the past several decades was a relaxation of the ban against hunting on Sundays (Caughley, 1985).

*Broader public interest.*—Although regulation of hunting changed little in postwar years, public interest in non-game species has increased substantially. Concern over rare and endangered species led to passage of the first Endangered Species Act in 1966. More symbolic than substantive, the Act did little more than authorize the Secretary of the Interior to develop and maintain a list of vanishing wildlife threatened with extinction.

The environmental movement in the late 1960s led to passage of the Endangered Species Act of 1969, curbing imports on wild animals (and parts thereof) threatened in their native lands. Four years later another Endangered Species Act retained refined elements from its two predecessors and extended federal protection to native wildlife threatened with extinction. Section 6 of this Act provided for federal funds for use by state wildlife agencies on behalf of endangered species. Since the Act's Section 7 protected critical habitat of endangered species from any development using federal funds, it provided for interagency consultation to resolve conflicts and suggest alternatives (Yaffee, 1988).

In 1972, Congress passed the Marine Mammal Protection Act (MMPA). This Act applied to all marine mammals and placed a moratorium on their harvest or harassment. It also established regulatory authority over commercial use of marine mammals and products made from them. Finally, recognizing that marine mammals play important roles in marine ecosystems, the Act prohibited reduction of marine mammal populations to the point that they cease to perform their ecological functions (Dunlap, 1988; Trefethen, 1975).

*Exploitation vs. protection.*—One of the most persistent controversies in wild mammal conservation is the conflict over controlled exploitation versus preservation. With its long and generally successful tradition in game management, wildlife conservation in the United States and Canada generally leans toward controlled exploitation, principally through sport hunting. Not only can sport hunting help populations recover, it can provide landowners with incentives to maintain natural habitat and can generate important revenue. Nonetheless, the preservationist view—that the best way to ensure survival of wild animals is through complete protection from exploitation—has gained favor during the past 2 decades. Management of endangered species in most cases precludes exploitation. Populations of many furbearing and, especially, marine mammals have recovered well when afforded complete protection. Each approach can work under some conditions, but decisions often are clouded by ideological divisions between the two camps. This division prevents some private conservation organizations from working together more effectively and presenting a united front on broader conservation issues.

Given proper habitat, most North American game mammals fare quite well, whether subjected to regulated hunting or afforded complete protection. Wild species found in increasingly crowded developing nations, however, may not be so fortunate. While tourism attracted by the large mammals of East Africa offers justification for protection of wildlife in national parks, unchecked human population growth in nations like Kenya may soon overcome that advantage (Myers, 1979, 1985). Rather than have parks steadily converted to subsistence farms, a better strategy may be to employ would-be farmers in a sustainable harvest of wild mammals and in processing them for sale. Unfortunately, there is no clear answer. Just as either controlled harvest or complete protection can ensure the survival of most species of wild mammals in North America, either strategy could result in extinction in the poorer, more crowded developing nations.

Even in North America, the debate over

exploitation continues among professional mammalogists and wildlife managers. One important example is game ranching, used in various forms in Europe, New Zealand, South Africa, the United States, and Canada. Game ranching is practiced on private land and involves to some degree the "privatization" of what is usually regarded as public property. Proponents argue that game ranching offers important economic incentives to private landowners who would otherwise convert wildlife habitat to more profitable uses. While the practice may require intensive management and acceptance of some rather artificial conditions, it may offer the only real hope for retaining large wild mammals on private lands.

Legislation aimed at encouraging private game ranching in Alberta, Canada, recently generated sharp controversy. Geist (1988) argued that privatization would undermine what has generally been successful wildlife conservation. Further, any shift from public to private ownership would leave populations of large wild mammals at the whims of market forces. When market demand was high, incentives to overharvest would be powerful. Conversely, when market demand slacked off, neglect would ensue.

If Geist's (1988) arguments are valid, and if they apply to wild mammals outside of Alberta, then they challenge a basic premise of the IUCN's World Conservation Strategy. Can wild mammals be exploited on a sustainable basis by market forces? Put another way, can markets themselves become sufficiently stabilized to ensure the long-term survival of wild mammals? And, if privately owned wild mammals are successfully established, will their wild counterparts be regarded as competitors to be destroyed?

