

THE FINDINGS IN
NORTH AMERICA
OF THE
MIND AND SPEECH

Edited by

FRANCIS J. YOUNG
WILLIAM B. STILES, JR.

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JOHN W. HARRIS

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**BIRD BANDING IN
NORTH AMERICA:
THE FIRST HUNDRED YEARS**

MEMOIRS OF THE NUTTALL ORNITHOLOGICAL CLUB,
NO. 15

William E. Davis, Jr. and Jerome A. Jackson, Memoir Series Editors

**BIRD BANDING IN NORTH AMERICA:
THE FIRST HUNDRED YEARS**

Edited by

JEROME A. JACKSON,

WILLIAM E. DAVIS, JR.

and

JOHN TAUTIN



CAMBRIDGE, MASSACHUSETTS
Published by the Club
2008

MEMOIRS OF THE NUTTALL ORNITHOLOGICAL CLUB

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15. Bird Banding in North America: The First Hundred Years. Jerome A. Jackson, William E. Davis, Jr. and John Tautin, editors. 2008. 280 pp., 62 figures.

Nuttall Ornithological Club
Cambridge, Massachusetts
© 2008 by Nuttall Ornithological Club
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Printed in the United States of America
ISBN 1-877973-45-9

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Preface

The year 2002 marked the 100th anniversary of scientific bird banding in North America. It all began in 1902 when Dr. Paul Bartsch of the Smithsonian Institution banded 23 Black-crowned Night-Herons at Washington, D.C. He used serially numbered bands with a “Return to Smithsonian Institution” address. Bartsch had his first band recovery in September 1902 and published his work in 1904. Others soon took up bird banding in the US and Canada, and it became a universal and indispensable tool for studying the movement, survival, and behavior of birds. Few, if any, tools have advanced our knowledge of birds as banding has. One need only review recent issues of scientific journals such as the *Auk* and *Journal of Wildlife Management* to grasp the significance of banding to ornithology and the conservation of migratory birds. Few if any tools used by ornithologists have had such a history and culture with devotees, paraphernalia, organizations, publications, and lore.

Today’s North American bird-banding program is remarkable in its scope, diversity, and value to birds and our society. It has expanded greatly from its start in 1902 when one person with simple objectives banded one species at one location. Today, it stretches from the Canadian Arctic to the tropics of Latin America, from Newfoundland to the far Pacific islands, and beyond to places like Siberia, Greenland, and Antarctica. Wherever North American birds go, bird banding is there.

Nearly all living species are, or have been, banded. Currently, 1,200,000 birds are banded, and 85,000 recovered, each year through the North American banding program. More than 66,000,000 birds have been banded since the beginning of the program, and 3,700,000 have been recovered and reported to the banding offices. Millions more have been recaptured or re-sighted by banders.

Banders include federal and state conservation agencies, university associates, avocational ornithologists, bird observatories, environmental centers, nongovernmental organizations, environmental consulting firms, and other private sector businesses. Served by the U.S. Bird Banding Laboratory and the Canadian Bird Banding Office, more than 6000 banders currently operate in the U.S., Canada, and Latin America.

Today’s banders augment traditional capture and banding methods with advanced technology. Many use auxiliary marking techniques such as colored leg bands, coded neck collars, and radio transmitters. Many take

blood and feather samples for chemical assays and DNA analysis, and many use sophisticated statistical models to analyze data. Some use satellite transmitters to track birds in real time over long distances.

Migration was the focus of the earliest banding studies and migration studies continue. But today banding has many broader applications, being used to study avian behavior and ecology, monitor populations, restore endangered species, assess the affects of environmental disturbances, set hunting regulations, educate people about the environment, and to address concerns about human health, safety, and economy. Results from banding studies support national and international conservation programs such as the North American Waterfowl Management Plan, and Partners in Flight.

The knowledge gained from the first 100 years of bird banding in North America led to remarkable accomplishments in ornithology and the conservation of birds. Few, if any, other tools available to the ornithologist were as productive. To recognize banding's critical role in North American ornithology and celebrate its rich history, the symposium "Celebrating 100 years of Bird Banding in North America" was held September 26, 2002 at the Third North American Ornithological Conference, New Orleans, Louisiana.

The Symposium was organized by committee chair John Tautin, who was then Chief of the U.S. Bird Banding Laboratory, Laurel, Maryland; by Lucie Metras former Chief of the Canadian Bird Banding Office, Ottawa, Ontario; by Robert Blohm, then Chief, Branch of Surveys and Assessment for the U.S. Fish and Wildlife Service, Arlington, Virginia; by Sara Morris, Canisius College, Buffalo, New York; and by Beverly McBride, then acting Chief of the Canadian Bird Banding Office, Ottawa, Ontario. Jerome Jackson, Florida Gulf Coast University, Fort Myers, Florida, and William E. Davis, Jr., Boston University, Boston, Massachusetts, were enlisted to edit the proceedings of the Symposium.

The Symposium consisted of a series of oral presentations by accomplished ornithologists who had close associations with banding during their careers. It opened with a historic review of the early formative years of the North American bird-banding program. The main body of the Symposium consisted of presentations covering particular areas of study where banding had been critical, e.g., migration and behavioral ecology. The presentations were scholarly, historic reviews illustrating the importance of banding to the subject area, with empha-

sis on scientific achievements attained through banding. The Symposium concluded with a look to the future of bird banding in North America.

“Celebrating 100 years of Bird Banding in North America” was a great success. It was comprehensive and inclusive, reflecting the diversity of the North American bird-banding program, and chronicling its rich history. It is fitting that the many fine contributions of Symposium participants are compiled for posterity in this volume of the *Memoirs of the Nuttall Ornithological Club*.

John Tautin

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The Early History of Bird Banding in North America

*Jerome A. Jackson*¹

Abstract.—The early history of bird banding in North America has, in previous accounts, almost ceremoniously begun with accounts from early Greeks and Romans, miscellaneous chance encounters of marked birds in Europe in recent centuries, and, of course, with the marking of Eastern Phoebes (*Sayornis phoebe*) by John James Audubon in the early 19th century. I offer my own versions of such here as I describe factors that made the late 19th and early 20th centuries the “right” time for the development of systematic bird banding as a scientific tool.

Born of scientific curiosity, made possible by the metallurgical qualities of aluminum and discovery of an inexpensive process for its manufacture, bird banding in North America was attended and nourished in its youth by young amateur naturalists and local and national news media that reveled in each new report of the travels of marked birds. The incorporation of bird banding into the tool-box of scientists came about as a result of the persistence and influence of a few visionaries. Some were academics. Some were wealthy and could devote much time, energy, and money to banding as they discovered the many kinds of questions that banded birds can help us answer. War, money, and success in an age without computers were impediments along the way. Government control and funding, and leadership from the ranks of amateurs, academics, and government scientists, led to a cascade of discoveries about the mysteries of bird migration, the home life of birds, and the dynamics of bird populations. Bird banding and its many enhancements, by the end of its third decade in North America had become an essential key to understanding and the conservation of birds.

The conspicuousness of birds, their seasonal migrations, and use for food and as “tools” for hunting have for millennia stirred human curiosity and provided reasons for identifying birds as individuals by their natural markings. Stable human communities led to domestication of birds for meat, eggs, and feathers; the keeping of birds as pets; and

¹ Department of Marine and Ecological Sciences, Florida Gulf Coast University, 10501 FGCU Boulevard South, Ft. Myers, Florida 33965

use of birds for racing and sending messages. Such uses of birds as human property led to marking them with symbols of ownership.

Close association of humans with wild birds led to observations of their predictable return to nests and roosts. This knowledge led to use of pigeons, swallows, and occasionally other species taken from nests or roosts and released at a distance to convey messages. Birds were sometimes temporarily marked with daubs of paint or colored threads to identify individuals or to convey a specific message. Marking those birds led to improvements in markers to provide greater durability, less compromise of the bird's welfare, and more information about the bird. Brief written messages were sometimes sent on parchment or other material secured around a bird's leg or neck, giving rise to the use of homing pigeons during war in both eastern and western cultures (Lincoln 1927).

The mysteries of bird migration have always intrigued and challenged observers, and early experience with naturally identifiable individuals provided some answers. Birds identified with a unique, relatively permanent marker that included a return address, thus facilitating help from other human observers, could be a means for better understanding of migration and learning about longevity, the nature of social interactions, and other behaviors. Human curiosity was no doubt a major factor in the early history of bird marking, but early efforts were but minor preludes to the eventual systematic use of bird banding in scientific study of bird migration, other aspects of bird behavior, bird longevity, and other aspects of bird population dynamics.

CONVERGENCE OF INTERESTS AND TECHNOLOGY AND THE BIRTH OF MODERN BIRD BANDING

The marking of birds with metal rings—some on a leg, others around the neck—dates back at least to the sixteenth century (Wood 1945). Many of these birds were the falcons of royalty, but wild birds were marked as well. A Gray Heron (*Ardea cinerea*), found in Germany in 1710 with several metal rings on its legs, might represent an early attempt to systematically mark a bird to later determine its identity if it were recaptured or found dead. The Turkish bander and his or her purpose are unknown. The several rings on its legs, suggest the possibility of multiple captures, although possibly the multiple rings had been used

to visually distinguish this individual from others marked with more or fewer rings (Lincoln 1921, 1938).

The first “bird banding” in North America has been attributed to John James Audubon who, in the spring of 1804, marked with silver “thread” [thin wire] the legs of five nestling Eastern Phoebes (*Sayornis phoebe*; he called them “Pewee Flycatchers”). These were in a nest at the entrance to a cave on his father’s property along Perkiomen Creek in eastern Pennsylvania. He was curious as to whether the nestlings would return to the same area the next year. He had found the old nest prior to arrival of adults in spring and had followed the nest closely, watching as the birds refurbished it and began laying. At first he marked the nestlings with “light thread” which “they invariably removed, either with their bills, or with the assistance of their parents.” He “renewed them, however, until [he] found the little fellows habituated to them; and at last, when they were about to leave the nest, [he] fixed a light silver thread [wire] on the leg of each [nestling], loose enough not to hurt the part, but so fastened that no exertion of theirs could remove it.” At least two of his marked birds returned to nest in the area the next year (Audubon and Chevalier 1840:227).

Since Audubon only marked his birds with wire and included neither numbers nor a return address, the fruits of his experiment, as well as those of his predecessors and many who followed him, were limited to his own observations. Another century passed before the development of systematic banding as we know it today.

Systematic use of bird banding in science followed the meteoric rise of bird banding as a popular endeavor at the beginning of the twentieth century. It was an endeavor brought about by the convergence of several intertwined factors:

- (1) A period of affluence in western nations and increased leisure time as a result of the availability of electricity allowed development of a widespread “nature-study” movement.
- (2) The nature-study movement resulted in the recognition that overhunting and market values for birds and their feathers for ladies’ fashions had diminished populations of many bird species. Professional ornithologists also took note and their attention began to turn from the naming of new species and subspecies to studies of geographic distribution and ecology. At the 1884 meeting of the American Ornithologists’ Union a Committee on the Migration and Geographic Distribution of

North American Birds was established with one charge being to document patterns of bird migration. To achieve this, the Committee sent out 6000 circulars soliciting observers for a unified effort to collect migration, and migration-related data. They were successful in recruiting over a 1000 observers and established observation stations in “every state in the Union, and in every Territory excepting Nevada” (Merriam 1885). This effort resulted in a tremendous volume of data on the timing and general geographic patterns of migration. Ornithological journals and government publications providing the results of these efforts further popularized and promoted the study of bird migration and began to identify questions that needed answers. In addition to notable ornithologists, this continent-wide study of bird migration also involved an army of amateurs. What was missing from the effort was a means by which the movements of individual birds could be monitored, something that was to come with the development of systematic bird banding.

- (3) During the late 1800s, advances in aquaculture led to marking fish in order to learn of their movements and survival (McFarlane et al. 1990), a practice that inspired those interested in bird migration. See also the description of Leon Cole’s work with fish in the paragraphs below.
- (4) Dramatically improved avenues of global communication and widespread media reports of recoveries of marked birds and fish in the final years of the 19th century fed a growing momentum of public interest in migration—creating a corps of observers anxious to join in this early “citizen-science” effort. A public aware of marked birds and the potential to learn of their travels through reporting their recovery was essential to the development and growth of bird banding.
- (5) The crowning factor that facilitated the birth of systematic bird banding at the end of the 19th century was the new, inexpensive availability of aluminum, a metal that was light weight, could easily be flattened, bent, and engraved, and would not rust into oblivion in a short time. It had to bear numbers and an address, the basic information needed for scientific documentation and public participation, and it had to survive the environments birds frequented from season to season.

While other metals had been used to mark birds, it was aluminum and its alloys that would ultimately fill most needs of scientific bird banding. In “support of” the comment by Lincoln (1921:218) that aluminum was not “extensively worked” in 1710 when the Gray Heron banded with metal rings in Turkey was captured in Germany, aluminum had not been discovered until 1808 and it wasn’t until 1854 that it was first commercially produced. It remained more valuable than gold until an electrolytic process was developed in 1886 that allowed massive aluminum production and general availability. The first aluminum companies were founded in the United States, France, and Switzerland in the late 1880s and aluminum didn’t become readily available until several years later (Aicheson 1960, International Aluminium Institute 2000). [The spelling “aluminium” is the international standard in the sciences although the spelling “aluminum” is the common spelling used in the United States.]

In 1890 Hans Christian Mortensen, a teacher in Viborg, Denmark, experimented with banding by marking two European Starlings (*Sturnus vulgaris*) with leg bands made of zinc. He watched those marked birds and concluded that his experiment was a miserable failure; the zinc bands were too heavy and affected movements of the birds (Lincoln 1922a, Preuss 2001). He retained the idea, however, and when aluminum became available in 1899, he tried again, using strips of aluminum that included a number and return address. He was successful in marking 165 starlings (mostly adults) and for his efforts is given credit for initiating scientific bird banding.

Mortensen focused on learning of the movements of the birds he marked and his efforts and returns were widely publicized in newspapers. His choice of starlings as subjects was deliberate and no doubt contributed to his success: Starlings live in areas near humans where they are readily observed, and they nest in nest boxes where they can easily be captured. Mortensen later worked with several other species and in six years he banded over 1500 birds (Preuss 2001).

CARP, LOBSTERS, SNAILS, AND THE BIRTH OF NORTH AMERICAN BIRD BANDING

Although his efforts may have been known to some American ornithologists, it doesn’t seem to have been until 1921 (Lincoln 1921)



Figure 1. Leon Jacob Cole shown later in life. When in his 20s, Cole was the first in North America to suggest the scientific value of bird banding and the first President of the American Bird Banding Association. Photo from McCabe 1979.

that Mortensen's work was acknowledged in American ornithological journals (digital search of SORA [Searchable Ornithological Research Archive]). The idea for systematic banding of birds in North America seems to have arisen independently with Leon Jacob Cole in 1901 (Figure 1). At the Michigan Academy of Science meeting held in March 1901, Cole gave a presentation in which he described the efforts of the U.S. Fish Commission to learn of the movements of fish by attaching numbered tags to them. This, he suggested, might also be done with birds, allowing us to learn of the movements of individuals (Cole 1903a, Wood 1945). Cole was also familiar with Francis Hobart Herrick's (1895) study of the habits of American lobsters (*Homarus americanus*) and was intrigued by the success Herrick had in learning of their movements through individually marking them (Cole 1922).

Cole, from Grand Rapids, Michigan, graduated in the spring of 1901 with an A.B. degree in Biology from the University of Michigan (Dickerson and Chapman 1989). With this interest and perhaps lack of a better offer, Cole stayed on at Michigan as an “Assistant in Zoology,” working on a project to investigate the habits of introduced German carp (*Cyprinus carpio*). He worked on that project for the U.S. Bureau of Fisheries from 1901 to 1903. No doubt the prospect of his new position had been the catalyst for his interest and presentation at the Academy meeting. During his efforts with the project he tagged about a hundred carp with small numbered copper tags attached by copper wire either to a spine of the dorsal fin or to a pectoral fin. These were released into Lake Erie and adjacent waters. He saw none of them again (Cole 1905, 1922), but the experience furthered his determination to tag birds in a similar fashion, understanding that it might help unravel the mysteries of bird migration. Perhaps refinement of the idea came as a result of a method of fish marking that was used at the time: using a metal ring placed around the caudal peduncle—the constricted area just before the caudal fin (McFarlane et al. 1990).

Cole, who had been an active member and Secretary of the Michigan Ornithological Club (Cole 1897), wrote an essay about his bird-banding idea and published his suggestions in the Report of the Michigan Academy of Science, Arts, & Letters (Cole 1902, McCabe 1979). He elaborated on those ideas in the Bulletin of the Michigan Ornithological Club (Cole 1903a) and continued to espouse the scientific potential of bird banding throughout his life (e.g., Cole 1909, 1922).

Percy A. Taverner of Detroit, also a member of the Michigan Ornithological Club, expanded on Cole’s suggestion (Taverner 1904:50-51; Figure 2), suggesting the use of aluminum bands “stamped with a number and bent in the form of the letter C.” These, he said, should be “issued by some central body to avoid confusion and duplication of numbers.” He advocated a central entity for maintenance of records and correspondence concerning returns and recoveries and the need for an address on the bands, although he suggested that adding anything beyond the number was “hardly practicable.” By 1904 he had about 200 bands made and had begun to distribute them to colleagues. True to his belief in a central repository for banding information, he apparently had made arrangements with the AOU, the American Museum of Natural History, and the Postal Service: in addition to a seri-



Figure 2. Percy A. Taverner shown later in life. Taverner and Cole were both members of the Michigan Ornithological Club and Taverner provided additional insight as he elaborated on Cole's idea of banding birds to study their migration. Taverner helped foster the early years of bird banding and was instrumental in recruiting banders in Canada. Photo from McAtee (1948); courtesy of *The Auk*.

al number he included included the message "Notify the Auk, N.Y." on each band (Figure 3). A Northern Flicker (*Colaptes auratus*) banded in Iowa with one of these bands in 1905 was found later that year in Louisiana. The resulting publicity further raised public interest and the recognition of the scientific value of banding.

Bird banding in Canada began in a limited way when Taverner sent bands to James H. Fleming of Toronto, Ontario. Fleming received the bands from Taverner in May 1905, and banded his first bird, an American Robin (*Turdus migratorius*), on 24 September 1905 (J. H. Fleming letter to F. C. Lincoln, 25 April 1922, from the files of the U.S. Bird Banding Laboratory, Patuxent Wildlife Research Center, Laurel, Maryland). Taverner also taught the technique of bird banding to John Thomas "Jack" Miner of Kingsville, Ontario, whose efforts did much to popularize bird banding in its formative years (McNicholl 2007).

Although Cole and Taverner raised the *possibilities* of bird marking, the earliest truly scientific bird-banding efforts in North America

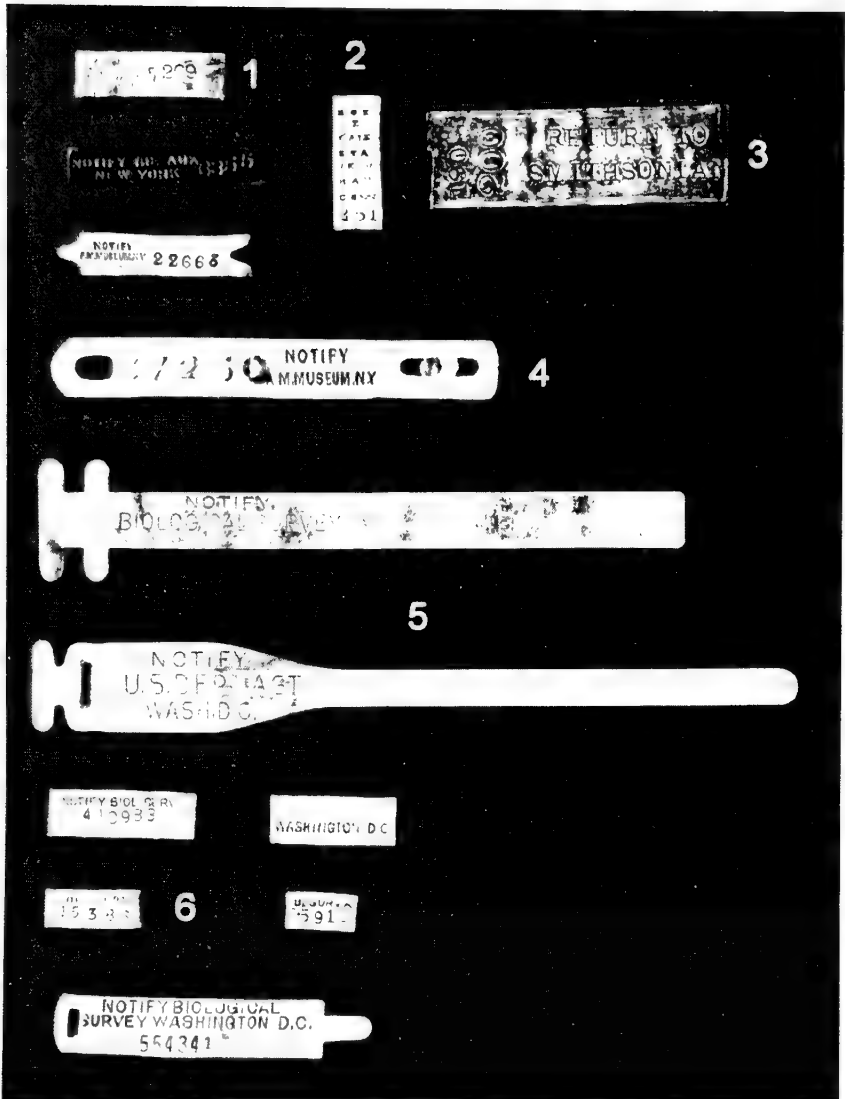


Figure 3. Examples of various bands used in North America: (1) The type of band distributed by the New Haven Bird Club in 1909, including the message "Notify the Auk, N.Y." (2) Earliest type of band used by the New Haven Bird Club with Yale address on it. (3) Type of band used by Paul Bartsch in banding Black-crowned Night-Herons near Washington D.C. in 1902-1903. (4) American Bird Banding Association band; used in about 1910. (5) Types of bands (above and below) used by Alexander Wetmore in banding ducks, 1914-1916. (6) A Biological Survey band on which the abbreviation "Biol" was erroneously printed as "Boil" during the 1920s. Legend has it that the error led to a letter from a finder of a banded bird about having followed the cooking instructions on the band. Original photo courtesy of Bird Banding Laboratory files; edited by J. A. Jackson.



Figure 4. Paul Bartsch, a Smithsonian scientist, banded Black-crowned Night-Herons in 1902-1903, becoming the first person to use bird banding for scientific purposes in North America. Photo courtesy of Bird Banding Laboratory files.

were those of Paul Bartsch of the U.S. National Museum (Figure 4). Bartsch was interested in the dispersal mechanisms of aquatic snails and it occurred to him that snails might move onto the feet and legs of aquatic birds and thus be carried by them from one body of water to another. He was familiar with a nesting colony of Black-crowned Night-Herons (*Nycticorax nycticorax*) and banded 23 nestlings in 1902-1903 (Bartsch 1904).

As with Bartsch's work, other early banders focused their efforts on nestlings. There were three reasons for this: (1) nestlings were easy to "capture," (2) many of the early bands were solid rings cut from tubular aluminum, thus they had to be slipped over a nestling's foot before the foot had grown to adult size (bands that could be slipped over an adult's foot could just as easily slip off), and (3) aluminum that was produced at the time was somewhat brittle and did not bend easily without breaking, thus the solid rings which required no bending were sturdier.

Through 1910, most of the bands provided by the American Bird Banding Association (see discussion of this organization below) were solid rings. The two drawbacks of solid rings were that (1) they were much more difficult to engrave, and (2) they limited the activities of banders to work during the nesting season (Cole 1909).

Perhaps the definitive statement as to the nearly simultaneous and explosive birth of scientific bird banding that was underway is the one *not* found in the Proceedings of the Fourth International Ornithological Congress, held in London in June 1905. There is no mention of bird banding, bird ringing, or any similar effort to mark birds, although already there were several bird-banding projects underway in Europe (Lincoln 1925). Bird migration, however, was a major topic. At the opening session on migration, Otto Herman (1907:44) declared that our understanding of bird migration “will only be arrived at by systematic observations extending as far as possible over the whole area covered by the migrations.” He went on to suggest: “The methods . . . hitherto followed cannot . . . lead to any positive result, and ought to be altered. . . . Our chief aim should . . . be the organization of a uniform process and an attempt to carry it out as far as possible.” Little did he know that the methods of studying bird migration were already being altered in a major way.

The efforts of Mortensen and others in Europe, and those of Leon Cole and Paul Bartsch in North America, while reaching public media, were not yet well-known within the American scientific community. In 1903 Cole (1903b) noted the banding efforts of the German Ornithological Society at Rossitten, but later (Cole 1910) suggested that initially he had been unaware of the work of Mortensen, the several banding efforts that had been underway in Europe, and the work of Bartsch at the U.S. National Museum. Bird banding, did, however, meet with some interest from “officialdom” by 1907: Henry Oldys (1908), then in charge of game protection for the U.S. Bureau of Biological Survey had been informed of a hen Canvasback (*Aythya valisineria*) that had been shot in October 1907 in Massachusetts and was bearing a band with the inscription “T. J. O. D. 48.” He published a note in *The Auk* seeking the identity of the bander, noting: “It would be interesting to know who banded this duck and for what purpose.”

THE NEW HAVEN BIRD CLUB AND THE BIRTH OF ORGANIZED BANDING

On 3 April 1907, Leon Cole was among the 60 birders who met in New Haven, Connecticut, to organize the New Haven Bird Club. Their focus was on learning about birds through observation rather than through collections. Under Cole's influence, bird banding quickly became a major focus of their activities. Cole chaired a committee that also included Louis B. Bishop and Clifford H. Pangburn whose goal was to begin an active bird-banding program.

In the fall of 1908, they acquired aluminum bird bands stamped with unique numbers and the return address "Box Z, Yale Sta., New Haven, Conn." At first they primarily used "closed bands" (solid metal rings) and focused efforts on banding nestlings. Strips of aluminum with the same address stamped on them were sometimes used to mark adults, but the aluminum of the time was somewhat brittle and difficult to work with. Bands of different sizes were created in the manner of those made by P. A. Taverner: long strips of aluminum were cut off to create a band of an appropriate length for each bird.

Cole described the New Haven efforts at the American Ornithologists' Union meeting in Cambridge, Massachusetts, in November 1908 (Cole 1910). His presentation obviously generated considerable interest: along with mention of his paper in the proceedings of the meeting is the note that "Remarks followed by Drs. Hodge, Fisher, Bryan, Roberts, the author, and Messrs. Murdoch and Ells."

The New Haven Bird Club banding was the first truly collaborative banding effort in North America and Cole (1909), in an article in *The Auk*, used it as a model to "outline a plan by which it is hoped that much data of a definite kind can be secured, not only as to the great migrations of birds, but regarding their minor movements as well." His proposal took note of his friend P. A. Taverner's earlier notice in *The Auk* (Taverner 1904) soliciting information from ornithologists who found one of his banded birds, and also Taverner's use of the simpler address message: "Notify The Auk N. Y." Use of unique numbers for every band, publicity about banding, and a single, simple address for reporting information about banded birds might be more likely to produce results. Cole's proposal also echoed Taverner's recommendation of a central office for maintenance of records and issuance of bird bands. (Taverner 1904, McAtee 1948).

The response to Cole's proposal was swift: 5000 (Cole 1910) to 7500 (Wood 1945) numbered bands of up to eight sizes were prepared following Taverner's lead with the three-line inscription:

NOTIFY
THE AUK
NEW YORK

According to Wood (1945) some of the bands bore the inscription: "Notify Am. Museum, N.Y." or "Notify A.M., N.Y." "Something over 5000" (Cole 1910:157) bands were distributed before the end of the 1909 nesting season. Only 800 (Wood 1945) to perhaps 1000 (Cole 1910) of them were placed on 73 species of birds by 44 individuals (Wood 1945). By the end of 1909, about 30 returns had been received (Cole 1910, Cleaves 1913). Cole summarized the results of 1909 banding efforts under the New Haven Bird Club auspices, noting that most of the bands were closed rings, meaning that only nestlings could be banded and that multiple sizes were needed for banding a diversity of birds. He noted that flat bands would allow adults to be banded and suggested that "two sizes of which have been found practicable to use on birds ranging in size from warblers to ducks and the larger owls" (Cole 1910:156). The long bands were cut by the bander to an appropriate length or were overlapped to fit. Those who had responded to Cole's offer of bands included individuals from several states including Oregon, Montana, and several Midwestern as well as east-coast states.

THE AMERICAN BIRD BANDING ASSOCIATION

On 7 December 1909, in New York, at the next AOU meeting, Cole presented the results of banding efforts that had taken place during the previous year. His paper was again followed by remarks of others. The next day Cole's collaborator from New Haven, L. B. Bishop, who apparently was not officially on the program to present a paper, "explained a proposed method of Tagging Wild Birds, and called attention to an association in Connecticut recently organized to study this subject" (Sage 1910). The purpose of his "impromptu" addition to the program was likely to call attention to a meeting that evening at the Hotel Endicott (where AOU members had dinner) for the purpose of organizing the American Bird Banding Association (ABBA). At dinner

that evening, Cole and his colleagues circulated a paper describing their proposed organization of a banding organization and asking for signatures of those interested in joining them. The group met after dinner. The meeting was independent of the AOU meeting and not mentioned in the AOU minutes. Among those in attendance were such ornithological luminaries as Arthur A. Allen, Charles F. Batchelder, Arthur Cleveland Bent, Ruthven Deane, Jonathan Dwight, Jr., Edward Howe Forbush, Bruce Horsfall, Lynds Jones, Waldon DeWitt Miller, T. Gilbert Pearson, Thomas S. Roberts, and Witmer Stone. About 30 individuals became charter members of the ABBA, paying annual dues of one dollar. Leon Cole was elected President of the organization; C. J. Pennock, Secretary-Treasurer; and Louis B. Bishop, Glover M. Allen, and Thomas S. Roberts were additional members of the Executive Committee (Cole 1922).

Although there were many supporters of this new activity, banding was looked at by some—even within the scientific community—with skepticism. Cleaves (1912:280) noted that efforts to raise funds to support the work of the ABBA were met with some letters of protest “setting forth the cruelties involved in such a practice.” Others refused support because banding had not yet proven itself. In the spring of 1910, the ABBA Executive Committee distributed a flier seeking membership and financial support for banding (Cole et al. 1910), noting:

“For the benefit of any who may fear that the prosecution of this work may be detrimental to bird-life, it should be stated that the Association is thoroughly in sympathy with the conservative efforts of the Audubon Societies of this country. The shooting of birds for the recovery of bands is in no way a part of the scheme. It is desired to have banding done only by reliable persons, and should it be found that the banding of any species is doing harm, either from disturbing of the nestlings, or from other causes, such work on that species will be discountenanced. As a guaranty of good faith it may be mentioned that the present membership includes not only many of the foremost members of the American Ornithologists’ Union but also leaders of the Audubon movement in America.”

Less than six months after its founding, the ABBA faced an important crisis. Its new president, who had been so instrumental in stirring interest in the region and in the founding of the organization, left New

England to assume a new position at the University of Wisconsin. Cole continued as President until the spring of 1911 when he left for Europe for the summer. Ernest Harold Baynes of the Meriden [New Hampshire] Bird Club then took over direction of the organization and the task of raising funds (Cole 1922). Almost nothing was accomplished by the ABBA in 1910 or 1911. In the fall of 1911, however, W. W. Grant of the Linnaean Society of New York offered the services of the Linnaean Society to sponsor the ABBA's work. A Linnaean Society committee was formed to raise funds for the purchase of bands, record forms, and filing cabinets. Grant, and Howard H. Cleaves, ABBA's new Secretary, handled the fundraising, record keeping, and correspondence that were needed to keep the banding program moving forward. Seven-thousand-five-hundred bands of the same style as those used by *Country Life, London*, were purchased. These included eight different sizes according to Cleaves (1913), although a record of bands purchased by ABBA during the years 1912-1915 (handwritten table in ABBA records at the U.S. Bird Banding Laboratory) suggests that there were only seven sizes in 1912. By 1914, there were 11 sizes being used.

Instead of using the inscription "Notify the Auk N.Y.," however, the bands read: "Notify Am Museum N.Y."—an inscription more readily recognized by the general public. In the spring of 1912, notices of the availability of bands and the efforts desired appeared in *The Auk*, *Bird-Lore*, and *Country Life in America*. At least 4173 bands were distributed to 44 individuals from across North America: north to Nova Scotia, south to Florida, and west to Montana. Seventy-three species including at least 800 individuals were banded under the ABBA program in 1912. Among the banders were A. A. Saunders of the U.S. Forest Service in Montana; Ernest Harold Baynes of Meriden, New Hampshire, who helped organize a nest-box program through the Meriden Bird Club and banded a diversity of cavity nesting birds; and Harrison F. Lewis of Yarmouth, Nova Scotia, who organized children to locate nests, thus enlisting their help in banding (Cleaves 1913).

By 1912, bird banding was generally recognized in Europe and North America, yet, while scientific ornithology greeted bird banding as having some promise, it was also greeted with skepticism. In a treatise on *The Migration of Birds*, T. A. Coward (1912:71) noted:

"The custom, now fortunately becoming wide-spread, of marking birds by affixing a numbered metal ring to one leg, may help elu-

cidate . . . many . . . problems, but until a large number of results are collected it is unwise to draw conclusions. Almost every month the recovery of some of these marked birds is noted in the scientific journals, but so far, beyond indicating the minimum distance travelled [sic] by individuals, little can be proved.”

Howard Cleaves championed bird banding and guided the efforts of the Linnaean Society on behalf of the ABBA. He noted (Cleaves 1913:253) that bird banding “is not the work of a limited circle but the duty of many. . .” fostering involvement of Americans of all ages and walks of life in the effort to learn the intricacies of bird migration. Cleaves acknowledged that many had been skeptical of the practicality and utility of banding, but by 1912 notable returns were already being

**DIRECTIONS
FOR
BANDING BIRDS**



A BANNED BIRD

AMERICAN BIRD BANDING
ASSOCIATION

AMERICAN MUSEUM OF NATURAL HISTORY
NEW YORK CITY

Figure 5. Pamphlet distributed by ABBA during the second decade of the 20th century to explain banding and recruit banders. Louis Agassiz Fuertes provided the illustration of the banded Yellow Warbler (*Dendroica petechia*). Photo by J. A. Jackson.

reported—both by banders and the public. Records of the ABBA at the U.S. Bird Banding Laboratory indicate that 7500 bands had been purchased in 1912, 6700 in 1913, 12,800 in 1914, and 11,000 in 1915.

A pamphlet distributed by ABBA (Figure 5), with a cover illustration of a banded Yellow Warbler by Louis Agassiz Fuertes, provided information on how to band birds and what we might learn from banding. Some individual banders, through eccentricities of their efforts, kept banding in the news.

One of the most colorful and well-known among early avocational bird banders was John Thomas “Jack” Miner of Kingsville, Ontario. Although born in Ohio, Miner’s family moved to Kingsville during his youth. There the family produced ceramic drain tiles, a business that provided them a secure income. In 1904 Jack established a bird sanctuary on his property, taking advantage of ponds resulting from the removal of clay for manufacture of bricks. He began with a pair of Canada Geese (*Branta canadensis*) whose wings had been clipped (Miner 1931, 1934), using the geese as lures to attract wild birds. He also provided housing and feeders for species ranging from Purple Martins (*Progne subis*) and Eastern Bluebirds (*Sialia sialis*) to ducks and geese. By providing food and a safe environment, he soon had flocks of migrant geese using his ponds during migration. In 1909, intrigued with news stories of banded birds being recovered at distant sites and curious about the origins and destinations of the birds visiting his sanctuary, Miner produced serially numbered bands with his address and began banding ducks. It wasn’t until 1915 that Miner banded his first wild Canada Goose that had been attracted by his captive birds. Miner’s work generated considerable publicity for banding because he included a Bible verse on each band, using the banded birds as flying missionaries.

In North America, World War I took a toll, but so too had persistent problems with obtaining supplies of bands and keeping up with the flow of incoming banding reports of birds banded, and recoveries and acknowledgments to those who had submitted recoveries (Cole 1922). The resources of the ABBA and Linnaean Society were limited and all filing and correspondence were done by hand. Banding continued and grew in many areas, but public interest waned and growth, in a sense, was mired in success. While many individuals and institutions in Europe initiated banding programs, the diversity of countries, govern-



Figure 6. Samuel Prentiss Baldwin, founder of the first true banding station in North America and the individual who showed us the possibilities of banding and learning from banding songbirds. Photo from Kendeigh (1940); courtesy of *The Auk*.

ments, cultures, and languages, as well as the exigencies of two World Wars, prevented development of a uniform banding scheme and overall coordination of returns there.

S. PRENTISS BALDWIN, BANDING STATIONS, AND THE BANDING OF ADULT BIRDS

Samuel Prentiss Baldwin (Figure 6) graduated from Dartmouth and earned a law degree from Western Reserve University in 1894, but quit his law practice in about 1900 (Herrick 1939, Kendeigh 1940). He had married the daughter of a prominent industrialist and was financially independent. Devoting much of the rest of his life to studying birds, he erected numbers of bird houses around his estate at Gates Mills, east of Cleveland, Ohio. To his dismay, many of the nest boxes were usurped by House Sparrows (*Passer domesticus*) and, in about 1913-14, Baldwin began a program to eliminate House Sparrows from the area

and simultaneously became interested in bird banding. His banding efforts were stimulated in part—and certainly enhanced—by the promotion of sparrow control and publication in 1912 of plans for what came to be known as the “government sparrow trap” (Anonymous 1912).

Although it was the House Sparrow that led Baldwin to begin trapping birds, he had a specific interest in House Wrens (*Troglodytes aedon*) and his work with House Wrens and other birds he trapped put a major focus on the broad range of things that might be learned by systematic trapping and banding of birds (e.g., Baldwin 1919; 1921a, b; 1928). Although he had been active in the ABBA, he was a relatively new member of the American Ornithologists’ Union in 1919 when he presented a paper at their annual meeting on “Bird Banding by Systematic Trapping.” He stunned the audience with the wealth of information he had obtained from marked birds (Lincoln 1932). Baldwin’s presentation at the AOU meeting was followed a month later by publication of his monograph of the same title by the Linnaean Society of New York. When Fred Lincoln became head of the Bird Banding Laboratory for the Bureau of Biological Survey, Baldwin seemed to serve as his non-governmental assistant, the needed liaison to the cadre of amateur banders working with songbirds. “Bird Banding by Systematic Trapping” was used by the new Bird Banding Lab as their first instruction manual for banders (Baldwin 1931). Baldwin’s methods of systematic trapping were also incorporated into early government bird-banding manuals (Lincoln 1924, Lincoln and Baldwin 1929).

At the 1922 AOU meeting, the second issue of *The Auklet*, an occasional irreverent spoof of AOU members and the AOU’s journal, *The Auk*, was distributed as a banquet favor. In it, Baldwin’s leadership role in the growing bird banding movement was parodied with reference also to William I. Lyon, then secretary of the Inland Bird Banding Association, Fred Lincoln, and Massachusetts ornithologist and president of the New England Bird Banding Association, Edward Howe Forbush: “Bandmaster Baldwin is said to be Lyon low Forbushes in which Lincoln’s Sparrows may be trapped.”

During the 1923 AOU meeting in Cambridge, Massachusetts, Baldwin, then President of the Inland Bird Banding Association, continued his broader leadership role among bird banders. He hosted banders in his hotel room for the purpose of delineating boundaries for regional banding organizations. Those present included representatives from Canadian and U.S. banding offices and from the New England, Eastern,

and Western bird-banding associations (Lyon 1923). As a banquet favor, attendees at the AOU meeting received a copy of *The Auklet*, which again included a satirical piece on Baldwin and the rising tide of bird banding among ornithologists.

Baldwin was also active on the political front on behalf of bird banding (Baldwin 1923). In an insert mailed with the December 1923 *Wilson Bulletin*, as President of the Inland Bird Banding Association, he urged readers to support the Game Refuge bill then before Congress. A similar bill had narrowly failed in the previous session of Congress and he advised readers to find out how their Congressman “voted on this matter and, if any opposed it, write to the Congressman and find out *what is the matter with him.*”

In recognition of his accomplishments and leadership in the development of songbird banding, Baldwin was given the unique distinction of being made honorary President of the Northeastern, Eastern, Inland, and Western bird-banding associations (Kendeigh 1940).



Figure 7. Alexander Wetmore, independent of other banding efforts in North America, and using bands with a Biological Survey return address, demonstrated the promise of banding as a tool in wildlife management. Photo courtesy of Bird Banding Laboratory files.

THE DAWN OF GOVERNMENT RECOGNITION, CONTROL, AND USE OF BIRD BANDING

Between 1914 and 1916, Alexander Wetmore (Figure 7) of the Biological Survey studied massive mortality of waterfowl in the Bear River marshes at the north end of the Great Salt Lake in Utah (Wetmore 1918, 1921). In the course of his efforts he banded 1241 birds including individuals of 23 species. Most were ducks. These were banded with bands provided by the Biological Survey rather than by the ABBA. They included a unique number and one of two messages: (1) "Notify U.S. Dept. Agt., Wash., D.C."—the "Agt." being a bizarre abbreviation for "Agriculture." And (2) "Notify Biological Survey, Washington, D.C." Wetmore received 182 returns from his banding, enough to impress Edward W. Nelson, then Chief of the Biological Survey (Lincoln 1933:69).

Wetmore's work with waterfowl, in combination with Baldwin's work with songbirds, demonstrated the feasibility of capturing large numbers of birds. Nelson was convinced of the utility of banding for population studies and wildlife management. On 26 November 1919, Nelson, as Chief of the Biological Survey, wrote to the Linnaean Society of New York and offered to take over the management and coordination of North American bird banding (Lincoln 1933). On 9 December 1919, his offer was accepted, and on 1 March 1920, Frederick C. Lincoln reported for work as head of the government bird-banding effort. E. W. Nelson, Chief of the Biological Survey announced the transition in several major scientific publications as well as in the popular press, seeking to gain support and alleviate bander fears that they might not be able to continue banding (e.g., Nelson 1920).

THE SHIFT TO GOVERNMENT CONTROL AND THE EFFORTS OF FREDERICK LINCOLN

Frederick Lincoln had been Curator of Birds at the Colorado Museum of Natural History from 1913-1918, then, although still nominally in that position, during 1918-19, he served in the U.S. Army Signal Corps helping to direct their carrier pigeon program through the

Smithsonian. His museum and carrier pigeon administrative experience seemed to make him the perfect person for the job (Gabrielson 1962). [Photos of Frederick Lincoln are included in other chapters in this volume.]

Beginning in 1920, bird banding in North America was coordinated between the U.S. and Canadian governments, with a uniform banding scheme, centralized supply of bands and data collection, and considerable uniformity in language and culture. It was poised to facilitate great progress in our understanding of bird migration, longevity, and other aspects of population dynamics. Lincoln was quick to recognize the advantages of centralized control and used these arguments with banders to further justify government involvement and to promote collaborative efforts (Lincoln 1925). Banding remained an effort that was largely carried out by volunteers and Lincoln continuously sought new banders. In 1922, for example, he expounded on the information that was being obtained from banded waterfowl and its importance to managing game birds, yet also noted that there were then only five volunteer banders who were focusing on waterfowl (Lincoln 1922b).

In 1921 Leon Cole reviewed the growth and history of bird banding in North America for the *Wilson Bulletin* (Cole 1922). He noted the recent resurgence of interest in banding, attributing it to S. Prentiss Baldwin's development and promotion of methods to capture and band adult birds rather than the "haphazard banding of nestlings" (Cole 1922:112).

Banders themselves sought new banders and took every opportunity to recruit them. They were energized perhaps by the novelty of banding, perhaps by the government endorsement, perhaps by the potential reward of having one of their banded birds found at some distant place. Beginning in 1922 the Wilson Ornithological Club (now the Wilson Ornithological Society) provided pages in the *Wilson Bulletin* for a special section called the "Bird Banding Department." These pages provided opportunities for reporting returns and news of banding operations. In March 1925, "Bird Banding Department" became "Bird Banding Notes." In the next issue, "Bird Banding Notes" became "Bird Banding News" and the section continued publication under that title through September 1928, under the direction of William I. Lyon of Waukegan, Illinois. Beginning in 1923, a special section of *The Condor* called "With the Bird Banders" filled a similar niche in western North America.

A recurring theme of these pages in the *Wilson Bulletin* and *Condor*—and to some extent the pages of the regional banding journals and *North American Bird Bander* which were their successors—was the need for more banders. Through the 1920s the theme was a campaign. As Talbot (1922) put it: “WANTED—More Bird Banders, anywhere, everywhere. If you cannot be one yourself, make it your duty to catch and tag someone else.” Lincoln (1923) promoted bird banding as “the sport which is also a Science.”

While much had been learned and the essence of modern bird banding was in place by the time the government took control, the foundation of scientific bird banding was merely a few bricks high. Stability and rapid growth of bird banding as a scientific tool (largely among serious avocational ornithologists), and widespread use of bird banding data, came quickly after 1920. The growth was powered by the government control and endorsement facilitated by Lincoln and was very much dependent on the growing cadre of volunteer bird banders, reports of returns and recoveries in news media, and a receptive and responsive public.

The hundreds of volunteer banders had not only their enthusiasm and license and encouragement from the Biological Survey, but also a strong leader in Frederick Lincoln. Lincoln provided direction and summaries of accomplishment not only through scientific publications and the banding pages in the *Wilson Bulletin* and later in regional banding journals, but also through *Bird Banding Notes*, a periodic “unofficial” publication of the Bird Banding Laboratory. Curiously, in the inaugural issue of *Bird Banding Notes* (and on the first page of subsequent issues) it was noted that *Bird Banding Notes* was “not a publication in any sense of the word, being issued merely for the information of our collaborators, not for general distribution” (Anonymous 1922a). In the second issue, however, bird banders were also cautioned that: “As these Notes are issued solely for distribution among bird banding collaborators they are therefore the official means of bird banding communication and every station operator should bear this fact in mind” (Anonymous 1922b).

