

QL
151
N864
NH

**SEVEN NEW WHITE-WINGED DOVES
FROM MEXICO, CENTRAL AMERICA, AND
SOUTHWESTERN UNITED STATES**



NUMBER 65

**UNITED STATES
DEPARTMENT OF THE INTERIOR
BUREAU OF SPORT FISHERIES AND WILDLIFE**



NORTH AMERICAN FAUNA

This publication series includes monographs and other reports of scientific investigations relating to birds, mammals, reptiles, and amphibians, for professional readers. It is a continuation by the Bureau of Sport Fisheries and Wildlife of the series begun in 1889 by the Division of Ornithology and Mammalogy (Department of Agriculture) and continued by succeeding bureaus—Biological Survey and Fish and Wildlife Service. The Bureau distributes these reports to official agencies, to libraries, and to researchers in fields related to the Bureau's work; additional copies may usually be purchased from the Division of Public Documents, U.S. Government Printing Office.

Reports in NORTH AMERICAN FAUNA since 1950 are as follows (an asterisk indicates that sale stock is exhausted):

- *60. Raccoons of North and Middle America, by Edward A. Goldman. 1950. 153 p.
- *61. Fauna of the Aleutian Islands and Alaska Peninsula, by Olaus J. Murie; Invertebrates and Fishes Collected in the Aleutians, 1936-38, by Victor B. Scheffer. 1959. 406 p.
- *62. Birds of Maryland and the District of Columbia, by Robert E. Stewart and Chandler S. Robbins. 1958. 401 p.
- *63. The Trumpeter Swan; Its history, habits, and population in the United States, by Winston E. Banko. 1960. 214 p.
- *64. Pelage and Surface Topography of the Northern Fur Seal, by Victor B. Scheffer. 1961. 206 p.
- 65. Seven New White-winged Doves From Mexico, Central America, and South-western United States, by George B. Saunders. 1968. 30 p.

SEVEN NEW WHITE-WINGED DOVES
FROM MEXICO, CENTRAL AMERICA, AND
SOUTHWESTERN UNITED STATES

By
George B. Saunders

Wildlife Biologist, Division of Wildlife Research
BUREAU OF SPORT FISHERIES AND WILDLIFE



NUMBER 65

UNITED STATES
DEPARTMENT OF THE INTERIOR
Stewart L. Udall, *Secretary*

Stanley A. Cain
Assistant Secretary for Fish and Wildlife and Parks

FISH AND WILDLIFE SERVICE
Clarence F. Pautzke, *Commissioner*

BUREAU OF SPORT FISHERIES AND WILDLIFE
John S. Gottschalk, *Director*



North American Fauna, Number 65

Published by
Bureau of Sport Fisheries and Wildlife
May 1968

UNITED STATES GOVERNMENT PRINTING OFFICE

• WASHINGTON •

1968

CONTENTS

	Page
Abstract	iv
Introduction	1
Methods	4
New races	5
<i>Zenaida asiatica peninsulae</i>	5
<i>Zenaida asiatica grandis</i>	8
<i>Zenaida asiatica monticola</i>	10
<i>Zenaida asiatica palustris</i>	14
<i>Zenaida asiatica insularis</i>	15
<i>Zenaida asiatica collina</i>	17
<i>Zenaida asiatica panamensis</i>	20
Discussion	21
Summary	28
Literature cited	29
TABLE—Measurements of 12 subspecies of white-winged doves .	22
FIGURES	
1. Map of breeding ranges	24
2. Statistical comparison of wing measurements	25
3. Statistical comparison of tail measurements	26
4. Statistical comparison of culmen measurements	27

Approved for publication, January 4, 1968.

ABSTRACT

Seven new subspecies of *Zenaida asiatica* are described: *Z. a. peninsulae* of the Yucatán Peninsula, México; *Z. a. grandis* of the upper Big Bend area, central western Texas; *Z. a. monticola* chiefly of the Mexican interior plateaus and highlands; *Z. a. palustris* of the central and southern Pacific coastal plains of México; *Z. a. insularis* of the Tres Mariás Islands, Nayarit, México; *Z. a. collina* of Central America, chiefly on the Pacific Piedmont and coastal plain from the Isthmus of Tehuantepec, México to Costa Rica; and *Z. a. panamensis* of the northeast coast of the Azuero Peninsula, Panamá.

INTRODUCTION

Of the white-winged dove, *Zenaida asiatica*, five subspecies have been generally recognized by taxonomists: *Z. a. asiatica*, *Z. a. mearnsi*, *Z. a. australis*, *Z. a. meloda*, and *Z. a. alticola*. Ranges of the races *asiatica* and *mearnsi* extend as far north as the southwestern United States, *australis* is in some of the lowlands of Central America, and *meloda* is in western South America (Peters, 1937, p. 87-88; Hellmayr and Conover, 1942, p. 499-503). Later the race *alticola* was described from the Altos, the high mountain region of western Guatemala, and neighboring highlands (Saunders, 1951).

Van Rossem (1947) described a subspecies *clara* from the Cape region of Baja California, pointing out that it was paler than *mearnsi*, but *clara* was not generally accepted (Friedmann et al., 1950). The series of 23 males and 14 females from Baja California examined during the present study do not show sufficient differences from *mearnsi* to justify separation from that race. The peninsular birds have longer wings and tail than *mearnsi*, but in adult males these differences are only 2 millimeters in average length of wings and 3 millimeters in average length of tail. The Baja California whitewings seem to be relatively sedentary—apparently they do not migrate beyond that State. Additional research may reveal other differences from *mearnsi* in habits and ecology.

The present paper describes seven new subspecies. Apparently, ornithologists have assumed that *asiatica* is the resident form in much of Central America because their collections, made mostly in the autumn and winter months, include so many of this race; other white-wings have been lumped as *asiatica* with the observation that this race shows wide variation (Dickey and van Rossem, 1938; Griscom, 1932; and Ridgway, 1916). While many *asiatica* winter as far south as Costa Rica, they do not breed in Central America (Saunders, 1959, 1962). It now appears that the race *asiatica* is much less variable in color and size than was formerly believed.