*The international wildlife trade.*—Just as unregulated market hunters in the United States depleted wild mammals in the 19th Century, unregulated international commerce in wild mammals and parts thereof began to threaten numerous species by the mid-20th Century. After a decade of prompting by the IUCN, a Convention on International Trade in Endangered Species (CITES) convened in Washington, D.C., in March, 1973. The Convention decided to list the more imperiled species in its Appendix I and to require both an export permit from the country of origin and an import permit from the country of destination. Species less critically threatened, but nonetheless rare, are listed in its Appendix II and require an export permit from the country of origin. In both cases, permits are issued by a "scientific authority," typically a wildlife or natural resource management agency.

Practically speaking, legal trade of Appendix I is negligible between signatories. Appendix II listings, however, allow trade at the discretion of the originating country but require record keeping and regular reporting. These public records prove useful in monitoring trade and population trends for periodic status review.

At the 1976 review meeting of the Convention in Berne, Switzerland, members voted to adopt strict criteria for listing and delisting species. Under these "Berne criteria," the information required for listing a species need not be as detailed or conclusive as that for delisting. This arrangement reversed the traditional burden of proof, placing it on those who advocate exploitation rather than on those who urge protection. Predictably, controversy ensued, but the rationale of erring on the side of protection prevailed.

*Projections of global declines in wild mammals.*—Despite the considerable progress in conservation during the 1960s and '70s, the 1980s opened with extraordinarily pessimistic projections for the Earth's wild species. Deforestation, particularly of the little-known but species-rich tropical moist forests, was accelerating. Field studies showed that the recovery potential or resiliency of tropical moist forests was far lower than that of temperate forests. International trade in wildlife and products from wildlife increased, spurred by rising demand in consumer nations and by increasing effort to use natural resources, such as wildlife and forest products, to balance trade and to offset growing indebtedness incurred by producer nations.

Besides local habitat losses and heavier commercial exploitation, wild species began facing threats from large-scale impacts to their environments. Ocean dumping and its resulting pollution increased in both scope and intensity. Atmospheric threats, first from acid precipitation and later from depletion of atmospheric ozone and increases in "greenhouse" gases, caused unprecedented effects upon entire biomes. Thus, *The Global 2000 Report to the President of the United States* in 1980 projected that from 15 to 20% of the world's wild species, if current trends continued, would be extinct by the year 2000 (Barney, 1980).

While the task force labored over *The Global 2000 Report* . . . the IUCN developed a comprehensive plan to offset some of the report's more dire projections. The *UCN's World Conservation Strategy* recognized that humanity would continue to exploit the Earth's seas and soils, but sought to thwart exploitation's impact by shifting it toward *sustainable* development. This basic change is analogous to the difference between mining a nonrenewable resource and cropping a renewable one.

Insofar as wild mammals were concerned, the *World Conservation Strategy* offered several recommendations, aimed principally at large mammals. First, a series of large nature reserves (of sufficient size to sustain wild populations of large mammals) should be established. Second, controlled exploitation, ranging from traditional sport hunting to less conventional game cropping, should be permitted in or around such areas. Properly done, such harvest would allow sustainable exploitation of meat and trophies, as well as providing employment and revenue. This is especially important in developing nations. Finally, the *World Conservation Strategy* recommended preserving wild species of mammals because of the genetic diversity their populations contain, potentially useful for the improvement of existing livestock and for the creation of "new" domesticated animals in the future (IUCN, 1980). In short, the IUCN's plan presented conservation as an integral part of economic development, rather than as the antithesis to it.

Many conventional types of development clearly are not sustainable. One of these is the large-scale clearing and conversion of tropical moist forests, either for commercial logging or for conversion of lowland forest to farms and pastures. Once the primary forests are cleared, recovery of the ecosystems to anything resembling their original state becomes unlikely. Tropical forests hold their nutrients not in soils, but in decaying plant and animal matter near the soil surface. Clearing and burning deprives the altered ecosystem of nutrients needed for recovery, and land surfaces become exposed for the first time to the direct effects of sun and wind. Insect and pest outbreaks follow, and remaining patches of tropical moist forest succumb to isolation and the combined physical and biological changes along their edges (Lovejoy et al., 1986).