Bird Banding Notes, an irregular mimeographed series published between 1922 and 1966, included information about permits, trap designs, collaborative studies, baits, methods for handling and holding birds, unusual captures, predators at traps, information on numbers of banders, new banders, numbers of birds banded, returns, and of course,

the perennial problems with obtaining bands and admonitions to get banding schedules in on time (see also Tautin, this volume). Significantly—and unlike its current resurrection as *Memoranda to All Banders* (MTABs)—*Bird Banding Notes* in its early years was a “non-publication” of the banders as well as one for the banders. It became a repository of anecdotes submitted by banders and the publication of these anecdotes not only provided interesting reading, but likely was important in increasing bander interest, morale, understanding, development and improvement of new techniques, and participation in cooperative efforts. These “bander to bander” functions of *Bird Banding Notes*, however, were ultimately passed on to regional banding organizations (see also Morris et al., this volume).

PROMISES FULFILLED AND PROSPECTS FOR THE FUTURE

Leon Cole ended his 1922 review of the history of bird banding by pointing to the formation of the New England Bird Banding Association (later to become the Northeastern Bird Banding Association and today the Association of Field Ornithologists) (Davis 2000). He recognized that banding had fulfilled his hopes as a tool that would unlock some of the secrets of migration. He saw prospects for other banding organizations and predicted their need and the need for permanent banding stations—ones that “have a greater permanency than can be assured on the basis of purely voluntary cooperation.”

In 1923 the New England Bird Banding Association recognized a need for banders to become better educated on bird biology and got Glover M. Allen, then president of the Nuttall Ornithological Club, to give a series of ten lectures on *Elements of Ornithology*. These were to be complemented by another lecture on bird banding, to be given by Professor Alfred O. Gross of Bowdoin College. All were then to be made available in printed form for a small fee (Wilson 1923, Gross 1925).

In a less “enlightened” moment in 1924, in response to bander problems with shrike predation at traps, Henry C. Wallace, the Secretary of Agriculture, issued a blanket permit allowing banders to kill shrikes (*Lanius* spp.; Wallace 1924). The Secretary’s Order stated “the holders of Federal permits for capturing migratory birds for scientific banding

purposes may kill shrikes in any manner, except by the use of poison, when found in the immediate vicinity of bird-banding stations, for the purpose of preventing them from killing other birds in or around the traps." Not only was the killing approved, but the birds thus killed "and every part thereof," were to "be totally destroyed as promptly as possible, and shall not be possessed, transported, or shipped in any manner except for the purpose of destruction in the immediate vicinity where the bird was killed." Apparently no mention of this was made in the primary ornithological journals (search of SORA database). The possibilities of studying the "collected" shrikes or their preservation as scientific specimens were not considered.

In 1925 Joseph Grinnell published an interesting prelude to what was to become one of the most important tools of bird banding—mist netting. During the first two decades of the twentieth century there was a massive immigration (more than four million) of working class Italians. There had been political upheaval in Italy and these were the resulting refugees of economic woes. In Italy the prototypes of our mist nets had been used to capture songbirds as a staple of their diet. The new Italian immigrants brought their nets with them and continued to net songbirds in North America—to the dismay of those in the growing conservation movement and in violation of the international agreement between the U.S. and Canada calling for the protection of migratory birds.

In the fall of 1923, Grinnell, then Director of the Museum of Vertebrate Zoology at Berkeley, was the recipient of 133 dead birds that had been confiscated when four Italian men had been arrested for illegally killing them. The men had used five bird nets and had driven birds into the nets. The birds had been captured within an hour and a half in one ravine. Grinnell prepared the birds as museum specimens and found that they showed no signs of trauma and their plumage was intact and in good shape. Immediately he thought how much more efficient the nets were than the shotgun used for collecting. But then he also realized that if the birds were caught unharmed "the possibilities in netting birds for banding loom up. The avowed aim of bird banders under the leadership of the Biological Survey, is to band birds in *quantity*—the more the better. . . . The method of netting, which the 'Italians' can teach us if we grasp the opportunity to be taught, is the only adequate wholesale method in the banding campaign that has yet been suggested for the usual run of small land-birds" (Grinnell 1925:250). He petitioned the

California Fish and Game for the nets that had been confiscated so that he might test their potential for scientific use, but was turned down. They expressed surprise at his “audacity,” suggesting that if his request were honored, “a bad example would be set to ‘Italians’” (Grinnell

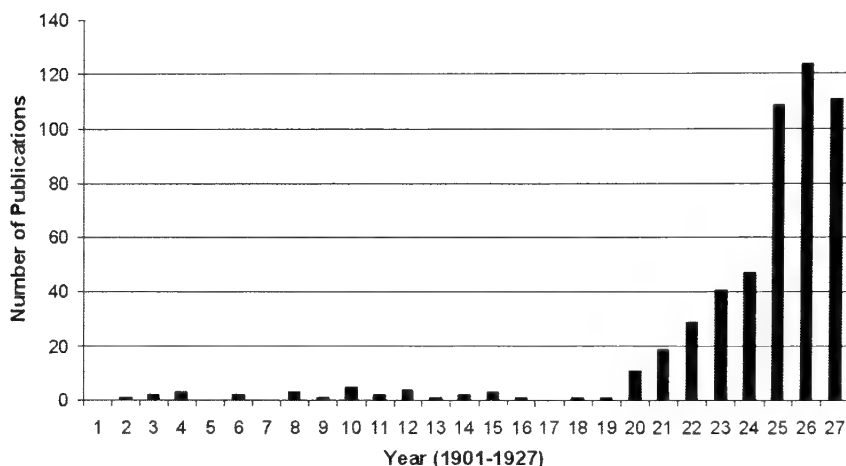


Figure 8. Growth in the numbers of bird-banding-related publications by year, 1901-1927. Data based on entries in the annotated bibliography of banding by Lincoln (1928).

1925:249). It would be more than two decades before mist nets were used for banding in North America.

Lincoln (1928) published an annotated bibliography of bird banding in North America covering the major ornithological journals, including the then new banding journals, and whatever other publications he could find from its inception through 1927. Analysis of his bibliography demonstrates an initial slow growth in scientific bird banding followed by the tremendous impact of government control of banding (Figure 8): Of 513 titles listed, only 32 were published prior to 1920, followed by near geometric growth thereafter. Bird banding had come of age as a scientific tool.

Missing from Lincoln’s (1928) bibliography was an interesting paper on “Bird banding and bird migration work at Rossitten on the Baltic Sea” that was published in *The Auk* in 1923 (Ahrens 1923). This paper, on the face of it, had nothing to do with bird banding in North America. It not once mentioned anything about banding in North

America—hence its logical exclusion from the bibliography. On the other hand, it also had much to do with the *prospects* for bird banding in North America. The station at Rossitten had been founded by the German Ornithological Society for the study of bird migration and began operations in 1901. Between 1903 and 1919, nearly 8000 birds had been banded there. While focusing on Rossitten, Ahrens drew attention to the many things that could be learned through banding and the handling of birds during banding. He mentions, for example, the examination of birds for molt and plumage characteristics and their changes, and he may well have provided seeds that facilitated the development and goals of banding stations and bird observatories in this country. He demonstrated how migration routes of particular species had been delineated through banding. He ended by indicating that “Observations now extending over 19 years have proved conclusively, that banding is not injurious to the birds and that it does not disturb or change their habits.”

Many of the techniques in use today were developed by trial and error by 1925. By 1927 color bands were readily available and were being used in studies of social behavior (Whittle 1927, McDonald et al. this volume). Each new issue of the banding journals brought new ideas for trap designs and solutions to problems reported. From the beginning there had been concern that banding might be injurious to birds; questions were continually raised and banders adopted as normal operating procedure that the welfare of the birds had to come first.

ACKNOWLEDGMENTS

I thank William E. Davis, Jr., and my wife Bette J. S. Jackson for their careful reading of an earlier draft of the manuscript and excellent suggestions that have improved it. Additional insights and assistance were generously provided by Stuart Houston, John Tautin, Mary Gustafson, and Monica Tomosy.

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Roles and Contributions of Banding Organizations to the North American Banding Program

*Sara R. Morris¹, Brenda Dale²
and
Mary Gustafson^{3, 4}*

Abstract.—Banding organizations have served valuable roles in the education and training of banders, dissemination of banding data, and development of cooperative banding projects. North American banding associations have been important in coordinating efforts of banders, initially by providing bands and helping revise the bird banding manual. More recently, the North American Banding Council was established to help promote standardization of skills among banders and to encourage ethical treatment of birds, and the dissemination of the results of banding studies. Regional banding associations, which began in the 1920s, have provided banders with regular meetings and publications, and their meetings have traditionally been opportunities for banders to learn or refine skills, present or learn about banding projects, and develop collaborations. These organizations have provided banders with publications that focus on banding techniques and results, thus both encouraging banders to publish and providing banders with new field methods. Additionally, the Northeastern Bird Banding Association was instrumental in increasing the availability of mist nets to bird banders. Bird observatories have provided additional opportunities for the training of banders and for cooperative projects and long-term studies. Banding associations and bird observatories have linked avocational and professional ornithology, providing for the growth of each and the advancement of bird banding as a scientific endeavor.

Banding and the use of banding data have been greatly enhanced by a variety of organizations ranging from North American and regional banding associations to bird observatories. Their contributions are var-

¹Canisius College, Buffalo, NY 14208

²Canadian Wildlife Service, 200-4999 98th Ave., Edmonton, AB T6B 2X3 Canada

³USGS Patuxent Wildlife Research Center, Bird Banding Laboratory, 12100 Beech Forest Road, Laurel, MD 20708-4037,

⁴Current address: Texas Parks and Wildlife Department, 2800 S. Bentsen Palm Drive, Mission, TX 78572

ied and have led to significant advancements in the scientific quality of bird banding and our understanding of birds. Coordination among banders, continued bander education, sharing information about banding techniques, encouraging cooperative banding research, disseminating the results of banding studies, and providing small grants for research are among the important contributions of these organizations. The number of organizations established during the first hundred years of bird banding in North America and their continued support by both professional ornithologists and avocational banders is testament to their importance to the North American banding program.

NORTH AMERICAN BANDING ORGANIZATIONS

American Bird Banding Association.—The early history of North American banding efforts, which were coordinated by the American Bird Banding Association, is described in Cleaves (1913) and Wood (1945) and Jackson (this volume). This organization, founded in 1909, was centered at the American Museum of Natural History, provided bands to members, began organized communication among banders, and maintained files of bands issued and recovered. In 1920, the American Bird Banding Association dissolved and turned its bands over to the U.S. Department of Agriculture, Bureau of Biological Survey, which formally took over the role of coordinating banding activities, issuing bands, and maintaining and processing banding records in the United States (Wood 1945, Jackson this volume).

The North American Council of Bird Banding Associations (NACOBBA).—In 1958, the North American Council of Bird Banding Associations was formed to be a liaison group among regional banding clubs (the Northeastern, Eastern, Inland, and Western Bird Banding associations), and the Ontario Bird Banding Association joined in 1959 (McNicholl 1994). The council was involved in revising the bird-banding manual for the Bird Banding Office of the Fish and Wildlife Service during the 1960s. There is little information about the other roles of the council, although in 1963, the chair of the council announced that President John F. Kennedy had signed a bill exempting mist nets from duty. The council gradually became inactive and was dissolved by 1973, when the Northeastern Bird Banding Association council minutes indi-

cate that the remaining treasury of the North American Council of Bird Banding Associations was to be donated to the Frank M. Chapman Memorial Fund at the American Museum of Natural History. Following its dissolution, there was no continental-level organization representing bander interests, although its role of communication was taken on when *North American Bird Bander* was created (C. J. Ralph, pers. comm.).

The North American Banding Council (NABC).—In March 1995, nineteen individuals—representing observatories, banding associations, academia, and government—met in Mill Valley, California, in a forum hosted by the Institute for Bird Populations. Attendees represented a variety of bird specialties (landbirds, hummingbirds, raptors) and shared a concern for the future of bird banding. They met to discuss ways to standardize competence at banding skills, improve the quality of banding data, and increase involvement of banders in standardized research and monitoring programs in North America. Forum participants reviewed permitting systems in seven nations outside North America and used this as a basis for discussing training, evaluation criteria, certification, ethics, and partnerships, and for identifying potential models for an improved banding community in North America. They recognized a variety of ways that knowledge and competence could be acquired. These included: independent use of written, photographic, and specimen resources; intensive courses; and work under experienced banders, in combination with experience and self-evaluation. They recommended formation of the North American Banding Council with members from the Ornithological Societies of North America and the bird-banding associations (Figure 1). They also provided a preliminary list of goals that were mainly related to standards, education, and testing.

After consultation, the list of member organizations to be invited was expanded to embrace groups representing waterbirds, shorebirds, and waterfowl. Not all of these groups have remained active in the NABC. Continental representation was ensured through the inclusion of all regional banding associations, the Society of Canadian Ornithologists, and one Canadian member from the International Association of Fish and Wildlife Agencies. Representatives from the Canadian Bird Banding Office and United States Bird Banding Lab were made *ex officio* members of NABC.



Figure 1. The North American Banding Council was established in 1996 and includes representatives of the American Ornithologists' Union, the Association of Field Ornithologists, the Cooper Ornithological Society, the Eastern Bird Banding Association, the Inland Bird Banding Association, the International Association of Fish & Wildlife Agencies, the Ontario Bird Banding Association, the Pacific Seabird Group, the Raptor Research Foundation, the Society of Canadian Ornithologists, the Waterbird Society, the Western Bird Banding Association, the Western Hemisphere Shorebird Reserve Network, the Wilson Ornithological Society, the Canadian Wildlife Service Bird Banding Office (ex-officio), and the USGS Bird Banding Laboratory (ex-officio).

The first meeting of the North American Banding Council was held in April 1996 in Laurel, Maryland. The mission of NABC was, "to promote sound and ethical bird-banding principles and techniques in North America." Its goal was "to increase skill levels of banders by preparing and disseminating standardized training and study materials and establishing standards of competence and ethics for banders and trainers." Short-term goals were set for developing a certification and evaluation program, production of training materials, identification and certification of an initial training pool, and encouraging cooperative efforts in the use of banding. It was clearly set out that evaluation and certification were to be separate from permitting, but efforts to improve standards would indirectly benefit government-regulated banding.

Meetings of the NABC are held at least annually, often in association with scientific or banding association meetings (Figure 2).



Figure 2. North American Banding Council meeting at the Big Sur Ornithology Lab in Andrew Molera State Park, California, in March, 2002. Photograph by Sara R. Morris.

Meetings have been held in Arizona, California, Florida, Louisiana, Manitoba, Maryland, and Missouri, attempting to include banders from a wide geographic range. A web site was established in 1999 and communication among Council member representatives and certified Trainers is electronic.

Good progress has been made on many of the short-term goals. A *Banders' Study Guide*, a *Trainers' Manual*, and group-specific manuals for passerines and near passerines, hummingbirds, raptors, and shorebirds have been completed (Gratto-Trevor 2004, Hull et al. 2001, North American Banding Council 2001a,b,c, Russell et al. 2001). Some of the guides have been translated into French (courtesy of the Canadian Wildlife Service) and Spanish (with the assistance of the Ornithological Council). In 2006 the waterfowl manual was nearing completion and efforts to develop seabird and woodpecker manuals had begun.

An initial pool of trainers was identified by nomination and certified by fiat. Processes were then established for attaining certification as a trainer or bander and for renewal of certification every five years. Protocols for evaluation and certification at both bander and trainer level for landbirds and hummingbirds have been approved and used,

although they continue to be improved. Efforts to develop testing protocols for raptors are in development. The Eastern, Inland, Ohio, and Western Bird Banding associations have all hosted evaluation sessions using North American Banding Council guidelines (Figure 3). Additionally, NABC has begun to create collections of specimens and photographs for bander education and to set new short-term goals in relation to training exercises and workshops.



Figure 3. Bob Yunick and Bob Pantle discuss band removal during a North American Banding Council evaluation session at Braddock Bay Bird Observatory in October 2001. Photograph by Sara R. Morris.

REGIONAL BANDING ASSOCIATIONS

Banding associations are the primary coordinating organizations for many banders that work through observatories or as individuals. Many, if not most, banders have worked solitarily or with a small group of other banders. Since the 1920s, one of the primary mechanisms of interacting with other banders has often been through membership and participation in one or more of the regional banding associations (Figure 4). Annual or semiannual meetings of these organizations have a role of fostering communication and exchange among banders. For many avocational banders these meetings and association publications provide a



Figure 4. Regional banding associations represent large regions of the continent (i.e., Eastern Bird Banding Association [a], Inland Bird Banding Association [b], and Western Bird Banding Association [c]) and smaller organizations represent specific states or provinces (e.g., Ohio Bird Banding Association [d]).

major mechanism of continued training and an important outlet for sharing banding results. These associations also provide grants for projects specifically using bird banding. While grants provided by regional banding associations are usually small, they have encouraged numerous well-defined, meaningful banding efforts. These grants have been particularly important because they provide important recognition of bander efforts and are often the only sort of funding available to students and avocational banders.

The regional banding associations have also joined forces on several publications that have provided scientific information to banders. From 1929 to 1967, the Northeastern Bird-Banding Association, Eastern Bird Banding Association, and Inland Bird Banding Association

jointly published the journal *Bird-Banding* (see NEBBA account below). The Eastern Bird Banding Association and Western Bird Banding Association began publishing a joint quarterly journal, *North American Bird Bander* (NABB), in 1976. This journal was established to fill the “exclusively for banding” niche abandoned by Northeastern Bird-Banding Association and to again provide a less technical publication about banding that would also include more news of the banding social scene. Although controversial at the time, the proponents of the joint venture hoped that merging small regional journals would provide banders with a journal that would encourage a greater exchange of ideas and the scientific study of birds using banding (Jackson 1983). Despite substantial opposition within the group, the Inland Bird Banding Association joined Eastern Bird Banding Association and Western Bird Banding Association in the publication of *North American Bird Bander* in 1982. This merging of the associations to share a common journal was known as the “Great Journal Joining,” or GJJ. Even after the journal became the official publication of the three associations, discontent among some members threatened to break apart the collaborative effort (Jackson 1983).

Since its inception, *North American Bird Bander* articles have focused on banding techniques and results of banding studies. Numerous papers on molt, and age and sex determination have increased bander abilities. Other articles in *North American Bird Bander* focus on experiences unique to banding and netting that may assist other banders. For example, in 1989, George Wallace introduced “gracklepox,” a form of poison ivy that develops when the toxin is “injected subcutaneously by the sharp claws of grackles or similar species, or alternatively rubbed into scratches caused by the birds” (Wallace 1989). Cathers and Shrader (1989) described capturing a kestrel in the large open spaces of a nearly-complete pet-food store.

In addition to general articles and recent literature, each of the three associations also provides information to its members in *North American Bird Bander*; this includes information about banding in the region and information about regional meetings. In 1976, Erma J. Fisk summarized the membership of EBBA by describing the diverse membership of the association based on a survey of members (352 of 628 members responded; Fisk 1976). Her survey indicated that 75 members held Ph.D.s, 166 held other degrees, members represented 71 profes-

sions and lived in all parts of the country, although most were from the eastern states and provinces.

The New England Bird Banding Association and its successors, the Northeastern Bird-Banding Association and Association of Field Ornithologists.—The New England Bird Banding Association was founded in 1922 to provide for regional interaction among banders. The membership of the association was expected to include banders from Connecticut, Massachusetts, Maine, New Hampshire, Rhode Island, and Vermont. Two years later the association was renamed the Northeastern Bird-Banding Association (NEBBA), when Quebec and the Maritime Provinces were included. Initially, the group met annually, but by the early 1950s, it met twice each year, once in the spring for a field meeting and once in the fall for its annual meeting. In 1977, it returned to a single annual meeting. The history of the organization was compiled by Davis (2000), and its early history and the context of its origin is described by Jackson (this volume).

In 1925, NEBBA began publishing the *Bulletin of the Northeastern Bird-Banding Association*, which became *Bird-Banding* in 1930 when the journal was published for the Northeastern, Eastern, and Inland Bird Banding associations, thus sharing control of content with these organizations. From its inception, this journal included articles and notes involving banding studies and reviews of recent literature relating to or involving banding. Techniques articles have contributed greatly to the process of banding. For example, Blake (1954) provided a summary of band sizes for different species of birds, Dennis (1955) presented results of experiments to increase the number of birds captured in traps, Stewart (1972) discussed skull pneumatization and the reliability of age determination, and Whitaker (1972) described a new method of using mist nets high above the ground in forests. Numerous articles also described methods of age and/or sex determination in a variety of birds. Additionally, major articles relating to banding have included “Ectoparasites and Bird Banding” (Peters 1930), “Bird Photography for Bird-Banders” (Fischer 1952), and “The Topography of a Bird” (Blake 1956). Some articles were very specific for bird banders and provided unique, creative solutions to banders’ problems. For example, Roslien (1974) described the use of the cassette case from oral contraceptives as a reusable band-storage device. The recent literature section initially involved reviewing books and entire volumes of ornithological journals.

In 1934, the section was reorganized. Individual articles, rather than whole volumes, were generally reviewed, the number of reviews was increased, and the reviewed articles were arranged in groups to help banders identify problems that needed to be studied. Margaret Morse Nice, who had begun receiving articles for review at the end of 1933, specifically targeted foreign literature. She authored hundreds of reviews during her nine years as review coordinator and through 1971, just three years before her death at the age of 90. These reviews brought (and still bring) banding news and techniques from around the world to banders. *Bird-Banding* incorporated a “Notes and News” section beginning in 1951, providing information about annual meetings, requests for information, grant competitions, and committee memberships. Beginning in 1957, the journal explicitly encouraged field ornithology studies, particularly of migration, whether or not banding was included. The Northeastern Bird-Banding Association reclaimed complete control of *Bird-Banding* in 1968, although that year the organization also created an editorial advisory committee that included representatives of the Eastern, Inland, Ontario, and Western bird-banding associations.

In 1980, *Bird-Banding* was transformed into the *Journal of Field Ornithology*, to better reflect its broader scope of all field studies, rather than only banding studies. In 1986, this regional banding association was transformed into an international ornithological society, the Association of Field Ornithologists (AFO). Its new focus and stature were reflected in its membership in the Ornithological Societies of North America (OSNA), an organization providing efficient communication among ornithologists and the major North American ornithological societies (Davis 2000). In the same year, the *Journal of Field Ornithology* began publishing abstracts in Spanish, reflecting its international scope.

In 1957, the NEBBA began the sale of mist nets from Japan, primarily through the efforts of E. Alexander Bergstrom. This activity was important to ornithologists who were thus able to obtain nets much more easily. After Bergstrom died in 1973, Manomet Bird Observatory agreed to take over the mist-net business for the NEBBA, and continues that service today for AFO. Through sound management, the NEBBA not only provided a welcome service, but also made a profit. The organization used profits to offset financial constraints, including increased costs associated with printing of their journal. The availability and sale of high-quality mist nets have clearly been one of the most important

contributions of NEBBA and AFO to banding and to ornithology. Mist nets, especially quality mist nets, were often difficult to obtain. There were no manufacturers of mist nets in North America, and the nets generally came from Japan and Mediterranean countries. The efforts of Eking Arnold, E. Alexander Bergstrom, and William H. Drury, Jr., through NEBBA were responsible for getting mist nets exempted from custom duties in 1960.

Inland Bird Banding Association.—The Inland Bird Banding Association (IBBA) was organized in 1922 at an American Ornithologists' Union meeting in Chicago, Illinois (Stevens 1940). William I. Lyon of Waukegan, Illinois, spearheaded the development of the organization that covered Alabama, Arkansas, Illinois, Indiana, Iowa, Kansas, Kentucky, Louisiana, Michigan, Minnesota, Mississippi, Missouri, Nebraska, North Dakota, Ohio, Oklahoma, South Dakota, Tennessee, Texas, Wisconsin, Manitoba, and Saskatchewan (both the Inland and Western bird-banding associations have claimed Alberta, which lies in migration routes of both regions; Stevens 1940).

The first issue of *Inland Bird Banding News* was published in 1929, with a listing of the councilors and the number of permits for the region by state. The newsletters were punched for a three-ring binder and were usually published quarterly, with three issues in 1929 and 1930. IBBA provided its members with "IBBA Form 1," a page for tabulation of bandings of a given species by month and year. Reports from the banding offices appeared as well, with excerpts from a paper read by F. C. Lincoln at the annual meeting about how bird banding was faring under the Biological Survey (Lincoln 1931). State reports as well as trap designs and success, totals for banders, returns by year, and longevity records are prominent in *Inland Bird Banding News*.

Annual meetings are held in the fall at locations that range throughout the IBBA area. Banding sessions are usually a focus of the meetings (Figure 5), as are a paper session, banquet, and social. Hands-on workshops to provide additional bander training are often offered. At the 1999 annual meeting in Ottumwa, Iowa, IBBA sponsored the first North American Banding Council certification session in addition to offering workshops to improve banding techniques, particularly for determination of age and sex of birds captured. Recent meetings have been held at diverse locations including a field station, refuge, nature center, and a college. IBBA sees its roles and the roles of its members as including



Figure 5. Grassland mist-netting demonstration during the Inland Bird Banding Association meeting at the Nature Conservancy's Tallgrass Prairie Preserve in Bartlesville, Oklahoma, in 2004. Photograph courtesy of Jennifer Maxwell.

disseminating information about banding to the public and educating the public about the importance of reporting bands found on birds.

Eastern Bird Banding Association.—The Eastern Bird Banding Association (EBBA) was formed in 1923 by Arthur Allen, Frank Burns, Maunsell S. Crosby, Beecher Bowdish, Howard Cleaves, John Gillespie, John Nichols, Witmer Stone, and Rudyerd Boulton at the American Museum of Natural History in New York. Arthur Allen was elected the first president of the association. The association covered the District of Columbia, Delaware, Florida, Georgia, Maryland, New Jersey, New York, North Carolina, Pennsylvania, South Carolina, Virginia, West Virginia, and Ontario. After the Northeastern Bird-Banding Association became the Association of Field Ornithologists, the New England states and Maritime provinces were umbrellaed under the Eastern Bird Banding Association. The history of the Eastern Bird Banding Association has been summarized in part by Beecher Bowdish (1958) and Dorothy Foy (1980; 1981a,b; 1982a,b).

The first publication of the Eastern Bird Banding Association was the *Bulletin of the Eastern Bird Banding Association*, which was issued in October of 1924, 1925, and 1927. In 1938, the Eastern Bird Banding Association was ready for a newsletter again and began publishing *EBBA Nus*, which later became *EBBA News*. *EBBA Nus* and *EBBA News* used the slogan "Let Us Band Together," a fitting double entendre for a group that had a self-stated primary purpose of increasing communication among banders. The newsletter was issued from three to twelve times a year, often with a hand-colored masthead. The newsletter highlighted the annual meeting as well as regional meetings, and there were several regional meetings in some early years. Articles in *EBBA News* included information on how to make presentations on banding, cooperative projects, notes from members on longevity records and trapping success, and many articles on trap design.

EBBA has always been a very social group, with annual meetings that brought banders from the EBBA region together to meet and talk about banding and banding techniques. The meetings have been big events for the year, with the newsletter and later the journal maintaining the ties between meetings. EBBA meetings have traditionally had a raffle, as a fund raiser for the organization, and a paper session. For many years meetings generally were held at banding stations, allowing opportunities to handle birds. That has become less common in recent years, but the trend seems to be changing back to holding meetings near banding stations and including some field time as a part of the meeting. At the 1976 EBBA meeting in Chevy Chase, Maryland, a young Peter Pyle won the bird quiz for the second year running. We're sure the participants had no idea just how much Peter Pyle would develop his interest in aging and sexing techniques for birds (e.g., Pyle 1997)!

Western Bird Banding Association.—The Western Bird Banding Association (WBBA) was founded by members of the Los Angeles Bird Banding Chapter of the Cooper Ornithological Club in 1925. The association was established for the banders in the western states and provinces: Alaska, Alberta, Arizona, British Columbia, California, Colorado, Idaho, New Mexico, Northwest Territories, Oregon, Utah, Washington, Wyoming, and Yukon. Geographic coverage of the association now includes Hawaii and Mexico. Their first meeting was held in 1926 and several committees were set up, including one to gather data on banders in what they called the "Western Province." Other commit-

tees dealt with annual reports, a “card file” for regional banding data, and establishing an emergency band supply. The “card file” was an effort to have all banders in the west report their bands received from the Washington Office to the coordinator, so that any banded bird that was trapped could be identified to bander quickly.

Early meetings were annual and took place such varied locations as a library, private estate, and colleges. The meetings were similar to today’s association meetings, with talks, field trips, trap demonstrations, and films. The lunch on the private estate under the spreading live oaks and another picnic lunch on a field day were likely very different from the meals at meetings today, but that is unfortunately left to the imagination.

The Western Bird Banding Association newsletter, titled *News from the Bird Banders*, first appeared in January 1926 and was issued quarterly for the entirety of its fifty-year run. The newsletter was retitled *Western Bird Bander* in 1961, and in 1976, Western Bird Banding Association joined Eastern Bird Banding Association in publishing *North American Bird Bander*. A brief history of the Western Bird Banding Association was written by Barbara McKnight (1982). The Western Bird Banding Association archives were unfortunately burned in a wildfire in 1991, making any future effort of a more complete historical account that much more difficult to undertake (Kay Loughman, pers. comm.). However, some information including a listing of Western Bird Banding Association Presidents, Business Managers, and Editors was included in the last issue of *Western Bird Banding*, as was a chart of the number of birds banded in the region by year (Stoner 1975).

Newsletters were punched for a ring binder, and included regular features on meetings, news from banders, annual reports from stations, a tabulation of birds banded each year starting in April 1928 for 1927 data, reviews of publications on birds, news from the banding office, and a column titled “Gossip.” Interesting early discussions on whether “bird banding” should be “bird-banding” and what constitutes a return, recapture, recovery, or discovery appeared over several years. The newsletter also contained trap designs, instructions to improve trap capture rates, trap baiting suggestions, discussions on the need for more members (a recurring theme today), and news from Chapters, including the Los Angeles Bird Banding Chapter and the Northern California Chapter. Another interesting tidbit sure to make staff at the modern Bird

Banding Laboratory cringe was a discussion of how a bander lacking the appropriate band instead manufactured a band to fit a Cackling Goose (*Branta hutchinsii*) and used the number from a size 5 band in their possession on their creation (Webb 1937).

Cooperative projects appear in the 1950s as a way to concentrate bander effort on a particular question or species. For Western Bird Banding Association, these included a project on winter age ratios of White-crowned Sparrows (*Zonotrichia leucophrys*) (Anonymous 1956) and a color-banding project on Golden-crowned Sparrows (*Zonotrichia atricapilla*) (Cogswell 1957). Western Bird Banding Association members participated in Operation Recovery, a coordinated effort, largely based on the East Coast, to study autumn migration and potentially capture migrant birds from other stations (Wilson 1962).

Recent meetings have been held annually in autumn at varied locations across the west, with a joint meeting with the Western Foundation for Vertebrate Zoology in 2004. These meetings have included a scientific paper session, field trips, a social and a banquet with speakers following. As with the Inland Bird Banding Association meetings, banding is usually an important part of the Western Bird Banding Association meetings, occurring each day of most meetings.

Ontario Bird Banding Association.—The Ontario Bird Banding Association (OBBA) held its first meeting in March 1956 in Toronto, at which time attendees agreed to hold monthly meetings from September through June and to produce a monthly newsletter. A thorough review of the founding of the association and its subsequent activities appears in McNicholl (1994).

Currently the Ontario Bird Banding Association holds a general winter or spring indoor meeting and a fall event for the public. Although the newsletter has not always been produced at its intended monthly interval, it continues to serve its original purpose as a mechanism of informal exchange of banding news and ideas. In 1966, the Ontario Bird Banding Association launched a quarterly journal—*Ontario Bird Banding*—that is now published once a year.

A number of cooperative banding projects, e.g., on Cliff Swallows (*Petrochelidon pyrrhonota*), House Finches (*Carpodacus mexicanus*), waterfowl and bluebird nest boxes have been undertaken by OBBA members (McNicholl 1994); studies of Snow Buntings (*Plectrophenax nivalis*), Horned Larks (*Eremophila alpestris*), and Lapland Longspurs

(*Calcarius lapponicus*), started in a single location but expanded to cover southern Ontario.

One of the most outstanding accomplishments of the Ontario Bird Banding Association was its role in the creation of the Long Point Bird Observatory and its resultant pioneering work on monitoring North American landbird migration. Volunteers started the Long Point project in 1959 and some 95,000 birds were banded in the first 9 years (Woodford 1969). The observatory became a separate entity in 1968 but remained associated with the Ontario Bird Banding Association (Hussell 1970).

Other Bird-Banding Associations.—In areas with numbers of banders, and especially in the very large IBBA region where regional association meetings have sometimes been too distant for local banders to attend, more local banding associations have been organized. All have had the purpose of promoting interactions among banders, encouraging continued training and skills development, and providing social opportunities for people interested in birds and banding (Figure 6).

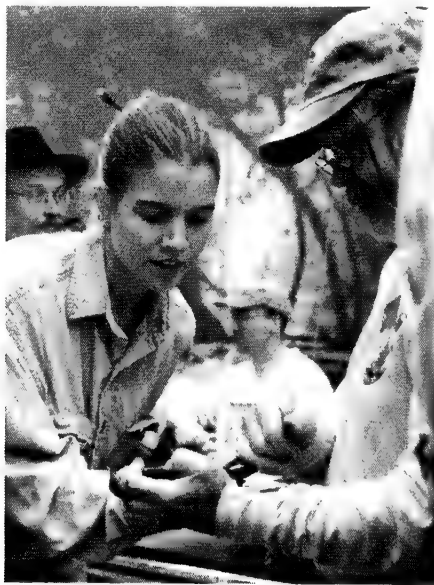


Figure 6. Tom Bartlett and Anne Smedley examine a Gray Catbird at the Ohio Bird Banding Association meeting in 2001. Photograph courtesy of T. K. Tolford.

As an example, the Ohio Bird Banding Association (OBBA) was established in 1981 and began meeting in August of that year. Although part of the Inland Bird Banding Association region, the number of active banders and assistants to banders in Ohio led to the creation of their own association, especially because the Inland Bird Banding Association meetings were often held in the Chicago area or other locations in the north-central part of the region (Jerome A. Jackson, pers. comm.). The Ohio Bird Banding Association meets twice each year, once in the spring and once in the fall. It publishes a quarterly newsletter, holds an annual spring banding weekend called the "Bandout," and encourages the involvement of anyone interested in birds.

Other groups devoted to banding have been established for communication among banders in specific areas. These groups include the Michigan Field Ornithologists and Bird Banders, the Texas Bird Banding Association, the Northeastern Nebraska Bird Banders, and the Mid-Atlantic Bird Banding Group.

Other groups have been established devoted to particular taxa. One of the most active recently is the Hummingbird Research Group. Initiated in 1986 as *Hummingbird Hotline*, a newsletter for active hummingbird banders, the Hummingbird Research Group began meeting every other year in 1995 at Lakeside Country Club south of Little Rock, Arkansas. It has since met in Arizona, Texas, and California. These meetings combine presentations of hummingbird research results and workshops devoted to bander training including forming hummingbird bands and making hummingbird traps (Figure 7).

BIRD OBSERVATORIES

A tremendous amount of information about bird distribution, migration patterns, survival, and longevity has been accrued through the incremental efforts of many observatories. The Canadian Banding Atlas for passerines and near-passerines relied on the efforts of all Canadian banders and observatories (Brewer et al. 2000). Long-term monitoring projects and educational efforts were pioneered in the late 1950s and early 1960s by observatories like Long Point in Ontario, Manomet in Massachusetts, Powdermill in Pennsylvania, and Point Reyes in California. Banding at bird observatories has led to better, more accurate and precise methods for making in-hand determinations of age and



Figure 7. Hummingbird banding at the Hummingbird Research Group meeting at the Kern River Preserve in Kernville, California, in July 2003. Photograph courtesy of Brent Ortego.

sex of birds captured. For example, work on skull pneumatization at Powdermill and molt limits at Powdermill and Point Reyes has provided tools now used by banders throughout North America. Observatories provide important training opportunities for both those who are learning how to band and those who are improving their skills. Perhaps most importantly, bird observatories have provided early hands-on opportunities for countless volunteers and interns, often college or graduate students who later pursue careers in field ornithology. Educational efforts at observatories range from the informal to workshops or classes charging tuition; participants vary from local bird lovers to students from Latin America hoping to start research programs. Through 2006, the Braddock Bay Bird Observatory (New York) and the Klamath Bird Observatory (Oregon) have hosted most of the North American Banding Council certification sessions.

Long Point Bird Observatory (LPBO).—Long Point is a 40 kilometer long sand spit jutting east into Lake Erie. One of those who participated in the initial banding foray to the end of the point in 1959

described it as follows, "When we arrived . . . the weather was beautiful but that night the temperature dropped, the wind rose, the rain descended and so did two of our three tents. However, a few birds were banded that week-end and thus began the Long Point Bird Observatory" (Woodford 1969:6). Initial trips to "The Tip" in 1959 by Ontario Bird Banding Association members were on foot carrying nets and poles for many kilometers, but soon a 1947 Jeep was used to travel the 30 kilometers of beach. In 1960 a small cabin and the first Heligoland trap were built and organized banding by volunteers began in earnest. By 1961 LPBO banders were on their way to combining banding with a daily census and other observations, which became the program known as "migration monitoring." A second banding station, named Breakwater, was established one-third of the way out the point in 1961. Mist nets, Heligoland traps, and other traps were employed at the Tip and Breakwater sites and near the base of the peninsula where much of the duck trapping and banding was done (Woodford 1969). The first permanent resident caretaker was hired in 1965 and David Hussell, one of the initial instigators of the project, became the first full-time staff person when he was hired as Executive Director in 1974 (Woodford 1969). In a report on the accomplishments of the first 10 years, Hussell (1970:4) describes the value of the observatory: "It is fair to say that the people involved believe that by taking part in a co-operative project . . . they can make a more worthwhile scientific contribution to ornithology than would be practical for them working alone, and at the same time benefit in terms of recreational enjoyment. . . . An observatory such as that at Long Point can make a valuable contribution by encouraging a high level of interest and participation by amateur naturalists. Furthermore, it provides unique opportunities for mutually beneficial contacts between amateurs and professionals."

From the early days Long Point was involved in the development of standardized banding and census methodologies. Migration studies and work on Tree Swallows (*Tachycineta bicolor*) were the focus of early work in the 1960s and continue today. A third station at Old Cut was established near the base of the point in the 1980s to complement the Tip and Breakwater stations. The Old Cut station, accessible by road, increased the ability of the Observatory to offer educational opportunities to the public and groups. Through its strong internship program Long Point Bird Observatory has played a central role in the training of many banders.

Bird Studies Canada (BSC) began, in 1994, as a committee of Long Point Bird Observatory, but in 1998 the roles were reversed with the creation of Bird Studies Canada as a national organization with a committee and separate endowment fund for Long Point Bird Observatory. Bird Studies Canada is the coordinating agency for the Canadian Migration Monitoring Network.

Powdermill Avian Research Center.—The long term year-round banding program at Powdermill Nature Reserve began in 1961. M. Graham Netting, the Director of the Carnegie Museum of Natural History at the time, invited Robert C. Leberman to establish the banding program at Powdermill, the museum's 2,200-acre (890-hectare) field research station. An earlier limited attempt by an Antioch College student to capture and band birds at Powdermill in the summer of 1959 using only wire traps was not very productive. By contrast, the results of four months of mist-netting and banding in the summer and fall of 1961 showed Powdermill's potential to be a productive site for long-term monitoring of landbirds, despite its geographic location away from any of the classic migration bottlenecks. In 1961, Leberman, with help from a few volunteers, banded over 1,500 birds of 80 species (Figure 8). Since then, the Powdermill banding program has consistently banded about 10,000 birds each year and has recorded 2,000-3,000 recaptures. By 2006, the program's database had grown to well over 575,000 records of 190 species.

A major strength of Powdermill's banding program has been the scientific underpinning and expert direction it received from curatorial staff at Carnegie Museum's Section of Birds: Kenneth C. Parkes and Mary H. Clench (1960s through the 1970s) and D. Scott Wood (1980s to the early 1990s). Powdermill's very ordinary setting in a broad mountain valley in the western Appalachians of Pennsylvania has proved to be an asset. Powdermill has provided data on species composition, migration timing, population trends, and population demographics for comparison with results obtained at the other contemporary bird observatories, most of which were intentionally situated in coastal or lakeshore settings to take advantage of the concentrating effect on migrants of large ecological barriers. Comparative studies include Ralph (1981), Hagan et al. (1992), Woodrey and Chandler (1997), and Marra et al. (2005).



Figure 8. Bob Leberman banding at Powdermill. Photograph courtesy of Bob Mulvihill.

Powdermill's early banding research efforts focused on banding processes, with emphasis on improving banding methods and the eventual scientific value of the data being collected through banding. In a seminal paper, Bob Leberman and Mary Heimerdinger (Clench) studied possible capture biases associated with use of the two predominant mist-net mesh sizes used by songbird banders (Heimerdinger and Leberman 1966). For several years, a reprint of their paper was included with every mist-net order filled by the NEBBA. Leberman's work on skull pneumatization documented the timing and pattern of pneumatization in different species (e.g., Leberman 1970) and helped promote more widespread use of "skulling" for making accurate in-hand age determinations.

Since he began helping with the Powdermill banding and education programs as a volunteer college intern in 1978 (joining the full-time staff in 1983), Bob Mulvihill has been at the forefront of the study of molt and molt limits (e.g., Mulvihill 1993, Mulvihill and Winsted 1997, Mulvihill and Rimmer 1997, unpubl. data extensively incorporated into Pyle 1997). His work has further refined and extended the ability of



Figure 9. Bob Leberman and Bob Mulvihill banding at Powdermill. Photograph courtesy of Bob Mulvihill.

banders to determine the ages of many landbirds. Currently, Mulvihill and Mike Lanzone, his full-time assistant, are working on a series of photographic guides to ageing and sexing of North American birds.

Another notable feature of the Powdermill banding program is that through its first 50 years, there have been only three Banders-in-Charge (Leberman, Mulvihill, and Adrienne Leppold; Figure 9), and all three have continually calibrated their determinations and measurements both within and among themselves. This level of standardization in all likelihood renders Powdermill's one of the most internally consistent banding databases. In addition to the banders, dozens of dedicated volunteers have provided essential help over the years as both scribes and net runners, especially during the busy migration seasons. Unsupervised collection of banding data, however, even by well-trained volunteers, rarely occurs at Powdermill.

Powdermill has been a leader in producing useful summaries of its voluminous banding data. The Powdermill data have been used to quantitatively assess and describe patterns of differential timing of migration of distinguishable age and sex classes of landbird species (Leberman and Clench 1968, 1970, 1971) and have been used in two major compilations of body mass and wing-length information (Clench and Leberman 1978, Mulvihill et al. 2004). Powdermill was also among the first large-scale banding operations to present timely information about

birds and bird banding to a worldwide community of birders, banders, and field ornithologists through a dynamic website launched in Fall 2000. The Powdermill bird banding website contains thousands of high quality digital photographs (many of these instructive to banders for making in-hand age and sex determinations), hundreds of pages of information including extensive Powdermill banding data summaries, and continually updated banding totals. The website's popularity grew rapidly by word of mouth, and in April 2006 it received its three millionth "hit."

Powdermill has been involved with informal bander training since its earliest days, with many volunteers, visitors, academic ornithologists, and field interns developing their banding skills at the station. The legacy of training continues today with up to three Bander Development Workshops offered each spring and fall since 2003; these have always been filled to capacity.

PRBO Conservation Science.—Founded in 1965 as Point Reyes Bird Observatory (PRBO), PRBO Conservation Science is dedicated to conserving birds and other wildlife in both aquatic and terrestrial ecosystems through innovative scientific research and outreach. The organization grew substantially since 1995 and by 2006 was hiring over 120 biologists annually as permanent and seasonal staff in the United States and Latin America. PRBO scientific expertise (in bird banding and many other fields) is used in major regional, national, and international initiatives and has resulted in more than a thousand papers in peer reviewed scientific journals.

Banding at PRBO's Palomarin Field Station began in 1966, and banding on Southeast Farallon Island began in 1969. These ongoing banding programs represent two of the oldest databases on land bird populations in western North America. Results of these studies have contributed significantly to the process of banding (e.g., Pyle 1997, Howell et al. 2003) and to current protocols now used to monitor and assess bird populations throughout the Americas (e.g. Ralph et al. 1993, 1996, Geupel and Warkentin 1995, Nur et al. 1999, Thomas et al. 2004, Latta et al. 2005). Scientists at PRBO Conservation Science have also intensively studied a community of coastal scrub birds using banding, color marking, and nest monitoring, a project that has validated the use of mist nets, banding, and other methods to monitor demographic processes (Martin and Geupel 1993, Silkey et al. 1999, Nur et al. 2004,

Ballard et al. 2004). This work has provided insight into the influence of life history strategies, weather, fire, and plant succession on land-bird populations dynamics (Geupel and DeSante 1990, Chase et al. 2005 a, b) and is now being replicated by biologists from PRBO Conservation Science and its partners throughout the west, with results being used to guide land management, fire, restoration, and other decisions that may impact bird populations and their habitats.

The Farallon Islands station hosts the longest running study of seabirds in North America. Banding studies on the seabirds there have provided insight into seabird life history strategies and factors influencing seabird and fish populations (e.g., Ainley and Boekelheide 1990). Seabird research has expanded to Antarctica and other sites throughout the California Current, leading to innovative research on penguin ecology and development of state-of-the-art bands for seabirds (Ainley and DeMaster 1980, Dugger et al. 2006). Other long-term PRBO studies using marked individuals have led to the listing and conservation of Snowy Plovers (*Charadrius alexandrinus*) and identification and conservation of important stop-over sites for shorebirds using the Pacific flyway (Warnock and Bishop 1998, Bishop et al. 2005).