My interest in this problem began in 1940 when some of the whitewing nestlings we banded in southern Texas in summer were reported during autumn and winter in Guatemala and El Salvador. In 1942 I visited these countries for the first time during winter and spring to study the numbers and distribution of these doves and the factors affecting them.

It was during this survey that *alticola* was found in the Altos of Guatemala (Saunders, 1951), and other series of whitewings were collected in different parts of Guatemala and El Salvador. Further collecting was done there in 1946 and 1947, and in México from

1940 through 1960. Other specimens were borrowed from the principal museums and from several universities and individuals. When the breeding specimens were sorted out and their distribution studied, there appeared to be several undescribed races. A statistical analysis of the measurements of specimens was made to determine whether this method would substantiate the presence of new subspecies.

It is very significant that more than 450 *Z. a. asiatica* banded in Texas have been reported from localities in Latin America south of their breeding places and on wintering grounds as far away as Costa Rica. More than 250 banded *Z. a. mearnsi* from Arizona have been reported from western México. The patterns of these recoveries are an invaluable aid to understanding racial distribution of this species.

The extent of migration of the races that breed in Central America is not yet adequately known. Some subspecies appear to be mostly sedentary, such as *alticola* in the Altos of Guatemala (Saunders, 1951). Skutch (1964, p. 224) reported that they nested in March and April in the Sierra de Tecpán, Guatemala, up to 9,000 feet above sea level, but after the rainy season began in mid-May they disappeared until late in the following November. This indicates that in part of their range there is a seasonal movement, perhaps mostly altitudinal. But we lack specimens of this race to show its distribution south of Guatemala.

Members of the Bureau of Sport Fisheries and Wildlife to whom I am especially indebted include John W. Aldrich for advice on taxonomic questions, Ralph Andrews for field assistance on our Mexican survey in 1960, Richard C. Banks for advice on taxonomy, Earl Bay-singer for tabulations of banding and recoveries, Thomas D. Burleigh, formerly with the Bureau and now retired, for skins for study, Allen Duvall for suggestions in studies of banding, Aelred D. Geis and Robert G. Heath for statistical assistance, Mary W. Mann, artist, Bird and Mammal Laboratories, for the distribution map and figures, and Lester L. Short, Jr., formerly with the Bureau and now with the American Museum of Natural History, for help with taxonomic questions.

On the surveys in Guatemala in 1947, Charles O. Handley, Jr., U. S. National Museum, aided in obtaining specimens, as did Clarence Cottam, Director, Welder Wildlife Foundation, on the 1957 survey in México.

I also wish to thank the following institutions and individuals for lending specimens essential for this study and for assistance when I visited and studied some of the collections: Academy of Natural Sciences of Philadelphia (R. M. deSchauensee and James Bond); American Museum of Natural History (Dean Amadon); British Museum (J. D. MacDonald); Carnegie Museum (Arthur C. Twomey and Kenneth C. Parkes); Field Museum of Natural History (E. R. Blake and the late Boardman Conover); Colorado Museum of Natural History (Alfred M. Bailey and Robert Niedrach); Louisiana State

University, Museum of Zoology (George H. Lowery, Jr., and Robert Newman); Texas A. & M. University, Department of Wildlife Management (W. B. Davis); U. S. National Museum (Philip S. Humphrey); University of California, Berkeley, Museum of Vertebrate Zoology (the late Alden H. Miller); University of California, Los Angeles (the late A. J. van Rossem); University of Florida, Department of Zoology (Pierce Brodkorb); University of Kansas, Museum of Natural History (Richard F. Johnston); and University of Michigan, Museum of Zoology (R. W. Storer and the late J. Van Tyne).

Others to whom I am grateful for specimens or information are Rollin H. Baker, Michigan State University; Alvaro Collado M., San José, Costa Rica; Robert W. Dickerman, then with the Oficina Sanitaria Pan Americana, México, D. F., and now with the Cornell University Medical College, New York, N. Y.; Herbert Friedmann, then Curator of Birds, U. S. National Museum, and now Director, Los Angeles County Museum; Roland W. Hawkins, Pittsburgh, Pa.; Hugh C. Land, Northwestern State College, Natchitoches, La.; D. B. Legters, Mérida, Yucatán; the late Luis Macias A., Chief, Department of Game, México, D. F.; Burt L. Monroe, Jr., University of Louisville; Allan R. Phillips, Instituto de Biología, Universidad Nacional Autónoma de México, D. F.; Albert Schwartz, Miami, Fla.; Gilbert Shaw and William Stone, U.S.D.A., Laboratorio Entomológico, México, D. F.; Alexander F. Skutch, San Isidro del General, Costa Rica; Austin P. Smith, Zarcero, Costa Rica; and Helmuth Wagner, Ubersee Museum, Bremen, West Germany.

Several ornithologists and other scientists now deceased gave me helpful information or other assistance in earlier years: Lee Arnold and Frederick C. Lincoln, Bureau of Sport Fisheries & Wildlife; Wilfred H. Osgood and Karl P. Schmidt, Field Museum of Natural History; James L. Peters, Museum of Comparative Zoology; Charles Plummer, U. S. Department of Agriculture, México, D.F.; and John T. Zimmer, American Museum of Natural History. My thanks go also to my fellow biologists and other field men of the States of Arizona and Texas, who have banded many thousands of white-winged doves since 1940 to obtain information on migration, mortality, and other important subjects. Without so many band recoveries of *asiatica* and *mearnsi* to help in clarifying the distribution of these birds in migration and on the wintering grounds in Latin America, the relationships of several races would continue to be much more puzzling.

To Alexander Wetmore I am much indebted for his advice on taxonomic and distributional problems, for his generosity in giving me access to field journals of his 1948 and 1963 collecting trips in Panamá, and for the privilege of describing the subspecies *panamensis*.