## *New Approaches to the Conservation of Mammals*

Threats to the long-term survival of free-living wild mammals are larger and more complex than ever before. Participants in a recent conference in Washington, D.C., examined the effects of atmospheric changes, largely the "greenhouse effect," on biodiversity (Peters, 1988). The climatic changes brought about by increasing levels of atmospheric carbon dioxide could trigger significant geographic shifts in plant and animal communities. Thus national parks and other reserves, already suspected as being of insufficient size, may prove even less effective at sustaining wild mammals as climates shift. One possible solution would be to leave or develop north-south corridors of natural habitat between protected areas in an effort to accommodate climatically-induced shifts in geographic ranges.

As threats increase in scale, so must efforts in ecological research. Ecological studies of wild mammals, particularly large species, increasingly are being carried out with the replication and controls needed in good experimental designs. In addition, the larger the scope of ecological investigations, the greater the cost. Thus, large-scale studies can become prohibitively expensive. One elegant and straightforward solution to these problems is the systematic use of wildlife management as scientific research (MacNab, 1983). Rather than apply one general management practice to a region the size of a state, wildlife agencies could deliberately vary practices, be they harvest levels, habitat improvements, or other options, in ways that would allow direct comparisons and evaluations. Some areas could be left alone to serve as "controls." This systematic approach to management would require more careful planning and more detailed monitoring, but their potential benefits would certainly be worth the extra effort.

A similar framework with which to integrate wildlife management with research is called comprehensive planning (Crowe, 1983). Adopted to varying degrees by some state wildlife agencies, comprehensive planning provides for periodic review of management practices using pre-established criteria. A particular program in wildlife management is planned, implemented, reviewed, and then reassessed routinely, thus allowing for improvement or, if necessary, replacement. Done properly, comprehensive planning not only provides important new research, but also reduces the political machinations that occur within agencies. Rather than deciding on a program's fate purely through competing political forces, agencies can evaluate it through analysis of field data. Even when a management program completely fails to meet its objective, useful information can be obtained and the effort justified.

A potentially far-reaching technique for large-scale field studies is a collection of computer software packages known as Geographical Information Systems (GIS). GIS links attribute data (e.g., biogeographical province, biome type, species occurrence, topographic features) with positions on the earth (McLaren and Briggs, 1993). Two principal approaches are *inventory,* consisting of descriptive data, mapping, and database management, and *analysis,* comprised of modeling and statistical treatments (Berry, 1993). Commonly used in natural resource management since the 1980s, GIS applications also are indispensible in detailed spatial studies of mammalian ecology (August, 1993).

Gap analysis is a particular application of GIS designed to target spatial "gaps" in statewide habitat protection systems. Once identified, such "gaps" often can be filled to ensure adequate protection of threatened species and rare natural communities. Gap analysis offers the advantages of identifying needs of several species at once as well as presenting a more proactive approach in which conservation measures may be taken before situations become desperate (Scott et al., 1991).

*Wild mammals and the maintenance of biodiversity.*—Wildlife conservation began as game management, with the aim of producing a "surplus" for sport hunting. Game management could be improved by field studies of the ecology of a game species in general and its responses to harvest and changes in land use in particular. Thus, game management succeeded by meeting the needs of game species one at a time. It seemed only reasonable in the early days of endangered species conservation to continue this tradition from game management, except that the objective was restoration rather than harvest.

Effective as it was for mostly temperate game mammals, this single-species management proved inadequate in the face of such serious and widespread threats as deforestation and increased international trafficking of wildlife. Of the roughly 4,100 species of mammals on Earth, only a small fraction has been studied sufficiently to permit development of detailed conservation plans. Conservationists began to realize that there was neither enough time nor resources to rely exclusively on single-species management. New challenges required new approaches. Professional wildlife conservation began to shift from efforts to save "species A" (typically a large mammal with popular appeal) to preserving biodiversity on an ecosystem level.