Manomet Bird Observatory.—Manomet Bird Observatory was founded in 1969, although the bird-banding program at Manomet began in 1966 as part of Operation Recovery. Kathleen Anderson was the first Executive Director from 1969 to 1983. Trevor Lloyd-Evans and Brian Harrington joined the Manomet Bird Observatory in 1972 as the first scientific staff. Lloyd-Evans increased the study of molt as one of his primary interests and Brian Harrington increased the study of shorebirds. One of the important contributions of Manomet banders to bird banding was development and adoption of a detailed banding data sheet (see Salvadori and Youngstrom 1973), which has been adopted or adapted by numerous other bird banding stations (Kathleen Anderson, pers. comm.). Each year, the observatory runs 50 mist nets during both spring and fall migration in the same locations and during the same time period. Over 350,000 birds had been banded at Manomet by 2005. These banding data have been used in numerous publications including age ratios and patterns of migration (Ralph 1981), a comparison of methods of studying migration (Williams et al. 1981), documenting site fidelity of shorebirds to stopover sites (Smith and Houghton 1984), comparing

survival of shorebirds at different sites (Harrington et al. 1988), and studies of molt (Lloyd-Evans 1983). Many volunteer assistants and banding/education interns receive valuable training and provide educational opportunities for countless visitors during migration. Manomet's formal intern program was unique among early observatories, allowing students to experience all aspects of a scientific study. These interns worked on many different projects, helped maintain the facilities, listened to lectures from visiting scientists, and interacted with them over the kitchen table (Kathleen Anderson, pers. comm.). By 1997, over 400 interns and many other shorter-term volunteers had assisted in this program.

From the beginning, in the quiet times during landbird banding, Manomet banders would relocate to the beach to capture shorebirds (Kathleen Anderson, pers. comm.). With the addition of Brian Harrington, shorebird banding increased and included the use of rocket netting, different colored nets, and banding in areas away from Manomet, often in cooperation with the Canadian Wildlife Service. Manomet has taken the lead on shorebird conservation in the western hemisphere, first by organizing, in 1974, the International Shorebird Surveys to gather information on shorebirds and the wetlands they use and as a co-founder, in 1985, of the Western Hemisphere Shorebird Reserve Network (WHSRN) in 1985. WHSRN was established to protect important shorebird habitats in both North and South America. Manomet has had staff working on the network since its inception and the executive offices of the network have been located at Manomet since 2000 (Linda Leddy, pers. comm.). As the role of the bird observatory expanded beyond banding to many conservation issues, the organization became, in 1996, the Manomet Center for Conservation Sciences, and the bird observatory became one of several programs run by the center.

Institute for Bird Populations.—The Institute for Bird Populations was established in 1989 by David F. DeSante as a tax-exempt, non-profit California corporation. The creation of the Monitoring Avian Productivity and Survivorship (MAPS) Program, which provides critical conservation and management information for populations of landbirds breeding within the United States and Canada, was the Institute for Bird Populations' initial project. Monitoring Avian Productivity and Survivorship uses constant-effort mist netting and banding of birds at a

continent-wide network of monitoring stations that has grown since 1989 from 16 to over 500 stations. Currently, nearly 100,000 captures of about 200 species of landbirds are annually added to the Monitoring Avian Productivity and Survivorship database.

In response to growing concerns over the lack of standardized bander training and certification, the Institute for Bird Populations championed the promotion of scientifically sound and ethical banding practices through its Monitoring Avian Productivity and Survivorship materials, its bander-training classes, and by facilitating the establishment of the North American Banding Council. By 2006, the Institute for Bird Populations had offered over 60 introductory and advanced bander-training classes and provided rigorous training in mist netting, bird banding, ageing and sexing techniques, and bander ethics to well over 400 persons in United States, Canada, and Latin America.

Because Monitoring Avian Productivity and Survivorship data indicated that processes on the winter grounds may be driving population declines for some Neotropical migratory landbird species, the Institute for Bird Populations began work in 1998 on the overwintering ecology of wood-warblers in Cuba. This led to the creation in 2002 of the Monitoring Overwintering Survival (MoSI—Monitoreo de Sobrevivencia Invernal) Program, a spatially-extensive network of over 80 standardized mist-netting and banding stations in Mexico, Central America, and the Caribbean designed to assess Neotropical migratory landbirds' winter habitat quality and develop management and conservation plans for Neotropical migratory landbirds on their wintering grounds. In 2003, the Institute for Bird Populations established the analogous Monitoring Avian Winter Survival (MAWS) Program, now with about 40 stations, for temperate-wintering species.

The Institute for Bird Populations' monitoring programs are providing a cornerstone for successful conservation of landbird populations by providing habitat-specific estimates of vital rates throughout the annual cycle based on banding. Beginning with inventory work in Yosemite National Park in 1998, the Institute for Bird Populations has also become a leader in developing avian inventory and monitoring protocols for national parks throughout the Pacific States. As part of its Sierra Nevada Research Program, the Institute for Bird Populations has conducted cutting-edge research on the effects of forest-thinning practices and stand-replacing fire on avian community dynamics and established the Sierra Nevada Important Bird Area. Since 1990, the Institute

for Bird Populations has published *Bird Populations*, a global journal of avian biogeography and demography.

Canadian Migration Monitoring Network.—Migration monitoring grew from the semi-standardized efforts of the Long Point Bird Observatory volunteers beginning in 1962. These sites use daily banding, censuses, and observations to calculate a daily estimated total migrants for each species at the site. These daily estimates are used to develop a total for a season, which when corrected for weather conditions that might have influenced the nocturnal movements of migrants creates a population index for each species (Hussell 1981). In 1993 a workshop was held to examine the long-term migration programs at Long Point Bird Observatory, Manomet, Point Reyes Bird Observatory, and other locations. The consensus was that, especially if properly standardized, banding migrants could yield population-trend information for northern breeding species poorly covered by other monitoring techniques and that a series of long term monitoring sites should be established (Blancher et al. 1994). An international committee was formed that established standards for conducting Migration Monitoring (revised by Hussell and Ralph 1998) and stations in Canada who met these standards were invited to join the Canadian Migration Monitoring Network. Currently there are 25 member stations and there is at least one in every province but Prince Edward Island (Figure 10). Trends by station are posted on the Bird Studies Canada web site.

Landbird Migration Monitoring Network of the Americas (LaMMNA).—The Klamath Bird Observatory, working with the U. S. Forest Service, Bureau of Land Management, Cornell University's Laboratory of Ornithology, and Point Reyes Bird Observatory, organized this network. Initially conceived in 1991 as part of the Migration Monitoring Council, a joint venture of the United States and Canada, the Landbird Migration Monitoring Network of the Americas was not formally established until 2005. This network is open to constant effort operations in Latin America and the United States and is intended to be a companion network to the Canadian Migration Monitoring Network. LaMMNA coordinators have identified approximately 230 bird observatories, banding stations, and other organizations that might contribute to their efforts. In 2006, the network spearheaded monitoring migratory birds for avian influenza in the Americas.



Figure 10. The Canadian Migration Monitoring Network includes 25 stations across Canada. (1) Rocky Point Bird Observatory, Victoria, British Columbia; (2) Teslin Lake Banding Station, Yukon Territory; (3) Mackenzie Nature Observatory, British Columbia; (4) Vaseaux Lake Migration Monitoring Station, British Columbia; (5) Inglewood Bird Sanctuary, Alberta; (6) Lesser Slave Lake Bird Observatory, Alberta; (7) Beaverhill Bird Observatory, Alberta; (8) Last Mountain Bird Observatory, Saskatchewan; (9) Delta Marsh Bird Observatory, Manitoba; (10) Thunder Cape Bird Observatory, Ontario; (11) Whitefish Point Bird Observatory, Michigan; (12) Bruce Peninsula Bird Observatory, Ontario; (13) Pelee Island Bird Observatory, Ontario; (14) Long Point Bird Observatory, Ontario; (15) Haldimand Bird Observatory, Ontario; (16) Tommy Thompson Park Bird Research Station, Ontario; (17) Prince Edward Point Bird Observatory, Ontario; (18) Innis Point Bird Observatory, Ontario; (19) McGill Bird Observatory, Québec; (20) Observatoire d'oiseaux de Tadoussac, Québec; (21) St. Andrew's Banding Station, New Brunswick; (22) Atlantic Bird Observatory, Nova Scotia; (23) Brier Island Bird Migration Research Station, Nova Scotia; (24) Point Lepreau, New Brunswick; and (25) Gros Morne National Park Migration Monitoring Station, Newfoundland. Map provided by Bird Studies Canada.

Observatories, on their own or in combination with academic or government institutions, have been involved in work that is increasing our understanding of demography, migration paths, migration ecology, and wintering biology of birds. For example, important demographic insights have been gained from a long-term study of hummingbirds at a single observatory (Hilton and Miller 2003) and on many species using information from a network of sites (Alexander and Ralph 2001). Data collected at Canadian Migration Monitoring Network observatories have contributed to understanding stopover ecology (Dunn 2002) and have made links between breeding and wintering grounds (Wassenaar and Hobson 2001). Observatory studies have improved our ability to sex young birds (Hobson et al. 2000).

Over the last 100 years, banding techniques have become more complex and specialized. The development of banding in the New World would have been delayed without bird banding associations and bird observatories coordinating banding records and cooperative projects, sharing skills and equipment, and training banders. Only recently has the use of the internet for disseminating and sharing information made the role of bird banding associations and bird observatories less critical for the sharing of information among banders. These organizations still play a vital role, providing a chance for banders to exchange knowledge with and learn additional skills from other banders.

ACKNOWLEDGMENTS

We thank Kathleen Anderson, Andrew Couturier, Dave DeSante, Erica Dunn, Geoff Geupel, Audrey Heagy, Jerry Jackson, Bob Leberman, Linda Leddy, Elaine Mease, Lucie Metras, Bob Mulvihill, Brent Ortego, Bob Pantle, C. J. Ralph, Chandler Robbins, Jennie Robbins, Chris Rose, Jr., Tim Tolford, Ellie Womack, and Bob Yunick for their contributions to this manuscript. Additional information about each of the banding organizations can be obtained at their websites.

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A History of the Bird Banding Laboratory: 1920-2002

*John Tautin*¹

ABSTRACT.—The U.S. Bird Banding Laboratory (BBL) has had a long and rich history beginning with its founding in 1920 by the visionary Frederick C. Lincoln. During the 1920s, Lincoln laid the foundation for the banding program and established many principles, procedures, and policies that stand today. He also led the banding lab and nurtured the banding program through the 1930s and most of the 1940s when economic depression and war made for difficult times in the United States. From 1947 to 2002, the five BBL “Chiefs” who followed Lincoln led BBL to further achievements and service to the banding community. In every decade of its existence, BBL has had to attend to practical matters such as issuing permits, supplying bands, and managing records while adapting to programmatic changes in the field of avian research and management. In this chapter I highlight the early formative years of BBL, the dominance of waterfowl management concerns, major programmatic and scientific developments between 1970 and 2000, and how they all influenced BBL operations.

Most national bird-banding programs in the world are supported by a service and administrative center. The U.S. center is the Bird Banding Laboratory (BBL) located at the U.S. Geological Survey’s (USGS) Patuxent Wildlife Research Center at Laurel, Maryland. Working in cooperation with the similar Canadian Bird Banding Office (BBO), BBL offers banders and others “one stop shopping” for services and information. BBL: issues permits and bands; supplies banding software, instructional materials, and technical advice; coordinates the use of auxiliary markers such as neck collars and radio transmitters; serves as the repository for banding records and the clearing house for reports of banded birds; disseminates data to researchers and managers; and assists in the development and coordination of banding projects. BBL is a large and complex operation, with a long and rich history. Herein, I attempt to present the BBL history, but not the equally long and rich his-

¹20117 State Highway 98, Conneautville, PA 16406

tory of BBO. Jackson (this volume) and others, e.g., Cole (1922) have ably presented the history of the broader North American bird-banding program, including its early administration by the American Bird Banding Association (ABBA).

The broader banding program became 100 years old in 2002, spanning the period between Paul Bartsch's banding of Black-crowned Night-Herons (*Nycticorax nycticorax*) and the present (Bartsch 1904, Tautin 2005a). To celebrate the century of remarkable achievements in North American bird banding, BBL organized a symposium at the 2002 North American Ornithological Conference at New Orleans, Louisiana. The presentations made at the symposium serve as the basis for this volume.

Like many aspects of migratory bird conservation in the U.S., BBL's foundation is laid on the principle of federal pre-eminence in migratory bird matters. The 1916 Convention for the Protection of Migratory Birds, agreed to between the United States and Great Britain (for Canada), established federal pre-eminence, and the subsequent 1918 Migratory Bird Treaty Act made it law in the United States. Looking back on these events, one might see them as the pretext for an overbearing government to take over a private sector (ABBA) function; however, this was not the case. The banding community encouraged the entry of the federal government into the management of bird banding. Support for ABBA had waned during World War I, and there was need for an entity with sufficient resources and authority to manage bird banding.

As the 1920s approached, federal migratory bird programs were being administered at Washington, D.C. by the U.S. Department of Agriculture's Bureau of Biological Survey (Survey). Survey biologists already had experience with banding (Wetmore 1915). Survey administrators, notably Chief Edward Nelson, and Harry Oberholser, head of bird studies, were supportive and recognized the need for a well-organized, central banding office. Thus, in 1920, in one of the most fortuitous appointments in the history of North American ornithology, they put Frederick C. Lincoln (Figure 1) in charge of organizing the office that would later be referred to as the "banding lab."

Lincoln was born in 1892 at Denver, Colorado. His early interest in birds led to a job as an assistant in the bird department at the Colorado Museum of Natural History. In 1913, at the age of 21, he became Curator of Ornithology at the Museum. He held that position until 1920,



Figure 1. Frederick C. Lincoln, founder of the U.S. Bird Banding Laboratory. Photograph courtesy of the U.S. Bureau of Biological Survey, U.S. National Archives.

with time out for World War I service as a “Pigeon Expert” in the U.S. Army Signal Corps. During his tenure at the Museum, Lincoln became acquainted with Alexander Wetmore, thus establishing a connection with the Biological Survey.

When Lincoln got to Washington in 1920, he approached the daunting task of organizing the banding lab with the characteristic professionalism, thoroughness, vision, and dedication that would see him become an accomplished biologist, writer, and administrator over the next three decades. Lincoln successfully organized the U.S. bird-banding lab in that first year of its history, 1920, and he stayed in charge of it until 1946. Behind the scenes, he developed numbering schemes and record-keeping procedures, established standards, recruited banders, and fostered international cooperation. Lincoln was a visionary. He promoted banding as a tool in scientific research and management, becoming famous for such things as the Lincoln Index (Lincoln 1930), that later proved to be a true population estimator (Nichols and Tautin this volume), and the Flyway concept (Lincoln 1935a) still applied today in waterfowl management.

Lincoln wrote prolifically about bird banding, chronicling the history of the banding lab as he was creating it. He did this in occasional articles in both government publications (e.g., Lincoln 1928a) and scientific journals (e.g., Lincoln 1926), but more importantly, in the long-running series *Bird Banding Notes*, which he developed to be the official communication between the banding lab and banders. *Bird Banding Notes* was never intended to be a publication, rather it was a circular designed to reduce correspondence with individual banders while communicating general information to all banders. Because it had limited distribution, *Bird Banding Notes* is not often found in libraries. Throughout this chapter, I rely heavily on *Bird Banding Notes* for information about the first decades in the history of BBL.

THE BBL HISTORY BY THE DECADES

The banding lab of the 1920s—laying the foundation for the North American bird-banding program.—The 1920s were perhaps the most important years in the history of BBL and the broader North American bird-banding program. The responsibilities and functions of the 1920s banding lab were remarkably similar to those of the modern day BBL. Many of the principles, philosophies, procedures, partnerships, and problems still evident in today's banding program developed in that first decade.

Much of banding lab's work in the 1920s was procedural and concerned with practical matters such as enabling banders to do their work. In those days, the government wanted volunteers to band birds and build a banding database for scientific analysis. The original process for obtaining authorization to band is not clear, but from the start, a federal permit was required (Figure 2). Banding and other forms of "hands on" research with migratory birds were considered a form of "take" to be regulated under the Migratory Bird Treaty Act. Banding permits not only gave people the legal authority to capture and band, but also facilitated record keeping and forced banders to work within one national, centralized system. Private banding schemes were not condoned. This concept of tying permits to participation in the common system was critical and still stands today. It enabled bird banding in North America to advance in a far faster and more organized manner than banding did in Europe where many disparate schemes developed.

Collaborator's Permit No. 324 Expires December 31, 1922.

UNITED STATES DEPARTMENT OF AGRICULTURE

PERMIT FOR CAPTURING MIGRATORY BIRDS FOR SCIENTIFIC BANDING PURPOSES

WASHINGTON, D. C. December 10, 1921

Permission is hereby granted under Regulation 9 of the Migratory Bird Treaty Act Regulations to F. C. Lincoln of Washington, D. C., to trap, in any State of the U. S. except on Federal or State bird or game reservations, at any time during the year nineteen hundred and twenty two migratory birds for banding purposes, and to possess such birds only for such period of time as may be necessary securely to band the same. good until verified

This permit is issued subject to the conditions printed on the back hereof and is not valid unless countersigned by the Chief, Bureau of Biological Survey.

W. S. Kesterson
Acting Chief, Bureau of Biological Survey.

Frank M. Beach
Secretary of Agriculture.

Figure 2. Frederick Lincoln's 1921 bird-banding permit. Note that, at the time, permits were signed by the Secretary of Agriculture. Photograph courtesy of BBL and Kinard Boone, USGS Patuxent Wildlife Research Center.

Another important, enabling concept involved the government (banding lab) procuring bands in bulk and distributing them free of charge to banders (Figure 3). This provided an inducement to banders, and it was cost effective when viewed holistically. It also facilitated record keeping and, to some degree, quality control. The concept of free bands stands today, having withstood the occasional challenge by budget-cutting bureaucrats. Although sensible in concept, providing free bands would pose chronic difficulties for the banding lab, mainly because of budget constraints, but sometimes due to difficulties with manufacturers. Some of the banding lab's early communications about bands would sound very familiar to today's banders. In addition to supplying bands, the early banding office had to attend to technical matters such as band-numbering schemes and inscriptions. This would remain the case well into the 1990s.

Information was also crucial to enabling banders to work in effective, acceptable ways, and the early banding lab worked hard to provide information. The first bird-banding manuals were published during the 1920s (e.g., Lincoln and Baldwin 1929) and supplemented with material in *Bird Banding Notes*. Banding techniques were emphasized in these manuals. Through *Bird Banding Notes* and other publications (e.g.,

6001 - 27

From	To incl.	Size	Ordered	Delivered	Mfg.	Cost.
6001	7000	1	✓	✓	✓	18.00
7001	8000	1	✓	✓	✓	18.00
8001	9000	3	✓	✓	✓	21.00
9001	10,000	1	✓	✓	✓	21.00
10,001	11,000	1	✓	✓	✓	21.00
11,001	12,000	1	✓	✓	✓	21.00
12,001	13,000	1	✓	✓	✓	21.00
13,001	14,000	1	✓	✓	✓	21.00
14,001	15,000	1	✓	✓	✓	21.00
15,001	16,000	2	✓	✓	✓	21.00
16,001	17,000	2	✓	✓	✓	21.00
17,001	18,000	2	✓	✓	✓	21.00
18,001	19,000	3	✓	✓	✓	21.00
19,001	20,000	4	✓	✓	✓	21.00
20,001	21,000	5	✓	✓	✓	21.00
21,001	22,000	1	✓	✓	✓	18.00
22,001	23,000	1	✓	✓	✓	18.00
23,001	24,000	3	✓	✓	✓	18.00
24,001	25,000	1	✓	✓	✓	18.00
25,001	26,000	1	✓	✓	✓	18.00
26,001	27,000	1	✓	✓	✓	18.00
27,001	28,000	1	✓	✓	✓	18.00
28,001	29,000	1	✓	✓	✓	18.00
29,001	30,000	1	✓	✓	✓	18.00
30,001	31,000	1	✓	✓	✓	18.00
31,001	32,000	1	✓	✓	✓	18.00
32,001	33,000	1	✓	✓	✓	18.00
33,001	34,000	1	✓	✓	✓	18.00
34,001	35,000	1	✓	✓	✓	18.00
35,001	36,000	1	✓	✓	✓	18.00
36,001	37,000	1	✓	✓	✓	18.00

Figure 3. Early band procurement records. Note near the bottom that in 1922 some bands were procured from Gey Band & Tag Company of Norristown, Pennsylvania. In 2002, the Bird Banding Laboratory was still procuring some bands from Gey Band & Tag Company. Photograph courtesy of the BBL and Kinard Boone, USGS Patuxent Wildlife Research Center.

Lincoln 1926, 1928b) the banding lab also apprised banders of results of the banding program by reporting totals of birds banded, highlighting interesting recoveries, and reporting on the studies of individual banders.

Organizing banders to work cooperatively would prove to be important to the advancement of the banding program. Recognizing the power of partnerships, the banding lab of the 1920s promoted the development of regional banding associations. Most of the regional associations still exist and cooperate with the BBL (Morris et al., this volume). Most meetings of regional banding associations were, and continue to be, attended by representatives of the banding lab.

Record keeping was another practical matter addressed by the banding lab in the 1920s. At the time, both banding and return records of individual birds were kept on the same card, and thousands of birds were banded annually. Even with the help of a clerk, Myra A. Putnam, and Russell Carpenter who issued bands (Duvall 1968), Lincoln's banding office had a tremendous job in keeping records straight. On top of that, banders made mistakes, necessitating the development of editing procedures. Thus, in the 1920s, the banding office began the endless process of improving record-keeping procedures to keep pace with growth of the banding program and advancements in technology. Throughout the subsequent history of the banding lab, virtually every communication it issued, whether *Bird Banding Notes* or its successor *Memoranda to All Banders (MTAB)* would contain procedural matter aimed at facilitating records management.

Bander adherence to record-keeping procedures was necessary, but not always forthcoming. Consequently, throughout the history of BBL, the office has had to remind, cajole, admonish, or even threaten banders to submit records in a timely and correct manner. As early as 1922 the banding lab got tough on banders, issuing stern admonishments. In the 1980s, some of the more obtuse communications coming out of the BBL would be dubbed "nastygrams" by the banders.

The banding office of the 1920s sometimes also had to adopt unpopular policies to assure that banding work was in the public interest. The banding lab was funded by annual appropriations from Congress, i.e., tax dollars, and the Survey had a responsibility for migratory bird conservation that would increasingly depend on having quality data from bird banding. Many banders would be in the program a long time, hopefully contributing, but certainly at some government

expense. With fiscal responsibility in mind, the banding lab supported, even encouraged, almost any banding project having reasonably plausible benefits. However, purposeless, pointless banding, referred to as “picnic banding,” was discouraged, and in 1928, the banding lab used some strong wording in discussing what constituted legitimate banding and why some rigor and scrutiny in the banding program were necessary. For example, (Lincoln 1928c):

“In offering the banding method to ornithologists and bird students of America, the Biological Survey serves its own ends in the study of migration, a responsibility delegated under the Migratory Bird Treaty Act, and also serves to increase other knowledge of the life habits of birds and to further the cause of bird protection.”

“Consideration of the application at the Washington office is a cold-blooded business proposition.”

“. . . permits and bands are not issued to every person, who, lost in transient enthusiasm, thinks he would like to participate.”

“Bird banding is not a plaything.”

Most banders did credible work worthy of the banding lab’s support, but at times deadbeat banders had to be culled. In later decades, “picnic banding” became known as “ring and fling banding,” and unproductive banders were “inactivated” rather than culled. Although the terms changed, the underlying policy remained: the banding lab, with a responsibility to serve the taxpayer and conservation as well as banders, always has to be mindful of the purposes and costs of banding.

While seemingly overbearing and bureaucratic, the 1920s banding lab’s emphasis on order, procedure, and policy provided a sound foundation for the future North American bird-banding program, and also served as a model for other programs. Having one, uniform, cooperative system would pay big dividends for migratory research and management in the years to come.

The 1930s—the Great Depression affects bird banding.—The 1930s banding office became a sort of crossroads of ornithology, witness to many developments, most progressive and gratifying, but some

very sad. On 1 April 1931, Alfred O. Gross, of Brunswick, Maine, and Thornton W. Burgess of Springfield, Massachusetts had captured the last Heath Hen (*Tympanuchus cupido*) and banded it with two bands, one aluminum, one copper, one each leg (Lincoln 1931).

The Bird Banding Lab did not escape the Great Depression that affected the U.S. during the 1930s. Congressional appropriations were reduced, and bands were in short supply. Although new staff came on board, the banding office apparently had inadequate resources to handle the workload generated by banders. In 1933, the banding lab placed a moratorium on the issue of new permits, and later purged 300 banders who had not reported banding in the previous three years (Lincoln 1933):

*“Limitation on Issuance of Banding Permits.—*Because of reduced appropriations, funds are not available for the purchase of the increased stock of bands that would be demanded by further expansion of work. The Biological Survey accordingly feels that its resources should be utilized for the benefit of those stations already operating. With this in mind, and effective at once, additional banding permits will not be issued until further notice.”

The situation began to improve in 1934 with a reorganization and expansion of the Survey’s migratory bird programs and a move to the new south building of the Department of Agriculture. A Bureau of Budget attempt to eliminate the Survey’s funds for scientific investigations in Fiscal Year 1935 did not pass Congress. Optimism returned (Lincoln 1935b):

“Cooperators may have confidence that birdbanding has come to stay: the Biological Survey is more than ever ‘sold’ on this method of obtaining original information relative to our native birds. During the present emergency special emphasis is being placed upon migratory waterfowl, but bird students in general may be assured that there is no lack of interest in the nongame species.”

During the 1930s, the banding lab maintained communications and continued to refine techniques, procedures, and policies. The banding lab broached the use of nets to capture birds and, as a result of pioneering studies of birds as individuals by Margaret Morse Nice and Wilbur

K. Butts, considered providing colored celluloid bands to banders and encouraged their use (Lincoln 1933). A new band-numbering scheme using the fiscal year of purchase as a prefix was established. Codes indicating how a banded bird was recovered were addressed, with some of the same codes mentioned in 1933 still in use today (e.g., 00 found dead, 01 shot). Data management entered the electronic era with the adoption of new return cards (Form Bi-137) designed for “the electric sorting machine.” The soon to be perennial issue of who had what rights to banding data was addressed, the banding lab taking the position that any serious researcher should have access to the data (Lincoln 1934a). And, as it would forever, the banding office of the 1930s continued to admonish banders to follow procedures.

During the 1930s, the Survey regionalized and reorganized under the dynamic leadership of J. N. Darling. A Migratory Waterfowl Division directed by J. C. Salyer was set up in 1934, and the banding lab was placed in a new section, the Distribution and Migration of Game and Other Birds, all of which was directed by Fred Lincoln, who reassured banders that “No change is at present contemplated in the status of bird-banding cooperators . . .” (Lincoln 1934b).

During the 1930s, the banding lab also became a key operation in migratory bird conservation, which gained great momentum with the founding of such organizations as Ducks Unlimited (founded 1937), and with the increased emphasis placed on waterfowl management by the Survey. In 1937 the Biological Survey appointed four Flyway Biologists to conduct and coordinate waterfowl investigations.

Despite the difficulties of the 1930s, the banding lab continued to grow in stature and importance. It expanded its scope geographically by beginning to sponsor banding in Latin America. For example, the banding lab sent a supply of bands to L. A. Summerhayes, of San Jose de Guatemala, so that he might open a banding station there (Lincoln 1939). But the banding office remained cautious about increasing the number of banders. A moratorium on new permits continued into the later 1930s, and in 1939, the banding lab culled 500 more permittees, paring the program back to about 1800 active banders.

The 1940s—World War II slows the banding program.—Following a 1939 Presidential Order, the banding lab’s parent organization, the Biological Survey, was transferred from the Department of Agriculture to the Department of the Interior. This set the stage for a significant

reorganization in 1940 in which the Biological Survey and the Bureau of Fisheries were merged to form the U.S. Fish and Wildlife Service (Service). This strengthened federal involvement in wildlife conservation, particularly waterfowl conservation. Shortly thereafter, in a prelude of things to come, the Service and banding lab established a new policy that waterfowl banding would be done chiefly in the public domain. That policy gave the Service and state wildlife agencies complete control over the planning and execution of waterfowl banding, something that was becoming increasingly important to their management endeavors, particularly the setting of annual hunting regulations. With minor exceptions, the policy still stands today, and as will be seen, it has had major long-term implications for the banding lab.

World War II profoundly affected the bird-banding lab as it did most American institutions. Even before the United States declared war in December of 1941, the banding lab saw difficult times coming, at least in the area of band supply. Difficult times indeed came soon, and the banding lab put a moratorium on new permits and discouraged large-scale banding of colonial waterbirds. Further evidence of difficulty is suggested by the paucity of communications from the banding lab. Apparently, only one issue of *Bird Banding Notes* was produced between April, 1942 and June, 1946, something most unusual considering that the prolific writer, Fred Lincoln, was still in charge of the banding lab during that period.

The War also prompted administrative moves that would affect the future bird-banding lab. During the summer of 1942, in accordance with President Roosevelt's decentralization order, the main offices of the Service were moved temporarily to Chicago. However, the bird-banding and other migratory bird files, together with the staff members who worked with those files, were moved to the Patuxent Research Refuge, located between Laurel and Bowie, Maryland, where space in one of the laboratory buildings was available. After the War, the Service returned to Washington D.C., but the bird-banding lab stayed at Patuxent where it remains today. This was most fortunate for bird banding, because Patuxent would eventually become a world-class center for migratory bird research and management. The co-location of the bird-banding lab with scientists who developed methods for analyzing banding data, and with management-oriented biologists who used the data, proved to be mutually beneficial.

At Patuxent, the bird-banding lab was housed in Nelson Laboratory, with the official address of Patuxent Research Refuge, Laurel, Maryland. However, into the late 1940s, the banding lab retained a Washington, D.C. telephone number.

Although Fred Lincoln had assumed additional, higher responsibilities over the years, he remained “in charge” of the banding lab through 1946, apparently maintaining a Washington, D.C. office and delegating on-site (Patuxent) management to subordinates. Lincoln had management assistance from May Thacher Cooke, from two clerks, Marge Stewart and Lois Horn, from biologist Chandler Robbins beginning in 1943, and from John Aldrich who would have transitional responsibilities for bird banding following Lincoln’s impending retirement (Duvall 1968). Lincoln retired from the Service in 1947, having been directly or indirectly responsible for the banding lab since 1920. He left a remark-



Figure 4. Seth H. Low, the second BBL Chief, at the BBL then housed in Nelson Laboratory at the Patuxent Wildlife Research Center. Photograph courtesy of Chandler Robbins.

able legacy and truly was the founder of the bird-banding program as we know it today. Much has been written about the career and achievements of Fred Lincoln (Terres 1947, Gabrielson 1961, Reeves 1984, Tautin 2005b; additional material on Lincoln can be found at the National Archives, The Frederick C. Lincoln Collection, Record Group 22, Stack Area 150, Row 3, Entry 254, Box 33, College Park, Maryland).

Seth H. Low (Figure 4) assumed leadership of the bird-banding lab on 5 January 1948 (Steele 1948). Low was a bander with a particular interest in waterfowl banding. He previously had been manager of Salt Plains National Wildlife Refuge in Kansas, a position that made him well acquainted with migratory bird conservation.

The first issue of *Bird Banding Notes* (volume 4, number 1) under Low's tenure went out to banders in June 1948. In what must have been a dubious introduction to the banding community, Low had to inform banders of post-War shortages of bands, insufficient funds, a staff too small for the banding lab workload, and the consequent necessity to cull 500 inactive banders from the rolls. But amid all of the bad news in that June, 1948 issue of *Bird Banding Notes*, there was a sure sign that the banding office was returning to normal after World War II: it resumed admonishing those uncooperative, thoughtless banders about record keeping.

The best year of the decade for the bird-banding lab was 1949. The budget was reasonable, a good supply of bands was on hand, the permanent staff was increased to six (Low, the biologist/leader and five clerks), and two temporary clerks were hired for "the rush season," i.e., the hunting season when reports of banded waterfowl increased greatly. Banding was picking up and expanding geographically with cooperators in the Pacific region, the Virgin Islands, and Cuba. The banding lab overhauled operations to keep pace. The last issue of *Bird Banding Notes* for the decade (volume 4, number 2, August 1949) contained so much policy and procedural information that it was almost a mini-bird-banding manual.

The 1950s and 1960s—waterfowl management dominates bird banding.—As the Nation got back to normal after the War, resources gradually became available to support a growing interest in waterfowl management. Young war veterans were going to college in great numbers under the GI bill, with many entering the developing field of

wildlife management. With the availability of trained biologists, surplus aircraft for surveys, and reliable funding from programs like the Federal Aid in Wildlife Restoration Act, the states, as well as the federal government, invested heavily in waterfowl management. Their efforts were stimulated in part by the upswing in waterfowl hunting that occurred after GIs returned home and sporting ammunition became readily available. The development of cooperative bodies such as the four Flyway Councils led to further growth in waterfowl management. By 1960, cooperative, large-scale breeding-ground surveys, harvest surveys, and banding programs designed specifically to yield data for waterfowl management were in place. Hawkins et al. (1984) provide a most interesting and comprehensive history of these developments.

As early as 1950, the banding lab recognized that the growth of waterfowl management was dominating bird banding in general, and office operations in particular. With minor exceptions, permit policy limited waterfowl banding to federal and state agencies, and a new data policy reserved game-bird data for the use of the Service and states in meeting their management responsibilities. From all of this emerged an unarticulated, but well-understood, distinction between the relative importance of game and non-game bird-banding, as seen by the Service, ergo the banding lab. Clearly, game-bird banding was the emerging priority in the 1950s, and distinctions between amateur and professional banders began to be drawn. The former were seen largely as amateurs interested in independent banding of non-game birds for personal reasons, while the latter were seen as professionals involved in large-scale, cooperative banding of game-birds for programmatic reasons. This would remain the case for years, but gradually the body of banders, both game and non-game, would become largely professional, i.e., banding for vocational, job-related reasons (Tautin 1991).

The priority given to game-bird banding was reflected in both policy and procedure at the banding lab. For example, banding permits for wildlife agencies were issued more or less automatically, and were good until revoked or surrendered by the agency. All banding and recovery records were modified to include codes for Flyway, and all recovery records contained a "hunting seasons survived" code, even for non-game birds. Large numbers of waterfowl banded reflected the emphasis on game-bird banding, and soon the Mallard (*Anas platyrhynchos*) became the number one bird banded in North America, a distinction that it holds to this day.

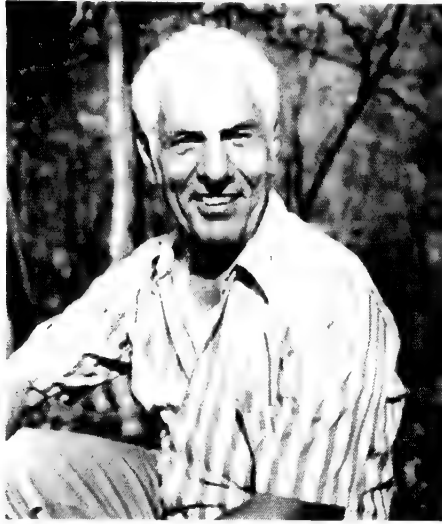


Figure 5. Allen J. J. Duvall, the third BBL Chief. Photograph courtesy of Matthew Perry and the Washington Biologists' Field Club.

In 1954, Allen J. J. Duvall (Figure 5) transferred from the U.S. National Museum to Patuxent where he was put in charge of migratory bird work, including the banding lab. In a 1961 reorganization at Patuxent, the banding lab was formally designated the Bird Banding Laboratory (BBL), and its leader, Duvall, was designated "Chief." Duvall remained BBL Chief until 1964 when he assumed a position with the Pesticides Review Board in Washington, D.C. The designations BBL and "Chief" remain today. Although these designations were not used until Duvall was in office, for purposes of continuity herein, I consider Lincoln and Low to be the first and second BBL Chiefs.

Neither Low nor Duvall was the communicator that Lincoln had been. During Low's tenure the banding office issued three *Bird Banding Notes*, and during Duvall's, none. Most communications to banders during Duvall's time are thought to have been in the form of memoranda. However, a compendium of them is not known to exist, and tracing specific developments at BBL during this time is difficult. It is known, though, that BBL managed to continue admonishing banders about record keeping and threatening to suspend permits of delinquent banders.

BBL biologist Willet T. Van Velzen revived *Bird Banding Notes* for two issues in December 1964 and April 1965. He praised Duvall for his leadership during difficult times for the bird-banding program, including the administrative aftermath of a disastrous fire that destroyed many banding records in 1959. BBL staff and other Patuxent personnel spent approximately two years reconstructing files.

In one way, though, the fire had a positive impact on BBL and other migratory bird programs at Patuxent; it accelerated their entry into the newly emerging field of electronic data management. Tons of punched data cards had accumulated at BBL and other Patuxent offices (Figure 6). More efficient and secure ways of managing the millions of records were needed. The solution came with the installation of an IBM computer in the mid-1960s. BBL staff, the banders, and people who reported bird bands all had to adjust to new procedures, but computers were clearly the way to the future. Converting millions of old banding records from various media and formats to magnetic tape was a monumental task, and BBL had to contract for private keypunching. Given the limitations of BBL staff and time, contracting out made sense, but it proved to be less than fully successful. The private contractor made so



Figure 6. Keypunching at BBL. Photograph courtesy of BBL, USGS Patuxent Wildlife Research Center.

many mistakes that BBL had to re-punch many records. “Re-punch” took years.

Shortly after Allen Duvall’s move to Washington in the fall of 1964, Earl B. Baysinger became the fourth BBL Chief (Figure 7). Engaging and energetic, Baysinger was reform minded, and he added much impetus to modernization efforts at BBL. Under Baysinger, BBL began communicating formally with banders via sequentially numbered *Memorandum(a) To All Banders* which quickly became known as *MTABs*. *MTABs* were shorter and were issued more frequently than *Bird Banding Notes* had been, but the content was similar, including the omnipresent admonishments of banders. BBL would continue *MTABs* as late as 2007.

Although *MTABs* were already being issued, BBL compiled one last issue of *Bird Banding Notes* (volume 6, number 1) in March of 1966. At 61 pages, it was the largest ever compiled, reflecting the major overhaul of BBL operations that was occurring. The contents included much on new procedures and policies, plus philosophical discussions about the purposes of bird banding, and pragmatic discussions of what BBL could and could not afford to support, given limited resources in the face of record numbers of birds being banded. With new policies



Figure 7. Earl B. Baysinger, the fourth BBL Chief, in 2004, at BBL. Photograph courtesy of Kinard Boone, USGS Patuxent Wildlife Research Center.

spelled out in the last issue of *Bird Banding Notes*, and later a revised *Bird Banding Manual*, BBL began steering the banding program toward more applied, purposeful banding. Recreational banding was discouraged, and requirements for obtaining banding permits were raised. A limited moratorium on new permits was implemented and once again inactive or uncooperative banders were culled. BBL was in a strong position to do all this, because it now had full signatory authority for banding permits, that authority having, since the 1920s, been gradually delegated downward from the Secretary of Agriculture's Office.

Significantly, that last issue of *Bird Banding Notes* carried the logo of the Canadian Wildlife Service, parent organization of BBO, on an equal heading with the Fish and Wildlife Service logo. This was a clear indication of how internationally important the banding program had become. Canada and the U.S. had long used the same bands and record formats, and had exercised similar policies with regard to banding and permits. But now the program was being managed cooperatively by BBL and BBO, and it was expanding geographically with U.S./Canadian bands being used as far away as Antarctica.

The international importance of BBL was recognized at the highest agency levels in Washington, D.C. In January 1967, the General Services Administration announced plans for the construction of a \$1.1 million Bird Banding Records Center at Patuxent (Anonymous 1967). Construction was completed promptly, and before the end of the decade, BBL was housed in its new, state of the art, home. The building had far more space than BBL needed and was soon filled by other offices of the Migratory Bird Populations Station. The building was named Gabrielson Laboratory (U.S. Fish and Wildlife Service 1972) in honor of Ira N. Gabrielson, an accomplished ornithologist, conservationist, and former Director of the U.S. Fish and Wildlife Service. BBL remains housed in Gabrielson Laboratory at Patuxent to this day.

The 1970s and 1980s—non-game bird banding comes of age.—Earl Baysinger left BBL in mid-1971 to take a job in the Service's Office of Endangered Species and International Activities at Washington, D.C. In August 1971, George M. Jonkel (Figure 8) became the fifth BBL Chief. Jonkel had been with the Service for many years and had been an active bander of both game and non-game birds. He most recently had been supervisor of the Service's Wetlands Acquisition

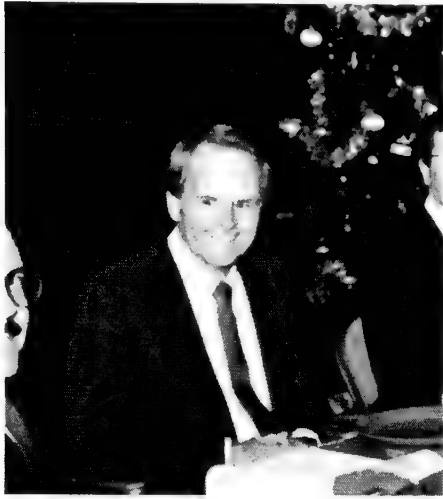


Figure 8. George M. Jonkel, the fifth BBL Chief, during the late 1970s at BBL's annual Christmas luncheon. Photo is courtesy of BBL, U.S.G.S. Patuxent Wildlife Research Center.

Office at Huron, South Dakota, a position with close ties to other migratory bird programs.

The BBL of the 1970s and 1980s was influenced strongly by external developments. Game-bird considerations continued to dominate, but non-game bird banding gradually became more prominent. The Endangered Species Act of 1973 formally charged the Department of Interior with responsibility for the listing and recovery of threatened and endangered birds, most of which were non-game birds. This stimulated much work and required that BBL cooperate with Service endangered species offices to manage the banding of threatened and endangered birds. Outside government, more ornithologists were being employed by universities and colleges, and by the end of the 1980s, nearly one third of all banders would have an academic affiliation. Academic banders, being more scientific, were apt to use auxiliary markers such as colored leg bands, neck collars, and radio transmitters, requiring that BBL invest more time in developing and managing marking protocols with the banders. Throughout the 1970s and 1980s, BBL encouraged and supported non-game bird work by both professional and amateur banders, and it maintained close ties to the regional banding associations that represented the latter.

BBL's role in international conservation continued to grow throughout the 1970s and 1980s. Foreign delegations came to learn the workings of BBL and the broader North American bird-banding program. BBL participated in workshops to train biologists from Latin America, issued more permits for work in Latin America, and helped Brazil develop its national banding program. Working relations with BBO were strengthened in the 1970s and 1980s.

During the 1970s and 1980s BBL and the banders were constantly adjusting to the rapid advance of computer technology. New record-keeping procedures ranging from processing band recoveries to extracting data would be altered or developed to take advantage of computers. An Electronic Data Processing section provided comprehensive computer support to BBL, covering everything from data entry to data-base development and management. Functions such as permits management and band issue became increasingly dependent on, and enhanced by, computer support. By the end of the 1980s personal desktop computers were widely available, and software for managing and submitting banding schedules was being developed.



Figure 9. John Tautin, the sixth BBL Chief, and Monica Tomosy, the 7th BBL Chief, at the 2005 annual meeting of the Eastern Bird Banding Association, Rochester, New York. Photograph courtesy of John Tautin.

Although much changed during the 1970s and 1980s, some things did not. As in all previous decades, BBL had to cope with sometimes inadequate budgets, band supply problems, and of course, those uncooperative banders who needed the occasional “nastygram” from BBL staff to remind them to follow procedure.

At the end of 1988, John Tautin (Figure 9) became the sixth BBL Chief. Tautin was a career employee with the Service’s Office of Migratory Bird Management, and had just finished a tour in the Washington office. He was a bander and had worked as a biologist in BBL during the mid 1970s. He came with a good understanding of the North American bird-banding program and BBL’s role in it. Tautin would serve as BBL Chief through the 1990s, and into the new millennium until his retirement in October, 2002.

The 1990s—partisan politics present a challenge, but science has the greater influence on BBL operations.—BBL had always been influenced by external developments, particularly programmatic developments, but in the 1990s, for first time in its history, raw, partisan politics would affect BBL. Democrat William J. Clinton was inaugurated as the 42nd President of the United States in January, 1993. Clinton appointed former Arizona Governor Bruce Babbitt to be Secretary of the Interior. Babbitt had good credentials and a conservation ethic, and he was reform minded.

During his formative years, Babbitt had worked for the U.S. Geological Survey (USGS), and the experience had made a lasting, positive impression on him. Immediately into his term at Interior, Babbitt set about to create a new agency, the National Biological Survey (NBS). NBS was to be modeled after USGS and provide other Interior agencies and the Nation independent, unsullied biological science. Undaunted by a lack funds, little support in Congress, and widespread concerns among other Interior agencies, states, and conservation groups, Babbitt used his executive powers to create NBS. He accomplished it by transferring all research functions and facilities from other Interior agencies, mainly the Service and the National Park Service, into NBS. BBL was caught up in the bureaucratic whirlwind, and in the fall of 1993 found itself in the NBS.