To my wife, Dorothy Chapman Saunders, I owe the principal acknowledgment for her assistance in collecting and preparing specimens, making color comparisons, statistical calculations, and editorial suggestions.

METHODS

Since differences in coloration, especially of females, are often subtle, some of the races can generally be separated most accurately on the basis of body size and dimensions. Differences in ecology, time of breeding, and extent of migration also help in characterizing some subspecies.

When field observations and study of laboratory skins suggested differences in a particular population, a statistical analysis was made to determine the possible significance of morphological differences. Mayr considers the conventional level of subspecies difference to be 90 percent or more (Mayr, Linsley, and Usinger, 1953). The criterion used here in determining the validity of races was whether 95 percent or more of the specimens of a population were separable from 95 percent or more of the specimens of the adjacent race or races. To determine the degree of difference and the percentage of joint nonoverlap between characters of races, the standard error was calculated for each mean. Confidence limits were determined for the .05 probability level as the mean \pm "t" times the standard error. The means, confidence limits, and ranges are given in the table and in figures 2 to 4. When the confidence limits do not overlap, statistically significant differences are indicated.

In this review, 463 adult specimens and several juveniles were studied. They represent most of the known populations from Arizona and Texas south to Ecuador and Peru. The largest series were those of the Fish and Wildlife Service collection in the U. S. National Museum that I had obtained in México and Central America. Specimens from the West Indies were not included. Birds from Jamaica, Cuba, Haiti, Dominican Republic, the Bahamas, and Old Providence Island were examined, but additional breeding specimens are needed before some puzzling questions can be answered and an adequate appraisal made of their taxonomy. The specimens of *asiatica* included in the present tabulation of measurements were from breeding grounds in southern Texas and northeastern México.

Measurements used in this study include length of wing (chord), tail, culmer, and tarsus, although the tarsus is not included in most of the comparisons as it is not of significant diagnostic value. Statistical differences in dimensions are shown in the table and in figures 2 to 4 (see pages 22-27). Plumage colors were studied under natural light in most instances. A few were determined under special lights which approximate daylight in the Bird Division, U.S. Museum of Natural History. Color names are from Ridgway (1912).

Since migrant subspecies may mingle with resident birds during the winter, it is essential that full information, particularly condition of gonads and amount of fat, be recorded in the field. In México and Central America it was usually possible, from February to April, to separate the resident and migrant forms by the greater development

of the gonads and the much smaller amount of fat in the residents.

In the following comparisons of specimens, males are referred to unless females are specified. In general, males show more racial differences in dimensions, as well as color, than do females, and consequently are of greater value for taxonomic study.

In the original determination of taxonomic differences in any migratory animal it is essential to use specimens that are representative of breeding populations. It would be desirable to have more specimens in fresh plumage for comparison, but by the time the postnuptial molt is completed, considerable migration away from the breeding ground may have occurred, and specimens taken together at that time may represent two or more subspecies. Therefore, the descriptions of these seven new races are based on specimens in breeding condition, with due consideration of adventitious effects of wear and fading. In contrast, the type specimen of *australis*, taken at Cerro Santa María, Costa Rica, January 9, 1908, (Peters, 1913) is in fine, fresh plumage, so it is not directly comparable with specimens in breeding plumage. It should be noted that no breeding white-winged doves have been reported from that locality. This is an example of doubtful situations which can arise from using wintering or freshly molted specimens in original descriptions.

NEW RACES

The series of white-winged doves from the Mexican States of Yucatán, Campeche, and Quintana Roo examined in this study exhibits considerable variation. It includes some wintering birds with dimensions and coloration of typical *asiatica* and others that were smaller and mostly paler. Fifteen of these birds which were collected by Gaumer have no date, and many of them have no locality other than "Yucatán." However, the general season during which they were obtained could be determined by molt and wear of the plumage. When the specimens were sorted according to season, it was found that almost all of those in worn breeding plumage had shorter wings and tails than typical specimens of *asiatica* in comparable plumage. Field study and this review of specimens have shown that the breeding population of the above area is a distinct subspecies which may be called:

Zenaida asiatica peninsulae, new subspecies Yucatán White-winged Dove

CHARACTERS

Nearest to *Z. a. asiatica* but with shorter wings and tail. In breeding plumage the back averages slightly paler and grayer than that of most specimens of *asiatica* seen. The crown of the male is paler and a lighter purple, and in some specimens is more suffused with

brown than in *asiatica*. The latter has more extensive purple that extends farther back on the hindneck. In most of the specimens of *peninsulae* seen the underparts are slightly paler, and some have a cinnamon tone to the throat and upper breast that occurs in relatively few *asiatica*.

DESCRIPTION

Type, Field Mus. Nat. Hist. No. 13223, adult male, San Felipe, near the mouth of the Río Lagartos, northeastern Yucatán, collected June 6, 1893, by W. W. Brown. Crown and hindneck vinaceous drab; back drab; tertiaries buffy brown; middle rectrices olive brown; throat wood brown basally with cinnamon tips; breast light drab; abdomen pearl gray; and flanks pale olive gray.

MEASUREMENTS

Males (14 specimens): wing 148.5–156.3 mm. (av. 151.5), tail 97.1–108.0 (103.5), and culmen 18.0–21.3 (20.2). **Females** (18 specimens): wing 143.0–155.0 mm. (av. 148.6), tail 93.0–104.0 (99.6), and culmen 18.4–21.7 (20.0). Most of these specimens were taken during the breeding season.

Ridgway (1916, p. 379) gave the average measurements of wing, tail, and culmen of 9 males from Yucatán as 156.4, 103.6, and 19.7 mm., and of 7 females as 149.6, 99.4, and 20.2 mm. Judging from the large average wing length there was no sorting of these specimens according to season, and apparently several wintering *asiatica* males were included.