This biodiversity approach offers two distinct advantages over single-species management. First, it allows more efficient allocation of time and resources. Instead of 4,100 management plans for wild mammals, it can rely on protecting reserves located in the roughly 193 biogeographical provinces or principal habitat types on which those 4,100 mammals depend for survival in the wild. Second, it recognizes the imperative of saving self-sustaining ecosystems, a goal consistent with the IUCN's view of sustainable uses of natural resources.

Concern for preserving biodiversity began attracting biologists from outside the traditional ranks of wildlife management. Population geneticists and evolutionary ecologists started to supplement their basic research with investigations into sustaining biodiversity. A new field, conservation biology, appeared along with an edited book of the same name in 1980 (Soulé and Wilcox, 1980). In 1987, the Society for Conservation Biology was established with its journal, *Conservation Biology.*

This new discipline is more broadly based than conventional wildlife management. Although conservation biology is interdisciplinary and includes many specialties, two of the more longstanding ones featured here are conservation genetics and insular ecology.

*Conservation genetics.*—The importance of conservation genetics escaped the notice of most wildlife managers, who knew that genetic depletion posed a problem for domesticated mammals but saw little evidence of its practical significance to wild ones. Thriving populations of white-tailed deer, for example, founded from only a few individuals, suggested that wild species had a greater resistence to genetic problems imposed by small, isolated populations.

The first clues that wild species might suffer from inbreeding appeared in studies of captive-bred zoo mammals in which more inbred populations consistently produced fewer surviving offspring than did less inbred ones (Ralls et al., 1979). Why was there such a marked difference between the zoo populations and their free-living, transplanted counterparts? Part of the answer stems from the fact that small populations of wild animals lose genetic variation in two stages (Franklin, 1980). The first is the so-called "founder effect" (Mayr, 1963), which occurs when a population undergoes sudden and severe numerical reduction, leaving only a small number of surviving "founders." Fewer founders mean that rarer genes are likely to be lost for future generations, reducing genetic variation.

The founder effect may be followed by additional genetic loss through inbreeding, genetic drift, or both. At low numbers, close relatives are likely to breed with one another. Also, small populations suffer from genetic drift, the loss of rarer genes by chance. These processes deplete genetic variability for each generation that a population is kept at low numbers.

Zoo populations have been subjected to both stages of genetic losses. Reintroduced game populations typically experience only the founder effect, quickly increasing their numbers and reducing the effects of inbreeding and genetic drift.

*Insular ecology.*—Insular ecology is an applied version of the classic theories of island biogeography (MacArthur and Wilson, 1967). These theories predict that islands will be colonized by wild species at a rate inversely proportional to distance from the mainland. Moreover, species on islands become extinct at rates inversely proportional to island size, the rationale being that the smaller the island, the smaller the populations, and the smaller the populations, the greater the threat of extinction.

These basic theories seem simple and plausible enough, and they are supported by studies of land-bridge islands separated from mainlands since sea levels rose at the end of the Pleistocene (Wilcox, 1980). When the islands were peninsulas, they presumably contained the same levels of species diversity that occurred on the mainland to which they were connected. Since the time of isolation by rising sea water can be reliably estimated, comparisons of historical levels of species on those islands can be compared with diversity on mainlands. The resulting differences compare closely with those predicted by island biogeography (Wilson and Willis, 1975).

Protected areas of natural habitat are increasingly fragmented and isolated from one another in human-dominated landscapes. The species preserved on such habitat islands may be subject to the same general patterns of extinction incurred by species on land-bridge islands. To the extent that the analogy holds (a matter of some debate at the time of this writing), isolated habitat preserves may lose many species. Mammals seem to be the class of vertebrates most vulnerable to this effect of insular ecology (Wilcox, 1980). Except for bats, mammals are more limited than birds in their dispersal, so their prospects for recolonizing isolated habitat preserves are limited. Mammals have higher metabolic demands than do reptiles and amphibians, and thus require larger areas over which to forage. Large mammalian carnivores, empirically recognized as "extinction prone" (Terborgh, 1974), require the largest areas of all and it may be that this area requirement is at least as important in their demise as conflict with human activity. Indeed, one recent model predicted that no national park or other habitat reserve anywhere in the world was large enough to sustain a population of large carnivores indefinitely (Belovsky, 1987).