Despite Babbitt’s promise of prosperity for NBS, BBL and most other NBS offices immediately saw their budgets cut as NBS officials co-opted funds to establish headquarters staff and new programs. The

situation worsened quickly. Within a few months of taking office, Babbitt ran afoul of governors and Congressional delegations from western states where he had tried to implement controversial management reforms on public lands. Congress quickly put Babbitt in check. Checkmate came shortly after mid-term elections in November 1994, when Republicans gained control of the House of Representatives. They stripped Babbitt's NBS of its identity and made it a Division under USGS. BBL, one of the Nation's longest running and most critical migratory bird operations, was now in the geology agency. Said one disgruntled bander, "They must have rocks in their heads." Of course, they did not, but the road ahead for BBL in USGS certainly was rocky.

Initially, neither NBS nor USGS understood fully what BBL did and how important it was to migratory bird research and management. To its credit though, NBS made a concerted effort to learn. In 1994 it commissioned a distinguished panel of experts to review BBL operations and recommend improvements. The panel was led by long-time bander and USGS scientist Paul Buckley. Unfortunately, the panel's report was not completed until 1998 (Buckley et al. 1998). In the interim, serious disputes over budgets, staffing, and other matters arose between BBL and higher administrative levels. The influence of BBL's long-time supporters, particularly the Service and the state wildlife agencies, would be brought to bear at critical times to assure that BBL had the resources it needed to serve the banding community. BBL also did what it could "in house" to improve efficiencies and control its workload. Among other things, it culled hundreds of inactive banders from the rolls and required stronger justifications for new permits.

The review panel did a thorough job and made sound recommendations for "re-engineering" BBL operations in the areas of permitting procedures and practices, operational issues, data management, organization and staffing, and implementation. USGS accepted a number of the panel's recommendations, added its own, and directed BBL to make major enhancements. The panel had not recommended that BBL reduce or discontinue any current functions, so most of the new directives added to BBL's already heavy workload, and some directives, particularly permit directives, proved contentious to BBL and banders. Unfortunately for all, USGS did not provide the additional staff that the review panel had wisely recommended as necessary for a successful re-engineering of BBL. Consequently, progress was generally slow, with the overhaul of BBL's complex computer operations proving particular-

ly difficult and taking years to accomplish. However, reasonable permit policies were maintained, and the most important operational changes were made.

On the positive side of things, the review panel's report added impetus to ongoing efforts by BBL to make the banding program more scientific. Back in the 1970s, at Patuxent and other places, a quiet, but profound, revolution in banding-data analysis had begun with the development of the so called Seber-Robson-Brownie models for estimating survival and recovery rates from band recovery data (Nichols and Tautin, this volume). As was historically the case with many developments in bird banding, this one was also driven by game-bird management priorities. Waterfowl management and the setting of annual hunting regulations were becoming more complex, and federal and state agencies needed better scientific results from banding (Tautin 1993). The development of analytical models moved rapidly beyond game-bird band-recovery models to include more versatile mark-recapture models well suited for non-game bird studies. By 1990, a suite of versatile and powerful models with accompanying software was available to the banding data analyst.

BBL recognized the value of these analytical tools and began to promote them in the banding community. BBL publicized them in *MTABs*, participated in international technical conferences held to advance the models, organized workshops at ornithological meetings, and otherwise encouraged banders to use the modern analytical models. Preference was given to permit applicants who designed banding studies with the intention of using the models, and BBL steered new and existing banders toward participating in cooperative projects like the Institute for Bird Populations' Monitoring Avian Productivity and Survivorship (MAPS) (DeSante and Burton 1994). MAPS was revolutionary in concept and scope, and in its design that made full use of contemporary analytical models and constant-effort mist-netting.

During the 1990s, BBL made several operational changes to support a more scientific banding program. In cooperation with Bird Studies Canada and BBO, new computer software (BAND MANAGER) was developed to enable banders to manage their banding data more efficiently and to submit data electronically to BBL. BBL also worked closely with the North American Banding Council (NABC) (Morris et al., this volume) to develop a bander-training and certification program. The program was designed to increase the number of

skilled banders capable of participating in the more scientific banding projects such as MAPS. In a significant policy advancement in 2001, BBL began accepting NABC certification as evidence of qualifications for a banding permit.

The most significant operational change made by BBL in the 1990s was to establish a toll-free telephone number for people to call and report bird bands. A late 1980s study (Nichols et al. 1991) had determined that only 32% of hunters who killed a banded Mallard actually reported the band. This rate was unacceptable with respect to the new, data-hungry analytical models and adaptive management principles being applied in a more scientific approach to setting hunting regulations. More and better band-recovery data were needed, and the convenience of a toll-free band number was the solution identified.

After negotiating bureaucratic hurdles, modifying computer systems, retraining staff, and obtaining bands with the 1-800-327-BAND telephone number stamped on them, BBL implemented the toll-free band-reporting system at the beginning of the 1995-1996 waterfowl hunting season. The toll-free number was an immediate success. BBL received so many calls reporting bird bands that staff could barely keep up. In subsequent years, BBL had to contract with outside answering services to help handle the volume. Within three years the Mallard band-reporting rate increased to 80%, much to the delight of federal and state agencies involved in waterfowl management.

Eventually, the 1-800 phone number was placed on all bird bands, and reports of non-game bird-band recoveries increased accordingly. These additional recoveries were useful and appreciated, but for most non-game-bird studies, recaptures and resightings of previously banded birds were more valuable. Untold millions of these data were accumulating and not being stored at a central location for archiving and use by persons other than the original banders. These data were well suited for use in contemporary analytical models and could be applied to a plethora of non-game-bird research and management questions. Thus, at the end of the 1990s, supported by a key Buckley review-panel recommendation, BBL turned its attention to developing a recapture/resighting database completely new in concept.

While politics, re-engineering and science were in the spotlight during the 1990s, behind the scenes BBL and its staff of 25 clerks, biologists, and computer specialists continued to address the everyday prac-

tical matters of supporting some 2000 banders and their 3000 subpermittees who were banding 1.1 million birds annually. As in every previous decade, BBL had to deal with a host of perennial issues, including, of course, band supply and exhorting banders to follow procedures!

2000 and beyond: reflecting on the past and looking to the future.—The new millennium brought historic anniversaries for both BBL and the broader North American bird-banding program. Dating back to Frederick Lincoln's founding of the banding office in 1920, BBL became 80 years old in 2000. With a rich and productive history, it was, and still is, one of the longest running, most successful offices in the history of wildlife conservation.

Tomorrow's bird-banding program will differ from today's as technology advances and new research and management needs develop. But as the banding program evolves, the past, present, and foreseeable future will remain linked by the fundamental need to uniquely identify individual birds to study their movement, survival, and behavior. Bird banding, or marking in some form, will remain a universal and indispensable tool in avian conservation. Thus, the histories of the banding program and of BBL will likely extend far into the future. May there be at least another 100 years of bird banding in North America, for as Bartsch (1904) said in the beginning, "There are still many unsolved problems about bird life"

ACKNOWLEDGMENTS

The staff of the BBL, particularly Florence Soehnlein, kindly assisted in locating, and provided access to, historic file materials at BBL. Kinard Boone of the USGS Patuxent Wildlife Research Center provided digital copies of several figures presented in this chapter. Matthew Perry located a key photo for the chapter and provided leads to information on former BBL Chiefs. Chandler Robbins, Kathy Klimkiewicz, and Nancy Mullis shared recollections of BBL history. Lynda Garrett allowed access to the extensive collections of the USGS Patuxent Wildlife Research Center's library. William E. Davis, Jr. and Jerome A. Jackson provided helpful editorial suggestions.

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The Role of the North American Bird-Banding Scheme in Bird Population Monitoring

Charles M. Francis¹

Abstract.—Bird banding has been a significant component of many programs to monitor changes over time in population size and demographic parameters of bird populations in North America. Uses of banding data have ranged from developing simple indices of relative abundance based on capture totals, to sophisticated mark-recapture models to estimate population size and demographic parameters. Standardized banding totals, adjusted for weather and time of year effects, have been used to provide an index to numbers of birds stopping each year at migration monitoring stations. Capture-recapture methods could be used to improve these indices by providing estimates of stopover duration and the proportion of birds newly arrived at a site. Banding, especially in combination with auxiliary markers, has been used to identify individual birds and estimate numbers of breeding pairs; this is a valuable approach for testing assumptions of other count-based monitoring methods. For demographic monitoring, data on age ratios collected during migration or breeding-season banding have been used to monitor annual variation in productivity. The greatest value of banding data has been for monitoring avian survival rates, which are nearly always dependent on recapture, resighting or recovery data from banded birds. Monitoring temporal changes in survival and recovery rates has been historically very important for management of waterfowl populations, especially to evaluate impacts of changes in hunting regulations. Monitoring changes in survival is increasingly an option for passerines and other non-game birds as a result of long-term single-species studies, as well as large-scale constant-effort programs such as MAPS (Monitoring Avian Productivity and Survival), combined with new developments in analysis techniques. In the future, we can anticipate greater use of banding combined with other sources of data as part of integrated population monitoring programs.

Bird population monitoring can be defined as measuring changes over time in various parameters of bird populations. Although monitoring is usually thought of primarily in the context of detecting changes in population numbers, monitoring programs can also track changes in demo-

¹National Wildlife Research Centre, Canadian Wildlife Service, Environment Canada, Ottawa, Ontario, Canada K1A 0H3

graphic parameters, such as survival and recruitment. Such monitoring can provide valuable information for bird management and conservation (Rich et al. 2004).

In the early development of banding in North America, monitoring of population change was not explicitly considered one of the objectives. Lincoln (1921) highlighted two major types of data provided by banding: information on movements, including migration routes, site fidelity, and dispersal that can be obtained when marked birds are recaptured; and information on life histories, mating strategies, etc. that can only be obtained when individual birds can be recognized. Nevertheless, he also emphasized the potential importance of banding to game-bird management. Of particular interest was delineation of connections between breeding and wintering areas, as well as information on whether these changed over time. Nelson (1920) noted similar benefits of banding, additionally highlighting the potential to understand migration speed and avian longevity.

The concept of using banding data to estimate population sizes of waterfowl was developed soon thereafter (Lincoln 1922, 1930). Lincoln (1930) estimated population sizes for many species of North American waterfowl by comparing the proportion of banded birds that were harvested with estimates of the total numbers of birds in the harvest (derived from hunter surveys). Although this approach did not lead to an ongoing monitoring program, the results were useful for setting waterfowl hunting regulations at the time.

For waterfowl, a great deal of information can be obtained from recoveries of birds reported shot by hunters, but for most other species, especially songbirds, few bands are encountered away from the original banding location. Baldwin (1921) demonstrated the value of repeatedly trapping birds at the same banding location to enhance encounter information. The importance of repeated trapping was emphasized by Nelson (1920) and Lincoln (1931) in their reviews of banding in North America. Multiple captures of individuals provide the basic data to follow the demography of individual populations. In one of the most thorough early population studies of birds in North America, Nice (1937) used intensive banding, combined with observational data, to estimate demographic parameters for her local population of Song Sparrows (*Melospiza melodia*). Subsequently, intensive studies of individual populations have relied on banding as an important tool for estimation of

demographic parameters. Data from band recoveries have also been used to estimate survival for many species (e.g., Hickey 1952), although it was not until the development of modern statistical methods for band recovery analysis (e.g., Brownie et al. 1978) that temporal changes in survival could be reliably monitored.

From those early beginnings, bird banding has grown to play an important role in many aspects of bird population monitoring in North America. Monitoring changes in population abundance has involved banding data in various ways, from simple indices based on capture totals, to sophisticated mark-recapture models to estimate population sizes, to use of banded birds to evaluate other monitoring techniques. Monitoring of survival, recruitment, and harvest rate has been dependent almost entirely on banding data, through analyses of recaptures, resightings, or recoveries.

In this paper, I provide an overview of some of the ways that bird banding has been and could be used as part of bird population monitoring programs, particularly in North America. I first discuss the role of bird population monitoring in management and conservation. I then consider separately the use of banding for monitoring population size, and the use of banding for monitoring demographic parameters such as survival and recruitment. I close with a brief discussion of future directions for banding in integrated population monitoring programs in North America.

ROLE OF POPULATION MONITORING IN MANAGEMENT AND CONSERVATION

Many monitoring programs take place over long time periods at large geographical scales to assess integrated impacts of both natural and anthropogenic factors on continental or regional bird populations. This type of monitoring provides the foundation for many conservation and management actions (Dunn 2002). For example, long-term declines in bird population numbers may indicate a need for conservation action to protect a species. In the United Kingdom, long-term monitoring programs have led to major conservation initiatives to protect and restore populations of farmland birds (Greenwood 2003). In North America, Partners in Flight uses information on trends in population numbers, especially declines, to help set bird conservation priorities (Rich et al.

2004). Changes in demographic parameters, such as survival rates, productivity, or age of first recruitment can provide valuable information to help identify possible causes of population changes (Baillie 1990; DeSante et al. 1995, 1999; Greenwood 2003). In turn, such information helps to determine appropriate conservation or management actions.

Monitoring programs also can (and should) be integrated into specific management activities to assess the impacts and effectiveness of the management activities. This can happen at scales ranging from land management on individual refuges to hunting regulations at a continental scale. Rarely do we know enough about bird-habitat relationships, or the effect of management practices on resultant habitat quality, to predict with certainty the impacts of particular management activities on bird populations. Management designed to enhance the value of habitat to particular bird species should be accompanied by monitoring of bird populations on that site to assess the effectiveness of the management. Well-designed monitoring can both enhance our understanding of the system and allow more effective management in the future.

In the case of waterfowl-harvest management in North America, this integration of monitoring and management has been formalized into an adaptive management framework (Williams and Johnson 1995, Williams et al. 1996). Management options (harvest regulations) are selected using a modeling approach that explicitly recognizes uncertainty in the impacts of regulations on harvests and in the impacts of harvests on bird populations. Carefully designed monitoring of bird population responses (including population size, harvest and survival rates), provides feedback into this process that helps to reduce future uncertainty and improve the management process (Williams et al. 1996).

For all of these programs, techniques ranging from counts of birds detected visually (either from the ground or from aerial surveys) or by song, to sophisticated capture-recapture/resighting models based on individually marked birds have been used to monitor population parameters.

USE OF BANDING TO MONITOR CHANGES IN POPULATION SIZE

For most species of birds in North America, the primary large-scale programs to estimate changes in population numbers are based on visu-

al and/or acoustic observations in the field. In many cases, though, data from banding programs have been used, or could be used, to supplement and improve these methods. In some cases, banding data are part of the primary method for estimating population sizes or trends. More frequently, banding data have been used to support population/trend estimates derived from other surveys, or to evaluate assumptions of other monitoring methods.

For most inland-breeding waterfowl species in North America, aerial transect surveys, combined with ground counts to develop visibility correction factors, are currently used to estimate breeding populations each year (Smith 1995). These surveys are considered to provide relatively unbiased estimates of total population size, at least for those populations breeding in the prairies. However, long before the development of these aerial surveys, Lincoln (1930) estimated population size for ducks based on the proportion of banded birds recovered by hunters, combined with estimates of the total number of birds harvested by hunters. His estimation method, which came to be known as the "Lincoln-Petersen estimator," became the basis for development of more sophisticated mark-recapture models over the past several decades (Nichols and Tautin this volume). Results from Lincoln's analyses also played an important role in setting waterfowl hunting regulations at the time, by giving managers, for the first time, information on the total numbers of waterfowl in North America.

Although no longer systematically used as part of the core waterfowl monitoring programs, mark-recapture estimates are still used to validate population-size estimates obtained from other survey methods for various species. Hestbeck and Malecki (1989) used mark-resighting models to evaluate the accuracy of population estimates derived from aerial surveys of Canada Geese (*Branta canadensis*) wintering in the eastern United States. Similarly, a Lincoln-Petersen estimate derived from resighting data of color-banded birds was used by Gonzalez et al. (2004) to assess results from aerial surveys of Red Knots (*Calidris canutus*) on their wintering grounds in Argentina and Chile (Morrison et al. 2004). In the latter case, the independent mark-resighting estimate was particularly valuable to show that observed large declines in aerial survey counts were probably due to declines in the populations rather than changes in wintering habitat or distributions. Gunnarsson et al. (2005) used resightings of color-marked Black-tailed Godwits (*Limosa*

limosa) on spring staging areas to estimate adult population size, and compared these with winter counts to make inferences about the wintering distributions of the Icelandic subspecies.

For many species of birds, particularly songbirds, the primary large-scale monitoring programs are based on survey methods such as point counts that only provide an index of population size. Thus, changes in population size can only be inferred from changes in population indices by assuming that the relationship between the index and true population density has not changed over time. The Breeding Bird Survey, the most widely used multi-species survey for landbirds in North America (Robbins et al. 1986), involves aggregating counts from fifty 3-minute point counts along randomly selected roadside routes throughout much of the U.S. and southern Canada. Point-count methods are also used in a wide range of regional and habitat-specific surveys across North America (see examples in Ralph et al. 1995).

Diverse methods have been proposed to estimate the relationships between point count indices and actual population densities to test the assumptions inherent in using these indices (Bart et al. 2004). Methods include use of double-observers to address variation in detection abilities among observers (Nichols et al. 2000), removal models to estimate numbers of birds and species that were not detected (Farnsworth et al. 2002), distance sampling methods to convert estimates of numbers of birds into densities (Buckland et al. 2001), and double sampling methods (Bart and Earnst 2002) in which a subset of sites is sampled more intensively to estimate true density. Each of these methods has its own assumptions and limitations, and further validation is required to determine which of these approaches (if any) will prove most effective for integration into large-scale surveys. The major role of banding in these programs has been for evaluation of some of these techniques.

DeSante (1986) showed that density estimates derived from variable circular plots (a distance sampling variation on point counts) were similar to those derived from mapping territories of individually color-banded birds (Figure 1). Tarvin et al. (1998) compared densities of nesting pairs of Blue Jays (*Cyanocitta cristata*) in a color-banded population with estimates derived from various point-count techniques and found that none of the methods worked particularly well. Other studies have used territory mapping of unmarked birds (spot-mapping) as a standard for evaluation of survey techniques, but that method is subject to observer bias (Verner and Milne 1990). Thus, there is considerable



Figure 1. Dave DeSante with a Northern Parula (*Parula americana*) in Cuba, 3 March 1999. Photograph by Hillary Smith.

potential for more use of territory mapping of individually marked birds to develop better validation methods of other monitoring techniques. Intensive observations of marked birds can also be used to test assumptions of other monitoring methods. For example, Jones (1992) used intensive observations of a color-marked population of Least Auklets (*Aethia pusilla*) to test assumptions about the proportion of birds that was visible at any one time on a colony.

In theory, banding could also be used as part of a double-sampling program, by estimating densities using mark-recapture methods in a subset of surveyed areas, to convert indices of population size to actual estimates of population size. In practice, mark-recapture methods have rarely been used to estimate population sizes directly for landbirds in any type of study. Nichols et al. (1981) reviewed the use of mark-recapture methods to estimate bird population sizes, and found few published

studies using these methods, most of which were for game birds. Nichols et al. (1981) used open-population models to analyze a number of existing data sets for various species, including several songbirds, and found that the coefficient of variation for population size estimation was often quite large, except in a few cases with high capture probabilities (indicating that most individuals of the population had been marked). Casagrande and Beissinger (1997) compared density estimates for a small neotropical parrot based on four sampling methods, including distance methods and mark-resighting. They found population estimates were comparable from all methods, but the mark-resighting analyses required the greatest effort to collect data, had the lowest precision, and had problems with model assumptions. Zakaria and Francis (1999) used open population capture-recapture models to estimate sampled populations of understory tropical forest birds in Southeast Asia, but had to make arbitrary assumptions about the area being sampled in order to convert these into densities (Francis and Wells 2003). They found that relative abundance of species was quite different from that estimated by capture totals, due to large interspecific variation in capture probabilities, and highlighting the value of using mark-recapture models rather than simple indices of numbers captured for comparisons among species.

Even in cases where banding data have been used in capture-recapture analyses to estimate population size, they have rarely been integrated into longer-term monitoring of population numbers. One notable exception is in the case of endangered species with very small populations for which a high percentage of the population can be marked. For Kirtland's Warbler (*Dendroica kirtlandii*), with a total population size estimated at about 300-350 males in recent years, up to 50% of males have been banded in some areas (Probst et al. 2003). This intensity of banding facilitates validation of other sampling methods, and provides data to monitor demography and movements. In an extreme case, the total world population of California Condors (*Gymnogyps californianus*), both wild and captive, was banded, allowing tracking not only of population size and demographics, but also genetic pedigrees (Ralls and Ballou 2004). At one point, the last-known surviving Heath Hen (*Tympanuchus cupido cupido*) was banded (Gross 1931), in part so that it could be recognized to determine whether it was, in fact the only remaining bird.

An alternative form of mark-recapture analysis estimates population growth rate (i.e., trend) directly from banding data, rather than first estimating population size (Nichols and Hines 2002), providing a potentially interesting alternative approach to population monitoring. This analysis method has been used on a variety of data sets, including Roseate Terns (*Sterna dougallii*; Nichols and Hines 2002) and Snail Kites (*Rostrhamus sociabilis*; Dreitz et al. 2002). However, such models require many of the same assumptions as population size estimation using open-population mark-recapture models, and estimates are particularly subject to bias if detection probabilities of animals are affected by initial capture (Hines and Nichols 2002). Bias in this respect may be reduced if analyses are based on resightings rather than recaptures, as was the case for the study by Dreitz et al. (2002). Data from these approaches can also be integrated with count data from other sources to enhance the precision of the estimates (Nichols and Hines 2002). It remains to be seen whether this approach will be practical in an operational monitoring program.

Capture totals from banding operations have often been used in monitoring programs as indices of population abundance. Karr (1981) outlined approaches for using mist nets to sample bird populations, particularly in tropical areas, as they have the advantages over other survey methods that sampling effort can be well standardized and is not dependent on observer skills. Since then, mist nets have been used in a diversity of monitoring programs, as outlined in a series of papers brought together by Ralph and Dunn (2004) (Figure 2).

Valid interpretation of indices derived from simple capture totals in mist net samples is critically dependent on the assumption that capture probabilities do not vary (Sauer and Link 2004). Capture probabilities are particularly likely to vary among species, even for species with similar ecology (e.g., Francis and Wells 2003). Thus, comparisons among species should be based either on more sophisticated approaches that estimate detection probabilities (e.g., mark-recapture analyses), or at least cross-validation among several sampling methods (e.g., visual surveys as well as netting).

With appropriate standardization of factors such as sampling effort, habitat, and location, capture totals may be useful for monitoring population trends within species (Dunn and Ralph 2004, Ralph et al. 2004). Standardized banding may be particularly useful for monitoring birds on migration, when few birds are singing and methods such as point



Figure 2. Erica Dunn, shown here banding a Saw-whet Owl (*Aegolius acadicus*), has promoted and evaluated the use of standardized banding for bird population monitoring. Photograph courtesy of Erica Dunn.

counts, which depend on detecting singing birds, are less effective. Migration counts have been advocated as an approach for monitoring populations of birds that are not readily sampled on the breeding grounds, particularly those that breed in the boreal forest or arctic where few birders are available to survey them (Hussell 1981). Although migration counts can be based on a variety of sampling methods, most monitoring stations, at least for songbirds, incorporate a component of banding (Hussell and Ralph 2005). Incorporation of well-standardized banding into a migration monitoring protocol has advantages in terms of standardization, as mentioned above, as well as providing ancillary data on age, biometrics, and body condition of captured birds. Particularly useful is collection of feathers for isotope analyses which



Figure 3. David Hussell, 1968, Long Point Observatory. Hussell established monitoring protocols emulated by bird observatories across America, pioneered trend analysis methods for migration counts, and helped establish the Canadian Migration Monitoring Network. Photograph courtesy of Charles Francis.

can provide information on the breeding origins of the birds being counted (Wassenaar and Hobson 2001).

Dunn et al. (2004b) found that trends derived from banding capture totals compared well with those based on counts from standardized observations at Long Point Bird Observatory. Comparisons with independent surveys such as the Breeding Bird Survey also suggest that migration counts incorporating banding studies can detect trends reliably, at least for species undergoing substantial population change

(Hagan et al. 1992, Dunn et al. 1997, Francis and Hussell 1998, Kaiser and Berthold 2004). However, both for observational data and banding data, sampling can be sensitive to habitat change at the sampling area (Dunn et al. 2004b, Kaiser and Berthold 2004). To some extent, this can be addressed by avoiding sites undergoing rapid successional change, by sampling at multiple stations with different habitats unlikely to be subject to the same change patterns, and by managing habitats (Ralph et al. 2004, Hussell and Ralph 2005) (Figures 3, 4).



Figure 4. David Hussell, June 1976, holding one of the first Forster's Terns (*Sterna forsteri*) found nesting at Long Point. Photograph courtesy of Charles Francis.

In theory, it would be possible to take advantage of banding data to improve migration monitoring by estimating the numbers of birds present at the stopover site, using mark-recapture methods, thus reducing problems associated with changes in detectability with habitat change. However, at many migration sites recapture rates are too low to make this practical. Most birds are captured once and never seen again as they move out of the area. Mark-recapture methods have more promise for estimating stopover duration of birds that remain at a site (Kaiser 1995).

This can be relevant for interpretation of count data, particularly to correct seasonal counts for the number of individuals that may have been counted multiple times on different days. Schaub et al. (2001) used mark-recapture models to show that stopover durations of migrants at a stopover site in Europe were generally longer than those estimated based solely on the mean interval elapsed between first and final capture. Morris et al. (2005) further refined these models, estimating stopover durations of migrant passerines at Appledore Island, Maine. More research is needed to determine how well the assumptions of those models are met, and to consider the best ways to incorporate transient models that allow for different capture probabilities for birds that move quickly through a site without stopping, and those that stay for one or more days.

MONITORING DEMOGRAPHIC PARAMETERS

In contrast to monitoring of bird population size, for which banding data have usually been secondary to other survey methods, monitoring of demographic parameters such as survival and recruitment has been critically dependent on bird-banding data. Monitoring of survival and recruitment can provide information to help interpret changes in population parameters and infer possible causes. For example, in the United Kingdom, monitoring data showed that recent declines in some farmland bird species were associated with reduced productivity, but for most other species, declines were associated with reduced survival (Greenwood 2003). This suggested a problem with overwinter survival, apparently associated with reduced food availability on farms with more intensive agricultural practices. This information has been helpful in developing policies for more bird-friendly farm management.

In North America, banding data have long been used to estimate survival rates of birds. Many analyses were based on band recoveries, because these indicate date of death and thus seemed to be appropriate for life table approaches. Hickey (1952) published an extensive overview of survival rates for many species of birds based on life table analyses of band recovery data. He found an apparent strong relationship between recovery rates and annual mortality of ducks, suggesting that hunting mortality was additive to other forms of mortality. For most songbirds, relatively few recovery data are available, so analyses have

generally been based on recaptures or resightings of color-banded birds, starting with such early classic studies as that of Nice (1937). Until recently, most recapture data were analyzed using ad hoc approaches that estimate the number of birds that die each year based on those that were never seen again (see review in Martin 1995).

Unfortunately, there are a number of problems with those early analysis methods. Recovery models did not take into account possible annual or age-specific variation in the likelihood that a dead bird will be found and reported, or the sampling correlations among recovery and survival estimates (Anderson et al. 1981, Burnham and Anderson 1979). Recapture models did not properly take into account the fact that birds not seen in a particular year may still have been alive (Martin et al. 1995). Inappropriate models can produce biased results which may affect conclusions. For example, analyses of duck recovery data using more appropriate methods suggested that increased hunting mortality was largely offset by reduced non-hunting mortality (i.e., compensatory) rather than additive to other forms of mortality (Anderson and Burnham 1976, Burnham and Anderson 1984). However, this remains a controversial subject, and some more recent studies have found evidence that hunting mortality is additive, at least in some populations, meaning that changes in hunting mortality do lead to changes in overall survival rates (Trost 1987, Smith and Reynolds 1992, Francis et al. 1998). Similarly, recapture models without properly estimated capture probabilities often under-estimate survival, although the bias tends to be minimal for resighting studies of color-marked territorial birds or other very intensive studies in which nearly every bird is seen every year (Martin et al. 1995).

In the past few decades there has been tremendous progress in the development of sophisticated statistical models for analysis of banding data (Nichols and Tautin, this volume). These include models for using live recaptures and resighting data (e.g., Lebreton et al. 1992), or recovery data from birds found dead or shot (e.g., Brownie et al. 1978) along with sophisticated computer programs for their implementation (e.g. White and Burnham 1999). This ready availability of software and models has led to greatly improved analyses and increased interest in monitoring survival.

Many long-term banding studies, although not necessarily established as monitoring programs, have yielded data that provide information on changes in survival over time—the essential ingredient of a

monitoring program. Particularly extensive banding and recovery data sets are available for many waterfowl species, and have been used in various ways for monitoring temporal changes in survival, harvest rates, and movements. Although data are available for many species, I discuss here examples from four of the more intensively studied species.

In North America, the most extensive banding program is for the Mallard (*Anas platyrhynchos*). Banding of mallards is sustained in large part by government agencies interested in management of the species for hunting, although some banding also takes place as part of specific research projects. This extensive banding has yielded information on geographic and temporal variation in survival over much of the continent (Anderson 1975, Nichols and Hines 1987). Data have been used as the basis for studies evaluating the impact of hunting on survival (e.g., Anderson and Burnham 1976, Smith and Reynolds 1992), and are integrated into the Adaptive Harvest Management strategy (Johnson et al. 1993).

Ongoing banding programs for American Black Ducks (*Anas rubripes*) have also been important in monitoring geographic and temporal variation in harvest rates and how these have been impacted by changing regulations (Conroy and Blandin 1984) as well as the impacts of restrictive harvest regulations on survival (Francis et al. 1998). Statistical methods for analyzing these data continue to improve, allowing better use of data from widely scattered geographic areas (Conroy et al. 2005).

Annual banding of Snow Geese (*Chen caerulescens*), initiated as part of a research project on genetics by Fred Cooke and associates in 1969, has allowed monitoring of the consequences of increasing population size on demography (Francis et al. 1992). Survival rates of adults increased over time, as the proportion of the population being harvested by hunters declined, while immature survival decreased over time, as population increases in breeding colonies led to degradation of the food supply and reduced gosling growth rates (Francis et al. 1992). Analyses of subsequent changes in survival rates from this colony have also been important in predicting the likely impact of control measures to reduce goose populations (Cooke et al. 2000). More recently, banding programs have been initiated at a number of other colonies to assess the impacts of changing hunting regulations on survival and movements. Such programs, in combination with monitoring of population size, have been particularly valuable in showing that special hunting seasons

have been successful in increasing harvest rates, reducing adult survival, and hence controlling population size of Greater Snow Geese (*C. c. atlantica*; Calvert and Gauthier 2005) (Figure 5).

Extensive banding has also been carried out for Canada Geese (*Branta canadensis*), using not only standard leg bands, but also various colored bands and neck collars that can be read in the field without capture. Neck collar data have been particularly valuable for monitoring movements and estimating population sizes of various populations of geese (Hestbeck and Malecki 1989, Hestbeck et al. 1991). Unfortunately, neck collars appear to affect survival and/or recovery rates of geese (Castelli and Trost 1996, Sheaffer et al. 2004), reducing their value for survival monitoring. Nevertheless, sufficient banding data for birds both with and without collars have been available to show that annual variation in survival of Canada Geese is affected by harvest rates, although other factors are also important (Sheaffer et al. 2004).

For non-game birds, fewer long-term studies are available that provide sufficient data for analyses of temporal variation in survival based

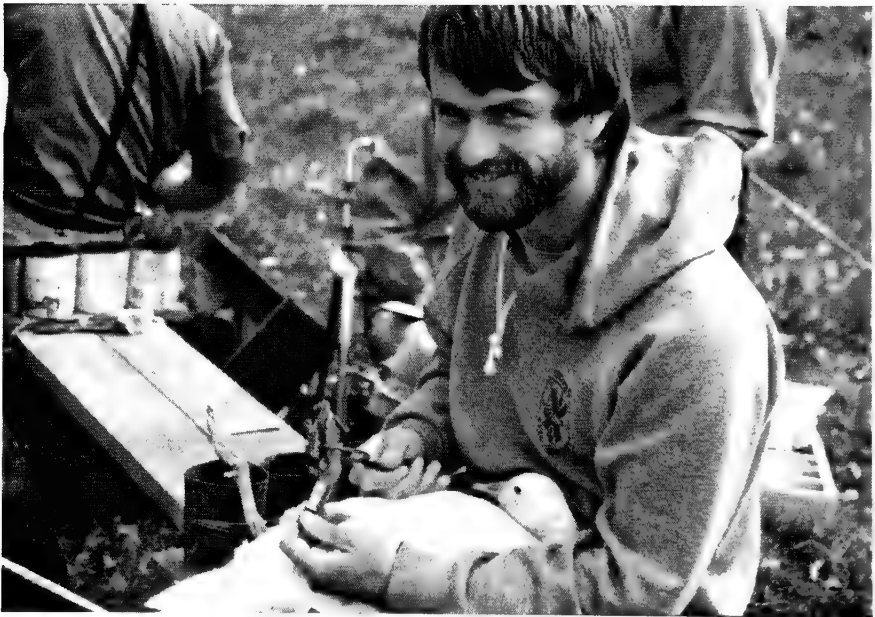


Figure 5. Charles Francis banding a Snow Goose at La Perouse Bay, 1988. Photograph courtesy of Charles Francis.

on recoveries. Houston and Francis (1995) were able to show that survival rates of Great Horned Owls (*Bubo virginianus*) of all age classes (young, yearlings, and adults) varied in relation to the snowshoe hare (*Lepus americanus*) cycle. Several authors attempted to analyze survival rates of gulls (*Larus* spp.) to understand long-term changes in population sizes on the Great Lakes, but estimates were not consistent with observed population growth rates (Ludwig 1972). Ludwig (1967) showed that survival estimates were severely biased by band loss, and proposed a method to adjust mortality estimates for band loss.

For most songbirds in North America, too few recoveries are available to estimate annual changes in survival rates based on recovery data (Francis 1995). Instead, it is necessary to rely on recapture data. Unfortunately, the banding office has not kept recapture data in a central location (a situation that will hopefully change in the future—Buckley et al. 1998), thus reducing the ability of researchers to compile data from many different banding stations to monitor geographic and temporal patterns in survival in the same way as is possible for waterfowl. Although mean survival estimates have been published for many species of passerines (Martin 1995), few analyses have used modern statistical approaches, and even fewer have examined temporal variation in survival – the key component to monitoring. Nevertheless, some individual researchers have long-term data sets, and a few of these have been used to estimate long-term changes in survival rates. One of the most thorough analyses is the study of Loery et al. (1997) who found a long-term decline in survival rates of Black-capped Chickadees (*Poecile atricapillus*) wintering at feeders in Connecticut, although they were not able to determine the cause. No doubt many similar analyses can be expected in the future, as researchers computerize historical data using newer data management software, and make use of readily available analysis software such as MARK (White and Burnham 1999).

Recognizing the potential strength of a large-scale integrated banding program, the Institute for Bird Populations initiated the Monitoring Avian Productivity and Survival (MAPS) program in 1989 (DeSante et al. 1995). This program has resulted in fairly good coverage for monitoring in several western U.S. states, and portions of the eastern U.S., although coverage in some central areas and in Canada is still rather sparse (DeSante and O'Grady 2000). Through this program, it has proven possible to estimate annual variation in apparent survival rates with reasonable precision by pooling data across moderate geographical

areas. DeSante et al. (1999) were able to show that observed population changes across large geographical areas were consistent with observed changes in survival and productivity in the western U.S.

Banding data can also be used to monitor annual variation in productivity, another key component of avian demography. For banding stations on the breeding grounds, variation in the proportion of juveniles caught in constant effort mist-netting sites, such as MAPS stations, appears to be a good measure of annual variation in productivity (DeSante et al. 1999), although it remains an index rather than an absolute measure. Nott et al. (2002) used MAPS data to show that annual variation in productivity in the Pacific Northwest of the U.S. was correlated with large-scale oscillations in weather patterns, as indexed by the El Niño Southern Oscillation and the North Atlantic Oscillation.

Age ratios from migration banding can also potentially be used to monitor productivity. However, many migrant concentration sites have highly skewed age ratios in autumn, with relatively few adult birds being caught. This means that annual variation in age ratios may be more dependent on conditions that influence capture of adults, rather than on the number of young being produced. Further research is required to determine to what extent migration age ratios can be useful for monitoring productivity (Hussell 2004, Dunn et al. 2004a).

FUTURE DIRECTIONS

Although population monitoring was not considered among the early objectives of bird banding in North America, banding has since been incorporated into bird population monitoring in many different ways. In general, banding data have been of secondary importance for estimating trends in population abundance. However, banding data have been essential for monitoring changes in demographic parameters, particularly survival and recruitment rates.

Bird population monitoring can be most effective if data from multiple sources are integrated to give information on many different parameters of bird populations, especially in the context of management and conservation actions. Thus, an effective monitoring program should provide information not only on temporal changes in population numbers, but also information on demographic parameters that can help to identify potential causes of population change. In the future, we should

look towards more integration of banding in the context of broader monitoring programs, especially for estimating demographic parameters.

In the United Kingdom, the British Trust for Ornithology has formalized this approach into an Integrated Population Monitoring program, involving the use of several concurrent monitoring programs to track bird populations (Baillie 1990). Breeding bird surveys provide information on changes in numbers, nest record schemes track changes in nesting success, and focused banding programs at constant effort sites provide information on changes in survival rates. Analysis of all three data sets in conjunction provides information not only on population changes, but also on the potential causes of change, and times of year when they may be operating (Greenwood 2003). Such information can, in turn, lead to specific management actions to restore declining populations and/or targeted research programs to identify specific management actions that may be effective. Ongoing monitoring of both population size and the demographic parameters that were targeted by management can then be used to assess effectiveness of the management actions, thus providing feedback.

In North America, the MAPS program (DeSante et al. 1995, 1999) was developed to fill a similar role to the United Kingdom constant effort program, providing information on temporal changes in survival rates of passerines, although the vastly greater scale of North America compared to the United Kingdom provides some challenges. The MAPS program can detect changes by combining data from multiple stations (DeSante et al. 1999), but has low power to evaluate patterns at small scales owing to limitations in sample size. In North America, nest records data are still relatively sparse, providing limited information on annual variation in productivity. However, the possibility of tracking variation in productivity through age ratios in MAPS banding data may help to fill this gap.

The adaptive management framework used to manage some waterfowl populations in North America is another example of an integrated monitoring approach (Johnson et al. 1993, Williams and Johnson 1995, Williams et al. 1996). Data from breeding ground aerial surveys provide information on changes in population numbers, brood counts provide information on annual variation in productivity, while banding and recovery data provide information on annual survival rates, as well as a measure of mortality due to hunting (based on the proportion of birds

that are reported shot). These data are evaluated in the context of explicit models that relate bird population responses to harvest management, and used to evaluate and refine those models.

Such integrated monitoring approaches can be used at a population-wide scale to evaluate integrated impacts of overall environmental change. They can also be used at a much smaller scale to evaluate impacts of specific effects such as management programs or environmental disasters. For example, banding combined with radio-tracking was used to estimate the impacts of the Exxon Valdez oil spill on the demography of bird populations (Esler et al. 2000, Peterson et al. 2003). Even several years after the spill, Harlequin Ducks (*Histrionicus histrionicus*) had lower overwinter survival rates in areas that had been affected by the spill, suggesting persistence of long-term toxic effects of the oil that were sufficient to lead to a declining population (Esler et al. 2000).

In the near future, one can anticipate a number of changes in the North American banding program as new technologies are developed to mark and to follow individual birds. Such technologies already include satellite transmitters, conventional radio-transmitters, and transponders; these are becoming increasingly smaller, thus expanding the range of species on which they can be used. Many of these technologies have the advantage that birds can be readily detected without the need for repeated physical captures, thus enhancing the amount and quality of data for individual birds. Such data are particularly valuable for monitoring bird movements, a population parameter which has not been considered in this paper, but is an important component of any conservation program for a migratory bird. They may also enhance encounter rates for other types of analyses. We can anticipate that the principle of individually marking birds, whether with traditional metal bands or other approaches, will remain an integral component of bird population monitoring. It is the only reliable means of estimating demographic parameters such as survival rates, a pre-requisite to understanding the underlying causes of bird population change. It is important that data management facilities at central locations such as the Bird Banding Laboratory adapt to accommodate and accept these new types of data (as well as more traditional data such as recaptures), to ensure that they can be incorporated into large-scale monitoring programs, and maximize their contribution towards bird conservation and management programs in North America.

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Bird Banding and the Restoration of Extirpated and Declining Populations

*Stephen A. Nesbitt*¹

Abstract.—Bands have been an important tool in securing several declining or critically low populations of birds. Pre-fledged Brown Pelicans (*Pelecanus occidentalis*) were taken from Florida and translocated to restore an extirpated population in Louisiana. Banding verified that the relocated pelicans remained in Louisiana and formed the foundation of a new population. In areas where Bald Eagle (*Haliaeetus leucocephalus*) numbers have declined or disappeared, populations have been bolstered through translocating birds from areas of abundance. Eggs were taken from Florida nests, chicks were reared in captivity then hacked in areas in the Southeast where the population was reduced or absent. The return of these marked individuals validated the success of these hacking efforts and has encouraged others.

Banded Snail Kites (*Rostrhamus sociabilis*) have demonstrated drought-related dispersal and double brooding. Subadult Red-cockaded Woodpeckers (*Picoides borealis*) have been successfully relocated to new areas to bolster or link declining populations, or to reintroduce the birds into suitable habitats from which they had been extirpated. Monitoring of color-banded individuals validated the success of this bold experiment. Banded Florida Grasshopper Sparrows (*Ammodramus savannarum floridanus*) have provided data to develop techniques and management strategies to maintain and reestablish viable populations of this non-migratory subspecies.

Twenty years of study of banded Sandhill Cranes (*Grus canadensis*) preceded efforts to reestablish extirpated populations of Whooping Cranes (*G. americana*). From studies of individually marked Sandhill Cranes have come three Whooping Crane restoration efforts. Whooping Cranes, derived from eggs laid and chicks reared in a captive setting, have been used to create experimental populations in an effort to prevent the species' extinction. Marked individuals have been important to monitor the progress of this endeavor. Complex behavioral characteristics, as well as movement and dispersal patterns, have been illuminated through banding and color marking in other declining species or populations.

The use of sequentially numbered leg bands has been used to identify sample populations of birds since banding was first introduced. The

¹Florida Fish and Wildlife Conservation Commission, 4005 South Main Street Gainesville, Florida 32601

addition of colored plastic bands in combination with numbered leg bands expanded the ability to differentiate among population segments or individual birds. Having individually recognizable birds has proven to be an important tool in efforts to reverse the decline of several species or populations of birds in North America. Numbered bands and colored bands have been used to uniquely mark representative members of bird populations and inferences have been made about the entire population based on data collected on the movements, behavior, and survival of these marked individuals. Based on these data, management plans have been developed or modified with the goal of reversing declining population trends. As a result, several species have been down-listed or delisted from the status of threatened or endangered species. The following examples illustrate some of the cases where banding and color marking have played a fundamental role in reaching the goal of species preservation.

BROWN PELICAN

Historically the Brown Pelican (*Pelecanus occidentalis*) population in Louisiana was estimated to number somewhere between 12,000 and 85,000 individuals (Holm et al. 2003). By 1963, pelicans had disappeared from the state (McNease et al. 1984), most likely a result of pesticide contamination, possibly Endrin (Holm et al. 2003). The pelican population in coastal Texas declined during this same period (King et al. 1977). In contrast, Brown Pelicans in Florida continued to thrive. In the late 1960s the Florida Game and Fresh Water Fish Commission (now Florida Fish and Wildlife Conservation Commission [FFWCC]), and the Louisiana Department of Wildlife and Fisheries developed a plan to restore the species to Louisiana. The plan involved removing young from nests in Florida just prior to fledging and transporting them to Louisiana. They were allowed to fledge normally from release pens erected near historic nesting habitat in coastal Louisiana. The birds were banded with numbered aluminum bands and colored plastic bands to document survival and dispersal. It was necessary to document that enough of these pelicans remained in the release area to justify continuing the relocation of more birds. The first shipment of 50 birds was made in 1968. Between 1968 and 1980, 1276 young Brown Pelicans were moved from Florida to Louisiana. Post-release survival was 89.6%

after two weeks and the first nesting effort among released birds occurred in 1971 (McNease et al. 1984). Because birds were uniquely marked, it could be determined that these initial nesting efforts were made by birds released in 1968. When they began nesting they were less than three years old and still in immature plumage (Williams and Joanen 1974). This population has grown to such a level that an estimated 34,461 young fledged in 2001 (Holm et al. 2003). This is a far greater number of young than could be accounted for by reproduction from the original population restoration effort (Holm et al. 2003). Data from a different banding study provided one possible explanation. Banding of nestling pelicans in Bay County in the Florida panhandle showed that pelicans fledged from a single colony disperse widely post-fledging (Wood et al. 1995). Banding data have given evidence of two phenomena occurring with Brown Pelicans in Louisiana: (1) successful reestablishment of a nesting population through relocation, and (2) natural immigration that has augmented the re-established population.

BALD EAGLES

Populations of Bald Eagles (*Haliaeetus leucocephalus*) in the conterminous United States declined by the middle of the 20th century to such a level that the species became one of the first to be declared endangered under the Endangered Species Act of 1973 (Buehler 2000). Since 1972, when the use of DDT was prohibited in the United States, the species has slowly increased in numbers. The nesting population of Bald Eagles in Florida has grown from 359 in 1981 to 1133 in 2003 (Florida Fish and Wildlife Conservation Commission 2003 unpublished Annual Report). To accelerate the process of re-establishment of Bald Eagles in the Southeast, eggs (from first clutches, to allow for re-nesting) were removed from eagle nests in central and north-central Florida (see Wood and Collopy 1993). The eggs were transferred to the Sutton Avian Research Center in Oklahoma, where incubation was completed. Young produced from these eggs were released (hacked) in other southeastern states where numbers of nesting Bald Eagles were below recovery goals. The young released at the various hacking sites were banded, allowing natal dispersal and recruitment (initiation of nesting near the release sites) to be monitored. A subsequent increase in new nesting pairs was documented (Nesbitt et al. 1998). As with the return of nest-

ing Brown Pelicans to Louisiana, hacking of Bald Eagles may merely have accelerated an already occurring natural process. The natural process alone, however, would have likely progressed at a much slower pace. Banding was vital to documenting the success of management efforts to recover the Bald Eagle as a nesting bird in the southeastern United States. The advent of the use of pop-rivet bands with eagles, giving band durability superior to that of traditional butt end bands, has improved the long-term efficacy of banding such species. Information on recruitment, natal dispersal, and longevity of normally fledged and relocated Bald Eagles is now being accumulated (Buehler 2000).