RANGE

The only breeding specimens seen were from areas of México including the northern half of Yucatán, coastal localities in Quintana Roo, the adjacent islands of Cozumel and Mujeres, and northern Campeche. A specimen from Jaina, Campeche, taken on June 15, 1900, by Nelson and Goldman, is referable to this form. The only breeder taken by Paynter (1955, p. 118) was a male collected at Vigía Chico, Quintana Roo, March 30, 1949. That locality is adjacent to Bahía de la Ascensión. Additional specimens from southern Yucatán and Quintana Roo are needed for clarification of the extent of the breeding range.

Based on the relative scarcity of this race in northern Yucatán during the winter, I believe that most of these birds winter farther south in the State, and possibly also in arid interior valleys of eastern Guatemala and Honduras. If so, *peninsulae* would be associated in some localities with a subspecies to be described further on, as well as with *australis*.

REMARKS

The white-winged dove was listed for Mujeres and Cozumel Islands, and was considered a well-known species on the mainland by Salvin

(1889). Cole (1906) was at Chichén Itzá in March 1904 and collected three specimens March 10–12.

Paynter (1955, p. 118) reported the habitat to be chiefly in coastal scrub and deciduous forest, but occasionally in clearings within the rain forest zone.

Peters (1913, p. 372) took two females on March 16 and 17, 1912, at Camp Mengel, on the Río Hondo, 36 miles southwest of Chetumal, Quintana Roo. I examined one of these specimens, MCZ No. 60754; it is a small bird, typical of *peninsulae*. Its rectrices are narrow, and its measurements are wing 145.0, tail 96.0, tarsus 22.5, and culmen 18.5 mm.

D. B. Legters, Mérida, who lived and hunted in Yucatán for many years, wrote me in 1961 that he found great numbers of white-winged doves on the northern coast of Yucatán between Dzilam and Telchac in April, May, and June, nesting among the coconut palms and mangroves. A very few remained through the year, mostly in the coconut groves. Chapman (1896) found whitewings in large numbers in the old cornfields near Chichén Itzá in March.

Dr. Allan R. Phillips wrote me in 1965 that he saw no whitewings in México on Isla Mujeres, January 15–18, only one on Isla Cozumel, January 19–23, and very few anywhere in Yucatán, or on the peninsula north or east of Isla del Carmen, where they should have been common. He found none on the Isla Cozumel during extensive daily field collecting, November 3–18, 1965.

During my field work in northwestern Yucatán in January 1960, the only white-winged doves seen or heard were several in the dry woodland south of Umán near the aguada (watering place) Xcamal, and one near the boundary with Campeche, a few miles north of Bolonchén de Rejón, both localities on the Mérida-Campeche highway.

Indians who live near the aguada Xcamal and who had learned a good deal about the "zac pakal," as the Mayas call this dove, said that they were more common during the nesting season, which begins in late March and extends through May, and that few were present the rest of the year. They added that nests were found in densely foliaged, thorny trees near the aguada, some of them placed quite low, and that only one brood was raised. I heard two sing briefly, and their songs were weaker in volume than typical *asiatica*. When flushed they flew low through the trees, more in the manner of white-fronted doves, rather than above the trees as whitewings usually do.

Three were collected and 20 seen at a watering place 16 miles east of the city of Campeche on January 31, 1960. One specimen was an adult male, the second an adult female, and the third an immature female with two juvenal primaries; all were *peninsulae*. Two birds there sang in the same low volume that characterized those noted at the aguada Xcamal. Two specimens from San José Carpizo, Campeche

(Storer, 1961), approximately 27 miles south of the capital, are immature females taken November 1 and 24, 1946. They are probably *peninsulae*, judging from their measurements.

A juvenile male of *peninsulae* less than 5 weeks old was collected at Santa Clara, Yucatán, September 2, 1950 (Yale U. No. 14384). It differs from juveniles of *asiatica* in having conspicuous buffy edging on many of the lesser coverts. The color of the underparts is slightly grayer, and the tips of the breast feathers are more tawny than in *asiatica*.

Additional proof that *asiatica* from the north occurs on the Peninsula in winter is found in two white-winged doves banded in Tamaulipas during the breeding season which were shot during winter in Tabasco and Campeche, and two banded in southern Texas which were recovered in Yucatán and Campeche.

SPECIMENS EXAMINED

México: YUCATÁN: Izamal, Santa Clara, Chichén Itzá, Sisal, San Felipe, and Xocempich. Some of those collected by Gaumer in Yucatán were not marked as to sex, locality, and date. CAMPECHE: Isla del Carmen near Puerto Real, Jaina, Champotón, and 16 miles east of the city of Campeche. QUINTANA ROO: Vigía Chico, Camp Mengel, Chetumal, and Isla Cozumel.

Field investigations in the Big Bend sector of Texas and the review of specimens collected there and elsewhere in the Southwest and in México proved that the white-winged dove of the Chinati Mountains and the adjacent valley of the Rio Grande in the upper Big Bend region of Texas is a distinct geographic race. As it is larger than the other known North American species, it is named:

Zenaida asiatica grandis, new subspecies Upper Big Bend White-winged Dove

CHARACTERS

It has longer wings, tail, and tarsus than *mearnsi*, *monticola*, and *asiatica*, but its culmen is shorter than that of *mearnsi*. It is grayer above and paler on the breast than *asiatica*, and slightly grayer than most *mearnsi*. The few specimens seen of *monticola* from the Chisos Mountains and northern México average very slightly browner on the back than *grandis*, with the purple crown of the male slightly less bright and more veiled with brown. The underparts are somewhat paler in *grandis* than in *asiatica*. It is similar to *Z. a. meloda* of South America in length of wing, tail, tarsus, and culmen, but it is much browner. The race *meloda* has a thicker bill, gray instead of white tips to the rectrices, and other differences in color of plumage.

DESCRIPTION

Type, U. S. Nat. Mus. (Fish and Wildlife Service Collection) No. 481592, adult male, breeding, active milk glands, near Ruidosa, Presidio County, Texas, altitude about 3,000 feet, May 25, 1957, by George B. Saunders, collector's number 2662.