*An increasing role for mammalogists.*—Perhaps the broadest question of all concerns the role that the discipline of mammalogy will and should play in conservation. Mammalogists concerned with conservation like to think that their research will lead to more effective conservation. Although distinguished authorities (Caughley, 1985; Geist, 1988) have argued that early wildlife conservation in North America succeeded despite the science of the day and not because of it, the situations in which we find ourselves today differ markedly from those that confronted Hornaday and Grinnell. The forces contributing to the loss of wild mammals are not just local market hunters, but large-scale habitat disruption, unprecedented atmospheric and oceanic pollution, and international trafficking. Many of these new threats are highly technical and require the technological assistance and conceptual innovation that can best be provided by science. Mammalogists will play an increasingly important role in ensuring the survival of wild mammals into the 21st Century and beyond.

## Summary and Conclusions

The conservation of wild mammals began largely with direct legal protection aimed at curbing excessive hunting and trapping. Such measures were based little on science, but the fact that many depleted populations recovered, especially those of North American ungulates, attested to the utility of legal protection in dealing with overhunting.

In recent decades, habitat alterations, habitat fragmentation, and genetic depletion have joined overharvesting as threats to the survival of wild species of mammals. These new threats have stimulated development of new scientific subdisciplines, such as conservation biology, and emerging technologies, including geographical information systems. In the future, the conservation and management of wild mammals will depend even more on mammalogy and related sciences.

## *Literature Cited*


August, P. V. 1993. GIS and mammalogy: building a database. Pp. 11–26, *in* GIS applications in mammalogy (S. B. McLaren and J. K. Braun, eds.). Oklahoma Museum of Natural History, Norman, 41 pp.

Barney, G. O. 1980. The global 2000 report to the President of the United States. Vol 1: the summary report. Pergamon Press, New York, 360 pp.

Belovsky, G. E. 1987. Extinction models and mammalian persistence. Pp. 35–57, *in* Viable populations for conservation (M. E. Soulé, ed.). Cambridge University Press, New York, 189 pp.

Berry, J. K. 1993. The application of GIS to mammalogy: basic concepts. Pp. 4–10, *in* GIS applications in mammalogy (S. B. McLaren and J. K. Braun, eds.). Oklahoma Museum of Natural History, Norman, 41 pp.

Caughley, G. 1985. Harvesting of wildlife: past, present, and future. Pp. 3–14, *in* Game harvest management (S. L. Beasom and S. F. Roberson, eds.). Caesar Kleberg Wildlife Research Institute, Kingsville, Texas, 374 pp.

Clements, F. E. 1916. Plant succession. Carnegie Institute Publication, New York, 242:1–512.

Crowe, D. M. 1983. Comprehensive planning for wildlife resources. Wyoming Fish and Game Department, Laramie, 143 pp.

Dunlap, T. R. 1988. Saving America's wildlife. Princeton University Press, Princeton, New Jersey, 222 pp.

Franklin, I. R. 1980. Evolutionary change in small populations. Pp. 135–149, *in* Conservation biology (M. E. Soulé and B. A. Wilcox, eds.). Sinauer Associates, Sunderland, Massachusetts, 395 pp.

Geist, V. 1988. How markets in wildlife meat and parts, and the sale of hunting privileges, jeopardize wildlife conservation. Conservation Biology, 2:15–26.

IUCN. 1980. World conservation strategy. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland, 40 pp.

Kallman, H. (ed.). 1987. Restoring America's wildlife, 1937–1987: the first 50 years of the Federal Aid in Wildlife Restoration (Pittman-Robertson) Act. U.S. Department of the Interior Fish and Wildlife Service, Washington, D.C., 394 pp.

Leopold, A. 1933. Game management. Charles Scribner's Sons, New York, 418 pp.

Lovejoy, T. E., et al. 1986. Edge and other effects of isolation on Amazon forest fragments. Pp. 257–285, *in* Conservation biology: the science of scarcity and diversity (M. E. Soulé, ed.). Sinauer Associates, Sunderland, Massachusetts, 584 pp.