SNAIL KITE

Banding and monitoring of color-marked Snail Kites (*Rostrhamus sociabilis*) that began in the 1970s have provided critical conservation information relative to survivorship and dispersal patterns of this endangered species in south and central Florida (Beissinger 1986; Beissinger and Takekawa 1983; Bennetts and Kitchens 1997a,b; Sykes 1983; Sykes et al. 1995). Resightings of banded individuals have shown that during drought events kites dispersed from areas of declining water levels to more suitable wetland habitats. Color-banded individuals also demonstrated that some kites were annually double brooded; they even nested at different wetland sites later in the same year. Modeling survivorship of adult kites, based on the large number of re-sighted individuals, is continuing.

RED-COCKADED WOODPECKERS

Translocation of individuals from areas of abundance to areas where the species has vanished or persists only in precariously low numbers has been successfully applied to the management of other endangered species. Red-cockaded Woodpeckers (*Picoides borealis*) are dependent on old-growth pine forest in the southeastern United States. Because of declining habitat and reduced numbers in much of its traditional range, the Red-cockaded Woodpecker was among the first species listed as endangered in 1973 (Hovis 1996). Red-cockaded Woodpeckers have been translocated to: (1) augment declining popula-

tions (fewer than 30 breeding clusters), (2) provide females for males-only groups, (3) redistribute birds and reduce the risk of isolated or disjunct clusters, (4) re-establish woodpeckers in vacant habitat, and (5) maintain genetic diversity (U.S. Fish and Wildlife Service 2003). Biological and permitting imperatives require researchers to band, color mark, and monitor the donor population prior to and during the moving of any birds. This is to identify individuals that are appropriate candidates for translocation, based on sex, age, and social status, and to insure that removing birds will not jeopardize the vitality of the donor population. Additionally, banding and color marking of the relocated population are necessary to document success of the relocations and to make adjustments in the structure of the relocated population. Monitoring woodpeckers provides the data necessary for developing and improving techniques to select donor populations and to refine relocation techniques.

FLORIDA GRASSHOPPER SPARROWS

Banding and color marking have been integral to the development of management guidelines for the Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*). This non-migratory subspecies of Grasshopper Sparrow is endemic to the grasslands of central Florida. It was feared extinct prior to the location of viable populations in the mid-1980s (Delany 1996). The subspecies was listed as endangered in 1986 (Delany et al. 1995). Studies of banded and uniquely color-marked individuals have provided information on minimum territory requirements and post-nesting movements.

Resightings of color-banded individuals have also been used to estimate survival and longevity of male Florida Grasshopper Sparrows (Delany et al. 1993). A feasibility study is underway to assess the efficacy of relocating sparrows into suitable but unoccupied habitat. Accurate assessments of the outcome of these efforts will depend on recapture or resighting of banded and color-marked sparrows to ascertain whether they remain to reproduce in the area of relocation.



Figure 1. Steve Schwikert (FFWCC) is about to capture a 60-day-old Florida Sandhill Crane chick. Dr. Marilyn Spalding (University of Florida, School of Veterinary Medicine) is in the background.

SANDHILL AND WHOOPING CRANE

The Florida Fish and Wildlife Conservation Commission began banding and color-banding Sandhill Cranes (*Grus canadensis*) in 1968 (Figure 1). One of the early products of the banding of cranes in Florida was the verification that there are two subspecies of Sandhill Cranes in Florida. Prior to these early marking efforts (Williams and Phillips 1972) it was only presumed that the population of Greater Sandhill Cranes (*G. c. tabida*) breeding in the Great Lakes region wintered in Florida. Recovery and resightings of Florida-marked Greater Sandhill Cranes in the early 1970s confirmed their Midwestern origins (Williams and Phillips 1972). Banding also verified that the non-migratory Florida Sandhill Cranes (*G. c. pratensis*) and the Greater Sandhills were sympatric during winter in Florida.



Figure 2. A Sandhill Crane is released back into the wild following banding and color marking in Florida.

In 1974 a system was initiated to uniquely color band individuals, with the objective of providing information on the behavior of individual cranes over a period of several years. Both patagial wing tags and alphanumeric tags were tried, but neither provided the long-term reliability of a simple multi-color banding system (Nesbitt et al. 1992). Eventually radio transmitters attached to colored leg bands (Melvin et al. 1983) became part of the marking system. The transmitters had an anticipated battery life of two to three years. Color-banded individuals have been successfully monitored for more than 10 years.

These data contributed to the development of techniques now being used to restore extirpated populations of Whooping Cranes (*G. americana*). Sandhill Cranes banded and color marked in Idaho were identified wintering on the Bosque del Apache National Wildlife Refuge in New Mexico (Drewien 1973). From 1975 through 1988 this population of Sandhill Cranes was used as foster parents to a new experimental migratory population of Whooping Cranes (Drewien and Bizeau 1978, Lewis 1995). Disease and high mortality rates among the young Whooping Cranes contributed to the failure of this effort to re-establish the species in the Rocky Mountain region.

Twenty years of study of individually color-banded Florida Sandhill Cranes preceded the effort to re-establish a non-migratory pop-



Figure 3. Steve Schwikert (Florida Fish and Wildlife Conservation Commission) has just removed a 9-month-old Whooping Crane from the shipping crate it arrived in. It is next in line for banding.

ulation of Whooping Cranes in the southeastern United States (Figure 2). Research demonstrated that foster rearing or soft releasing of captive-reared cranes could be employed to establish a non-migratory population of Whooping Cranes in Florida (Nesbitt and Carpenter 1993), replicating the extirpated population that once occurred in Louisiana. The first Whooping Cranes were introduced to Florida in 1993. Subsequently 14 to 47, captive-reared Whooping Cranes have been released annually (Nesbitt et al. 1997) (Figures 3, 4). There is now a



Figure 4. Marty Folk (FFWCC) applies a colored plastic leg band to augment the radio transmitter band (behind) and the USFWS numbered leg band at the foot.

population of 50 to 60 non-migratory Whooping Cranes on the prairies and agricultural grassland of central Florida.

This experimental population began nesting in 1999, and there has been an average of 3.5 nesting attempts every year since. Seven nests were monitored in 2002, six failed because the eggs were infertile or because the nest marsh dried up. One pair hatched both of their eggs. When the surviving chick fledged (the other was taken by a Bald Eagle the day of hatching) on 7 June, it became the first Whooping Crane to be produced by parents reared in captivity and released into the wild. This was a landmark event in the effort to prevent the extinction of the Whooping Crane. Efforts to augment the wild population began in the early 1960s, when the first eggs were removed to captivity from the sole remaining wild nesting population in Wood Buffalo National Park in the Northwest Territories of Canada. This was to establish a captive-breeding population to guard against a calamity that would destroy the solo surviving wild population.

For the safety of the species, new populations of Whooping Cranes are being founded in areas separate from the critically endan-

gered wild population that migrates from northern Canada to the coast of Texas. In addition to the non-migratory population being established in central Florida, efforts to establish a second migratory population of Whooping Cranes in eastern North America began in 2001 when 11 Whooping Cranes were led with ultralight aircraft from Wisconsin to winter in Florida. Based on the success during the first year, efforts are expected to continue for several more years (Clegg and Lewis 2001, Langenberg et al. 2002).

Captive-raised Mississippi Sandhill Cranes (*G. c. pulla*) have augmented the wild population of this endangered subspecies. Modifications to release techniques resulting from information gathered from observations of banded individuals have improved the success of these projects.

These are but a few examples of the how banding and color banding have been used in North America in the restoration of extirpated and depleted bird populations. The capability to uniquely band individual birds and monitor them in the field has been vital to the development of the techniques and management practices that have successfully stemmed the tide of decline in some populations. The need for banding and color banding will continue as long as there are wildlife populations that require our intervention to insure their survival.

COMMENTS ON SOME OTHER SPECIES

Banding and associated color banding have been instrumental in deciphering the intricate and distinctive social structure of the Florida Scrub-Jay (*Aphelocoma coerulescens*) (Woolfenden and Fitzpatrick 1984). Behavioral characteristics including cooperative breeding, sedentary life style, and restricted habitat requirements were deciphered after years of following marked individuals. These differences, identified through banding, were one of the reasons that this species was separated from the western scrub-jays (Woolfenden and Fitzpatrick 1996).

Banding has shown interchange among what were thought to be disjunct and endangered sub-populations of Least Terns (*Sternula antillarum*) (Boyd and Thompson 1985, Lingle 1993). This leads to the possibility of considering some regional populations together rather than as separated, and more precarious, individual units. California Condors (*Gymnogyps californianus*) were thought have two rather distinct sub-

populations that rarely overlapped. Through banding and radio-telemetry it was discovered that the two populations were not separate (Meretsky and Snyder 1992) and that interactions between the subpopulations occurred routinely.

These are but a few examples of how banding and color banding have been used in North America in the restoration of extirpated and depleted bird populations. The capability to uniquely band individual birds and monitor them in the field has been vital to the development of the techniques and management practices that have successfully stemmed the tide of decline in some populations. The need for banding and color banding will continue as long as there are wildlife populations that require our intervention to insure their survival.

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North American Bird Banding and Quantitative Population Ecology

*James D. Nichols*¹

and

John Tautin^{2,3}

ABSTRACT.—Early bird-banding programs in North America were developed to provide descriptions of bird migration and movement patterns. This initial interest in description quickly evolved into more quantitative interests in two ways. There was (1) interest in *quantifying* migration and movement patterns, and (2) rapid recognition that re-observations of marked birds provided information about other parameters relevant to population dynamics. These included survival rate, recruitment rate, and population size. The evolution of methods for estimating population size, survival, recruitment, and movement is reviewed and we show it to be closely tied to bird-banding data. These estimation methods have been used with bird-banding data to draw important inferences about evolutionary ecology, population ecology, and population management. Illustrative examples of such inferences are provided.

Early publications about bird banding in North America indicate that banders were interested primarily in information about bird movements, particularly long distance migration (Lincoln 1921). Recoveries of birds at locations distant from banding sites provided valuable information about movements of individual birds. Early investigators also recognized that banding could be used as a means of investigating other aspects of avian ecology, including disease (Wetmore 1915), behavior (Baldwin 1921), and population dynamics (Magee 1928, Whittle 1929). We will review the role of the North American bird-banding program in

¹U.S. Geological Survey, Patuxent Wildlife Research Center, 11510 American Drive, Laurel, MD 20708

²U.S. Geological Survey, Patuxent Wildlife Research Center, 12100 Beech Forest Road, Laurel, MD 20708

³Current address: 20117 State Highway 98, Conneautville, PA 16406

the development of quantitative animal-population ecology. It is our view that the role of North American bird banding and the people associated with this program have been important to progress in this area of ecology. We illustrate this view by tracing developments in this field and highlighting contributions of bird banding. We begin by focusing on methods for estimating parameters needed to make inferences in population ecology. We then single out landmark papers that have been especially influential with respect to estimation methods and to population ecology and management.

ESTIMATION METHODS

In the basic difference equation of population ecology (e.g., see Williams et al. 2002), abundance at time $t+1$ is written as a function of abundance at time t and births, immigration, death, and emigration occurring during the interval t to $t+1$. We will organize this review of estimation methods around these key variables of population ecology.

Abundance.—Abundance or population size is the state variable of interest in population management and studies of population dynamics. Frederick C. Lincoln was a pioneer of early North American bird banding who was a visionary in using banding information to understand and manage North American waterfowl populations. Lincoln joined the U.S. Biological Survey in 1920 and was put in charge of organizing the U.S. banding office. Among his contributions were numerous works that applied banding data to population-level issues in waterfowl management. He actively promoted banding as a tool of quantitative population ecology and management.

Lincoln (1930) developed an ingenious approach to estimate the population size of North American waterfowl using data from different sources. He had banding information that included the number of birds banded in the summer (denoted as n) and recovered (r) by hunters during the subsequent hunting season. Lincoln also considered a hunter reporting-program in which hunters reported their seasonal bags, from which the total number of birds harvested during the hunting season (\hat{H}) could be computed. Lincoln then reasoned that the proportion of banded birds harvested should be approximately equal to the proportion of the total waterfowl population that is harvested:

$$\frac{r}{n} \approx \frac{\hat{H}}{N},$$

leading to the intuitive estimator for abundance:

$$\hat{N} = \frac{\hat{H}n}{r}.$$

Although this estimator is known as the Lincoln Index, it is not an index at all but a true estimator that can be derived in several ways (Seber 1982, Williams et al. 2002). The estimator applies not only to the special case of harvested populations but also to any capture-recapture study. Indeed, all capture-recapture estimators of abundance can be



Figure 1. Frederick C. Lincoln is widely regarded as the founder of the North American bird-banding program. In addition to being an accomplished writer and administrator of the bird banding office, he was a scientist who applied banding data effectively to research and management questions. In 1930 he developed an intuitive estimator for waterfowl abundance that provides the basis for all subsequent capture-recapture modeling.

viewed as generalizations of the Lincoln Index. These include K -sample closed population models (Otis et al. 1978), open population models such as the Jolly-Seber model (Jolly 1965, Seber 1965, 1982), and the robust design (Pollock 1982, Pollock et al. 1990, Kendall et al. 1995) (Figure 1).

Because birds are easily heard and seen, abundance for most species is estimated by observation-based methods rather than by capture-recapture approaches. Nevertheless, in some situations avian abundance is estimated by capture-recapture studies of banded birds. For example, such methods have been used to estimate abundance of Wood Ducks (*Aix sponsa*; Haramis and Thompson 1984), Black-capped Chickadees (*Poecile atricapillus*; Loery and Nichols 1985, Loery et al. 1997), and Snail Kites (*Rostrhamus sociabilis*; Dreitz et al. 2002). Open-model abundance-estimators have been extended to the direct estimation of rates of change in abundance (Pradel 1996, Nichols and Hines 2002), and these have been applied to avian capture-recapture data as well (Dreitz et al. 2002, Franklin et al. 2004, Anthony et al. in press, Nichols et al. 2005).

Survival rate.—Annual survival rate can be defined as the probability that a bird alive at the time of banding in one year is still alive at the same time (banding period) the next year. It is one of the vital rates responsible for all changes in population size and is thus of great interest to population ecologists and managers. It is clear that bird-banding and recovery/recapture data carry information about survival. A bird banded one year and either recaptured or recovered dead 3 years later has survived the 3 years since banding. However, usually we do not know the exact age of the bird at banding, and we never recover all banded birds when they die, nor do we recapture all birds still alive. Estimators of survival rate must somehow deal with these sources of uncertainty.

Methods for estimating survival rate from bird-banding data can be divided into two general approaches based on the type of re-encounter data considered. One approach, capture-recapture, uses recaptures of birds by individual banders at specific banding locations. The other approach, band recovery, is based on recoveries of banded birds found dead or killed by hunters.

Capture-recapture.—Magee (1928) and Whittle (1929) were among the first to analyze data of this type in order to draw inferences

about survival. Their elementary analyses differed, but each concluded that the average life of Purple Finches (*Carpodacus purpureus*) was about two years. Neither discussed models, but Whittle (1929) equated the proportion of birds recaptured one year later with survival rate. Magee (1928) summarized and presented his data in a manner similar to that recommended subsequently by statisticians for use with band recovery (Table 1 of Magee 1928) and capture-recapture (Table 3 of Magee 1928) models. Similar capture-recapture studies by individual investigators in North America providing estimates of survival included those of Nice (1937) on the Song Sparrow (*Melospiza melodia*), Paynter (1947) on Herring Gulls (*Larus argentatus*), and Austin (1951) on Mourning Doves (*Zenaida macroura*).

Statisticians began to devote serious attention to capture-recapture models in the 1940s and 1950s (reviewed by Cormack 1968, Seber 1982). Hammersley (1953) developed a model in order to estimate survival for Alpine Swifts (*Apus melba*), and Orians (1958) used models and methods developed by Paul Leslie (Leslie and Chitty 1951; Leslie 1952, 1958; Leslie et al. 1953) to estimate survival rates for Manx Shearwaters (*Procellaria puffinus*).

The stochastic modeling approach used today for estimating survival rates began with the model of Cormack (1964), developed for use in estimating survival of Northern Fulmars (*Fulmarus glacialis*). This basic model was extended for use in estimating population size and recruitment independently by Jolly (1965) and Seber (1965). Pollock (1981) extended the basic Cormack-Jolly-Seber (CJS) model to the situation where multiple ages could be identified in the field, motivated by a Canada Goose (*Branta canadensis*) resighting study. Buckland (1980, 1982) and Loery et al. (1987), also motivated by bird-banding examples, considered models for age-specific survival where all birds were marked as young (hence age was always known). These different models saw relatively little use following their development, but they are now widely used for avian survival estimation by individual investigators (e.g., Loery and Nichols 1985, Karr et al. 1990, Blums et al. 1996, Sillett et al. 2000) and in large-scale monitoring programs (Peach et al. 1990, DeSante et al. 1995, 1999) (Figure 2).

The past 20 years have seen numerous extensions of capture-recapture models for survival estimation in open populations, and many of these extensions have been motivated by work on bird populations. For example, the trap-response model of Brownie and Robson (1983) devel-

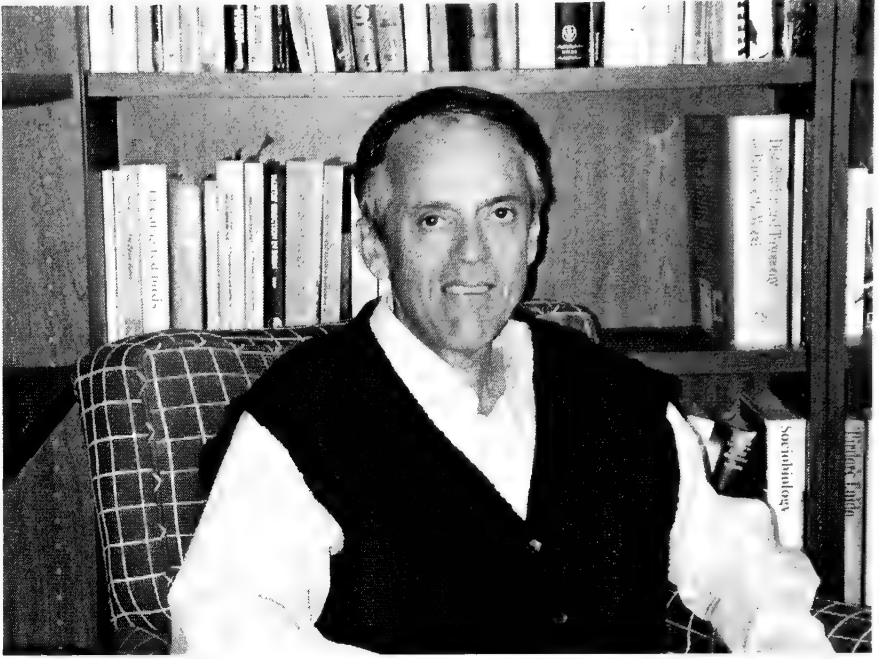


Figure 2. Kenneth H. Pollock has spent much of his professional career at North Carolina State University as Professor of Statistics, Biomathematics and Zoology. He has made numerous important contributions to estimating population parameters from bird-banding data using capture-recapture and band-recovery models.

oped for migrating shorebirds, permits different survival probability for birds after initial capture and marking than after subsequent recapture or resighting. Mist-netting studies of birds are frequently characterized by captures of both residents and transients; transients are birds with near-zero probability of being recaptured in subsequent years or seasons. Application of standard CJS models in such instances yields survival estimates that are negatively biased, prompting Pradel et al. (1997, also see Hines et al. 2003) to develop special “transient models” for estimation of resident survival in the presence of transients.

Band recovery.—During the 1930s and 1940s, the accumulation of band recoveries in the files of the Bird Banding Laboratory led to consideration of this data type for survival rate estimation. Early use of band-recovery data for survival rate estimation in North America was exemplified by the work of Farner (1945, 1949) and Hickey (1952).

Hickey reviewed and critiqued the life-table methods commonly used then to estimate survival rates. He noted how practical matters such as emigration and band loss could affect estimates and devoted a chapter to "Difficulties in Constructing Life Tables for Birds." Similar analyses were being carried out in Great Britain (e.g., Lack 1943a,b).

Lack enlisted the help of a statistician to move beyond ad hoc intuitive estimators and develop the first estimators with solid statistical underpinnings (Haldane 1953, 1955). These estimators were not based on general models in the sense that they required constancy of survival and recovery rates over time. The general model that forms the basis for modern band-recovery models was developed independently by Seber (1970), who was motivated by bird-banding data, and Robson and Youngs (1971), who were motivated by fisheries applications. D. R.

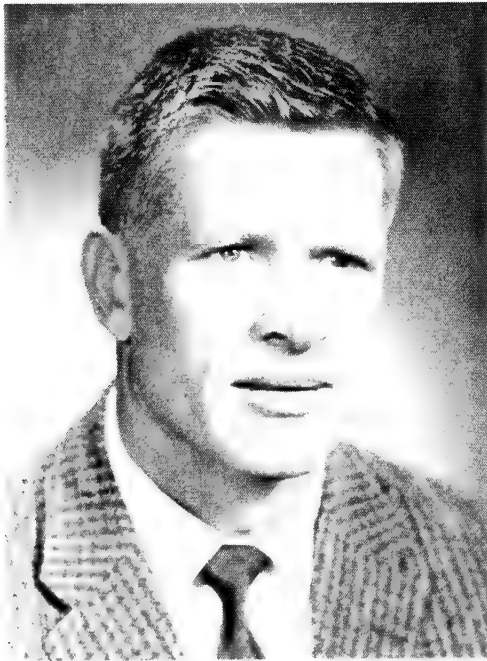


Figure 3. Douglas S. Robson spent most of his professional career as Professor of Biostatistics at Cornell University, where he served as mentor for several of the pioneers in modeling bird-banding data, including Cavell Brownie and Kenneth H. Pollock. Robson made important contributions to early models and estimators using band recovery data and capture-recapture data.

Anderson of the U.S. Fish and Wildlife Service recognized the importance of this modeling approach for drawing inferences about survival of hunted bird-species and funded additional research by D. S. Robson and his Ph.D. student, C. Brownie. This led to the extension of band-recovery models to deal with age-specificity in survival and recovery rates (Brownie and Robson 1976) and to a synthetic treatment of band-recovery models and estimators (Brownie et al. 1978, 1985); this handbook and its revision have become the most important publications concerning the analysis of bird-banding data (see later discussion) (Figure 3).

The classic handbooks of Brownie et al. (1978, 1985) include a set of models and associated estimators, and all of the models could be fit to band-recovery data sets using associated computer programs. The next breakthrough in data-analytic methods came when White (1983), Conroy and Williams (1984), and Conroy et al. (1989; Figure 4) devel-

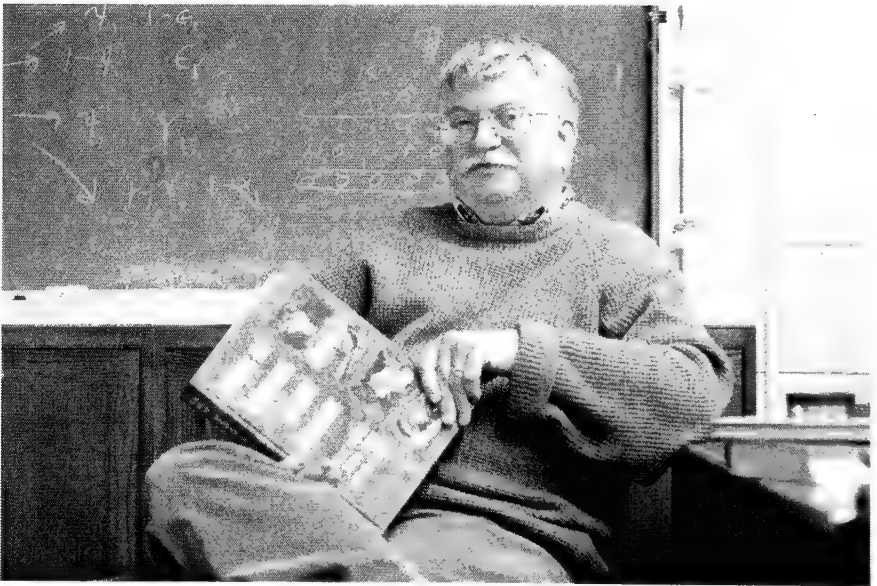


Figure 4. Michael J. Conroy, Assistant Leader of the Georgia Cooperative Fish and Wildlife Research Unit, has conducted bird-banding studies on a variety of species and has made important contributions to band recovery modeling, capture-recapture modeling and estimation of band reporting rate. Photograph by J. P. Bond.

oped flexible software that could be used to fit user-defined models to band recovery and other data sets. The user was no longer constrained to the specific models provided by software developers, but was free to develop new models that corresponded to any sampling situation. Evolution of such flexible software has led to the current program MARK (White and Burnham 1999), which is extremely powerful software for analysis of various kinds of data, including band-recovery and capture-recapture data.

As with capture-recapture modeling, new band-recovery models have been developed to extend basic models to address various questions and to better correspond to sampling situations. A model with a temporary (the first year following banding) banding effect on recovery rate has been useful for hunted species (Anderson 1975a, Brownie et al. 1978, 1985). Models based on banding at multiple times per year have permitted estimation of seasonal survival rates for a variety of waterfowl species (Brownie et al. 1978, 1985; Blohm et al. 1987; Hestbeck et al. 1989; LeMaster and Trost 1994; Reynolds et al. 1995).

In the case of hunted species, it is possible to estimate harvest rate from band-recovery data if ancillary data are available on band reporting-rate, the probability that a banded bird shot and retrieved by a hunter will be reported to the Bird Banding Laboratory. Birds banded with reward bands, specifying a reward for whoever reports the band, provide such ancillary data. Special band-recovery models have thus been developed for estimation of band-reporting rate and harvest rate from reward-band studies (Henny and Burnham 1976, Conroy and Blandin 1984, Conroy et al. 1989, Nichols et al. 1991, 1995).

Movement.—Early investigators drew inferences about movement patterns from bird-banding data by plotting recoveries resulting from bandings at specific locations to provide a graphic depiction of general regions of breeding, wintering, and migration (Taber 1930, Lincoln 1935a, Aldrich 1949). These data provided general inferences about bird movement at the population level and led to the development of the waterfowl flyway concept (Lincoln 1935b). Band-recovery distributions still provide descriptive information about bird distribution and movement (Anderson and Henny 1972, Nichols and Hines 1987). In addition, tests for differences between bivariate distributions (Mardia 1967, Cowardin 1977, Mielke and Berry 1982) have been used to test hypotheses about differences in recovery distribution patterns for birds

from different banding locations (Munro and Kimball 1982, Pendleton and Sauer 1995), different sex and age classes (Nichols and Hines 1987), and different species (Diefenbach et al. 1988).

Band-recovery models can be used to draw inferences about not only survival and recovery rates but also movement. Schwarz and Arnason (1990) describe a set of models that differ in assumptions about fidelity and the flexibility of movement patterns. For example, the models of Schwarz et al. (1988) permit estimation of location-specific survival rates when birds (Mallards, *Anas platyrhynchos*, in their application) from a single banding area represent a mix of birds from two or more wintering areas. Schwarz et al. (1993) also developed models for the situation in which banding and recoveries occur during the same season and illustrated their use with Mallard data (Schwarz 1993).

Capture-recapture models have also been developed to draw inferences about bird movements. Multistate models were developed to estimate location-specific rates of survival and movement in capture-recapture studies at multiple locations. After their initial development by Arnason (1972, 1973) these models saw little use until they were extended to deal specifically with bird capture-recapture/resighting data (Hestbeck et al. 1991, Brownie et al. 1993, Spendelov et al. 1995). Data for wintering Canada Geese prompted the extension of the Arnason-Schwarz model to "memory models" in which movement between times t and $t+1$ depends not only on location at time t but also location at time $t-1$ (Hestbeck et al. 1991, Brownie et al. 1993).

Capture-recapture/re-observation data have also been used to draw inferences about bird movement at migration stopover sites. The inferential problems associated with such studies are to estimate probabilities of departure from such sites, the average residence time of birds at such sites, and the total number of birds passing through such sites. Capture-recapture models and estimators useful for such purposes have been described and reviewed by Kaiser (1995, 1999) and Schaub et al. (2001).

Both band-recovery and capture-recapture data can be obtained from birds banded at a single banding station. The complement ($1 - \hat{\phi}$) of so-called "local" or "apparent" survival estimates obtained from capture-recapture studies includes both permanent emigration and death, because birds must return to the banding location in order to have any opportunity of being recaptured. However, the complement of survival estimates obtained from band-recovery data includes only mortality, as

recoveries can occur at any location throughout a bird's range. Anderson and Sterling (1974) and Hepp et al. (1987) recognized that this distinction could be used to estimate permanent emigration (and its complement, fidelity) using survival estimates obtained from separate capture-recapture and band recovery analyses. The rationale underlying this ad hoc estimation approach was then incorporated into a formal model by Burnham (1993), and this model has been used to estimate survival and fidelity for several North American and European waterfowl species (Szmczak and Rexstad 1991, Lindberg et al. 2001, Blums et al. 2002, Doherty et al. 2002). Barker (1995, 1997) combined standard capture-recapture data with ancillary resighting data (rather than band recoveries) in order to estimate movement parameters.

Recruitment.—Age ratios in the banded sample have long been used to provide information about reproductive rate (e.g., Bellrose et al. 1961). However, unless capture probabilities are the same for adults and young birds, such age ratios will be biased when used as estimates of true age ratio. For several bird species that are hunted in North America (e.g., Mourning Doves; American Woodcock, *Philohela minor*; most waterfowl species) there is another source of age-ratio information from harvested birds obtained via harvest surveys (Martin and Carney 1977). An estimator of age ratio in the population can be constructed by dividing the age ratio in the harvest sample by the ratio of age-specific band-recovery rates based on banded birds. This approach focuses on the age ratio of birds at the time of banding (just following the breeding season in many North American banding programs). The harvest age-ratio is then “adjusted” by the ratio of probabilities that birds of different ages appear in the harvest sample. These probabilities are estimated by the recovery rates. Thus, if the harvest age-ratio is even (50% young birds) and if the ratio of recovery rates is 1.5 (young at the time of banding are 50% more likely than adults to appear in the harvest), then the estimated age ratio at the time of banding is 1.5 young per adult bird. This approach has been used for some time to estimate fall age ratio, a surrogate for reproductive rate, for North American waterfowl species (Geis et al. 1969, Martin et al. 1979, D. Johnson et al. 1992, F. Johnson et al. 1997).

It has been recognized recently that capture-recapture studies sometimes provide information about such recruitment-related topics as adult-breeding probability and age-specific recruitment to the breeding

population. In many avian capture-recapture studies, sampling is conducted on the breeding grounds each year. Birds that do not “choose” to breed in a year may not return to the breeding location and are thus not available for capture or observation. Kendall and Nichols (1995) and Kendall et al. (1997) developed models to estimate temporary emigration, a phenomenon synonymous with nonbreeding in many of these situations. These models have been applied to estimate breeding probabilities for Snow Geese (*Chen caerulescens*; Kendall and Nichols 1995) and Canvasbacks (*Aythya valisineria*; Lindberg et al. 2001) in North America. The models rely on sampling at two different temporal scales, with multiple-sampling occasions within each of multiple seasons or years. Fujiwara and Caswell (2002) and Kendall and Nichols (2002) have also developed standard open-population models (a single temporal sampling-scale) that permit estimation of temporary emigration (probability of not breeding) in some circumstances.

A special case of such temporary-emigration models concerns birds such as seabirds in which newly fledged young depart the breeding grounds the year of hatching and do not return until they are ready to attempt breeding. Clobert et al. (1994) developed ad hoc capture-recapture estimators for age-specific probabilities of first breeding from banding data for birds marked as new young. Formal models were then developed to estimate age-specific breeding probabilities for bird-banding data from single (Spendelov et al. 2002) and multiple (Lebreton and Pradel 2002, Lebreton et al. 2003) sites. Other approaches to the estimation of age-specific breeding and recruitment probabilities from avian capture-recapture data include use of reverse-time modeling (Pradel et al. 1997, Pradel and Lebreton 1999) and a super-population approach (Schwarz and Arnason 1996). All of these approaches yield estimates of the age-specific probabilities that a bird that has not yet been recruited to the breeding population is recruited at that particular age.

LANDMARK PUBLICATIONS

The methods described above were developed for use in drawing inferences about population ecology and dynamics using data from individually marked birds. Many classic studies in vertebrate population-ecology have been conducted on marked birds using these methods (e.g., see reviews in Lack 1954; Newton 1989, 1998; Johnson et al.

1992). Some of the best examples of decision-theoretical approaches to the management of vertebrate populations are provided by programs for bird populations (Anderson 1975b; Johnson et al. 1993, 1997; Nichols et al. 1995; Williams et al. 2002). Bird banding has been an important tool in virtually all of these programs directed at investigating and managing bird populations. Here, we select one publication and one publication series that deal entirely with North American bird-banding data. We briefly describe these publications and their influences on animal population-ecology and management as a means of illustrating the substantive contributions of bird banding to these subject areas.



Figure 5. Left to Right: David R. Anderson, G. C. White, and Kenneth P. Burnham have spent their careers developing and promoting use of rigorous inference procedures for data resulting from bird-banding studies and related work on marked animals. They have contributed individually and collaboratively, and from 1988-2005 they worked together at Colorado State University, Anderson and Burnham as the Leader (recently retired) and Assistant Leader, respectively, of the Colorado Cooperative Fish and Wildlife Research Unit, and White as Professor in the Department of Fishery and Wildlife Biology.

Brownie et al. (1978, 1985).—In the late 1960s and early 1970s, David R. Anderson (Figure 5), then working at the U.S. Fish and Wildlife Service Migratory Bird Populations Station at Patuxent Wildlife Research Center, became aware of the new work on survival-rate estimation from band-recovery data published independently by Seber (1970) and Robson and Youngs (1971). Anderson was involved in research on Mallard population dynamics and management, and it was important that he be able to draw reasonable inferences about annual survival. The Seber-Robson-Youngs model permitted estimation of annual survival rates based on bird-banding and recovery data and was very general, permitting survival and band-recovery rates to vary by year.

Anderson recognized the potential for these models to bring statistical rigor and strong inferences to the study of hunted bird-populations. He worked with computer programmers to write code for computing estimates under this model (Anderson et al. 1974). He then provided



Figure 6. Cavell Brownie has spent much of her career as Professor of Statistics at North Carolina State University. Her Ph.D. work led to the monograph on band recovery models that has provided the basis for modern modeling of such data. She has made numerous other important contributions to band recovery and capture-recapture models.

funding support for the Ph.D. work of Cavell Brownie (Figure 6), a student under Douglas Robson at Cornell University. Brownie and Robson collaborated with Anderson and his new colleague, Kenneth P. Burnham, to develop a series of models and associated computer programs for analyzing band-recovery data for the purpose of drawing inferences about survival.

The collaboration led to the publication of the monograph, *Statistical Inference From Band Recovery Data—A Handbook*, by Brownie et al. (1978). This publication provided a detailed account of a set of models designed to permit inferences about survival from band-recovery data. Models were available for adult-only data and for data with both adults and young, and separate computer programs (ESTIMATE and BROWNIE) were developed to deal with these different types of data. The computer programs provided estimates of parameters of interest (e.g., survival and recovery rates) as well as of associated variances and covariances. The programs included goodness-of-fit and between-model tests for use in model selection. The monograph was intended for a biological readership and provided detailed explanations that would have been unnecessary for statistician readers. In addition to the models that were included in the handbook software, the monograph described other models (e.g., for two banding periods per year, for age-specificity extending to yearlings in addition to young and adult), presented test statistics useful for certain comparisons, and included a very useful chapter dealing with aspects of study design, including computation of sample sizes.

The Brownie et al. (1978) monograph became the most influential publication ever written on analytical methods for bird-banding data. It was so useful that a second edition was printed (Brownie et al. 1985) with new material and an appendix of related scientific papers. Beyond the influence on population studies of birds, this publication represents a landmark because, (1) it provided a model for subsequent efforts to introduce new statistical methods to biologists, and (2) it described multiple models and developed the issue of model selection, laying the groundwork for subsequent work on this topic.

The critical components of the Brownie et al. (1978) model for introducing statistical methodology were a writing style directed at biologists, a text that included many worked examples, models that were biologically motivated, and software that was designed to be user-friendly. An additional model component that cannot necessarily be

viewed as part of the monograph itself was a series of workshops and short courses conducted by the monograph authors for waterfowl biologists. The workshops introduced biologists to the modeling concepts and included many computer examples, providing participants with a working knowledge of the associated software. This model was extremely effective and resulted in use of the Brownie et al. (1978) estimators in a large fraction of papers dealing with waterfowl survival within five years. The model provided by Brownie et al. (1978) has been successfully followed numerous times now, including for closed capture-recapture models (Otis et al. 1978, White et al. 1982), distance sampling methods (Burnham et al. 1980; Buckland et al. 1993, 2001), and open capture-recapture models (Burnham et al. 1987, Pollock et al. 1990, Lebreton et al. 1992). We believe that this model is directly responsible for the relatively rapid assimilation of statistical methods in animal population-ecology and wildlife management.

We believe that the Brownie et al. (1978) monograph is also a landmark publication because of its introduction of the topics of multiple models and model selection to biologists and managers. The monograph described numerous models that could be fit to each data set, as well as a general strategy for selecting a single model for use in estimation. Prior to 1978, descriptions of new models for analyzing capture-recapture and band-recovery data were nearly always of single models. The concept of multiple models was prevalent in the general statistical literature for hypothesis testing based on linear models, but had not yet been extended to the topic of parameter estimation in animal population-ecology. The ability to fit multiple models to the same data set was new, providing the biologist user with flexibility in modeling. This ability to fit multiple models has been extended to modern software (e.g., MARK, White and Burnham 1999) that fits user-defined models and thus provides an extreme level of flexibility. We believe that Brownie et al. (1978) represented the beginning of this evolutionary march towards flexibility in biological modeling.

The model-selection strategy of Brownie et al. (1978) involved a goodness-of-fit test for the most general model in each model set, with the idea that adequate fit of the general model was important before proceeding to look at simpler models. Likelihood-ratio tests were then used to test the more general model against a nested, simpler model created by constraining parameters of the more general model. If the between-model test is significant, then the extra parameters of the more general

model are needed to adequately describe the variation in the data. However, if the test is not significant, then it is concluded that the models describe the data similarly well. The extra parameters of the general model are not necessary, so the simpler model is selected because the smaller number of parameters yields more precise estimates. This rationale is now referred to as the “Principle of Parsimony” (Burnham and Anderson 1992, 1998, 2002), but the objective of achieving a satisfactory compromise between bias and precision was well articulated by Brownie et al. (1978). Although the process of model selection is now viewed as an optimization problem, rather than a problem in sequential hypothesis testing, the underlying objective of obtaining a parsimonious description of the data remains the same.

Although the issue of model selection is sometimes viewed simply as a means of obtaining a parameter estimate with an optimal mix of bias and precision (e.g., as measured by root mean squared error, Anderson et al. 1994), Brownie et al. (1978) clearly recognized the relevance of this process to the conduct of science. For example, Model 1 of Brownie et al. (1978) was the Seber-Robson-Youngs model, in which both survival and band-recovery rates varied over time (year to year). Model 2 of Brownie et al. (1978) again modeled variation in recovery rates over time, but imposed the constraint that survival did not vary with time. Because band-recovery rates are good indices to harvest rates, Model 2 is closely related to the compensatory mortality hypothesis of Anderson and Burnham (1976), as survival is relatively constant in the face of variable harvest-rates. Thus, the competing ways of modeling band-recovery data represent important underlying ideas about population dynamics, and model selection provided a means of drawing inferences about the relative appropriateness of these models and their corresponding hypotheses. The model-selection philosophy presented by Brownie et al. (1978) can be viewed as a fundamental approach to the conduct of science when multiple hypotheses are considered (Chamberlin 1897, Hilborn and Mangel 1997, Burnham and Anderson 1998, 2002).

Mallard Report Series.—In the late 1960s, Anderson led a team of U.S. Fish and Wildlife Service biologists in the conduct of research on the population dynamics of North American Mallards. The work involved efforts to synthesize available information on Mallard populations and their responses to harvest management. The available infor-

mation was substantial, as it came from survey programs designed to inform the management of waterfowl, with emphasis on the Mallard, the number one bird in the waterfowl hunter's bag. The database included aerial survey data (Pospahala et al. 1974), harvest-survey data (Martin and Carney 1977), and, most importantly, band-recovery data (Anderson and Henny 1972, Anderson 1975a, Anderson and Burnham 1976, Munro and Kimball 1982, Nichols and Hines 1987). Anderson and Henny (1972) first used recoveries of birds banded in late summer just before the hunting season (preseason bandings) to define banding reference areas, aggregations of banding sites for which birds exhibited similar band-recovery distribution patterns. Anderson (1975a) then estimated age- and sex-specific survival rates and band-recovery rates (indices to harvest rates) for Mallards in each reference area and subsequently (Anderson and Burnham 1976) explored the relationship between survival and harvest regulations. Band-recovery data were also combined with harvest age ratio data as described above to estimate the age ratio of Mallards in the preseason population, an estimate of recruitment rate (e.g., Anderson 1975a).

The fifth monograph in the series (Anderson 1975a) provided a useful model for retrospective analyses of avian population-dynamics. Its primary focus was on sources of variation in Mallard survival rates and harvest rates. In addition to examining variation associated with age, sex, and geography (the different reference areas), Anderson (1975a) addressed questions about temporal variation associated with environmental variables, including habitat conditions on the breeding grounds. Anderson (1975a) also addressed the question of possible density dependence in Mallard survival rates. Estimates of survival and reproductive rates were incorporated in a population projection matrix and also in a more complex stochastic projection model. Such modeling was not common for bird populations at the time and represented an important effort at synthesizing available demographic information for the purposes of projection.

The sixth monograph in the series represented a serious effort to assess the influence of harvest regulations and hunting mortality on Mallard survival and population dynamics (Anderson and Burnham 1976). The authors first noted flaws in historical analyses of band-recovery data that led to incorrect inferences about hunting mortality. They then constructed two competing hypotheses about the influence of

hunting mortality on total annual survival rate and tested them with available data. Anderson (1975b) applied optimal stochastic control methods to demonstrate that these two hypotheses produced very different harvest strategies, thus emphasizing the importance of conducting the science needed to distinguish between the two alternatives.

The Mallard report series in general, and these two monographs (Anderson 1975a, Anderson and Burnham, 1976) in particular, presented important models for the conduct of science and management on bird populations. The careful demographic analyses of Anderson (1975a) were based on appropriate estimation models that were new to ecology. The use of competing models to draw inferences about sources of variation in survival rate was a new approach at the time, foreshadowing today's emphasis on model selection in multi-hypothesis science (Burnham and Anderson 2002). The development of deterministic and stochastic population projection models represented an important effort at synthesis that again foreshadowed today's widespread use of such modeling (e.g., Tuljapurkar 1990, Caswell 2001). The focus on harvest management using rigorous methods (Anderson and Burnham, 1976) provided an approach that has been followed since that time (e.g., Nichols 1991, Nichols and Johnson 1996, Williams et al. 2002). Careful construction of competing hypotheses and the proper treatment of sampling variances and covariances in testing them represented important departures from previous work. The general application of a formal decision-theoretical approach to harvest management and the specific use of stochastic dynamic programming as a method for developing optimal harvest regulations (Anderson 1975b) represented additional innovations that would be formally adopted by duck managers 20 years later. Finally, Anderson and Burnham (1976) recommended experimental manipulation of hunting regulations as a means of drawing unambiguous inferences about the relationship between hunting regulations and Mallard population dynamics. Indeed, the Mallard report series represented an extremely important step in the evolution of harvest management for North American ducks and was ultimately responsible for the adoption of the adaptive harvest management program by the U.S. Fish and Wildlife Service in 1995 (Nichols 2000).

CONCLUSIONS

We believe that North American bird banding has contributed importantly to the general fields of avian population ecology and management. Bird banding has contributed to the development of appropriate methods for the conduct of science on animal populations. This development includes not only the development of a wide variety of probabilistic models for parameter estimation, but also very general model selection approaches to inference with multiple hypotheses. Bird banding has been integral to the development of a decision-theoretical approach to waterfowl harvest management in the face of uncertainty that provides an important model for managing animal populations. In addition, it is important to note that many of the world leaders in quantitative animal population ecology and management have spent substantial portions of their careers working with North American bird-banding data. The North American Bird Banding Laboratory is housed at Patuxent Wildlife Research Center in Laurel, Maryland, and the collocation with research and management scientists has caused Patuxent to be an important training ground for quantitative animal population ecologists and managers.