Crown vinaceous drab; hindneck light purple drab; back and tertiaries drab; middle rectrices nearest olive brown; throat deep olive buff to avellaneous; breast light drab; abdomen pale smoke gray to pale olive gray; and flanks pale mouse gray.

MEASUREMENTS

Males (10 specimens): wing 166.0–175.0 mm. (av. 172.0), tail 120.5–133.0 (126.6), tarsus 26.0–28.0 (26.5), culmen 20.0–23.0 (21.5), length (2) 317–340 (332), extent (2) 518–538 (526). **Females** (5 specimens): wing 162.0–164.9 mm. (av. 163.5), tail 112.9–121.3 (116.5), tarsus 25.0–26.9 (25.8), culmen 20.7–22.3 (21.5), length (2) 304–306 (305), extent (2) 494–498 (496).

RANGE

Breeds in the Chinati Mountains and adjacent parts of the Rio Grande bottomland from near Presidio, Presidio County, north to Indian Hot Springs, Hudspeth County, Texas. It probably also occurs in the Sierra Vieja, as white-winged doves were seen flying to the bottomland near Porvenir from the direction of those mountains.

A few are reported to winter in the Big Bend region of Texas, but the majority journey farther south into México. How far they go at that season is not known, but a specimen taken in February near Presa Calles, Aguascalientes, México, at 7,000 feet, has the characteristics of this race.

REMARKS

When male specimens from the lower Big Bend (Lajitas, Castolon, Chisos Mountains) are compared with those from the Chinati Mountains and adjacent valley of the Rio Grande, in the upper Big Bend, it is apparent that the latter have significantly longer wings and tail. This is surprising since the two ranges are separated by less than 60 miles. In the collecting done from Chinati north to Porvenir, 9 of 10 males taken in the breeding season were typical *grandis* and the tenth was intermediate between *grandis* and *monticola*. The ecological differences between their habitats are believed to be the principal basis for the separation of the two populations.

Along the Rio Grande Valley the principal physical barriers between these two populations are the Colorado Canyon, 3.1 miles in length, and the Grand Canyon of Santa Elena, 7 miles in length. These are very narrow, deep canyons, with vertical rocky walls rising at each side of the Rio Grande, and no trees or shrubs bordering the river.

The upland on each side of the canyon walls is barren, with gravelly hills and no cover for whitewings. The only habitat between these two canyons is in small, isolated coves in the river bottom and at the mouths of tributary arroyos or washes where there are scattered clumps of tamarisk (*Tamarix*), mesquite (*Prosopis*), and associated trees.

Formerly there was much more nesting habitat in the river bottomland from Presidio to El Paso. From Presidio northward almost all river bottom woodland that was suitable for nesting has been cleared for agricultural crops for a distance of approximately 25 miles, except for an occasional thin fringe near the river. From near Chinati north to Ruidosa and locally beyond as far as Indian Hot Springs there are occasional coves of woodland, chiefly of dense tamarisk and mesquite, that offer nesting cover for whitewings. When this part of the Rio Grande was scouted by plane in 1949 no adequate cover for white-winged doves was seen north of Esperanza to El Paso.

Although most of the specimens of *grandis* were collected near Ruidosa where the eastern edge of the river bottomland meets the foothills, the doves flew in from the direction of the Chinati Mountains. This range is to the east, and its highest elevation, Chinati Peak, is 7,730 feet. Local hunters said the whitewings nested in the oak woodland of the mountains. How many *grandis* nest in the oak woodland of the Chinati Mountains and how many utilize other plant associations remains to be determined.

SPECIMENS EXAMINED

United States: TEXAS (Presidio County): Chinati, Ruidosa, and near Porvenir.

All white-winged doves in the interior highlands of México have been referred to the race *mearnsi* (Friedmann et al., 1950), but breeding specimens collected there have longer wings and tail, shorter bill, and average slightly grayer plumage than Arizona *mearnsi*. Birds from the more northern highlands, as in Nayarit and Durango, are slightly darker than those of Oaxaca and Puebla, but they too have longer wings and tail than *mearnsi*. Study of these highland birds confirms that they are a distinct subspecies which may be named:

Zenaida asiatica monticola, new subspecies Mexican Highland White-winged Dove

CHARACTERS

It has shorter wings and tail than *grandis*. Birds from the highlands of Nayarit, Durango, and more northern States average browner than *grandis*, but those from Puebla and Oaxaca average slightly

grayer. It is larger and longer in wing and tail than *asiatica* and *mearnsi*, and has a shorter bill than the latter. Similar in dimensions to an undescribed race on the Tres Mariás Islands, México, but with paler underparts; similar also to *Z. a. alticola* of the highlands of Guatemala (Saunders, 1951) but much paler above and below.

DESCRIPTION

Type, U. S. Nat. Mus. (Fish and Wildlife Service Collection) No. 481589, adult male, breeding, singing on territory, testes 6 x 12 mm., 11 miles south of Acatlán, Puebla, México, April 28, 1957, collected by George B. Saunders, collector's number 2648. Crown brownish drab; hindneck light brownish drab; back hair-brown; tertiaries buffy brown; middle rectrices clove brown; throat and breast light drab; abdomen pale smoke gray; and flanks light quaker drab.

MEASUREMENTS

Males (44 specimens, all seasons): wing 161.3–177.0 mm. (av. 167.2), tail 114.0–127.5 (120.4), and culmen 18.9–22.9 (21.1). **Females** (22 specimens, all seasons): wing 156.0–171.0 mm. (av. 162.8), tail 111.0–124.4 (116.2), and culmen 19.2–23.0 (21.0).