Lyster, S. 1985. International wildlife law: an analysis of international treaties concerned with the conservation of wildlife. Grotius Publications Limited, Cambridge, England, 470 pp.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, 203 pp.

MacNab, J. 1983. Wildlife management as scientific experimentation. Wildlife Society Bulletin, 11:397–401.

Matthiessen, P. 1987. Wildlife in America. (revised edition) Viking/Penguin Press, New York, 332 pp.

Mayr, E. 1963. Animal species and evolution. Harvard University Press, Cambridge, Massachusetts, 797 pp.

McLaren, S. B., and J. M. Briggs. 1993. Introduction. Pp. 1–3, *in* GIS applications in mammalogy (S. B. McLaren and J. K. Braun, eds.). Oklahoma Museum of Natural History, Norman, 41 pp.

McCabe, R. E., and T. R. McCabe. 1984. Of slings and arrows: an historical retrospective. Pp. 10–72, *in* White-tailed deer: ecology and management (L. K. Halls, ed.). Wildlife Management Institute and Stackpole Books, Harrisburg, Pennsylvania, 870 pp.

McHugh, T. 1972. The time of the buffalo. Alfred A. Knopf, New York, 339 pp.

Myers, N. 1979. The sinking ark. Pergamon Press, New York, 307 pp.

———. 1985. Conservation of Africa's cats: problems and opportunities. Pp. 437–446, *in* Cats of the world: biology, conservation, and management (S. D. Miller and D. D. Everett, eds.). National Wildlife Federation, Washington, D.C., 501 pp.

Peters, R. L. 1988. Effects of global warming on species and habitats: an overview. Endangered Species Update, 5:1–8.

Ralls, K., K. Brugger, and J. Ballou. 1979. Inbreeding and juvenile mortality in small populations of ungulates. Science, 206:1101–1103.

Reiger, J. F. 1972. The passing of the Great West: selected papers of George Bird Grinnell. Winchester Press, New York, 182 pp.

Scott, M. S., B. Csuti, K. Smith, J. E. Estes, and S. Caicco. 1991. Gap analysis of species richness and vegetative cover: an integrated biodiversity conservation strategy. Pp. 282–297, *in* Balancing on the brink of extinction: the Endangered Species Act and lessons for the future (K. A. Kohm, ed.). Island Press, Washington, D.C., 315 pp.

Shelford, V. E. 1913. Animal communities in temperate America. University of Chicago Press, Chicago, 362 pp.

Soulé, M. E., and B. A. Wilcox (eds.). 1980. Conservation biology. Sinauer Associates, Sunderland, Massachusetts, 395 pp.

Terborgh, J. 1974. Preservation of natural diversity: the problem of extinction-prone species. BioScience, 24:715–722.

Trefethen, J. B. 1975. An American crusade for wildlife. Winchester Press and the Boone and Crockett Club, New York, 409 pp.

Wilcox, B. 1980. Insular ecology and conservation. Pp. 95–117, *in* Conservation biology (M. E. Soulé and B. A. Wilcox, eds.). Sinauer Associates, Sunderland, Massachusetts, 395 pp.

Williamson, L. L. 1987. Evolution of a landmark law. Pp. 1–17, *in* Restoring America's wildlife, 1937–1987: the first 50 years of the Federal Aid in Wildlife Restoration (Pittman-Robertson) Act (H. Kallman, ed.). U.S. Department of the Interior Fish and Wildlife Service, Washington, D.C., 394 pp.

Wilson, E. O., and E. O. Willis. 1975. Applied biogeography. Pp. 522–534, *in* Ecology and evolution of communities (M. L. Cody and J. M. Diamond, eds.). Harvard University Press, Cambridge, Massachusetts, 545 pp.

Yaffee, S. L. 1988. Endangered species protection through interagency consultation. Endangered Species Update, 5:14–19.

~~New~~ DATE DUE

| | |
|---|---|
| | |
| | |
| | |
| | |
| | |
| | |
| | |
| | |
| | |
| | |
| | |
| | |
| | |
| | |
| | |
| | |