As a final observation, we note that the methods developed for the analysis of bird-banding data have been borrowed for application in other subject areas. With respect to animal and plant ecology, capture-recapture thinking and modeling have been extended to observation-based estimation problems in community dynamics (e.g., Burnham and Overton 1979; Boulinier et al. 1998; Nichols et al. 1998a,b; Cam et al. 2002) and in patch occupancy dynamics associated with metapopulation systems (e.g., Mackenzie et al. 2002, 2003). Band-recovery models developed for North American birds were adapted for use with fossil data for drawing inferences about taxonomic diversity and extinction probabilities in paleobiology (Nichols and Pollock 1983, Conroy and Nichols 1984, Nichols et al. 1986). Bird-banding estimation methods have also been borrowed for use in human biology and sociology for purposes ranging from estimation of criminal and homeless populations, to dealing with the U.S. Census undercount, to various biomedical estimation problems (e.g., Chao et al. 2001). Applications even extend to the estimation of the number of errors in computer programs (Chao et al. 1993) and to the number of human-launched objects in

outer space (K. H. Pollock, pers. comm.). We conclude that North American bird banding and associated methodological development have been extremely influential throughout the general field of animal population ecology and in various other disparate subject areas.

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The Role of Bird Banding in Management of Migratory Bird Hunting

Robert J. Blohm¹

ABSTRACT.—Bird banding in North America has a long and storied tradition, particularly with regards to those birds, such as ducks, geese, swans, and doves considered “migratory game birds” within the Migratory Bird Treaty. Beginning on a small scale with the efforts of Jack Miner and others at the onset of the 20th Century, banding activities of migratory game birds today have grown to include more than 20 million bandings and 2.8 million recoveries. It is common for 400,000 migratory game birds to be banded and nearly 100,000 bands to be recovered each year. Harvest management activities have their roots in banding and recovery information. Accumulated data from early banding efforts were instrumental in describing migration routes from patterns of recoveries, ultimately leading to the creation of four administrative flyways that have been the basis for establishing annual hunting regulations on the continent for over 50 years. Understanding fidelity to breeding, migration, and wintering areas; defining populations, describing the distribution and derivation of harvests; assessing harvest pressure; measuring vulnerability to the gun; helping to estimate the production of young; and providing estimates of survival are just some of the important uses of banding and recovery information for the wildlife management community. Recent advances in computer technology and analytical methodologies hold great promise in optimizing the utility of future banding programs and enhancing current capabilities to manage migratory game bird harvests in North America.

In North America, hunting has been at the heart of outdoor activities, providing valuable food, recreation, economic, and aesthetic benefits for millions of people (U.S. Fish and Wildlife Service 2001). Our shared migratory bird resource has traditionally been a significant component of wildlife harvest programs. Some have referred to waterfowl as the most prominent and economically important group of birds in North America. However, the necessary regulation of harvest activities, especially of a resource that extends from one end of the continent to the

¹U.S. Fish and Wildlife Service, 4401 N. Fairfax Drive, MS 4107, Arlington, VA 22203

other and beyond during the course of the annual cycle, presents challenges that are unique within the wildlife management community. One could argue that these efforts represent the most complex allocation of a renewable resource in all of North America, requiring vast amounts of reliable information that can support regulatory decision-making at all administrative levels.

My goal in this chapter is to review the role of bird banding as a key source of information in the management of migratory bird hunting in North America. More specifically, I will trace the history and uses of banding information in harvest management as biologists have strived to ensure that exploitation of migratory birds through hunting maintains the health and abundance of hunted species while providing sustainable recreational hunting opportunities among countries, states, and provinces.

REGULATING MIGRATORY BIRD HUNTING IN THE UNITED STATES

In the 19th Century, state and local governments developed and enforced their own regulations or laws governing the take of migratory birds (Hawkins et al. 1984, Nichols 2000). This situation provided widespread variability in methods of regulating the take of migratory birds, given the preponderance of conflicting views about how this valuable resource should be managed. In the early 1900s, it became obvious that numbers of many migratory bird species had plummeted to alarming lows, reflecting the pressures of spring hunting, market gunning, few if any bag limit restrictions, and a general decline in the health of key habitats on formerly undisturbed breeding and wintering areas.

These concerns prompted discussions at national and international levels and were directed specifically at remedying the downward spiral of migratory bird numbers on the continent (Day 1949). As a result, in 1916, the United States formally concluded treaty negotiations with Great Britain (for Canada) that ultimately outlined responsibilities for the preservation and management of migratory birds on the continent. In 1918, the Migratory Bird Treaty Act in the U.S. was passed and assigned ultimate responsibility and authority for the management of migratory birds to the federal government, including the development of annual migratory bird hunting laws (U.S. Fish and Wildlife Service

1988, Blohm 1989). Since then, various other treaties and amendments, with Mexico (1936, 1972), Japan (1972, 1974), and the Soviet Union (now Russia, 1978) have provided additional recognition of how far migratory birds travel within and outside the continent's borders throughout the year, and further clarified the list of birds to be protected under these agreements (Bean 1983). These conventions define migratory game birds as belonging to five taxonomic families, representing nearly 200 species. Today, 58 species of migratory birds within this group are hunted (U.S. Fish and Wildlife Service 1988).

Because of the magnitude of effort necessary to protect and manage this resource, partnerships between federal governments and states, provinces, and non-government organizations soon evolved, promoting effective resolution of management issues of mutual concern. Over the years, hunting regulations became a large and complex body of game laws. These reflect not only the desire to address longstanding inequities throughout North America for migratory game bird abundance in relation to hunter numbers, but increasing capabilities to manage the harvest of our wildlife resources. Of the more than 60 million bandings and 3.8 million recoveries that now reside in the Bird Banding Laboratory (BBL) in Laurel, Maryland, are more than 20 million bandings and nearly 2.8 million recoveries of migratory game birds, representing a formidable body of information that continues to support game-bird harvest-management programs throughout North America.

BANDING DATA AS TOOLS IN HARVEST MANAGEMENT

An understanding of the impact of harvest on exploited populations—in this case, migratory birds—is fundamental to any hunting program's success. Numbers of birds change as a result of demographic variables such as survival and recruitment, immigration, and emigration. Hunting or harvest may influence these variables to bring about population change. Over the years, biologists have become increasingly aware of the value of banding data in helping to inform them of the relative importance of each of these variables as well as any cause and effect relationships that might exist during each species' annual cycle that could help explain changes in status, distribution, and abundance. Because of hunting, biologists have benefited from a relatively large number of recoveries of banded migratory game birds each year. These

samples have assisted analytical procedures and strengthened inferences and conclusions from these data sets.

USES OF BANDING DATA

Describing migration routes.—Early banding programs focused on questions of migration and movement and whether patterns could be discerned from an inspection and analysis of band recoveries. (See Table 1 for key terms used in discussing the disposition and reporting of game-bird bands). Since key elements of band recovery usually include information on location of the recovered bird and date of recovery, all in relation to where and when it was banded, early investigators were able to ascertain with some degree of certainty the general direction the bird traveled and the amount of time required to make the journey from banding to recovery location (Lincoln 1935a, Aldrich 1949). Inspecting all recoveries from a banded sample provided a pattern that described the minimum range flown and the migration route that was used. Lincoln (1935b) appreciated the value of this information and analyzed thousands of band recoveries to delineate four major routes or flyways of waterfowl traveling among breeding, migration, and wintering areas in North America. Using radar technology, Bellrose (1968) further clarified these routes as migration corridors for waterfowl and other birds.

Table 1. Definitions of key terms associated with game-bird banding data.

Band Recovery	a report to the Bird Banding Laboratory of any band number from a previously banded bird.
Direct Recovery	bird recovered during the first hunting season after banding.
Indirect Recovery	bird recovered in any hunting season following the first hunting season after banding.
Reporting Rate	proportion of banded birds taken by hunters that are reported to the Bird Banding Laboratory following recovery.
Recovery Rate	reported proportion of banded birds taken by hunters.
Harvest Rate	proportion of the population alive at the start of a given year that is harvested in the same year.

Lincoln's work established a vastly improved understanding of the distribution and movement for a group of migratory birds of extreme interest to wildlife managers. These routes or corridors subsequently became functional administrative units or Flyways (e.g., Atlantic, Mississippi, Central, and Pacific flyways) that make up the foundation of harvest management on the continent today (Figure 1).

Other descriptive uses of recovery information of importance to harvest management have been derived from direct and indirect recoveries of banded birds. Lincoln (1927) noted distinct sets of recoveries early in the banding program in the United States. Later investigations with larger data sets have established degrees of similarity of recovery distributions for both direct and indirect recoveries. These suggest a level of fidelity to certain areas by birds in the banded sample, allowing managers to make useful inferences about how distinct populations are



Figure 1. Early efforts to follow waterfowl migration through banding and recovery information included tracking recoveries from Bear River Refuge. Such data contributed to the development of the flyway concept.

on breeding, migration, and wintering areas (Anderson and Henny 1972, Munro and Kimball 1982, Nichols and Hines 1987). Further examination of banding data and associated recoveries can also help clarify the *distribution* of the harvest from a given breeding area and the *derivation* of birds harvested in a particular area, both important considerations in regulations-setting. The distribution of harvest describes a pattern of how migratory game birds from an area of banding on the breeding grounds are distributed among the many harvest areas available during the hunting season. Similarly, the derivation of harvest gives managers some idea of which areas on the breeding grounds are most important in contributing to the harvest in a particular area, based on where the recoveries originated.

Assessing harvest pressure.— After managers have obtained a better understanding of migration patterns and the relationships between the breeding grounds and where birds are subsequently harvested during the hunting season, banding data can be useful in providing a direct measure of hunting pressure, resulting from a particular season or regulatory option within a season. For managers, it is important to understand two relationships that are integral to any harvest management program: the relationship between hunting regulations and harvest rates and the relationship between harvest rates and population status (Nichols and Johnson 1996). Recovery rates serve as a valuable index to harvest rates (the proportion of the hunted population harvested by hunters) for species, populations, and even sex and age cohorts of interest, given that the banded sample is representative and that reporting rates do not change much over time (Anderson 1975). Thus, changes in hunting regulations can be monitored following the conclusion of a hunting season through an assessment of recoveries of banded birds, helping to ensure that management programs continue to be consistent with harvest objectives, especially with the status of the hunted population.

Estimating population size.— Lincoln (1930) established the groundwork for future investigations of population dynamics and quantitative population ecology by developing a simple but reliable measure of animal abundance, using banding information. His method was based on the number of banded birds recovered (r) for the sample (n) of birds (in this case, waterfowl) banded the summer before the hunting season

they were recovered, and on seasonal hunter bag information (H) that estimated the total number of birds harvested during the same hunting season. Assuming that the proportion of banded birds that was harvested was about the same as the proportion of the total waterfowl population (N) that was subject to harvesting, Lincoln reasoned that the size of the total waterfowl population could be calculated as the only unknown. That is,

$$r/n = H/N, \text{ or}$$

$$N = Hn/r$$

This straightforward approach, based originally on banding data, has had widespread application in wildlife management. See Nichols and Tautin, this volume, for additional discussion of what has become known as the Lincoln Index. This approach to estimating game-bird populations has been reviewed extensively by biologists and statisticians and refinement of this methodology has benefited our understanding of changes in animal abundance for many species and populations (Williams et al. 2002).

Measuring vulnerability.— One of the underlying principles of harvest management is that, generally, young migratory game birds are more susceptible to the gun than are adults (Anderson 1975, Martin et al. 1979). Similarly, biologists have found that, within some duck species, males may be more vulnerable than females during the hunting season (Anderson 1975, Baldassarre and Bolen 1994). All of these differences can be measured using banding data. For example, at the time of banding, species, age, and sex information are recorded if possible for every bird banded. Consequently, for migratory game birds, if a banded bird is harvested and the band number reported to the BBL, the bird's age and sex can be determined from the original banding record. Recovery rates for each cohort of interest can be calculated (e.g., f_1 and f_2) and compared by dividing one rate by the other, and the resulting ratio is an estimate of *relative vulnerability* (e.g., $V_1 = f_1/f_2$). This value represents the degree to which young birds are more vulnerable to hunting than adults.

The reasons for these differential rates of recovery likely relate to a number of factors, including the level of exposure of young birds to

the gun, differential survival of young and adult birds to the later portions of the hunting season, variation in social behaviors between age and sex classes, differences in migration patterns of sex/age cohorts, and sex-specific regulations which may promote harvest of one sex over the other. Moreover, these rates may vary markedly from one year to the next, given population size, reproductive success, and hunting conditions. Relative vulnerability between age groups, in particular, is an important factor in providing unbiased information to managers on reproductive rates.

Estimation of production rates.— Production rate is one of the key demographic variables of interest to biologists involved in population management when it is necessary to understand the effects of exploitation or hunting on population size of migratory game birds. Estimating production rates directly from nesting studies for a variety of species over a broad geographic area is difficult and costly. Consequently, biologists have used alternative sources of information over the years to provide some insight on nesting season success and what might be anticipated in the fall flight. One source has been banding data and the ratio of young and adults in the banded sample (Bellrose et al. 1961). When used, these indices were of limited value because of potential bias in banded samples due to differential probabilities of capture of the different age groups (Figure 2).

Harvest surveys also provide indices to relative recruitment each year as biologists obtain sex and age information, by species, in Parts Collection Surveys of sampled hunters (Martin and Carney 1977), during the hunting season. However, these indices taken directly from the harvest survey are generally biased because of differential vulnerability of young and adult birds during the hunting season. Biologists have been able to successfully address this source of bias by adjusting age ratios from the harvest survey with the estimate of relative vulnerability obtained directly from banding data. The validity of this procedure depends heavily on the success and representativeness of banding efforts for migratory game birds on breeding areas prior to each hunting season. Given that these assumptions are met, this procedure provides harvest managers with a reliable measure of recruitment of birds into the fall population, which weighs significantly in many regulatory decisions each year (Geis et al. 1969, Martin et al. 1979, Johnson et al. 1992).



Figure 2. Aging waterfowl prior to banding. Accurate sex and age information obtained at time of banding can provide additional opportunities to use banding and recovery data in managing these migratory game birds.

Estimating survival rates.— Survival is another key demographic variable considered in many investigations of the dynamics of wild animal populations. By definition, (annual) survival rate is the probability that an animal alive at one point in time in one year is alive at the same time the following year. The value of banding data as a source of information on survival rates of bird populations has long been recognized. Generally, biologists have taken two approaches when using banding and recovery data sets for survival rate estimation. One approach is based on live, banded individuals and the frequency of recapture (or re-sighting) following banding (e.g., Magee 1928, Nice 1937, Blums et al. 1996). The other uses the number of banded birds found dead or recovered by hunters during each hunting season (e.g., Hickey 1952, Farner 1945, Brownie et al. 1978, Brownie 1985). Both methods have strengths and weaknesses, but in general, have proven to be useful in estimating this population parameter. In recent years, analytical methods have been

developed that allow investigators to estimate survival rates on an interval or seasonal basis within the annual cycle (see Blohm et al. 1987, Hestbeck et al. 1989, Reynolds et al. 1995).

Of particular interest and importance to harvest managers has been the variation observed in survival rates and how these rates change over time because of environmental phenomena (e.g., habitat conditions on key breeding, migration, and wintering areas) and harvest management options (e.g., liberal versus restrictive hunting seasons). For example, relationships, such as higher survival rates for Mallards (*Anas platyrhynchos*) when wetland numbers are abundant on important nesting areas, have provided managers with key insights during the regulations-development process each year (Nichols et al. 1982). The long-standing debate over the influence of hunting on population change, and whether hunting mortality is additive (e.g., in addition to natural mortality, such as disease and predation) or compensatory (changes in hunting mortality are compensated by concomitant changes in natural mortality below a certain threshold), has had its roots for more than 60 years in the analysis of banding data (e.g., see Hickey 1952, Geis 1963, Geis and Crissey 1969, Geis 1972, Anderson and Burnham 1976, Nichols et al. 1984, Burnham and Anderson 1984).

Despite information to suggest that both scenarios may be at work in migratory game bird populations at various times or under certain conditions, the topic remains controversial. Because of the obvious implications of this issue to harvest management programs, banding data will likely continue to play a key role in future efforts to further clarify the relationship of harvest and survival and the ultimate influence of harvest on population dynamics. Nichols and Tautin (these proceedings) have provided a comprehensive review of the evaluation of survival rate estimation from banding data, using both approaches.

ROLE OF AUXILIARY MARKERS IN BANDING STUDIES

Investigators have often used auxiliary marking devices alone or in conjunction with bands to assist in evaluating migration and distribution patterns and key demographic attributes of bird populations. Some examples of these alternative marking methods include colored bands (e.g., Spencer 1978); colored wing markers (e.g., Morgenweck and Marshall 1977); neck bands and collars (e.g., Huey 1965, Maltby 1977);

nasal tags (e.g., Bartonek and Dane 1964, Sugden and Poston 1968); back tags (e.g., Gullion et al. 1962, Frankel and Baskett 1963); web tags (e.g., Grice and Rogers 1965); and dyes, paints, and inks (e.g., Evans 1951, Swank 1952). In recent years, more “high tech” approaches have been developed and used in migratory bird investigations. These include such methods as radio-telemetry, (e.g., Cochran 1972, 1980), chemical and radioactive markers (e.g., Haramis et al. 1983, Griffin 1952). Today, the use of satellite tracking programs to monitor birds carrying radio-transmitters is common, providing investigators with frequently-updated and precise location information from marked birds (Miller et al. 2001, Takekawa and Orthmeyer 2001, Fleskes et al. 2002). More detailed description of the types and applications of auxiliary marking devices for migratory birds is provided in Samuel and Fuller (1996).

CURRENT CHALLENGES

The continued utility of banding data to support harvest management in North America depends on the sustained viability of the continental banding program. Despite a longstanding and highly successful banding operation for many migratory game birds each year, some species remain significantly underrepresented in banded samples. For example, banding records of more than 6 million Mallards and 3 million Canada Geese (*Branta canadensis*) exist in the files at the BBL; while fewer than 100,000 American Woodcock (*Scolopax minor*) and 200,000 American Wigeon (*Anas americana*) have been captured and banded during the same time period (1908–2003). These small samples are likely the result of many factors, including inherent difficulty in trapping certain species, and the cost of banding in areas where some species are normally found in reasonable abundance. These difficulties will not be easily overcome.

Another challenge is to continue to improve the willingness of those who recover bands to report them to the Bird Banding Lab. Until recently, the reporting rate for some migratory game birds, such as the Mallard, was approximately 33%. Only one-third of the birds recovered were reported to the BBL for subsequent use by biologists (Nichols et al. 1995b). Since the mid-1990s, an active band solicitation program has been in place in North America, encouraging those who recover bands

to report them to the BBL. This effort replaces the traditional use of the postal system to report recovery information and uses a 1-800 telephone number (1-800-327-BAND), inscribed on the band, to encourage hunters and others to forward recovery information for processing. Preliminary results from reporting rate investigations suggest a significant increase in reporting rates for many species. The impact of this increase should improve the efficiency of current banding programs because more information is returned (via recoveries) for each unit of banding effort. This increase in efficiency will help address concerns for those species not easily banded, by providing more information back to the BBL for even small banded samples. In 2004, the telephone-answering system was completed for all of North America, with the addition of Mexico to the system, and now recoveries in all three countries will be forwarded to the central repository at the BBL in Laurel, Maryland.

Since the mid-1990s, many in the wildlife management community have embraced the use of an adaptive approach to harvest management (Adaptive Harvest Management, AHM) (Johnson et al. 1993, Nichols and Johnson 1996). This approach relies heavily on banding and recovery information and uses many banding data sets to support complex modeling and analytical procedures that are critical to AHM's success (Nichols et al. 1995a, Johnson et al. 1997). Future success of AHM will depend heavily on the success and reliability of the North American banding program and the ability of field efforts to provide adequate, representative samples of migratory game birds.

Overall, the value of the continental banding program is only as good as the level of support provided by cooperating resource agencies and other organizations. Continued funding and a willingness of agencies and organizations to provide experienced field personnel in banding activities will depend on the sustained value of banding information in resource management and decision-making, particularly as administrators are challenged to support other resource management programs with limited budgets.

CONCLUSIONS

The importance of banding information to harvest management programs in North America cannot be understated. The long history and tradition of banding efforts for migratory birds, particularly migratory game birds, contributed significantly to the body of knowledge so fundamental to decision-making and the wise use or exploitation of these wildlife populations. Not only have we learned more about migratory patterns and behavior of birds on this continent through the close inspection and analysis of banding and recovery information, we have developed, and continue to develop, better field methods and analytical techniques that will enhance our ability to manage our migratory bird resource for future generations.

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The Role of Bird Banding in Avian Ecotoxicology: A Review

D. V. "Chip" Weseloh¹

and

Craig E. Hebert²

ABSTRACT.—In this review, we discuss the results of over 60 field studies that deal with bird banding as it has been applied to ecotoxicology. We identify four levels of banding studies, i.e., those that have used aluminum bands only, colored markers, VHF radio-transmitters, or satellite transmitters. The four levels of banding represent increasing degrees of remote sensing. VHF telemetry is considered to be the most powerful technique available for tracking birds that have been exposed to environmental toxicants. We discuss future methods of “banding” such as use of stable isotopes, genetic markers, and pollen to identify individuals and track movements.

Bird banding and avian ecotoxicology are inextricably tied together by the desire to know what happens to specific individual birds after they have been exposed to a given set of potentially toxic environmental conditions. However, the joining of these two activities is like combining father time and the new kid on the block. Scientific bird banding, in one form or another (marking birds for later recognition of individuals), has been used for more than a century, whereas avian ecotoxicology is a very new science, having emerged within the last half century.

The term “ecotoxicology” was coined by Truhaut (1977), but ecotoxicological studies superceded the name by at least three decades. Ecotoxicology is the science of the ecological impacts of poisons, whereas toxicology is the science of impacts of poisons on individual

¹Canadian Wildlife Service - Ontario Region, Environment Canada, 4905 Dufferin St., Downsview, Ontario M3H 5T4

²Canadian Wildlife Service, National Wildlife Research Centre, Environment Canada, Carleton University, Ottawa, Ontario K1A 0H3

organisms. The former is a natural extension of the latter and was first identified as such by Truhaut in 1969 (Truhaut 1977, Moriarty 1983). However, the recognition of ecotoxicology goes back to the first investigations of side effects of poisons on other than the intended target organisms. In avian studies this is at least to the time of the early studies of the effects of DDT on songbirds (Mitchell 1946, Stewart et al. 1946, Storer 1946, George and Mitchell 1947).

Our objective in this paper is to review the kinds of ecotoxicological studies that have been conducted using bird banding or bird marking. In doing so, we recognize and discuss four "levels" of banding. We also discuss new intrinsic methods and developments in recognizing a bird's origin and where it has been in the recent past (such as during migration), but only as they apply to avian ecotoxicology. We hope to provide researchers with descriptions of a cross-section of banding methods and discussion of the kinds of studies that can be done with different levels of banding.

METHODS

For this review, we liberally define bird banding to include the application of any device to a bird that allows it to be identified as having been previously handled. We consider four levels of banding. The simplest involves the use of a serially numbered aluminum band with an address to which a finder can report. The other three levels usually include use of a serially numbered aluminum band, but add (1) colored markers (Cottam 1956, Marion and Shamis 1977), and/or (2) a VHF radio-transmitter (Preide and Swift 1992, Brewer and Fagerstone 1998), or (3) a satellite transmitter (Howey 1992, Castles 1998). We conclude with a short discussion of potential future marking or banding systems. With few exceptions, we have dealt only with birds that have been free-flying (or were old enough to be free-flying) between the time of banding/marking and subsequent recapture or re-sighting. Thus, studies of birds marked and assessed for toxicological effects before fledging, were generally not included. Similarly, studies of banded birds that were caged during their entire study were not included. This is not a review of general avian ecotoxicology, but rather a review of avian ecotoxicological studies where banding has played an integral part in the study.

We have also tried to maximize the number of different species discussed.

In reviewing the literature, we initially confined ourselves to projects using North American bird-banding facilities and coordinated through the U.S. Fish and Wildlife Service and the Canadian Wildlife Service. Because results of computer searches of available literature were not specific enough to meet our above criteria, we hand-searched the following 13 journals (when available) from approximately 1950 onwards: *Auk*, *Condor*, *Bird-Banding*, *Journal of Field Ornithology*, *Wilson Bulletin*, *Environmental Pollution*, *Archives of Environmental Contamination and Toxicology*, *Bulletin of Environmental Pollution and Contamination*, *Colonial Waterbirds/Waterbirds*, *Ecotoxicology*, *Journal of Wildlife Management*, *Environmental Monitoring and Assessment*, *Environmental Toxicology and Chemistry*, and selected references cited in papers in these journals.

RESULTS

We selected at least 46 studies, involving shearwaters, pelicans and cormorants, herons, waterfowl, diurnal and nocturnal raptors, gulls and terns, grouse, and passerines to illustrate the four levels of banding. Thirteen additional studies were selected to illustrate new methods for the identification of a bird's origin. While these latter studies do not represent banding in the traditional sense of the word, they do allow for identification of the general origin of a bird and point to new directions in research for determining the natal site of birds.

Aluminum bands only.—Birds have been banded with numbered aluminum bands as their sole means of marking for about a century (see Jackson, this volume); again, much longer than the science of wildlife toxicology has been recognized. Data from aluminum leg bands have suggested the general migratory pathways of many bird species (Brewer et al. 2000), especially non-passerines where the return rate is often higher than for passerines. They also identify wintering areas of birds from known breeding areas and vice versa. One of the main features of studies using aluminum leg bands alone has been to show whether bird populations in a given area are migratory or resident. This information is vital to many wildlife toxicological studies.



Figure 1. Mike Gochfeld, another Common Tern aficionado. Photograph courtesy of Joanna Burger.

One of the simplest forms of using aluminum band data in ecotoxicology is in the retrospective analysis of deformity rates. Both Gochfeld (1975; Figure 1) and Fox et al. (1991), used numbers of terns (*Sterna* spp.) and cormorants (*Phalacrocorax* spp.) banded as a means of estimating the number of young examined and deformity rates. Gochfeld (1975), on western Long Island (New York), found that 104 of 7649 young banded Common Terns (*Sterna hirundo*) had one or more of seven different types of abnormalities. Fox et al. (1991), examining bill deformity rates in young Double-crested Cormorants (*Phalacrocorax auritus*) banded (or handled) across Canada and the Great Lakes, found that rates varied significantly from 0–52.1/10,000 (N=52,130).

In a massive undertaking, Deuel and others (Deuel 1984) banded over 12,000 Northern Pintails (*Anas acuta*). They dosed half of them

with two # 5 lead pellets and attempted to assess differential over-wintering mortality from band returns. Although nearly equal numbers of dosed and un-dosed birds were recovered (435 vs 419) and results were not significantly different, the study showed the extent to which band recoveries, on a large scale, could be used to assess specific mortality questions.

In another dosing study, Grue et al. (1982) banded both free-living and captive European Starlings (*Sturnus vulgaris*) to test whether results from captive birds could be extrapolated to free-living birds. All birds were nesting in boxes on the grounds of the Patuxent Wildlife Research Center. Birds were dosed with dicotophos, a potent organophosphorus insecticide and tested for two physiological responses: brain cholinesterase levels and body weight. They found that the physiological responses by the two groups were similar. However, they cautioned that this might not be the case for other variables.

One of the most common uses of the results of traditional banding studies is to determine the wintering areas or migration routes of birds. Such results are especially useful when a bird's egg-contaminant profile is not consistent with that of the food web on its breeding range. An egg-contaminant profile is a measure of the concentrations and ratios of specific contaminants in its eggs (e.g., its DDE:PCB ratio; Hughes et al. 1998) (DDE, dichlorodiphenyldichloroethylene, is the main breakdown product of the insecticide, DDT, dichlorodiphenyltrichloroethane; PCBs, polychlorinated biphenyls, are a mixture of up to 209 individual chlorinated compounds that were once used as coolants and lubricants). In a series of studies in the interior of the western United States, Henny (Figure 2), Findholt, and colleagues (Henny et al. 1984, 1985; Findholt 1984; Findholt and Trost 1985) found several wading bird species showing elevated contaminant levels, eggshell thinning, and poor productivity—fairly common features in some bird populations in the 1970s and 1980s. In Snowy Egrets (*Egretta thula*), egg contaminant profiles (DDT:PCB ratio = 58:1) did not fit with those of the local food supplies (2:1; Findholt 1984). Findholt concluded that the DDT-rich egg profiles had to be a result of contaminants obtained where DDT use was still high, as in northern Mexico, where banding records showed that the egrets wintered. In these studies past banding data furnished important information for current problems. When the contaminants were not thought to be of local origin, band returns were used to determine wintering areas.



Figure 2. Chuck Henny with an adult Osprey trapped along the Columbia River near Portland, Oregon. It was banded and marked with a satellite transmitter.

In examining contaminant levels in Arctic seabirds breeding on Prince Leopold Island, Braune et al. (2001) used banding data (Donaldson et al. 1997; Figure 3) and age-identifying plumage data to ascertain that Northern Fulmars (*Fulmarus glacialis*) which bred there did not winter off the coast of Newfoundland, as was expected, but rather off the European coast. Thus, eggs of fulmars which nest on Prince Leopold Island in the Canadian Arctic may reflect contaminants from European food chains, while developing young may reflect contaminants from near the breeding colony.

When large numbers of birds have been banded over many years, more sophisticated studies which attempt to correlate various contaminant-related parameters with known-aged birds are possible. Maness and Emslie (2001) captured 50 previously banded Royal Terns (*Sterna*



Figure 3. Garry Donaldson demonstrating the hazards of banding Common Murres (*Uria aalge*). Photograph courtesy of Grant Gilcrest.

maxima) at four breeding colonies in North Carolina, where young birds had been banded for more than 20 years. They took blood samples and by use of the Comet Assay, which had not previously been applied to birds, looked for genetic damage. The Comet Assay can be used to assess genetically damaging toxic exposure by detecting DNA strand breakage (Mitchellmore and Chipman 1998). They found 80-94% regional philopatry and variation in DNA damage by site but no relationship between damage and age. Many avian toxicologists have tried looking at contaminant levels and/or effects relative to increasing age of birds, often to no avail.

In a similar study, Mora et al. (1993) building on the more than 40 years of banding efforts by the Ludwig family on the Great Lakes (Ludwig 1965), examined 136 previously banded Caspian Terns (*Sterna caspia*). They, too, found significant variation in organochlorine levels by region but no relationship with age in 45 Caspian Terns banded as chicks, aged 4-29 years. However, they did reveal a negative relationship between mean PCB concentration in plasma (by region) and the percent of terns returning to their natal region, suggesting the more

highly contaminated colonies or regions may be sinks for young birds as they grow to become adults.

Gochfeld et al. (1996), capitalizing on a gull-control program at J. F. Kennedy International Airport (New York), analyzed five different tissues of shot Laughing Gulls (*Larus atricilla*) for six different metals. Among the hundreds of birds collected, they selected groups of five males and five females that had been banded 1, 3, 5, and 7 years previously as chicks at Barnegat Bay (New Jersey). Although they found significant correlations with age in 17 of 30 possible combinations, and most of those were positive, they concluded that, “. . . there is no clear pattern in metals levels with age for any metal or tissue.” Burger (1994; Figure 4), who has reviewed the use of feathers in analyzing for mercury, comments that most studies with feathers have failed to find any relationship with age.

On the pampas of Argentina, a die-off of thousands of Swainson's Hawks (*Buteo swainsoni*) occurred when the hawks received lethal doses of the organophosphorus insecticide monocrotophos that had



Figure 4. Joanna Burger with one of her favorite birds, a Common Tern. Photograph courtesy of Mike Gochfeld.



Figure 5. Chip Weseloh (L) and Craig Hebert (R) preparing for a boating course at Parry Sound, Ontario. Photograph courtesy of Glenn Barrett.

been sprayed onto crops to control grasshoppers (Goldstein et al. 1999, Hooper et al. 1999). Band recoveries were important in identifying the hawks' wintering habitat, their duration of stay in winter (November-March), and their natal/birth areas. Banding recoveries gave the extent of the wintering range and allowed determination of relative area (%) of winter range covered by the known kill area. Nine U.S. Fish and Wildlife Service leg-bands were recovered from birds banded in Saskatchewan, Alberta, Montana, and California suggesting a substantial mixing of North American birds on the wintering grounds.

Perhaps the most extensive use of data from aluminum leg-banded birds in an avian ecotoxicological setting is associated with the Herring Gull (*Larus argentatus*) Egg Contaminants Monitoring Program on the Great Lakes (Mineau et al. 1984, Hebert et al. 1999; Figure 5). Several authors, both before and after the contaminants work began in the 1970s, have used the banding data. Moore (1976) delineated movements of Herring Gulls banded on the Great Lakes showing that as adults, the gulls were non-migratory but did move around within the



Figure 6. Andy Gilman, definitely not in his bird banding garb. Photograph courtesy of Keith Lennon.

region. Gilman et al. (1977; Figure 6) further showed that most recoveries of banded adults were from their natal lake. Weseloh (1984; Figure 5) examined over 14,000 recoveries of Herring Gulls in the Great Lakes region and found that more than 99.5% of them had been banded there; only 0.1-0.2% had been banded outside the Great Lakes region, showing that it was essentially a “closed” system, with very little immigration. This negated any suggestion that declining contaminant levels in gull eggs were the result of contaminant-free birds coming into the Great Lakes. Later Hebert (1998) showed that in severe winters, Herring Gulls banded in the northern Great Lakes moved (wintered) south to the lower Great Lakes and had elevated egg-contaminant levels in spring. In mild winters, birds did not move as far south and contaminant levels were not elevated above long-term values.

A whole field of studies for which we found no examples is the assessment of longevity of birds in relation to contaminant exposure. For example, is there any difference in life span or expectancy of birds between the years of the “pesticide era,” approximately 1955-1975, and the 20-year periods before and after that era? Marshall (1947) discussed the potential utility of such a study, but it has yet to be done.

COLORED MARKERS

Colored markers used by banders today increase the visibility of an individually numbered bird (if anything is going to be legally attached to a wild bird in North America, it usually must also have the U.S. Fish and Wildlife Service band attached). As a result, identification can be made more quickly and larger numbers of birds can be identified. Various kinds of marking techniques have been summarized by Marion and Shamis (1977).

In a relatively passive use of banding, Hays and Riseborough (1972; Figure 7) color-banded over 5200 Common and Royal tern chicks in two years at Great Duck Island Long Island Sound, New York.



Figure 7. Helen Hays away from Great Gull Island.

By searching the island intensively later in the season, they noted up to 1.5% of grown chicks were unable to fly and had abnormalities of various types. It is sometimes difficult to keep track of the number of birds examined progressively over the course of a season, but banding facilitates this.

In a study using Golden Eagles (*Aquila chrysaetos*) as surrogates for California Condors (*Gymnogyps californianus*) potentially exposed to lead, Pattee et al. (1990) patagially-tagged 162 eagles and, from repeated observation, determined that 31% were resident (seen more than 60 days post-banding). However, there was no difference in blood lead levels between residents and migrants. Levels were elevated enough to suggest that condors would not fair well if released there and levels must be reduced if that area was to be a release site.

In one of the earliest ecotoxicological studies involving colored markers and dosing birds, Norris (1958) investigated the effects of x-irradiation on eggs, young, and adult female Eastern Bluebirds (*Sialia sialis*); nestlings and adults were color-banded. The dosage rate was 23.5 roentgens (r) /minute and most individuals received 200-600 r. There was no suggestion that pairs in which females were irradiated were less successful in producing fledglings than were pairs in which the females were not irradiated. However, two-thirds of the embryos or resulting nestlings from irradiated eggs died before leaving the nest. Unfortunately, results from non-irradiated eggs were not presented.

A straightforward study by White et al. (1983) showed that Laughing Gulls, color marked on the neck with rhodamine B (red) dye and dosed with parathion, a potent organophosphorus pesticide, maintained an altered incubation behavior for 2-3 days post-treatment, but after 3 days, showed no difference from control birds. Behavior modification such as this is common in non-lethal exposure to organophosphate and carbamate pesticides. In a complementary study using the same marking technique and the same species, King et al. (1984) found no difference in nest defense behavior and reproductive success between dosed and control gulls.

In another dosing study, Stromborg et al. (1988; Figure 8) patagially-tagged 121 European Starlings and dosed half of them with dicrotophos, an organophosphate insecticide. The birds fledged and Stromborg made twice a week searches for 7 weeks, keeping track of relocated individuals. Sightings of patagially-tagged birds recorded during weekly 2-day observation periods suggested that age at fledging,



Figure 8. Ken Stromborg on an eagle banding mission. Photograph courtesy of Paul Willems.

flocking behavior, and habitat use did not differ between exposed and non-exposed birds. More than 70% of birds that fledged were re-sighted.

McEwen and Brown (1966) used a combination of rectangular neck tags made of Naugahyde®, yellow dye, numbered white plastic leg bands, and an anodized aluminum leg band on Sharp-tailed Grouse (*Pediacetes phasianellus*) to determine the response of the 52 adult male grouse to a single oral dose of dieldrin, malathion, or lactose. Lethal doses of dieldrin ranged from 5.0 to 32.2 mg/kg (LD50 = 6.9 mg/kg) and for malathion it was 200-240 mg/kg.

Meyers et al. (1990) used a high dose, low dose, and control scheme of methyl parathion to examine the effect of a single oral dose of the organophosphate on the behavioral response, reproduction, and long-term (over-winter) survival of 40 color-banded adult female Red-winged Blackbirds (*Agelaius phoeniceus*). They found that parathion caused ataxia, lacrimation, and lethargy and significantly depressed cholinesterase activity, but there were no adverse effects on reproduction. Dosed females returned to their nests, resumed incubation, suc-

cessfully hatched, and reared their young. Nestlings of poisoned females did not have significantly different body weights at 8 d compared to controls, indicating parathion had not disrupted the females' ability to provide food for their young. There was no indication that dosed birds suffered greater over-winter mortality than control birds. Both groups returned and nested in similar proportions the following year.

Individually color-marked birds also allow one to age the birds when they are resighted rather than having to recapture the birds or read band numbers through a telescope. In this way, Ewins et al. (1999; Figure 9) examined contaminant levels in known-aged female Ospreys (*Pandion haliaetus*) on the Great Lakes. More than 1100 nestlings were color-banded over a 30-year period. They took 44 eggs from known-aged females and analyzed them for organochlorines. Females were aged from 3-15 years. There was no significant variation among year groups (3-4, 5-9, and 10-15 years of age) for levels of organochlorines. Their conclusion was that females reach a steady-state equilibrium with environmental contaminant levels by the age of first breeding.

In another study at this level, Knapton and Mineau (1995) color-banded 240 Song Sparrows (*Melospiza melodia*) in hedgerows along cornfields that were destined for imminent application of granular pesticides and cornfields that were not. Through repeated monitoring for the presence and absence of color-banded birds, they showed that there was no significant difference in disappearance rates or productivity of sparrows in exposed or control cornfields. Observations showed birds did not feed extensively in the fields and were probably not very exposed to the granular pesticides.

VHF TELEMETRY

VHF radio-telemetry has revolutionized avian ecotoxicology and has been described as the most powerful technique available for use in wildlife trials measuring exposure and survival and improving the chance of carcass location (Edwards 1990). It allows one to determine the precise location, and even the type of activity in which birds are engaged at any time of the day or night, including the precise time when a pesticide is applied. This can then be related back to specific exposure scenarios. There have been many applications of VHF radio-telemetry

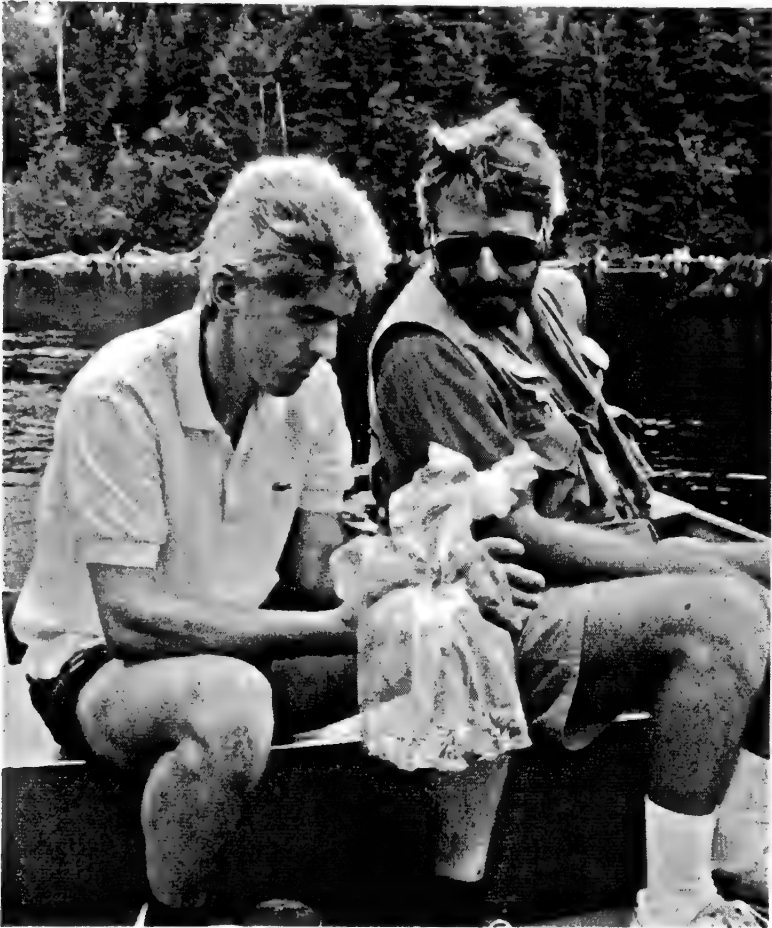


Figure 9. Pete Ewins (L) and CWS contractor (Mike Barker) look at a sample of prey remains from an Osprey nest, Kawartha Lakes, 1991. Photograph courtesy of Larry Benner.

to avian ecotoxicology. Various aspects of the subject have been reviewed thoroughly by Fairbrother (1998), Urban (1998), and more than a dozen other authors in Brewer and Fagerstone (1998) and Hoffman et al. (2002).

VHF radiotelemetry studies can be divided into at least four types. By far the most common is where birds are fitted with transmitters, released, then followed through the season as they live in a landscape where pesticides are used. A second type of study is where birds are captured, dosed with a regime of exposures, and then followed. A third type

is where birds are captured, their blood sampled, released, and followed. Results are based on birds considered exposed and not exposed. A fourth type of study, where birds are tagged and then followed to find their wintering grounds, is less common. Transmitters have also been used to determine residency of birds in a wintering area. In many ways, these studies are similar to those done with colored markers, but the return rate is much greater and data much more certain.

Hegdal and Colvin (1988) attached transmitters to 50 owls, mostly Eastern Screech-Owls (*Megascops asio*), in Virginia and monitored their movements daily and nightly before, during, and after rodenticide application for voles (*Microtus* spp.), assessing possible secondary poisoning. Minimum mortality was 58% of screech-owls for which more than 20% of their home range was treated, compared to 17% of those for which less than 10% of their home range had been treated; secondary poisoning was the most probable death in more than 25% of screech-owl deaths.

In a study of possible secondary poisoning in Great Horned Owls (*Bubo virginianus*) in Iowa, Buck et al. (1996) radio-tagged 22 birds before and after applications of the granular formulations of either COUNTER® or LORSBAN®, two organophosphorus insecticides, to cornfields over two years. They used transmitter signals to plot home ranges and habitat use of the owls. They found that owls made little use of treated areas, concentrating their hunting activities to non-treated areas. There was little evidence of exposure to the insecticide.

In a study of Prothonotary Warblers (*Protonotaria citrea*) along the Tombigbee River in south Alabama, Reynolds et al. (2001) used simultaneous triangulation from three radio receivers to plot the foraging areas of 29 tagged individuals. They attempted to use contaminant concentrations (especially DDT and mercury) in the soil within foraging areas to predict contaminant conditions in the diets and tissues of nestling warblers. In general, soil DDT levels did predict the variation of contaminants in adipose samples, while mercury levels in the soil accounted for 78% of the variation in kidney samples. The predictive value of relationships with other compounds was minimal.

Evaluating the success of rehabilitation efforts, post-exposure, Anderson et al. (1996; Figure 10) compared the survival and dispersal of oiled Brown Pelicans (*Pelecanus occidentalis*) after rehabilitation and release with survival and dispersal of un-oiled control birds. They found the rehabilitated birds disappeared at a higher rate than control



Figure 10. Dan Anderson (L) and Frank Gress (R) placing a conventional radio transmitter on a Brown Pelican. Photograph courtesy of D. M. Fry.

birds, remained farther from breeding colonies, and did not breed during the first two seasons post-rehabilitation. They concluded that oil and/or rescue and treatment results in long-term injury to Brown Pelicans, and current rehabilitation efforts do not restore them to breeding condition or survivability.

One of the most interesting studies in this category was that of Henny and Blus (1986). They found highly contaminated Black-crowned Night-Herons (*Nycticorax nycticorax*) in Nevada, but much less contaminated birds in Idaho. Egg-contaminant profiles of the Nevada birds did not fit local food sources, suggesting a wintering-ground contamination. However, band returns were not conclusive enough to determine precise wintering areas. So, they radio-tagged 29 night-herons in Idaho and Nevada with transmitters that had a range of 15-20 km when tracked by a receiver-equipped airplane flying at 300 m. They then spent 80 hours flying through southern Nevada, California, and coastal Mexico looking for their birds. Twelve of 29 radio-tagged night-herons were located. The contaminated birds were located in agriculturally rich areas of southern California, and Arizona. The cleaner

Idaho birds had leap-frogged over the others and were in clean coastal marshes of western Mexico.

In a dose and release experiment with Northern Bobwhite (*Colinus virginianus*) in Florida, Buerger et al. (1991) radio-tagged 197 bobwhites over three years. These had been orally dosed with sublethal concentrations of the organophosphorus insecticide methyl parathion, at rates of 0, 2, 4 or 6 mg/kg body weight. Birds were located twice daily, diurnally and nocturnally, and all birds alive at 14 d post-treatment were euthanized. Birds in the 6-mg group had significantly lower survival estimates than birds in the 0- or 2-mg group due to predation, not toxicity. There were no differences among groups in activity and both treated and control groups had similar brain cholinesterase levels.