RANGE

Interior plateau and some of the mountains from Oaxaca north of the Isthmus of Tehuantepec, northward in the mesquite and guamachil associations, thorn forest, tropical deciduous forest, and in some localities in oak-pine woodland, to northern Chihuahua, Coahuila, and Nuevo León of México, and the Chisos Mountains and lower Big Bend of central western Texas. Most were observed at elevations of 4,000 to 8,000 feet. They have also been found during summer in Hidalgo County, southwestern New Mexico, where 3 of 15 specimens examined were identified as *monticola*: 2 were collected in 1892, and 1 in 1933. The other 12 were nearer *mearnsi*. Northern Chihuahua and the southwestern corner of New Mexico may be a zone of intergradation between these two races, but this is an area where whitewings are scarce and local in distribution.

REMARKS

Although *monticola* is widely distributed in the highlands, there are many localities where it is absent. Most were observed in dry woodlands or thorn forest, but some were in agricultural valleys where large guamachiles (*Pithecellobium dulce*) and mesquites offered nesting cover and food, or in pecan groves of some of the valleys, and villages. A few others were seen in higher oak and pine woodland. In many localities their absence was due to a lack of suitable habitat, but conversely many places with what appeared to be a good habitat lacked whitewings. In field work during 1950, 1952, 1957, and 1960 they were observed in the highlands of every interior

State of México, and they were collected in Oaxaca, Puebla, Guerrero, Morelos, Jalisco, Michoacán, Nayarit, and Aguascalientes during this study.

This race was breeding in Oaxaca and Puebla during the first week in February, although the altitudes were from 4,000 to 7,000 feet. Also, they were breeding in the mountains of Guerrero and Nayarit in March when *mearnsi*, still heavy with winter fat, were in flocks there in the foothills, and on the coastal plain of these States.

Most *monticola* are believed to winter in or near their breeding range. Some at the northern end of the range move south for the winter for an undetermined distance, but there are winter flocks as far north as Coahuila and Durango. No specimens of *monticola* are known to have been collected from coastal areas or any locality south of the Isthmus of Tehuantepec.

Several individuals of *asiatica* banded in Texas and Tamaulipas, México, and recovered in the Mexican highlands, chiefly in the States of Morelos and Oaxaca, prove that some *asiatica* migrate through or winter in the range of *monticola*. Other winter specimens of *asiatica* have been collected in these southern highlands. Recoveries in the western highlands, and especially in the States of Michoacán and Jalisco, of many Arizona-banded *mearnsi* prove that many of this subspecies winter there with the resident *monticola*. If most of the museum specimens of white-winged doves were obtained in winter, it is not surprising that *mearnsi* was for so long thought to be the resident subspecies throughout the western highlands.

Peters (1937, p. 87), as well as Hellmayr and Conover (1942, p. 500), gave the range of *mearnsi* as extending southward and eastward in México to Puebla. The present study shows that much of this area is within the range of the new race *monticola*. Specimens from the southern highlands of México in Guerrero, D. F., Morelos, and San Luis Potosí, considered by Pitelka (1948) to be intermediate between *asiatica* and *mearnsi*, included some wintering *mearnsi* and *asiatica*, as well as summer and autumn *monticola*.

Several specimens taken in winter in Oaxaca and Puebla were unusually large, and may represent a different race that breeds in the higher mountains of those States and winters at lower elevations with *monticola*, or they may be *grandis* which wintered south of the principal range. The inclusion of their measurements with those of *monticola* is responsible for the upper limits of the wing and tail measurements of *monticola* exceeding those of *grandis*. Further field study of breeding populations in different parts of Oaxaca and Puebla is needed to give information on this subject.

Another interesting discovery concerns a population in the mountainous part of Durango, where dimensions of the sexes are about equal. The several females were sexed and labeled in different years

by two experienced collectors. They also may represent a separate race, for this characteristic is not true of any other known population of white-winged doves.

The white-winged doves from the interior highlands of Sonora at Tecoripa, Cerro Blanco, Opodepe, and Moctezuma probably are referable to *monticola*, judging from their dimensions, but inclusion in this race should await further study of specimens and ecology.

Several whitewings and a nest with a single nestling were found in northern Coahuila at Noria de Gilberto, by Walter P. Taylor and Clifford C. Presnall, April 9, 1945 (personal correspondence, 1945). These birds probably were of the race *monticola*, since it occurs north of this area in Brewster County, Texas (Van Tyne and Sutton, 1937).

The differences in habitats occupied by *monticola* in the lower Big Bend and by *asiatica* at the northwestern corner of its breeding range in Val Verde County, Texas, apparently serve as ecological barriers and seem to be effective in maintaining the separateness of these populations. In addition, the three long, narrow canyons of the Rio Grande and the barren hills between the breeding ranges of *monticola* and *asiatica* probably also assist in separating these races. Although a strong flier like the white-winged dove could easily fly this distance, no flights have been reported along this route. No specimen of either *monticola* or *grandis* has been taken near Del Rio, to my knowledge, nor do I know of a specimen of *asiatica* reported from the Big Bend.

SPECIMENS EXAMINED

México: AGUASCALIENTES: Presa Calles. CHIHUAHUA: Meoqui, Río Conchos, Río San Pedro. COAHUILA: Las Delicias, Piedra Blanca. DISTRITO FEDERAL: Pedregal. DURANGO: La Boquilla, Las Bocas, Río Sestin, San Juan (C. Lerdo). GUERRERO: Chilpancingo, Colotlipa, and Iguala. HIDALGO: Zimapán. JALISCO: Autlán, Bolanos, Hacienda La Venta, La Cienega, Santa Cruz, Tizapán el Alto (west of L. Chapala), Villa Corona, Zapotlán. MICHOACÁN: Zamora. MORELOS: Cuernavaca, Puente de Ixtla, Temilpa. NAYARIT: Amatlán de Cañas, Hacienda de Ambas Aguas, and Tepic. OAXACA: Cuilapán (near Oaxaca) and La Compañía (near Ejutla de Crespo). PUEBLA: Acatlán, Atotonilco, Chila, Huejotzingo, Matamoros, Tecamatlán. SAN LUIS POTOSÍ: Hacienda Capulín, Salinas Reg, and Santo Domingo. **United States:** TEXAS: Lower Big Bend (Black Gap, Boquillas, Castolon, Lajitas, Pine Canyon, Stillwell Crossing, and Wade Canyon. NEW MEXICO: Guadalupe Canyon and Animas Mountains, Hidalgo County. All seasons are represented by this series.