The study with perhaps the most dramatic results in this level was that of Blus et al. (1989) and dealt with Sage Grouse (*Centrocercus urophasianus*) in Idaho. After verified die offs of Sage Grouse in 1981, the authors captured 82 grouse, fitted each with a radio-collar, and released them. Daily activity patterns and habitat use were determined from transmitter fixes; the grouse fed in croplands and roosted and loafed in sagebrush (*Artemisia* spp.). Fifteen of the 82 tagged grouse were in an alfalfa field when it was sprayed with the organophosphorus insecticide, dimethoate. All but one became intoxicated and more than half of these were found dead. A flock of 200 grouse, some of which were radio-tagged, was in a large alfalfa field when it, too, was sprayed. Sixty-three of these birds were later found dead, some in the field, some in the sagebrush; their brain cholinesterase activity was depressed by 51-86% normal activity.

Our last example for this group is a study by Poche et al. (1998) in which a 1.5-g transmitter was attached to each of 560 songbirds (American Robins, *Turdus migratorius*; Brown Thrashers, *Toxostoma rufum*; and Blue Jays, *Cyanocitta cristata*) prior to the application of a "new insecticide" (an unnamed granular) on eight golf courses in Columbus, Ohio. The survival index on exposed portions of the courses was 89% but only 80% on unexposed (control) portions of the golf courses, suggesting the chemical application had little if any adverse effect on the test species.

SATELLITE TELEMETRY

Although satellite telemetry has been used to track bird movements for more than a decade (Fancy et al. 1988, Howey 1992), few researchers have applied it in great detail to avian ecotoxicology. Henny et al. (1996; Figure 2) trapped north-bound Peregrine Falcons (*Falco peregrinus*) in spring at Padre Island, Texas, and were able to locate the breeding grounds and subsequent wintering grounds in Latin America for half of their transmitter-equipped birds. This allowed them to better identify precise wintering areas and assess potential contaminant exposure.

Woodbridge et al. (1995), Hooper et al. (1999, 2003), and Goldstein et al. (1999) used satellite telemetry to locate the precise wintering grounds of Swainson's Hawks, which breed in western North America and winter on the pampas of Argentina. In so doing, they discovered and detailed the death of upwards of 20,000 hawks on their



Figure 11. Glenn Barrett examining an unexpected guest found in a kestrel nest box. Photograph courtesy of Kimberly O'Hare.

wintering range from monocrotophos, the potent organophosphorus insecticide that had been sprayed on crops in Argentina to control grasshoppers.

On the Great Lakes, Barrett et al. (2002; Figure 11) attached transmitters to 12 adult breeding female Herring Gulls on lakes Superior and Huron and determined the number of days each spent in autumn and spring migration and on wintering grounds in Lake Erie. These data will be used to model the impact of contaminant exposure from the lower lakes on the overall egg contaminant load of eggs in nesting areas on the upper lakes.

FUTURE DIRECTIONS: USE OF STABLE ISOTOPES, GENETIC MARKERS, AND POLLEN

It is often difficult to predict what new methods in any given area of research are on the horizon. However, over the years many of us have amusingly and jokingly wished that young birds would simply “register” themselves when they fledged and that would be a lot easier than all this banding we have to do. We are probably not too far from a situation that is akin to that. Some new intrinsic methods of marking are proving to be more and more like such a system.

Intrinsic markers, such as stable isotopes or DNA, have an advantage over traditional marking approaches in that every bird has, within its biochemical or genetic make-up, information regarding its origin and past movements. Naturally occurring stable isotopes of various elements (hydrogen, carbon, nitrogen, sulfur) have been used to discriminate among birds from different geographic areas (Caccamise et al. 2000, Wassenaar and Hobson 2000, Meehan et al. 2001), to link breeding and wintering areas (Hobson and Wassenaar 1997, Figure 12; Marra et al. 1998), and to gain insights into how contaminants may be passed through avian food-webs (Hobson et al. 1997, Hebert et al. 2000). The factors underlying geographic differences in the isotopic composition of avian tissues are the result of both natural and anthropogenic factors. Stable hydrogen isotopes in feathers show latitudinal trends that correspond with known isotopic patterns in precipitation (Hobson and Wassenaar 1997, Wassenaar and Hobson 2000, Meehan et al. 2001). Carbon and nitrogen isotopes have also been found to exhibit large-scale geographic differences in birds (Hobson 1999a,b, Wassenaar and

Hobson 2000, Hebert and Wassenaar 2001). However, studies using stable isotopes have provided information on movement patterns only at large geographic scales. Therefore, stable isotope data will not replace traditional banding studies but instead represent an additional source of information that will be particularly important for most individuals that are never included in banding studies.

Methods using genetic markers to discriminate among birds from different regions may also provide new insights into where birds breed and where they have been. To date, few such studies have been applied to the field of ecotoxicology. Chen et al. (2001) used molecular methods to show that Great Lakes Herring Gull populations were genetically isolated from those in Atlantic Canada. This lack of gene flow between regions corroborated the results from banding studies that had previously suggested Great Lakes Herring Gulls were non-migratory. This type of information is important for validating species as monitors of environmental conditions in specific regions.

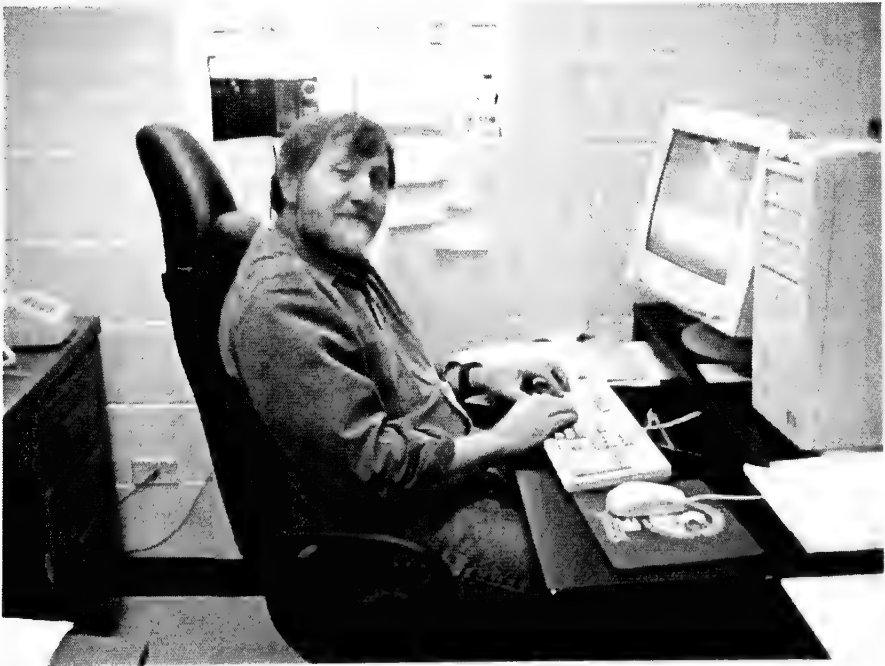


Figure 12. Keith Hobson analyzing more data and writing another paper. Photograph courtesy of Steve van Wilgenburg.

Finally, naturally occurring intrinsic and extrinsic markers may also be useful in tracking the movements of birds. Rintamaki et al. (1998) have discussed using area-specific genetic signatures of avian blood parasites to identify regions where birds may have picked up the parasites. Laursen et al. (1997) have found that pollen may be a useful indicator documenting bird migratory movements. Webster et al. (2002) review several new innovative technologies to unravel migratory connectivity.

DISCUSSION

Having identified and presented examples and studies from four levels of banding, it would be a useful summary to identify the most useful application of each method. This will show how the four levels of banding represent the evolution of a progressively greater degree of remote sensing. Aluminum banding alone is best used to identify a cohort of birds that may be later located on, mostly, a random or accidental basis. The exception to accidental relocation would be working within the breeding colony where adults or young had been banded. Those birds will tend to return to that site and could be re-located there with a fair degree of certainty. Still, the effort needed to re-trap banded birds or to read a bird's band number with a telescope is considerable. The number of re-sightings is severely limited by the time available to the researcher.

Color-marking birds, on the other hand, allows the identification or location of the marked cohort of birds within a visual distance. This is a much simpler and more productive task than just relying on returns from birds when they are found dead, re-trapped, or when their band numbers can be read without capture. In many situations, it is easy to obtain re-sightings on scores of individually marked birds in a single day. The numbers of birds initially marked limits the number of re-sightings one will make. Color-marking greatly increases the visibility of the bird and, with large obvious and unique markings, greatly increases the number of birds which can be identified in a given time. However, the researcher must still actually view the bird.

Marking birds with a VHF transmitter is best used to identify or locate the marked cohort of birds anywhere within an electronic transmission range (usually up to 15-20 km). Of course, this is an immense

increase in the range over which birds can be identified. VHF telemetry makes it possible to locate birds at will, day or night, as long as they are within the range of the radio receiver. This is the feature that made the Sage Grouse study (Blus et al. 1989) unique; it was possible to tell exactly where the birds were when the alfalfa fields were aerially sprayed; it was possible to tell which birds were sprayed and which were not. VHF transmitters make it possible to track all local movements of the study species in both natural exposure and dosing studies.

Satellite telemetry is perhaps the ultimate in long-distance tracking. One is able to identify or locate a cohort of birds over thousands of kilometers. Satellite telemetry is still a new technology, and smaller and more complex transmitters are being developed, and location identification is becoming more accurate.

The conclusion to draw from this analysis is simple: field studies of avian ecotoxicology would be almost non-existent if it were not for bird banding. True, agricultural fields would be sprayed, spills would happen, and dead birds would be found and counted, even analyzed for the causative agent(s). But controlled field studies with any level of sophistication would not be possible. Bird banding has been an immense aid to avian ecotoxicology and its importance will only continue to grow as methods become more sophisticated.

ACKNOWLEDGMENTS

We thank Tania Havelka, Kate Jermyn, and Cynthia Pekarik who assisted greatly in searching the literature. Colleagues Ken Stromborg and Tom Custer also provided reference material. Donna Stewart, Jerome Jackson, and William (Ted) Davis provided excellent comments on an earlier version of the manuscript. We also thank those who provided photographs.

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Contributions of Banding to Understanding Habitat Use by Birds

*Scott Schlossberg¹, Jeffrey P. Hoover²,
Courtney Blood³, and Jeffrey D. Brawn⁴*

Abstract.—Understanding how and why birds use different habitat types have been major goals of field studies in ornithology for decades. In recent years research efforts in this area have made several major advances, moving well beyond the mere description of habitats that predominated in early studies of habitat selection. Banding and marking of birds have played a central role in these advances. Here, we discuss three primary areas in which banding has increased our knowledge of avian habitat ecology. These include: (1) behavioral processes that underlie habitat selection, (2) how spatial factors influence habitat selection, and (3) how anthropogenic changes in avian habitats affect birds and how conservation efforts might be focused to counter those impacts. We also discuss two case studies in which banding and marking have produced important findings.

Habitat use and how habitat affects ecological and evolutionary processes have been central parts of ornithology for over 50 years (Karr 1980, Block and Brennan 1993). The study of banded birds as a means to develop an understanding of bird-habitat relationships also began early, but has become an integral part of bird-habitat studies only in recent decades. Understanding avian habitats can be as simple as describing the type of vegetation used by the species in question or by contrasting conditions in areas with and without the birds. While the

¹Program in Ecology and Evolutionary Biology, University of Illinois, 606 E. Healey St., Champaign, Illinois 61820

²Illinois Natural History Survey, 606 E. Peabody Dr., Champaign, Illinois 61820

³Department of Natural Resources and Environmental Sciences, University of Illinois, 606 E. Peabody Dr., Champaign, Illinois 61820

⁴Department of Natural Resources and Environmental Sciences and Department of Animal Biology, University of Illinois, 606 E. Healey St., Champaign, Illinois 61820

spatial scales and statistical methods used in this field have changed over the years (Stauffer 2002), descriptive studies of habitat use that do not involve marking birds remain a major area of research. This makes habitat use an unlikely area to consider in a volume focusing on how banding has contributed to ornithology.

In recent years, however, the study of habitat use has made a number of advances, moving far beyond the mere description of used and unused habitats. These discoveries, which have dramatically increased our knowledge of how birds select habitats, the consequences of habitat selection, and applied aspects of habitat use, were made possible by marking birds for individual identification. Because most of these advances have come since 1980, a review of how banding has contributed to the history of this field will mainly include contributions from the last few decades.

Our review focuses on how banding has improved our understanding of avian habitat use in three major areas: (1) the behavioral processes underlying habitat selection, (2) spatial aspects of habitat selection and dispersal, and (3) application of habitat ecology to conservation of birds in fragmented landscapes. We also discuss some interesting case studies where banding has played a major role. These include daily commuting patterns in Brown-headed Cowbirds (*Molothrus ater*) and post-breeding movements and survival of songbirds. Throughout, we focus on important North American studies, but include key papers from elsewhere when they have led to significant advances in the use of bird banding as a tool in understanding avian habitat ecology.

BEHAVIORAL ASPECTS OF HABITAT USE

Observed patterns of habitat use are the result of behavioral processes that birds use to select habitats (Hildén 1965, Klopfer and Hailman 1965, Jones 2001). In the past few decades, research with marked birds has revealed important behavioral mechanisms that determine how birds distribute themselves across the landscape and why populations vary in space and time. One of the most robust findings from research on habitat selection is that birds have higher site fidelity after they nest successfully than after failing to rear offspring (Greenwood and Harvey 1982). The earliest North American study to report this result was Nolan's (1978) long-term study of a marked pop-

ulation of Prairie Warblers (*Dendroica discolor*). Other early findings reporting similar results include Catchpole (1972) and Harvey et al. (1979) working in Europe. All of these studies were made possible by individually marking breeding birds, recording their nesting success, and then observing whether or not the birds returned the following breeding season. Since these pioneering studies, numerous studies of this phenomenon have been conducted, including important work on Bobolinks (*Dolichonyx oryzivorus*; Gavin and Bollinger 1988, Bollinger and Gavin 1989), Red-winged Blackbirds (*Agelaius phoeniceus*; Beletsky and Orians 1991), and Prothonotary Warblers (*Protonotaria citrea*; Hoover 2003).

While individual reproductive success can clearly influence site fidelity and, therefore, habitat selection, an intriguing finding of the past 10 years has been that a bird's social environment can also influence habitat selection. This research has led in two directions. One key finding is that birds often prefer to settle near where other birds have already established territories, a behavior known as conspecific attraction (Smith and Peacock 1990, Reed and Dobson 1993). While the importance of conspecific attraction is obvious in colonial birds (Burger 1988, Kress 1997), conspecific attraction had not been considered in territorial birds until recently, presumably because the primary purpose of the territory is to exclude conspecifics (Stamps 1994). Studies from a banded population of birds, however, showed that this phenomenon occurs in territorial species. Muller et al. (1997) reanalyzed data from S. Charles Kendeigh's (1941) study of banded House Wrens (*Troglodytes aedon*) conducted in the 1920s and 1930s. Muller et al. found that while previously banded birds returning to the population tended to pick the highest-quality nesting sites (i.e., those with the lowest predation rates), first-time breeders at the study site preferred nest boxes near established neighbors. This result has direct conservation implications because if territorial birds show conspecific attraction, then they can potentially be attracted to breed at new sites using playbacks and models, as with seabirds (Ward and Schlossberg 2004).

A second area of research on social aspects of habitat selection involves the use of "public information," information about the environment that birds obtain from other birds (Valone and Templeton 2002). Danchin et al. (1998), studying a banded population of Black-legged Kittiwakes (*Rissa tridactyla*), found that the nesting success of individual birds was not the best predictor of colony selection. Birds appeared

to use the reproductive success of the entire colony to determine where to settle, using information about colony-wide nesting productivity over their own nest success. Public information about nesting success of neighbors has also been found to influence site fidelity in Collared Flycatchers (*Ficedula albicollis*); banded birds were more likely to return to populations that had experienced high nesting success in previous years (Doligez et al. 1999, 2002). Thus, banding has revealed that birds are attracted to nest near conspecifics and that they use information about the nesting success of those conspecifics when selecting habitats.

Theoretical models of habitat selection suggest that birds should select habitats that maximize their fitness (Fretwell and Lucas 1970, Fretwell 1972). These models, however, have been criticized for making too many assumptions about the animals' ability to perceive environmental conditions (Gotceitas and Colgan 1991, Tregenza 1995). To test a model such as the "ideal free distribution" requires estimating fitness of individual birds in different habitats. While fitness itself cannot be measured, one can measure the productivity of individually marked birds over the entire breeding season, with the assumption that the more offspring one produces, the higher one's fitness. Using this method, in one of the first field tests of a theoretical model of habitat distribution, Petit and Petit (1996) studied habitat selection and productivity in a banded population of Prothonotary Warblers. The authors found multiple lines of evidence that the warblers conformed to the "ideal dominance distribution," with older males preferring areas near water and excluding younger birds. The birds nearer water had higher season-long productivity than those farther away. Similarly, Holmes et al. (1996) found that banded Black-throated Blue Warblers (*Dendroica caerulescens*) had higher season-long productivity in shrub-dominated woods, and correspondingly, experienced birds tended to prefer such habitat, forcing younger birds to use less desirable, more open forests.

SPATIAL ASPECTS OF HABITAT SELECTION

Spatial variation in habitat availability, structure, and quality can have significant impacts on bird populations. Research with banded populations of birds has revealed a number of patterns in how birds respond to this variation. For instance, the buffer effect is the tendency

for bird populations in high quality habitats to remain relatively constant because they are “buffered” by fluctuations in lower quality habitats (Brown 1969). Although named by Brown, this phenomenon was first described by Kluijver and Tinbergen (1953) based on their studies of an unmarked population of Great Tits (*Parus major*). The key demonstration of the mechanism for this theory was provided by Krebs (1971) who observed that banded Great Tits dispersed directionally from lower quality to higher quality habitats. Recent work with banded birds has provided further confirmation of the buffer effect. Murphy (2001) demonstrated directional dispersal from low to high quality habitat in Eastern Kingbirds (*Tyrannus tyrannus*), and Gill et al. (2001) showed that the buffer effect could act at a continental scale.

Another aspect of spatial ecology where banding has produced insights is metapopulation ecology and habitat connectivity. Marking of birds has revealed previously unrecognized connectivity between habitats in some studies or a lack thereof in others. In an elegant study, Stacey and Taper (1992) showed that annual productivity in an isolated population of banded Acorn Woodpeckers (*Melanerpes formicivorus*) was insufficient to maintain the population. Through a combination of modeling and observation of immigration events, made possible by having a banded population, the authors showed that the population was likely being maintained by immigrants. This provided a demonstration of the “rescue effect,” the maintenance of a sink population by immigration (Brown and Kodric-Brown 1977).

Several recent studies have used marked birds to test for connectivity among habitat patches with different levels of isolation. Farmer and Parent (1997) found that during stopovers, Pectoral Sandpipers (*Calidris pectoralis*) tended to stay in place at isolated wetlands but would freely move among individual wetlands that were located in larger complexes, suggesting these groups of marshes need to be managed as a whole rather than individually. Homing experiments, in which banded birds are removed from their nesting territories and released at a distance, have shown that birds can relocate their territories from some distance (e.g., Nice 1937). Bélisle et al. (2001) advanced on this research, showing that open areas posed a barrier to movements of forest-dwelling songbirds translocated from their home territories. Translocated birds were less likely to return to their home territories and took longer to do so in more fragmented environments. This suggests that openings in forests may hinder the movements of forest birds.

On a smaller scale, banding has shown that male and female birds may use habitats differently. Sexually dimorphic species frequently forage in distinct microhabitats (Selander 1966). For monomorphic species, some researchers have simply lumped both sexes together when analyzing habitat use. Research with banded birds of known sex has shown that failure to separate the sexes may hide substantial intersexual variation in habitat use. Red-cockaded Woodpeckers (*Picoides borealis*) cannot be reliably identified to sex in the field. Morse (1972), studying unbanded woodpeckers, found no difference in foraging microhabitat between the sexes. When banded birds of known sex were studied, however, major differences were found. Female woodpeckers forage on the trunks of larger trees while males on smaller branches high in trees (Ligon 1968). Such differences have significant implications for management of the woodpecker, as managers may need to provide distinct microhabitats for each sex.

APPLIED ASPECTS OF HABITAT SELECTION

Research with marked birds has provided key demonstrations of the effects of habitat fragmentation and degradation on bird populations. The first studies to show a negative impact of fragmentation on avian nesting success appeared in the 1970s and 1980s (Gates and Gysel 1978, Wilcove 1985). Many of these early studies, however, used artificial nests, which may not accurately reflect real predation rates. Some also examined the nesting success of unmarked populations of birds. Nesting success estimates from unmarked populations, however, may not accurately reflect season-long reproduction in birds that can re-nest. To remedy this problem, recent studies have examined the effects of habitat fragmentation on nesting success in banded populations of birds. These studies have demonstrated that over an entire breeding season, birds breeding in more fragmented forests tend to have lower productivity than those breeding in more continuous habitats. Porneluzi and Faaborg (1999) found that Ovenbirds (*Seiurus aurocapillus*) breeding in forested landscapes had roughly twice the productivity of those nesting in areas fragmented by agriculture. Trine (1998) found that in a fragmented landscape, nesting productivity of Wood Thrushes (*Hylocichla mustelina*) was low enough that even populations in large patches (2000 ha) were sinks. Use of season-long productivity in marked pairs of birds

allows precise estimation of productivity and determination of whether a given population is a source or a sink.

Research with marked birds has shown that besides affecting nesting success, habitat fragmentation can also influence survival rates. Bayne and Hobson (2002) found that apparent survival in a marked population of Ovenbirds was significantly lower in forest patches fragmented by agriculture than in continuous forest or landscapes fragmented by silviculture. While the authors could not distinguish between permanent dispersal and mortality in explaining their finding, this study was one of the first to show that mortality and/or return rates are influenced by anthropogenic changes in a habitat. Most research on the effects of habitat fragmentation in North America has involved migratory birds, but Doherty and Grubb (2002) showed that fragmentation may have a negative impact on survival rates of resident birds inhabiting fragmented landscapes. In a six-year study of forest fragments in an agricultural region, the authors found that survival of three resident species increased with patch area.

CASE STUDY 1: COMMUTING IN BROWN-HEADED COWBIRDS

Brown-headed Cowbirds are brood parasites that lay their eggs in the nests of a variety of bird species (Friedmann 1929). For birds lacking defenses against cowbird parasitism, being parasitized may seriously impair reproduction, and cowbirds are now a major threat to several bird species. Cowbirds are typically birds of open country and prefer to feed in areas such as pastures and feedlots where insects are abundant (Thompson 1994). Many cowbird hosts, however, live in woodlands, shrublands, or wetlands where cowbirds may not be able to forage effectively. This raises a problem for female cowbirds during the breeding season. They must spend time searching for nests each day but also must find enough food to produce eggs almost daily during their six-week breeding season (Lowther 1993).

Research with transmitter-equipped and banded birds has shown that cowbirds have a simple and elegant solution to the problem of disjunct feeding and breeding areas. The birds make a daily commute, spending the morning in breeding areas where they search for and parasitize nests. Then, in the afternoons, the birds travel to feeding areas.

Rothstein et al. (1984) were the first to document this behavioral pattern; they found that birds in the Sierra Nevada of California commuted 2-7 km daily between breeding sites in forests and feeding sites at corrals and bird feeders. Research in Missouri, Maryland, and most recently, New Mexico has corroborated this pattern (Thompson 1994, Gates and Evans 1998, Curson et al. 2000). In New Mexico, some cowbirds traveled 18 km between woodland breeding areas and foraging areas near cattle herds (Curson et al. 2000). This research has a major conservation implication: cowbird control requires landscape-level management of feeding sites. A single feeding location such as a feedlot can lead to increased parasitism several kilometers away.

CASE STUDY 2: POST-BREEDING MOVEMENTS AND SURVIVAL OF SONGBIRDS

Despite decades of research on bird nesting behavior, the period immediately following breeding remains something of a mystery. Having finished breeding, most passerines stop singing and become more cryptic. For recently fledged young, the post-breeding period is critical, as young birds are newly independent and learning survival skills. To learn about habitat use and demography of birds during this time, ornithologists have recently begun using banding and radio-tracking to follow birds. Research with individually marked birds in the post-breeding period has provided new insight into bird habitat requirements.

After breeding, adult birds may use different habitat types than they do during the breeding season. Vega-Rivera et al. (1999) found that two thirds of post-breeding adult Wood Thrushes dispersed from their territories during molt. Dispersers tended to use distinctive habitats, choosing areas with relatively dense vegetation that presumably offered better cover than their breeding territories. Vega-Rivera et al. (2003) reported similar findings for adult Scarlet Tanagers (*Piranga olivacea*). Roughly half of birds dispersed from their breeding territories during the molting period, although habitat use in dispersers was fairly similar to that of breeding birds.

Until recently, little was known about habitat use and survival rates of fledglings after they leave their natal territories. Using radio-tracking, both Vega-Rivera et al. (1998) and Anders et al. (1997) found that young Wood Thrushes used early successional or scrub habitats where

dense cover and fruit were available. This suggests that effective management for birds may require providing different habitat types for post-breeding periods. Overall, habitat use during post-breeding movements is a promising, new area of research where tracking individual birds may lead to advances in our ability to conserve and manage bird populations.

CONCLUSIONS

Banding and auxiliary marking such as use of colored bands or telemetry have made extensive contributions to our understanding of how birds use their habitats. The simple uniquely numbered metal band and/or other unique markers provide the identifier that assures researchers of the individuals they are working with. The ability to follow individual birds has transformed the study of habitat use from a largely descriptive field to one in which researchers can determine the behavioral processes that lead to observed patterns of habitat selection. The use of banding and radio-tracking have provided immense benefits for conservation, allowing determination of how birds use habitats at multiple scales and making possible the study of vagile species with large home ranges. In many respects, the quantitative study of habitat selection is a young field. Bird banding and the use of auxiliary markers such as color bands and radio transmitters have, in the past few decades, facilitated an explosive growth in our understanding of the relationships between birds and their habitats. The prospects for the future include incorporation of even more technology in concert with banding to open new horizons for understanding of avian ecology and conservation.

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Contributions of Bird Banding to International Waterbird Conservation

Brad A. Andres¹

Abstract.—Achieving effective bird conservation requires integration and cooperation across geographic scales, cultural experiences, and shared avian ecologies. Banding and color marking of migratory birds have greatly enhanced their conservation at the international level by expanding geographic scale and stakeholder participation in conservation efforts. Over the last century, bird banding and color marking have continually contributed to our knowledge of migration routes, breeding locations, and winter destinations of North America's migratory birds. Development of collaborative networks has allowed researchers to answer broad-scale questions about how birds function within their environments. With this knowledge came a greater appreciation not only of the birds' annual cycles but also a greater understanding of the critical need to consider bird conservation in a more holistic way—one that includes the full range of human experiences that affect birds and their habitats. Bird banding and color marking have set a strong foundation to pose questions that modern techniques, such as satellite tracking, genetics, and stable isotopes, may help answer. Banding certainly has a future in monitoring the response of migratory birds to our conservation and management actions.

Every continent is visited by migrant birds that breed in North America and migrant birds from every continent visit North America. Achieving effective conservation and management of such wide-ranging organisms is necessarily complex and challenging and can only be effective if efforts are coordinated and integrated across geographic scales, cultural experiences, and shared avian ecologies (Andrew and Andres 2002). Over the last century, banding and color marking of migratory birds have provided a biological foundation that has helped define the geographic scale of migratory bird conservation issues and catalyzed the formation of international networks of bird conservationists. European banders (ringers), in cooperation with their African and Asian

¹U.S. Fish and Wildlife Service, Division of Migratory Bird Management, P.O. Box 25486, DFC, Denver, CO 80225-0486

colleagues, used their collective bird-banding information as a basis to devise bio-political networks for the conservation of migratory birds (Davidson et al. 1999). In North America, early twentieth-century efforts directed toward game-bird management have evolved into the general acknowledgment of the need for a flyway perspective to manage and conserve all migratory bird species (Schmidt et al. 1999, Harrington et al. 2002). In this paper I use waterbird examples to illustrate how bird banding has contributed to international conservation efforts for migratory birds.

GEOGRAPHIC SCALE

Only scant information on the recovery of banded waterfowl was available when Great Britain (for Canada) signed the migratory bird convention with the U.S. in 1916. Shortly after the convention was signed, the two countries agreed to develop a single, bilateral bird-banding system (Crissey 1984)—an arrangement that has persisted for almost 90 years. The accumulation of banding data over the next two decades allowed Lincoln (1935) to delineate waterfowl migration flyways. Additional information on migratory bird movements catalyzed a bilateral migratory bird treaty with Mexico in 1936 and led to the first trilateral North American Wildlife Conference on migratory wildlife (Special Committee on Conservation of Natural Resources 1936). Although the term “flyway” is often used to portray an overly simplistic view of bird migration, the basic concept of a source breeding population moving across latitudes (or longitudes) to wintering destinations remains a useful principle for migratory bird management and conservation. Indeed, realization of the need to manage populations at a flyway scale persists in the current approach to waterfowl-harvest management. Likewise, initial waterfowl banding efforts have now transformed into a coordinated, statistically-rigorous program that provides information that is incorporated into the hunting regulation-setting process (e.g., Johnson et al. 2002).

Along with metal leg-bands, other marking methods (e.g., neck bands, wing streamers, leg flags) have been used to study movements of migratory birds and to establish links among breeding, stopover, and wintering locations. Neck bands allow relatively easy re-sighting of known individuals and have provided much information on migration

patterns of geese and swans in North America. Connections between contiguous U.S. wintering areas of Tundra Swans (*Cygnus columbianus*) and breeding sites in Alaska and Canada were discovered by using neck-banded individuals (Sladen 1973). Observations of neck-banded individuals also portrayed differences in fall and spring migration patterns in small subspecies of Canada and Cackling geese (*Branta canadensis*, *B. hutchinsii*; Hines et al. 2000). Migration chronology data gained from these studies are used to establish hunting seasons that minimize the harvest of northerly migrant populations (U.S. Fish and Wildlife Service 1995), although recent information suggests that reporting rates for neck-banded birds are higher than those for other band types (Sheaffer et al. 2004). Neck banding has been used to link Alaska breeding sites of Greater White-fronted Geese (*Anser albifrons*) to an important stopover in northwestern Texas and to wintering sites in the highlands of north-central Mexico (Anderson and Haukos 2003). Beyond establishment of migration corridors, uniquely marked individuals are valuable to investigations of a variety of ecological and behavioral questions.

The capturing and color banding of shorebirds (waders) have contributed greatly to the understanding of their range-wide distribution and to the identification of specific geographic linkages of populations across the globe (Fox 2003). In the Pacific Basin, observations of color-flagged individuals have illustrated the elliptical migration route of Bartailed Godwits (*Limosa lapponica*) from western Alaska to New Zealand and northward through the Yellow Sea (Gill et al. 2005). With knowledge of the migration pathway, biologists realized that godwits are subjected to a subsistence harvest, either underway or planned, at all points of their annual cycle (B. McCaffery, U.S. Fish and Wildlife Service, pers. comm.). Thus, a management strategy for Alaska-breeding godwits clearly needs to consider effects of harvest throughout their range. Also in the Pacific Basin, observations of color-marked Bristle-thighed Curlews (*Numenius tahitiensis*) were used as a basis for developing more detailed genetic studies that addressed linkage of segregated breeding populations to specific wintering locations (L. Tibbitts, U.S. Geological Survey, pers. comm.). Knowledge of population linkage is needed to development of management strategies that can address spatially explicit threats of subsistence hunting, habitat alteration, and invasive species predation (Sherley 2001). Beyond shorebirds, recoveries of American White Pelicans (*Pelecanus erythrorhynchos*) taken by

hunters in the Alvarado Wetlands of Veracruz, Mexico, indicate that pelicans wintering there originate from virtually all breeding sites in the U.S. and Canada (B. Andres, unpubl. data). Thus, any conservation strategy for American White Pelicans breeding in North America should consider the exposure to threats in the Alvarado Wetlands (Andres and Cruz-Carretero 2003).

Handling shorebirds during the capturing and banding process allows biologists to obtain morphometric data that are also useful in distinguishing population origins of birds captured at a specific site. In addition to being used for study of age and sex composition of populations, measurements of captured birds can be used to investigate functional relationships between birds and their environments. In Delaware Bay, for example, measurements of weight gain in stopover shorebirds have been used to assess the ability of the bay to provide adequate energetic requirements, via horseshoe crab (*Limulus polyphemus*) eggs (U.S. Fish and Wildlife Service 2003). Range-wide re-sightings of Red Knots (*Calidris canutus*) color-flagged during the banding process, usually applied as a batch mark, have been used to estimate adult survival and to relate it to body condition of knots in Delaware Bay (Baker et al. 2004). The technological development of individually coded color-flags will likely improve estimation of survival rates, over use of batch marks, of Red Knots that migrate through Delaware Bay (Atkinson et al. 2003). Using banded individuals, Pfister et al. (1998) suggested that the chance of Semipalmated Sandpipers (*Calidris pusilla*) surviving the over-water flight from Massachusetts to the coast of Suriname, and hence returning to the stopover the next year, was related to their fat levels at departure. Because maintenance of high quality stopovers has direct survival consequences, assessment of site health at all stopovers along a migration corridor would represent a true flyway approach to migratory shorebird conservation.

CULTURAL EXPERIENCES

The biological connectivity established through banding programs is often the foundation for developing international networks of people who are interested in the conservation of shared migratory birds. The hands-on result of banding birds offers a unique opportunity to bring together conservation stakeholders from a variety of societal perspec-

tives—not only biologists, but also policy-makers, educators, landowners, and industry representatives. Besides the melding of perspectives at a given site, cultural values and experiences need to be integrated across geographic scales to achieve effective flyway conservation. Beyond the biological information that international banding teams supply, they can also expand the outlook of participants and broaden the context of a local banding effort. For example, the cooperative color flagging of a small number of Dunlin (*Calidris alpina*) on Alaska's North Slope may be statistically insignificant to estimate survival, yet the outreach generated from the bilateral effort has significant, beneficial conservation implications in Japan (Andres et al. 2001). Cooperative, multilateral conservation networks leverage not only financial and biological resources, but also societal importance. Societal commitment for migratory bird conservation manifests itself in the development and implementation of multilateral flyway treaties and conventions (Boere and Rubec 2002).

Banding has played a central role in the development of a collaborative approach for investigating questions about the migration system of the Western Sandpiper (*Calidris mauri*). Cooperation across the entire migration and wintering range of the sandpiper has allowed researchers to address questions at a hemispheric scale (Nebel et al. 2002). Organized networks can provide training and capacity-building opportunities at numerous levels. University researchers involved in the network have supported and advised Latin American and Mexican students who, after completing their graduate work, have gone on to develop their own scientific training programs. Research projects undertaken by network participants also educate younger students about shorebird migration biology (e.g., Warnock 2003). Designed to connect students across flyways, the Shorebird Sister Schools Program has repeatedly used banded birds to pique biological interest and as a focus for shorebird and habitat conservation messages (Chapman and Andres 2003). A central tenet of the program is to link students, educators, biologists, and communities in shorebird and habitat conservation. Parallel flyway-scale educational efforts directed toward shorebird and environmental conservation are also underway in Australia and Japan (see Andres et al. 2005).

The “Western Hemisphere Shorebird Reserve Network” (WHSRN) was formed on the concept that conservation of long-distance migrant shorebirds requires a network of sites that collectively is

only as strong as the weakest link in the chain (Myers et al. 1987). Since its initial conception in the early 1980s, the WHSRN has endeavored to build linkages among network sites. Re-captures of color-flagged Semipalmated Sandpipers provide a direct link between stopovers in Canada and the U.S. and wintering sites on the coast of northern South America (Gratto-Trevor and Dickson 1994). The direct connectivity established by re-sighting or re-capturing a bird from a known origin provides tangible evidence useful for persuading conservation administrators and donors to expend funds outside of their immediate jurisdiction, and the sensational description of bird migration can catalyze broad conservation actions. Involvement of a variety of stakeholders was a fundamental step in building the Linking Communities Project among residents of Chaplin Lake, Saskatchewan (Canada), Great Salt Lake, Utah (U.S.), and Marismas Nacionales, Nayarit (Mexico). Connecting the breeding, stopover, and wintering sites of migratory shorebirds, the coalition has sponsored teacher exchanges, held site visits at each of the links, and developed cooperative conservation strategies for shared migratory bird species (Padilla et al. 2000).

CONCLUSION

Banding and re-capturing of migrant birds have played a significant role in the development of the concept of flyway conservation. Champions in the development of the African-Eurasian Migratory Waterbird Agreement and the Asia-Pacific Migratory Waterbird Conservation Strategy were bird banders who realized the importance of connecting places and people across migratory birds' ranges (Beintema and van Vessem 1999, Asia-Pacific Migratory Waterbird Conservation Committee 2001). Although newer genetic, telemetric, and stable isotope techniques will likely become more efficient at answering certain migration questions, bird banding will continue to play a role in monitoring the state and performance of migratory bird populations. In many instances, the utility of banding efforts could be enhanced by developing more open, collaborative, and hypothesis-driven projects (Nebel and Lank 2003). Transparent, collaborative networks, that cover all aspects of the conservation or management system, are really the only models for comprehensively addressing questions about the biology of long-distance migrant birds. Direct integration of

bird banding, and other scientific pursuits, into the conservation and management decision-making process should become standard operating procedures for conservation designers, practitioners, and administrators in the twenty-first century. Bird banding has helped make us aware of the necessity of broadening our geographic and cultural perspectives — in the next century, bird banding can help us find solutions to the pressing conservation challenges faced by migratory birds.

ACKNOWLEDGMENTS

Thanks to John Tautin for asking me to participate in the symposium. Octavio Cruz-Carretero's friendship and commitment inspired me to work harder on conservation issues. Special thanks to Chan Robbins and Barbara Dowell for introducing me to international bird research. The energy and ideas of Gerard Boere have greatly infiltrated my perspective on broad-scale conservation. Lastly, I thank the bird conservation community for providing interesting thoughts and inspirational actions.

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Use of Bird-Banding Information to Investigate Disease, Safety, and Economic Issues of Birds and Their Interactions with Humans

*Robert G. McLean*¹
and
*Stephen C. Guptill*²

Abstract.—Bird-banding efforts and the systematic collection and availability of banding data provide valuable information on the breeding sites, local movements, habitat use, migratory pathways, and wintering destinations of many species of birds. These data can reveal information about transmission, maintenance, and movement of pathogens; the bird species and populations responsible for agricultural damage, depredations, and nuisance; and safety hazards of birds related to air travel and other human activities. Banding recoveries help define the residency status of bird species in specific locations and the status varies within species and among populations. The residency of birds is a major factor in determining their role in local transmission cycles of certain diseases. The high fidelity of some bird species to breeding areas makes them good candidates to annually reintroduce and maintain disease agents within a disease focal area and band-recovery information on sampled birds helps define which species are important hosts. Sampling and testing blood samples from multiple captures of banded birds provides valuable information on local disease transmission rates and seasonal patterns for the principal host species and helps identify the habitats and locations where diseases occur. Accumulation, summary, and analysis of bird-banding records from multiple species in a migratory flyway, combined with testing samples from these species, help identify which bird species are potential disseminators of diseases, when and where dissemination is likely to occur, and the source and destination of the disease pathogen. Some avian species seriously impact agricultural production of crops as well as pose human safety problems. Banding operations enable researchers to identify responsible species and populations and to determine seasonal movement patterns, staging areas, population numbers, and reproduction and survival rates in order to better develop effective methods to alleviate these affects. The specific identification of individual birds permits focused investigations on their role in disease ecology, agricultural depredation, and human safety.

¹Wildlife Diseases Program, National Wildlife Research Center, WS/APHIS/USDA, Fort Collins, Colorado 80521

²Geographic Sciences Branch, U.S. Geological Survey, Reston, Virginia 20192

The specific identification of individual birds achieved through the use of numbered leg bands has added great value to a number of investigations on the involvement of birds with, and their role in, diseases of public health, domestic animal health, and wildlife health importance. It has also aided in the investigations and mediation of agricultural depredation, and investigations related to human safety hazards caused by birds. Banding records provide information to determine avian life history characteristics important for these investigations such as: residency status of local species; fidelity and tenacity of species to both breeding and wintering sites; population estimates; survival rates; habitat use; local and regional movement patterns; dates, routes, and speed of migration; and location of breeding and wintering sites. Banding recoveries have been most useful in delineating characteristics related to regional and migratory movement of birds; whereas, recaptures of banded birds at the banders' own study sites provided information on local life history characteristics and comprised most of the banding returns. Certainly the advent and use of radio telemetry has supplemented and in some cases replaced banding returns in describing specific life history characteristics, in identifying specific movement patterns or in determining precise habitat preferences. However, the bulk of information will continue to be obtained from banding records because only a limited number of birds can be fitted with transmitters and tracked.

BANDING INFORMATION FOR DISEASE INVESTIGATIONS

One of the earliest uses of banding information in the investigation of diseases was the ornithological work by H. E. McClure as part of a comprehensive study on the epidemiology of the arthropod-borne viral encephalitides in Kern County, California, in 1943-1952 (McClure et al. 1962). This study related information on avian ecology with the epidemiology of several human and equine viral diseases for which avian species were the primary natural hosts and mosquitoes the principal vectors. The value of studying wild bird populations through mist-netting and banding during disease studies gained more popularity (Stamm et al. 1960) and became an integral part of disease investigations (Lord et al. 1973). There are many important diseases of birds that have an impact on human health (zoonotic diseases), domestic animal health,

and wildlife health, but zoonotic diseases have received the most attention (McLean 1991; Friend and Franson 1999; Charlton 2000) (Table 1). Many disease investigators have used banding operations to aid in their studies and a few examples will be described.

Investigations of avian malaria.—One of the most common avian diseases of North American birds is avian malaria which is caused by a single-celled protozoan in the genus *Plasmodium*. Avian malaria is normally a benign disease transmitted between birds by mosquitoes, causing few problems except under certain circumstances and/or with a few species (e.g., impact on endangered Hawaiian bird species). R. D. Manwell described malaria in birds and its relationship to migration and life history habits of birds (Manwell 1934, Manwell and Herman 1935). Numerous investigations were conducted in subsequent years to determine the distribution of avian malaria and host species involvement. In

Table 1. Important diseases of birds of public health, domestic animal health, and wildlife health concern in the United States and the methods of transmission and disease impact.

DISEASE	METHOD	HUMAN	DOMESTIC	WILDLIFE
<u>VIRUSES</u>				
West Nile virus	Mosquito	High	High	High
Western equine encephalitis	Mosquito	High	High	Low
Eastern equine encephalitis	Mosquito	High	High	Low
St. Louis encephalitis	Mosquito	High	None	None
Newcastle disease	Direct	None	High	Low
Avian influenza	Direct	None	High	None
Highlands J	Mosquito	None	Low	None
Avian pox	Mosquito	None	Moderate	High
<u>BACTERIA</u>				
Lyme disease	Tick	High	None	None
Mycoplasma	Direct	None	Moderate	High
Avian TB	Direct	Low	Moderate	High
<u>PROTOZOA</u>				
Avian malaria	Mosquito	None	Low	Low

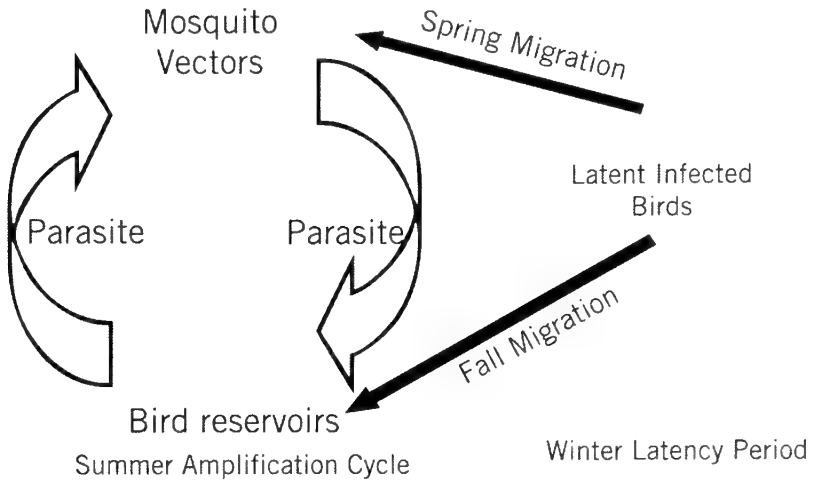


Figure 1. Transmission cycle of avian malaria in free-ranging passerine birds in the United States.

temperate climates in northern latitudes, parasite transmission and increases in bird infections (amplification) occur only during the summer months when vector mosquitoes are active and feeding on birds (Figure 1); however, the disease is able to persist in local bird populations during summers with greatly reduced mosquito activity. The mechanism by which mosquito-transmitted pathogens survive during the winter and during other times when mosquitoes are not active was a puzzle and was critical to the pathogen's long-term maintenance. As part of a five-year, year-round study of bird populations at a permanent study site in central Pennsylvania, the prevalence of avian malaria was determined by examining blood smears from a large number of permanent and summer resident species of birds for parasites (Beaudoin et al. 1971). The American Robin (*Turdus migratorius*), Northern Cardinal (*Cardinalis cardinalis*), and Wood Thrush (*Hylocichla mustelina*) had the highest prevalences of infection of the frequently captured species; 44%, 17%, and 16%, respectively. The prevalence of detectable infections in birds began to increase with the seasonal emergence of adult-feeding mosquitoes in the spring, peaked during the summer amplification period, and declined to undetectable in the fall. A high frequency of recaptures of individual birds at the study site allowed serial testing of

birds for malaria infection within the same summer transmission season and during subsequent years. This serial testing identified when each bird became infected initially at the site, followed their infection status through the summer, and detected the disappearance of parasites from the blood of these birds in fall. Banding had the additional benefit of limiting the number of blood samples taken from individual birds during each sampling period to reduce the risks of extra handling as well as not inflating the infection results from birds that are frequently recaptured.