Series of white-winged doves were collected in México on March 28–30 near San Blas, Nayarit, and on April 1, 1960, south of Escuinapa, Sinaloa. Study of these specimens, in addition to field observations on their distribution, habitat, and habits, showed clearly that at least two different populations were present. Most of the collecting was done in or near the mangrove swamps, and most of the specimens were of a darker population that was breeding in that habitat. The others seen were in drier upland habitats, were in flocks, were fat, and their gonads were little, if any, enlarged. The latter birds were obviously winter residents or migrants, and were identified as *mearnsi*. The darker breeding race has not been reported previously, so it is described as:

***Zenaida asiatica palustris*, new subspecies**
San Blas White-winged Dove

CHARACTERS

Nearest to *Z. a. mearnsi* (Ridgway, 1915) in size, but darker than that race, and with a shorter bill. It is darker in coloration and has shorter wings and tail than the Tres Mariás Islands population described beyond.

DESCRIPTION

Type, U. S. Nat. Mus. (Fish and Wildlife Service collection) No. 481591, adult male, breeding, near San Blas, Nayarit, México, March 29, 1960, collected by George B. Saunders, collector's number 2672. Crown and nape between vinaceous drab and dark vinaceous drab; back Prout's brown; tertiaries Saccardo's umber to cinnamon brown; middle rectrices between Prout's brown and mummy brown; breast nearest Saccardo's umber; belly pale ecru drab to smoke gray; and flanks light quaker drab.

Principal differences of diagnostic value are: *palustris* males average a shorter bill than *mearnsi*, but differentiation of these races is chiefly on the basis of the darker color of both sexes of *palustris*. In comparison with the Tres Mariás Islands population described beyond, *palustris* has a shorter wing and is darker in color.

MEASUREMENTS

Males (22 specimens, mostly breeding): wing 158.0–169.0 mm. (av. 163.2), tail 109.–123.6 (117.2), culmen 19.0–23.0 (20.7). **Females** (20 specimens, mostly breeding): wing 153.5–166.0 mm. (av. 159.5), tail 107.0–117.0 (112.2), culmen 19.8–23.0 (21.4).

RANGE

The specimens of *palustris* examined in this study were from the mangrove swamps near San Blas, Nayarit, and northward to near

Mazatlán, Sinaloa. This race also occurs in some mangrove swamps and adjacent woodlands southeast to localities in Guerrero, but further study of museum collections and additional field work will be needed to determine distribution in more detail. There are several specimens of *palustris* in museum collections from near Acapulco, Guerrero, and six in my series from there. Two of the latter were taken in the breeding season (February 6 and 11, 1949), and four in August and September, 1965 (from A. R. Phillips collection). Most of the specimens I have seen from Sinaloa, Nayarit, Colima (Schaldach, 1963), and Guerrero were taken in winter and were chiefly migrant and wintering *mearnsi*.

The northern limit of the range of *palustris* may extend to about Culiacán, Sinaloa. A male collected at Providencia, 15 miles west of Culiacán, April 11, 1963, by A. R. Phillips, is *palustris* both in coloration and dimensions, although its back is slightly paler than average. There is little mangrove swamp north of Culiacán, and no specimens of *palustris* have been seen beyond there.

SPECIMENS EXAMINED

México: GUERRERO: Laguna Coyuca, Laguna Cayaco, and Laguna Tres Palos, all near Acapulco; Ciruelar and Tuncingo. **NAYARIT:** San Blas and Quimeche River (Río Acaponeta). **SINALOA:** Escuinapa, Mazatlán, and Providencia (La Palma). Most of these were taken during the breeding season.

A review of specimens of white-winged doves from the Tres Marías Islands, Nayarit, México, and comparison of them with series taken on the mainland show that they are a separate race. The name proposed is:

Zenaida asiatica insularis, new subspecies

Tres Marías White-winged Dove

CHARACTERS

Similar to *palustris* of the adjoining mainland of Nayarit and Sinaloa, but with paler plumage and longer wings. It likewise has longer wings than *mearnsi* of Arizona and Sonora, but is slightly darker. It is similar in dimensions to *Z. a. monticola* of the Mexican highlands, but has darker underparts.

DESCRIPTION

Type, Acad. Nat. Sci. Phila. No. 150095, adult male, María Madre, Tres Marías Islands, Nayarit, México, July 12, 1941, collected by Dawson Feathers, Fifth George Vanderbilt Expedition. Crown deep brownish drab; hindneck brownish drab; back olive brown; tertiaries Saccardo's umber; middle rectrices sepia; throat wood brown to

sayal brown; breast wood brown; abdomen pale smoke gray to smoke gray; and flanks light mouse gray to pale mouse gray.

Two specimens collected on María Madre, May 7, 1897, by Nelson and Goldman are slightly paler than the type; the back is Saccardo's umber and the breast avellaneous.

MEASUREMENTS

Males (9 specimens): wing 163.0–176.0 mm. (av. 170.3), tail 114.0–126.0 (121.4), tarsus 25.0–27.0 (25.7), culmen 19.2–21.0 (20.5).
Females (4 specimens): wing 161.8–165.0 mm. (av. 163.3), tail 108.0–113.00 (110.0), tarsus 24.0–26.0 (24.6), culmen 20.0–22.0 (20.6).

RANGE

The Tres Mariás Islands, Nayarit, México, 60-75 miles west of San Blas, Nayarit.