Because of the high fidelity of species like the American Robin and Wood Thrush to breeding sites, a number of individual birds banded and tested during previous years were tested again in the spring for malaria. Previously infected birds relapsed following the stressful migratory and reproductive periods making malaria parasites available in their blood again to infect emerging mosquitoes. Multiple infected birds relapsed simultaneously to initiate the local summer transmission cycle thus providing a maintenance mechanism for the local survival of the parasites despite the departure of the vertebrate host during the winter months (Figure 1). This chronic infection and relapse phenomenon in the natural avian host species provides for the maintenance of the parasite even through summers with insufficient mosquito production to amplify transmission. The measurement of local movement patterns through recapture information also identified specific habitats that supported malaria transmission.

Investigations of St. Louis Encephalitis virus.—An extended investigation of the avian hosts of St. Louis encephalitis (SLE) virus in the urban environments of southern California during 1987-1996 used banding information from 52,629 birds captured and tested for infection with SLE virus (Gruwell et al. 2000). The virus is transmitted by mosquitoes between birds and occasionally spills over into associated human populations (Figure 2). A small human epidemic of SLE virus occurred in this area of southern California a few years prior to the study and a number of bird species and sites where transmission occurred were identified (McLean et al. 1988). During the later study, the highest capture rate as well as the highest recapture rate occurred in two urban species; House Finches (*Carpodacus mexicanus*) and House Sparrows (*Passer domesticus*). The large capture of 25,599 House Finches (37% recaptures) and 18,214 House Sparrows (42.5%)

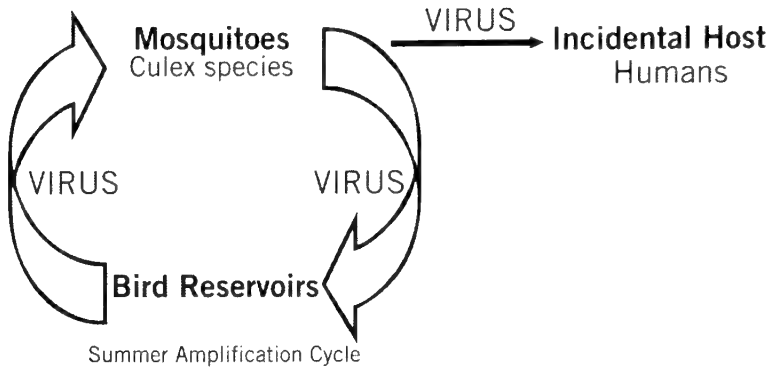


Figure 2. Transmission cycle of St. Louis encephalitis virus in the United States.

occurred because of their high densities, site fidelity, and short movement range. Only 1.1% of the birds were antibody positive for SLE virus, but the high recapture rate allowed for multiple serial bleeding of individual birds to test for conversions from negative to positive infections and to follow infections to define the temporal nature of virus transmission. The short movement distances of these species and little exchange between capture sites as determined by recapture information allowed for spatial separation of the disease data and identification of precise locations where virus transmission by mosquitoes was occurring.

The recapture information was used to calculate the average minimum longevity of each species; 714 days for House Finches and 559 days for House Sparrows. Age and longevity of avian hosts are important factors in understanding the epidemiology of SLE virus; e.g., understanding the effect of population turnover rates on the number of susceptible birds in the local population, which in turn affects the transmission potential of various host species. The banding information in this comprehensive study identified not only the crucial bird species for virus transmission (House Finch and House Sparrow) in this urban environment, but also the precise locations where the virus was optimally transmitted and maintained and the time periods when transmission occurred.

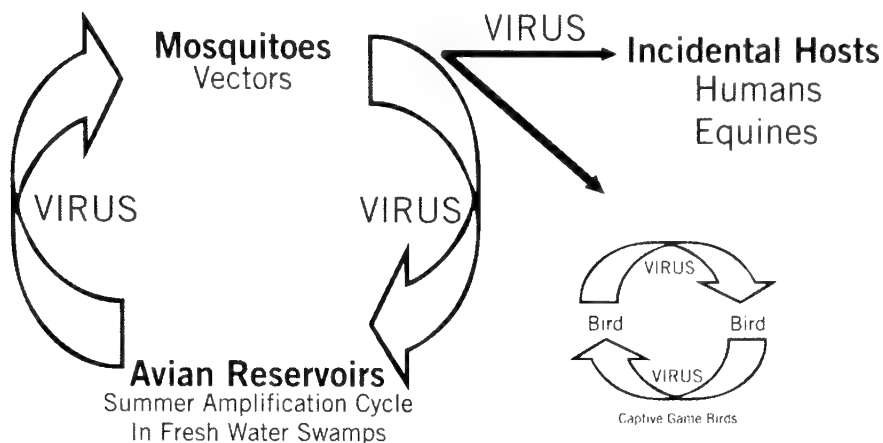


Figure 3. Transmission cycle of eastern equine encephalitis in the United States.

Investigations of eastern equine encephalitis virus.—An ecological study of eastern equine encephalitis (EEE) virus in avian communities in New Jersey freshwater swamps was conducted from 1980-1983 (Crans et al. 1994). This virus transmission cycle involves passerine birds and a specific mosquito vector (*Culiseta melanura*) in selected freshwater swamps along the Atlantic and Gulf coasts of the U.S. Virus transmission occurs during the summer and is restricted to coastal fresh water swamps (foci) where EEE virus is optimally transmitted and maintained because of specific mosquito and avian host species that inhabit the swamp habitats (Figure 3). The virus occasionally escapes from the swamp habitats and causes small numbers of human and equine cases annually and sporadic outbreaks. Historically, EEE virus was also introduced from the swamp foci into captive breeding farms for exotic game birds causing outbreaks that were perpetuated directly between birds by pecking and cannibalism. The use of vaccines, plastic protectors to prevent pecking, and improved sanitary conditions reduced the incidence of such outbreaks. During the study, 1848 individual birds of 69 species were captured and tested for virus and antibodies against EEE virus in a swamp that was a well-established enzootic focus for the virus. Nineteen (1%) birds were viremic (circulating virus in blood) at the time of capture, 494 (27%) birds were antibody positive, and 47 (68%) species were antibody positive for EEE

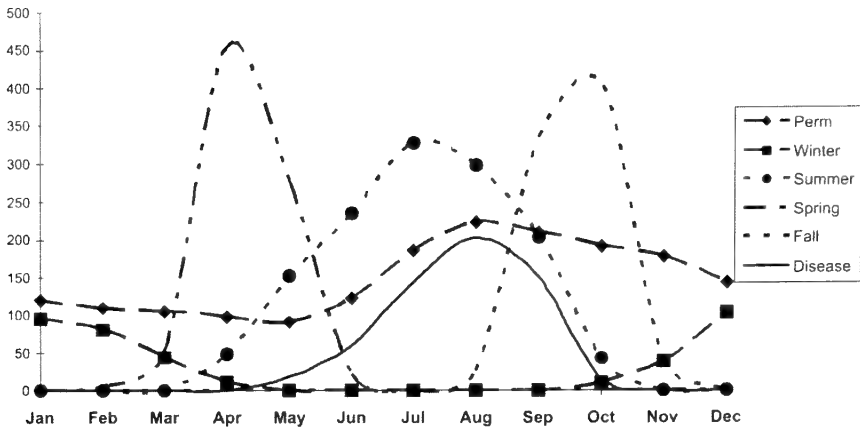


Figure 4. Hypothetical numbers of birds for various residency types at a local fresh water swamp habitat in relation to time periods for mosquito activity and disease transmission of eastern equine encephalitis virus.

virus. Because EEE virus is not transmitted throughout the year in swamp habitats in the northern latitudes (adult mosquitoes die or are inactive during the winter months), residency status of many bird species was critical in defining their role in amplifying and sustaining virus transmission (Figure 4). Banding information determined which species were locally important as host for the virus and determined the type of local residency status that was most closely linked to participation in the EEE transmission cycle. Avian species and subpopulations of species spending the greatest amount of time in the swamp in the summer had the highest prevalences of EEE antibody; permanent resident Blue Jay (*Cyanocitta cristata*) (62%), Tufted Titmouse (*Baeolophus bicolor*) (44%), and Carolina Chickadee (*Poecile carolinensis*) (39%), and summer resident Wood Thrush (60%), Gray Catbird (*Dumetella carolinensis*) (34%), and American Robin (30%). Transient migrant and winter resident birds had the lowest antibody prevalences.

As with the SLE study, serially testing of individually banded birds over time at the study site provided insights on the epidemiology of the disease not otherwise achievable. Band recoveries on birds tagged and sampled the previous year (69 birds, 4%) identified 29 of the recaptured birds (42%) that had seroconverted from antibody negative to positive;

12 (17%) seroconverted in the spring before EEE virus was detected in local mosquitoes. One Gray Catbird was antibody positive in May, 1981 and was viremic and thus capable of infecting mosquitoes when recaptured the next year on 8 June 1982. The banding information combined with serial sampling of individual birds enabled researchers to postulate that mosquito-transmitted viruses are able to survive through temperate winters when there is no mosquito activity as persistent and relapsing infections in birds to initiate early summer transmission cycles.

West Nile virus dissemination by migratory birds.—A strain of West Nile virus (WNV) introduced into New York City in 1999 caused a human epidemic and an epizootic in the local bird population (Eidson et al. 2001). This mosquito-transmitted virus of birds became established in the northeastern states and then rapidly expanded across the country within three years. By the fall of 2004, the virus was present in all of the continental 48 states (CDC 2004). The dissemination of WNV was most likely facilitated by the seasonal movement of migratory birds (McLean 2002). An investigation into the involvement of migratory birds in the spread of WNV was initiated in 2001 and more than 13,000 wild birds from 139 species at 17 sites in 12 states were captured and sampled (R. McLean, S. Guptill, and R. Dusek, unpublished data). Banding information combined with laboratory results from testing blood samples from this study will be used to determine which bird species are potential disseminators of the virus and the routes of dissemination. This information will be supplemented by the accumulation, summary, and analysis of historical bird-banding records to further define the avian host species, to predict when and where dissemination is likely to occur, and to evaluate the likely source and destination of the virus.

BANDING INFORMATION FOR INVESTIGATIONS OF BLACKBIRD DAMAGE TO AGRICULTURAL CROPS

Bird banding of some avian species that seriously impact production of agricultural crops enables researchers to identify responsible species and populations, determine seasonal movement patterns, determine staging areas, and evaluate prevention strategies. Blackbirds are a group of species that have negatively impacted agricultural production.



Figure 5. Locations of breeding populations in the north-central states and wintering populations in the south-central states of Red-winged Blackbirds that cause significant agricultural damage in the United States.

Blackbird populations have thrived in response to agricultural changes in the north-central and south-central states. Ripening sunflower crops in the north in the fall (Cummings et al. 1989) and rice crops in the southern states in the winter (Brugger and Dolbeer 1990) receive heavy blackbird depredation resulting in millions of dollars of damage. Changes in the prairie pothole wetlands in the northern Great Plains to dense stands of cattails made this area desirable for nesting and roosting blackbird populations and wintering flocks of blackbirds extend across the southern states supported in part by the winter rice crops (Figure 5). Bird-banding records indicate that the breeding and wintering Red-winged Blackbird (*Agelaius phoeniceus*) populations are linked (Brugger and Dolbeer 1990). Banding recoveries revealed that individual populations of blackbirds tend to stay together during the winter months in southern states and specific roosts were located that

contained banded birds from the sunflower damage areas in the Dakotas. The banding information allowed mass marking of the large identified blackbird roosts with aerially applied dyes to track the movement and destination of wintering blackbirds to the summer breeding grounds in the north (Knittle et al. 1987). Banding recoveries over five years indicated the fidelity of male blackbirds to specific breeding territories in the Dakotas (J. L. Cummings, unpublished data). This banding information enables researchers to identify specific wintering roosting sites in the south and migratory routes and staging areas of these same birds between their wintering grounds and breeding range in the north which allowed targeted management efforts to reduce specific crop depredation.

BANDING INFORMATION FOR INVESTIGATION OF AIRLINE SAFETY HAZARDS FROM BIRD STRIKES

Hazards to public safety from aircraft strikes of wildlife, especially birds, has steadily increased during the last few decades. Crashes of commercial and military aircraft have resulted in hundreds of deaths and significant economic loss to the airline industry and the military. Management strategies to reduce the number and frequency of strikes at airports included habitat management, bird deterrents, noise and visual harassment techniques, and shooting. The situation at John F. Kennedy International (JFK) Airport in New York City (NYC) was of particular concern because of an airline crash, airplane damage (especially to the Concorde), and an increasing number of bird strikes to airplanes (Figure 6). An expanding breeding colony of Laughing Gulls (*Larus atricilla*) adjacent to the JFK airport increased from 15 pairs in 1979 to 7629 pairs in 1990. In analyzing the bird strike data, Dolbeer et al. (1993) determined that 52% of the bird strikes were from Laughing Gulls, 35% from other gull species, and 13% from other bird species. All of the bird strikes due to Laughing Gulls were from May to September during the breeding season. Habitat management to reduce the local presence of Laughing Gulls was not possible because the large breeding colony was located in the Jamaica Bay Wildlife Refuge adjacent to the airport. The gulls flew from the breeding colony across the airport to multiple foraging areas in the NYC area. Shooting of gulls flying on the airport runways became the only viable option to reduce air strikes. Collection and

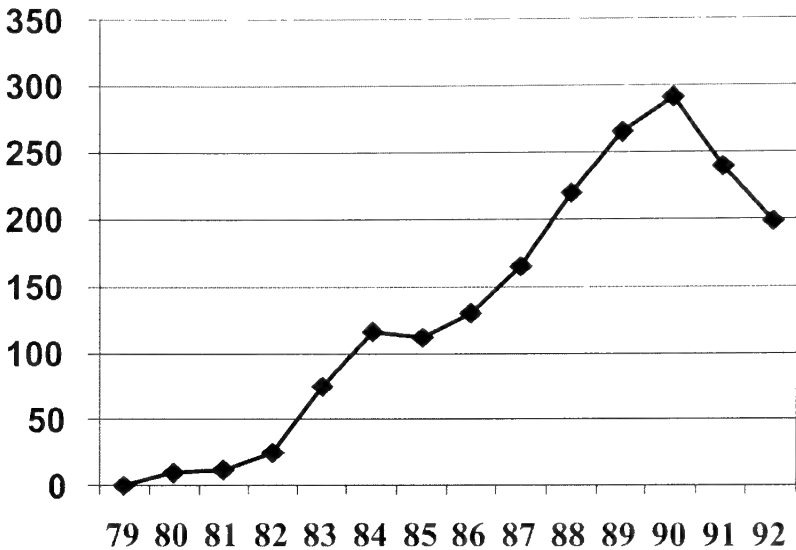


Figure 6. The number of bird strikes with airplanes at the John F. Kennedy International Airport, New York City, New York, 1979-1992 (modified from Dolbeer et al. 1993).

examination of the gulls shot at JFK airport during 1991-1992 revealed that 92% were Laughing Gulls of which 90% were brooding adult birds likely from the adjacent breeding colony since the nearest other breeding colony was 106 km away. Population control resulted in 68-89% reduction in airplane strikes during the first 2 years of the shooting program (Figure 6). Gulls shot were representative of gulls struck by aircraft as determined by the banding records of the birds. A similar percentage of the Laughing Gulls struck (2.4%) and the Laughing Gulls shot (2.2%) were banded and both groups had a similar species composition and age-sex ratios indicating that the shooting was specifically directed at the gulls causing the strikes. Of the banded gulls, 98% were banded as nestlings in New Jersey, 106 km from JFK; no banding of nestlings was occurring at the local breeding colony.

SUMMARY

The benefits of bird-banding information to disease investigations, regional investigations of depredation of agricultural crops, and investigations of human safety issues at airports have been illustrated. The greatest benefit from combining bird-banding operations with other investigations is during multiyear sampling studies in specific locations when a high frequency of multiple recaptures occur. The identification of individuals by banding and multiple serial sampling of tagged individuals provided the most useful tool in understanding disease dynamics in local bird populations. Historical banding information can be used in determining potential dissemination routes of diseases of wild birds. Bird-banding information can be complemented by radio telemetry to track both short-distance and long-distance movement patterns (satellite telemetry) and by stable isotope studies to determine the geographical breeding locations of fall migrants and even locations visited.

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History of the Role of Bird Banding in Avian Behavioral Research

M. Victoria McDonald¹, Jerome A. Jackson², and William E. Davis, Jr.³

Abstract.—Identification of individual birds is uniquely, and with certainty, the cornerstone of bird banding's contribution to North American ornithology. We (1) review the history of the integration and influence of banding as a tool in behavioral studies of birds and (2) address two questions with data based on a survey of ornithological and behavioral literature: (a) How has the frequency of published works relying on bird banding changed over time? And (b) what changes in the literature on the behavior of birds seem to co-vary with the growth of bird banding? The latter question was addressed using case-studies and other cited works on bird behavior found in major animal behavior texts.

The use of bird banding as a tool in behavioral studies of birds began early in the first decade of scientific bird banding in North America. Growth in the frequency of papers using bird banding in studies of bird behavior grew exponentially following demonstration of the scientific potential of systematic banding and control and coordination of banding by the United States and Canadian governments. Defining trends in questions asked in behavior papers using banding is difficult because, while the technique of bird banding has certainly influenced the growth of avian ethology, the growth of avian ethology has also influenced the development and growth of bird banding. The future of bird banding as an endeavor and tool for bird behavioral studies is tied to major forces pervading all field biology. We conclude with suggestions of potential future directions of behavior studies enabled by individual identification.

Papers and case studies cited in animal behavior texts suggest that the most classic research done in the past 50 years has used individually marked birds. Perhaps less appreciated, however, is the role of these

¹Department of Biology, University of Central Arkansas, Conway, Arkansas 72035

²Department of Marine and Ecological Sciences, Florida Gulf Coast University, 10501 FGCU Boulevard South, Ft. Myers, Florida 33965

³Professor Emeritus, Boston University, 23 Knollwood Drive, East Falmouth, Massachusetts 02536

studies in forging trends in some of the major theoretical bases of ethology. Nowhere in field studies of avian behavior is this more evident than in the study of the evolutionary consequences of mate choice and territorial behavior.

In this chapter we follow the integration of banding into behavioral studies of birds, and more importantly how bird banding as a tool has propelled the advancement of behavioral data collection and analysis—not merely for birds, but for other taxa as well. We elucidate by showing the cascading influence of banding, that is, which realms of ethology (specifically behavioral ecology) have grown as a direct or indirect consequence of being able to identify birds individually.

We begin with a practical and historical look at why individual identification, and banding in particular, is usually required for avian behavior research. Although the early major focus of bird banding was on understanding bird migration, within the first decade of scientific bird banding, some ornithologists recognized other values associated with having recognizable individuals. In an editorial, Lynds Jones (1923:44) of the Wilson Ornithological Club noted that “bird banding naturally lends itself to the more intimate study of individual birds . . .” Jones also provided an assessment of behavioral literature of the time and sage advice to students of bird behavior: “. . . it is all important that the telling of what has been seen shall be in simple language and without additions or subtractions—that is, just as it actually was. A vast deal of the reports of observations that find their way into popular print are padded with all sorts of interpretations. Cut that sort of thing out.”

S. Prentiss Baldwin, a pioneer bird bander, student of bird behavior, and proponent of systematic banding of adult birds, noted that by 1925 some ornithologists believed the “greatest value of banding [would] be in the intimate study of the daily life of the individual bird, and better understanding of the home life of each species” (Baldwin 1925). In addition, there have been benefits to the growth of avian ethology that have come about—in part independent of having marked birds—from closer observations of birds made through the processes of capture, handling, and release. Lyon (1922) and Dales (1925), for example noted individual variation in birds in the manner of their response to capture. Frederick Lincoln (1939), first and long-time director of the U.S. Bird Banding Laboratory, summarized the early progress in understanding bird migration made as a result of studying banded individuals

as opposed to the more general understanding that had been achieved through patterns discerned through study of species.

We trace the role of bird banding in the development of animal behavior as a discipline from the early 20th century to present. Our focus is not only on specific studies, but also on changes in the numbers and nature of papers and books dealing with bird behavior. We demonstrate the increasing proportion of studies using banding and the changes in trends of ethological questions both answered and enabled by the ability to individually identify birds. We conclude by suggesting potential future directions of behavior studies enabled by individual identification, using traditional banding techniques and/or other, newly emerging marking technologies.

IMPORTANCE OF BEING ABLE TO IDENTIFY INDIVIDUALS

Why identify?—Identification of individuals uniquely and with certainty is the cornerstone of the contribution of bird banding to North American ornithology. Beyond the obvious necessity of being able to recognize one's subject animals in order to associate behavior with other parameters, comes the capability to extrapolate from individual to population and from current time to the future. Research questions addressed at the population level often intersect or develop in tandem with questions asked by ethologists, particularly when dealing with the genetic basis and evolution of the behavior.

How can a researcher identify individuals?—Prior to the central administration of bird banding, all manner of bands and markers were applied to wild birds to aid in individual identification. Reasons for such marking varied from simple curiosity to field studies involving behavior. For example, Watson (1909, 1915) used daubs of paint applied to feathers to identify individual Brown Noddys (*Anous stolidus*) and Sooty Terns (*Sterna fuscata*) to determine their individual responses during displacement experiments and other behaviors.

Celluloid plastic was patented in 1870 (Anonymous 2007) and was used to make colored plastic rings for marking poultry and cage birds perhaps as early as 1902 in the United States (National Band and Tag Company 2007). These rings were occasionally placed on wild birds,

thus allowing their individual recognition (e.g., Lloyd 1925). On an Antarctic expedition in 1908-1909, Gain (1913) marked Adelic Penguins (*Pygoscelis adeliae*) and Blue-eyed Cormorants (*Phalacrocorax atriceps*) with colored plastic bands to allow him to distinguish age classes. Other early studies of marked birds involved use of colored celluloid poultry or cage bird bands in conjunction with numbered aluminum bands.

In England, J. P. Burkitt (1924, 1926) used aluminum bands and metal bands of "some dark tinny material" in various combinations so that he could identify individual Robins (*Erithacus rubecula*) without recapturing them. Although he is sometimes credited with having invented "color-banding," Burkitt was color blind, thus he depended not on color, but on shapes and shades of gray to identify the band combinations on his birds (Hutchinson 1999). The end result was the same as modern color-banding studies—he was able to discern individual behavioral attributes and interactions among specific individuals.

By 1925 colored plastic bands were readily available and those using them encouraged others to use them, noting the many questions that could be answered by the ability to recognize individuals on sight (Whittle 1925, 1927). As a consequence of the independence of the approach, most early markers were of use only to the individual who applied them. The lack of regulation and coordination of such markers meant that two or more individuals might apply similar markers such that observers could make errors of identity. By 1930 these problems were recognized by behavioral researchers interested in using marked birds that were individually identifiable at a distance (e.g., Butts 1930). Today, standard-issue metal U.S. Fish and Wildlife Service bands are often applied in conjunction with other markers (e.g., colored leg bands, patagial tags, neck collars, nasal saddles) and use of these auxiliary markers is also coordinated, regulated, and managed such that misidentification of individuals as a result of duplication of marking schemes is minimized.

Even without applied markers, individual identification is possible using variation in such natural attributes as song, plumage details, and physical deformities. Strong (1914) used slight plumage differences to identify members of a pair of Herring Gulls (*Larus argentus*) and studied birds at marked nests. Lawrence Kilham was a master at distinguishing individuals by plumage subtleties and made substantial contributions to our understanding of the behavior of woodpeckers, White-

breasted Nuthatches (*Sitta carolinensis*; 1972) and other species as a result of his careful observations.

The advantages and disadvantages of relying on natural marking, however, vary considerably with circumstances. Kilham, for example, raised White-breasted Nuthatches in captivity as well as studying them in the wild. He was intimately familiar with nuances in their plumage, something that only comes with considerable experience. A major disadvantage of relying on natural markers for bird identification is the lack of enough variation among individuals for most characters to allow sample sizes above a mere handful. Major limitations of this approach are that (1) without banding the sample size is always limited due to small natural variation in bird appearances, and (2) it is usually impossible to be absolutely certain that the identifying characteristic is unique within the population. Such limitations are perhaps what drove banding and associated auxiliary marking techniques to their prominence in avian studies.

Negative impacts of banding relative to studies of avian behavior.—Although banding has had an overall positive impact on the development of ethology, at times this tool may introduce a bias and create problems that call into question the validity of reported results or interpretation of data. Capture and recapture alone induce physiological stress (e.g., Wingfield et al. 1982), and was very early in the history of bird banding known to influence reproductive behavior (Baldwin 1921). The possible impact of use of aluminum and color bands and other markers on the behavior of birds has been a frequent subject of study and results provide some evidence of problems, although not in all species. Use of certain colors (especially red) on color bands for some species has been reported to alter social status of individuals, although most such reports have met with differing views. See conflicting reports and reconsideration of reported problems from: Burley (1981) and Zann (1994) for Australian Zebra Finches (*Taeniopygia guttata*); Beletsky and Orians (1989), Metz and Weatherhead (1991), Weatherhead et al. (1991), Metz and Weatherhead (1993) for impacts on Red-winged Blackbirds (*Agelaius phoeniceus*); and Hagan and Reed (1988, 1989) and Hill and Carr (1989) for Red-cockaded Woodpeckers (*Picoides borealis*). Color bands were not found to influence social status of Dark-eyed Juncos (*Junco hyemalis*; Cristol et al. 1992). Watt (1982) examined the hypothesis that if researchers can use color bands to identify

individuals, perhaps birds might be able to do so as well. She found no evidence of such ability in White-crowned Sparrows (*Zonotrichia leucophrys*). Clearly there seems to be a potential for problems, but certainty and severity of problems associated with influence of color bands on behavior have eluded us. Certainly awareness of potential problems and continued vigilance as behavioral studies are designed and implemented are in order. Discussions and analysis of the impacts of such techniques have contributed, and will continue to contribute to the volume of ethological literature involving use of banded birds.

Influence of bird banding on the growth of behavioral studies of other animal groups.—Bird banding and its systematic use to study bird behavior did not develop in an ethological vacuum. It had been preceded by efforts to learn of the movements of creatures as diverse as lobsters and fishes through the development of systematic marking programs (see Jackson, this volume). However, these earlier efforts were isolated and focused primarily on dispersal from the point of marking rather than intimate studies of complex behaviors. The use of bird banding in behavioral studies, once begun, grew rapidly and globally. A growing body of behavioral studies based on birds individually marked by banding, planted seeds of possibility within fertile fields of many taxonomic disciplines. While many of those seeds germinated into organized marking schemes, thus far much of the resulting research has been targeted at movement patterns and longevity rather than classical ethological studies. Birds are more often diurnal, more conspicuous, and thus easier to study in the field. Bat banding began at least as early as 1932 and was likely directly influenced by the successes of bird banding (Reyberg 1947). Most bats for which similar banding programs have been developed, because of their more nocturnal behavior, do not lend themselves to observation of marked individuals except in laboratory conditions (Greenhall and Paradiso 1968). Delaney (1978) provides a brief history of marking efforts for several animal taxa. Marking of insects for behavioral studies was begun in the 1920s and was common by the 1930s (Delaney 1978). These efforts, using paints and dyes and not part of a widespread, coordinated, marking scheme, began as numbers of publications of behavioral studies of birds identified by banding were growing geometrically.

BRIEF HISTORY OF ANIMAL BEHAVIOR AND ITS RELATION TO BIRD BANDING AND ORNITHOLOGY

The establishment of the federal bird-banding program was critical in the development of the study of animal behavior, propelling field studies on birds from mere collections of observations and descriptions to recognition as legitimate scientific research, with ensuing major contributions to ethology.

The beginning—ethology vs. comparative psychology.—The study of ethology (animal behavior) emerged as a recognized discipline early in the twentieth century. Until approximately the end of the 1960s the field was somewhat polarized, with lab-oriented behavioral-psychologists (e.g., B. F. Skinner) at one end of the continuum, and classical ethologists (e.g., Konrad Lorenz and Niko Tinbergen) using “natural experiments” (Tinbergen 1951, 1963) at the other end. Initially behavioral investigations using birds were more ethologically oriented, but, since the popularity of studies of behavioral modification and mechanisms of learning began to dominate the literature, there have been increased laboratory studies as well.

Beginning in the 1970s, the distinction between the ends of the comparative psychology-ethology continuum began to dissolve (e.g., Hinde 1970). Concurrently, the studies reflected in most published papers shifted from being mostly descriptive (e.g., mechanisms, immediate consequences, and development within an individual) to addressing questions pertaining to the evolutionary significance of the behavior. With this shift, the subject of study in both the laboratory and the field became less often an individual animal or small unit (e.g., pair, parents-offspring) whose behavior was documented over a relatively short period of time, and more often the population over a longer period of time. Studies began to emerge addressing the lifetime reproductive or even inclusive fitness consequences of certain behavioral traits. The need for marking and tracking of individuals became not only a convenience, but a necessity.

In North America, new societies and journals devoted to animal behavior were established mid-century, e.g., the Animal Behavior Society (in 1965; Schein 1994). Their popularity surged in the 1970s-1980s, while in Europe older journals were rejuvenated and/or renamed.

For example *Behaviour*, co-founded by Tinbergen and W. H. Thorpe in 1948, while still focusing on the causes of behavior and variation in behaviors among closely related species, also followed new trends in ethological research. *Zeitschrift für Tierpsychologie*, the journal of the Society for Animal Psychology (Ethologische Gesellschaft), began publication in 1937 and was initially co-edited by Konrad Lorenz. In 1986, this journal's name was changed to *Ethology*. Studies in recent volumes of all these journals have increasingly dealt with question-driven testing (vs. describing) animal behavior and its consequences—mostly in natural settings or at least under natural conditions. Again, the role of banding in field studies involving birds was indispensable.

With the publication of E. O. Wilson's book *Sociobiology: The New Synthesis* in 1975, a convergence of sorts occurred involving aspects of many realms of animal behavior. Some predicted sociobiology would subsume ethology, and others predicted ethology would become splintered into its component specialties. But neither seems to have happened. Bird banding has been directly affected little if any by the strict sociobiology paradigm, although one could perhaps trace some trend shifts to the topics and issues brought to the forefront by sociobiology.

Other impacts of changes in science during the last quarter of the 20th century.—At least five other changes in science, beginning with the last quarter of the 20th century, have had indirect but significant impacts on the use of bird banding in behavioral research: (1) There has been an increase in restrictions on research due to animal welfare concerns. (2) There is an expectation of statistical treatment in published works. (3) There has been growth in the diversity and numbers of conservation-related behavioral studies, in part a result of endangered species legislation and resulting programs to recover listed species. (4) There have been increased numbers of studies on relatedness enabled by molecular techniques. And (5) with the increased breadth of research possibilities facilitated by banding and recognition of the potential use of banding data in wildlife management, there has been an increase in career options requiring advanced training and thus an increase in graduate school opportunities and projects.

Impacts of restrictions on research activities.—Increased sensitivity to, and then discipline-wide guidelines and governmental regulation

related to animal welfare and humane handling, both in the lab and in the field, became central by the 1980s. Research prior to that time had more-or-less carte blanche when it came to experimental manipulations, and many questions asked were answered with methodologies that today would have a difficult time getting through Institutional Animal Care and Use Committees (IACUC; see a history of federal animal care guidelines and IACUC in Anonymous 2002). Banding, however, always has been relatively innocuous, and thus with the clamping down on extreme experimental manipulations came more studies designed to take advantage of what Tinbergen (1951, 1963) called “natural experiments.” Because time-consuming and expensive manipulations were not part of the protocol, these studies required, or allowed larger samples. The result was a mild resurgence in dependence on bird banding, necessitated among other reasons by the need to obtain sufficient sample sizes.

Expectations of statistical treatment of data.—Whether driven by the above, as a result of it, or both, as larger and statistically-robust samples became the norm, quantitative analysis became not only possible, but obligatory. Earlier research on bird behavior in the field had been somewhat exempt from such expectations (e.g., see pre-1970s papers published in *Behaviour*). Increased use of statistical analysis, and now the requisite application of statistical analyses to data associated with field studies (and the increased need for academicians to publish) contributed to the broader scientific community’s acceptance of bird behavior research as a credible sub-discipline.

With more demand for research questions to be cast as hypotheses, followed by data tested statistically, came the search for appropriate statistical tests. Ethologists discovered non-parametric statistics, a “discovery” that allowed them to treat their scant or lop-sided data sets statistically, yet side-step the rigid requirements of parametric statistics. Siegel’s 1956 book *Nonparametric Statistics for the Behavioral Sciences* became so popular in the 1980s that copies were hard to come by. This book’s simplistic approach allowed many field researchers to grasp intuitively and then apply valid statistical treatment to behavioral data. Obviously, with the need for larger samples came the necessity to economically and efficiently keep track of more individuals, and leg bands with longer numbers, or other unique marker(s) combined with leg bands filled this need.

In addition to aiding identification, banding provided another role that was important from the perspective of proper experimental design for statistical treatment. The advantage of numbered leg bands over more conspicuous markings, natural or human-applied, is that individuals in the sample group can be homogenous, differing only in the numbers on the bands, and not by more substantial but heterogeneity-producing marking or recognition schemes.

Growth in the diversity and numbers of conservation-related behavioral studies.— Another thread to the story, which has relevance to the rise of bird banding as an essential ingredient in post-1960s bird field research, can be traced back to the post-World War II increased prominence of higher education in North America. Along with more people entering and being born into the upper-middle class, and easier access to higher education for most people, came an emphasis on science in general. More students entered graduate school to pursue careers in biology. Along with more biology graduate students came more research projects, and thus the necessity to develop more and different questions—obviously necessary to avoid overlap or duplication with other students' projects. Academic mentors and advisors, departing from the old school, now demanded that their students' field research projects be aimed at answering specific questions rather than being studies entailing only observing and reporting natural behaviors. If one wanted to do academic research on bird behavior in the wild, then by and large the subject birds had to be banded, no matter whether one was going to study singing, foraging, mating, or parenting. For example, the long-term studies of cooperative breeding of Florida Scrub-Jays (*Aphelocoma coerulescens*; Woolfenden and Fitzpatrick 1984 and references therein) would not have been possible without a uniquely color-banded population.

Increased numbers of studies on relatedness enabled by molecular techniques.— With the advent of DNA fingerprinting techniques in the early 1990s, studies seeking to assign parents to offspring in order to determine other levels of relatedness and the fitness consequences of being related (or not) in altruistic behavior became immensely popular. Such studies have become even more common as expertise has increased and lab-related expenses decreased.

Along with its sister applied molecular technology tool—mDNA (mitochondrial DNA, used generally to determine evolutionary relatedness at the subspecies and higher taxonomic levels)—DNA fingerprinting has had probably a greater impact on field ornithology in general, and on avian behavioral studies in particular, than any other technique, except for banding and possibly the technological development of tape recording and subsequent quantitative analysis of avian vocalizations.

Expanded graduate school opportunities and projects.—Studies of vertebrate behavior aimed at expanding our overall knowledge of threatened, endangered, rare, or sensitive species have increased in recent years concurrently with heightened awareness of their potential extinction and thus permanent disappearance of their behavioral repertoire.

Conservation behavior, a contemporary sub-discipline of animal behavior, is growing in popularity and rapidly maturing. Newly-funded grant resources support research in this area. Examples of issues and applications can be seen in conservation-oriented journals (e.g., *Conservation Biology*; *Pacific Conservation Biology*), and sampled from web-based forums, e.g., the Animal Behavior Society's on-line newsletter "The Conservation Behaviorist" (<http://www.animal-behavior.org>). Studies that required individually marked birds, for example, studies of winter site fidelity in Neotropical migrant birds (e.g., Kricher and Davis 1983), have direct conservation implications concerning habitat destruction in the Neotropics.

By 2007, many survey-oriented research programs or government-mandated assessments expect at least some documentation of the natural behavior of sensitive species or populations. Particularly when potential litigation is a background concern, the design of field studies includes a behavior component. The description of behavior in these situations increasingly necessitates statistical rigor—and once again the adage that the more data the better means keeping track of more individuals with minimal manipulation, ergo banding.

THE USE OF BANDING IN PUBLISHED WORKS ON BIRD BEHAVIOR

In addition to reviewing the development of bird banding as a part of the emerging science of ethology, a second purpose through this chapter was to survey the literature for indications of changes in the numbers and nature of studies dealing with bird behavior since the advent of banding as a field technique. This was done by McDonald.

Specifically, we predicted the following: First, that an increasing proportion of published work would rely on banding, and second, that banding's widespread implementation would lead indirectly to more theoretical orientations and changes in levels of analysis. Pertaining to the latter, we expected more multifaceted studies would be attempted, given that tracking data in time and space had become more manageable using banding, as contrasted to methods used previously.

McDonald attempted to address the second prediction because she wanted to demonstrate that simply counting and categorizing papers does little to validate the critical role of bird banding has played in shaping the course of behavioral studies. Being able to track individual birds in time and space is critical not only for ornithology, but also in higher-level approaches to ethological questions, e.g., the evolution and development of behavior in birds.

As explained in more detail in the following sections, the results plainly bore out the first prediction. Data purporting to address the second prediction were not as straightforwardly assessable. Clearly, changes in trends of ethological questions have taken place during the past fifty years, but the degree to which these changes can be attributed to banding's role is not clearly discernable. Below we summarize the methods and results for the literature sampling McDonald undertook.

Methods.—*The first question—changes in proportions of published works relying on bird banding—*McDonald addressed by looking at samples of papers in ornithological and behavioral journals from two eras: early-banding (1905-1934), and recent (1995-2004). For each era and within each archive collection she did a random selection of about one issue from one volume per year, looked at its Table of Contents, and categorized the listed papers.

Access to the journals' tables of contents was effected through three on-line scientific paper portals, which overlapped in their cover-

age. First, she used SORA (Searchable Ornithological Research Archive, <http://elibrary.unm.edu/sora>), an open access electronic journal archive providing extensive ornithological literature of international scope, although the journals themselves are all North American in origin. Coverage dates back approximately 120 years to the first issue of *The Auk*. Specifically, the content of this site includes the following publications: *Auk* (1884-1999), *Condor* (1899-2000), *Bird-Banding/Journal of Field Ornithology* (1930-1999), *North American Bird Bander* (1976-2000), *Pacific Coast Avifauna* (1900-1974), *Studies in Avian Biology* (1978-1999), and *Wilson Bulletin* (1889-1999). The primary behavior journals surveyed were *Animal Behaviour*, *Behaviour*, *Ethology* (previously *Zeitschrift für Tierpsychologie*), *Behavioral Ecology and Sociobiology*, and *Behavioral Ecology*.

In addition to the ornithological journals indexed on SORA, two major on-line life sciences data bases provided access to many citations and abstracts for papers published after 1969: BioOne (BioOne, <http://www.bioone.org>) and DialogWeb (Thompson Dialog, <http://www.dialogweb.com>). Hard-copies of journals shelved in libraries sometimes supplemented the on-line research.

The second question—changes in ethological trends co-varying with bird banding's implementation and use over the past century—was addressed by McDonald using case-studies and other cited works on bird behavior found in major animal behavior texts. The texts selected for her survey were based on their frequency of use in North American college and university courses and are listed in Appendix 1.

Although this second data source, the texts, is much smaller than the first, we consider it to be an index, a representation of what broadly-read animal-behavior authors consider to be classic or noteworthy research involving wild birds. From the textbook source literature McDonald categorized cited ornithological work according to whether the study relied on banded individuals or not.

Results: Change in frequency of use of banding in behavior papers.—Prior to the establishment of the federal bird-banding office in 1920, research using “banded” or otherwise marked birds in the field was uncommon. After bird banding with federally-issued numbered bands was implemented, published papers using banding in their methodology appeared with rapidly increasing frequency in the literature stream (Jackson this volume).

Of the avian behavior papers published in the decades 1905-1934, the proportion using banding was approximately 4%, as indicated by surveying *Auk*, *Pacific Avifauna*, and *Wilson Bulletin* issues, compared to 77%, the proportion of bird-behavior field studies using banding that were published within the recent (1995-2004) decade's indicator journals (the six North American ornithological journals indexed by SORA, plus the North American bird papers published in the referenced behavior journals).

Survey Results: Trends in questions asked in behavior papers using banding.—More revealing than the simple percentages reported above, and more indicative of banding's contribution to science are the changes in direction and focus of questions asked (and sometimes answered) employing bird banding as a vital field technique.

One need only glance through a few recent issues of bird or behavior journals, and compare them with their counterparts of 80-120 years ago to see the obvious change-over. A hundred years ago the major bird journals published many relatively short papers describing birds found at a particular locality, "unusual" behaviors of a single bird, or perhaps behavior of novel birds (again, one or several individuals). Longer papers were more likely to contain more details, mostly descriptive, as well as educated speculation, but little in the way of analysis. Now, in most major journals, the structure is based on addressing questions, usually very specific, such as nest-area fidelity and its impact on inclusive reproductive success, or why populations increase or decrease in response to certain habitat changes. This characterization of older vs. modern literature points toward the extremes, but it does indicate the broad change-over of orientation during the past century.

In addition to changes in subject areas and the nature of the questions addressed, the levels of analysis have shifted also, and there are major differences in theoretical orientation. These changes are indicative of overall developments and trends in ethology and ornithology, but the realization that achieving "new" perspectives and approaches still rely on the "old" technique of bird banding, validates its versatility and reliability even when competing with more sophisticated technologies in bird identification, e.g., sound-recording analysis, molecular techniques, and digital imaging.

In some respects the increased use of banding over the years since its implementation parallels increased use of technology in general.

Banding itself is perhaps an offshoot or simply a requisite for the authorization to attach other devices, e.g., radio transmitters for tracking migration. But in most cases involving higher levels of technology, banding continues to serve as the indispensable identification component of such projects.

Despite the potential and perhaps expected trend that modern field studies engage in more and more elaborate technologies, this survey of recent journals and books suggests that the trend seems to have plateaued at about the same level as that of the 1980s. This may be a result of more restrictions on experimental manipulations of all kinds. A result, then, of such curtailment may be that Tinbergen-style “natural history experiments” have actually increased in recent years—and this still, as it was fifty years ago, can only be possible as true scientifically approachable questions with banded birds.

Along a similar line of analysis, one might have expected that as biological disciplines have become more and more specialized, so would also field studies on bird behavior. To the contrary, however, this survey revealed a steady stream of holistic behavioral studies on birds in the field that combine natural history with experiment.

CONCLUSIONS AND A VIEW TO THE FUTURE

Bird banding during its first century played a central role in paving the way for avian behavioral studies to be conducted with sample sizes sufficient to allow statistical analysis. With banding, field observations of birds could progress from anecdotal documentation to rigorous hypothesis testing and subsequent recognition by the scientific community, including publication of reports in major journals.

Banding continues today to reign as the key field technique, the base upon which nearly all avian behavioral research relies. More than merely serving as a facilitator for identification, the advent and subsequent wide-spread use of banding has enabled researchers to transcend describing behavior (either natural or that resulting from experimental manipulation). Theoretical questions seeking answers to the historical origins and the evolutionary consequences are addressed alongside the continual gathering of baseline descriptive data for lesser known or otherwise “special” (e.g., habitat destruction-threatened) species.

The North American Bird Banding Laboratory model of individual marking coupled with a centralized, coordinated, and a format-standardized database of records has been adopted by other regions of the world and has been implemented for other taxa. The recording, management, and long-term maintenance of banding data in a centralized data base are essential to this global success. Of all the marking schemes used on wild vertebrates, the bird-banding program administered collaboratively by the U.S. Fish and Wildlife Service and Canadian Wildlife Service is probably the best. Presumably, the adoption of newly emerging technologies will keep the North American program at the forefront.

The future of bird banding as a tool of science and tool for bird behavioral studies is tied to major forces pervading all field biology. For banding, and in particular for field studies seeking to unravel natural behaviors in wild birds, the two most important of these forces are conservation concerns and the use of electronics integrated with geospatial tools, e.g., GIS (Geographic Information Systems). Integration and miniaturization of relatively inexpensive electronic and digital devices and automated data collection are appearing in avian field studies. Research on natural behaviors is one of the primary beneficiaries of such technology due to the significant reduction in interference that tiny lightweight devices such as RFID (radio frequency identification) allow over earlier technology.

The huge potential utility of electronic-enabled data collection is important to the field of wildlife conservation. Growing concerns about reducing interference in research animals, animal welfare considerations, and the resulting guidelines and regulations—whether legislated or self-imposed for ethical reasons—are driving the elimination or reduction in handling and marking of birds in the field. Small devices, some capable of transmitting electronic data, and miniscule, non-visible entities such as bioinformatics-based identification techniques—are providing some alternatives to banding and use of visible auxiliary markers for reduction in interference with the birds' natural habits (Applegate et al. 2000, Gauthier-Clerc and Le Maho 2001). However, banding is still usually essential to the testing of these technologically sophisticated devices and is generally used as a backup identification method with them.

The challenge at hand is not so much the invention or application of emerging technologies to bird marking, as perhaps it should now be

called, but rather the regulatory office's (i.e., the U.S. BBL) ability to keep up with, or anticipate these developments and have the infrastructure in place to support and coordinate the swell of technological advances in marking techniques.

Finally, as important and basic to behavioral ecology as banding has been, its importance to the growth of the discipline has sometimes been taken for granted. For example, in his synthesis of "Historical patterns in the study of avian social behavior," Brown (1994) focused on the growth in ideas as reasons for trends and does not acknowledge the importance of banding and other marking techniques. Banding has been the essential tool that brought these ideas to fruition. Although new technologies involving molecular and electronic information may eventually replace traditional banding's central role in individual recognition, for the near future, at least, banding will remain as the best all-purpose, low-cost, and minimum-technology alternative for behavioral research requiring the recognition of individual birds in the field.

ACKNOWLEDGMENTS

We are indebted to John Tautin for having organized the symposium celebrating bird banding's first 100 years in North America and for bringing the idea for the symposium to a successful historical event as a part of the 2002 North American meeting of ornithological societies. We thank Bette J. S. Jackson for helpful comments on an earlier version of the manuscript.

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