REMARKS

Nelson (1899) was the first to record this species for the Tres Mariás. He found white-winged doves rather common residents on both María Madre and María Magdalena, and a few were seen on María Cleofás, breeding in the last half of May. The fact that Grayson did not report this species from the Tres Mariás on his trips there in 1865, 1866, and 1867 (Lawrence, 1874) led Nelson (1899) to think that these birds were recent residents on these islands. However, white-winged doves have been overlooked in many other places. They can be very local in distribution, especially under adverse ecological conditions.

McLellan (1927) found these doves fairly common at all places visited in Sinaloa and Nayarit, including María Madre, in the fall of 1925. The collection includes a male and female taken on María Madre, October 23, 1925.

The Fifth George Vanderbilt Expedition of the Academy of Natural Sciences of Philadelphia collected a good series including the type of *insularis* on María Madre from July 10 to 16, 1941 (Bond and de Schauensee, 1944).

Stager (1957) found *Zenaida* in considerable numbers on all islands of the Tres Mariás group, although they were outnumbered by *Leptotila* and *Columbigallina*. *Zenaida* was likewise the least abundant on María Cleofás, but could always be found in the forest margin directly behind the beaches on the eastern side of that island.

Grant (1965), in his taxonomic study of the birds of the Tres Mariás, examined a series of 10 male and 5 female white-winged doves from the islands and 9 males and 12 females from a nearby area on the mainland. He concluded that the two groups do not differ sufficiently to warrant taxonomic recognition. He probably reached this conclusion largely because some of his mainland specimens were *mearnsi* migrants and winter visitants from farther north,

and not the breeding subspecies of the Nayarit mainland. In discussing the disparity in male bill lengths between some of the mainland and the island birds, Grant correctly diagnosed the reason for this difference when he inferred that it might be due to the presence of migrants in the mainland sample.

The nearest breeding population on the mainland is near San Blas, Nayarit, mostly in or near the mangrove swamps. The 22 adult males I examined from this part of the mainland were breeders I collected mostly in that locality and near Escuinapa, Sinaloa, in April 1960. Their bills average almost 2 mm. shorter than those of *mearnsi*. In late autumn, winter, and early spring, the population of *mearnsi* in drier woodlands and fields of this coastal plain and foothills of these States, many of them from Arizona as proved by band recoveries, greatly outnumbers that of *palustris*, which is much more local in distribution.

A series of 25 specimens from the Mexican mainland of Sinaloa and Nayarit nearest the Tres Mariás includes no individuals that have the principal characteristics of *insularis*. The latter are distinctly different although these islands are only 65 miles offshore, west of San Blas, Nayarit.

SPECIMENS EXAMINED

México: NAYARIT: Tres Mariás Islands, María Madre.

Field studies in Guatemala in 1942, 1946, and 1947 provided many observations on the biology of white-winged doves there. A series of specimens from the dry woodlands was first recorded as *mearnsi* (Saunders et al., 1950). Later study showed that these represented a new race whose principal range is in the dry woodland of the Pacific piedmont hills of Central America. This new race may be called:

Zenaida asiatica collina, new subspecies Piedmont White-winged Dove

CHARACTERS

Compared with *alticola*, *collina* is paler and smaller and has shorter wings and tail. It has shorter wings and tail than *monticola*. It is slightly larger than *australis*, averages paler on the underparts, and lacks the cinnamon brown tone to the breast and upperparts which usually characterizes that race. Also, it is grayer on the back and rump, and usually more purple on the crown than *australis*. Compared with *panamensis*, *collina* has longer wings and averages darker on the breast and upperparts. Compared with *asiatica*, *collina* is slightly larger, and its wings and tail are longer. Compared with

mearnsi from Arizona, it averages browner, the wing of the male is longer and the culmen shorter; in the female the tail and culmen are shorter.

DESCRIPTION

Type, U. S. Nat. Mus. (Fish and Wildlife Service Collection) No. 481590, adult male, breeding, near Progreso, Department of Jutiapa, Guatemala, elevation approximately 3,100 feet, March 13, 1942, collected by George B. Saunders, collector's number 1622. Crown dark vinaceous drab; hindneck vinaceous drab; back olive brown; tertiaries Prout's brown; middle rectrices mummy brown; throat and breast nearest buffy brown; abdomen pale drab gray; and flanks pale quaker drab.

MEASUREMENTS

Males (52 specimens): wing 158.0–169.9 mm. (av. 162.6), tail 108.0–121.9 (113.0), culmen 17.5–22.0 (20.0). **Females** (22 specimens): wing 151.0–165.6 mm. (av. 157.4), tail 103.7–111.0 (107.0), and culmen 18.1–22.1 (20.1).

RANGE

Southernmost México from southeast of the Isthmus of Tehuantepec (Oaxaca and Chiapas) through Central America to the Guanacaste district of Costa Rica (Carriker, 1910), chiefly on the Pacific slope.

REMARKS

Field studies and specimens indicate that *collina* occurs in the dry woodland and thorn forests of the coastal plain foothills and lower mountains of the Pacific slope, and in many of the arid interior valleys, including some in the Caribbean drainage. In some places, as at Punta Piedra, Costa Rica, on the Gulf of Nicoya, *collina* breeds locally in the coastal lowlands. It is not known whether it also nests in mangrove swamps there.

In some localities on the Pacific slope of Guatemala and El Salvador during winter months every white-winged dove I collected was *asiatica*; in other places they were in equal numbers with *collina*, and in yet other habitats only a few miles away I found only *collina*. In some instances *collina* was the only race present in the thorn forest, and *asiatica* was often more common in valleys that had extensive weed fields and farms with grain.

One specimen of *collina*, labeled Panama, is probably from Guatemala. Ridgway (1916, p. 380) wrote, "There is a specimen in the collection of the Carnegie Museum labeled Natá, Coclé, Panama (no. 20777; Heyde and Lux, collectors); but this is evidently referable to the larger and grayer form from western Mexico, and if really from

Panama must have been a cage bird; indeed its appearance suggests its having been kept in confinement." This adult male has its primaries and rectrices moderately worn, but no more so than many other breeding white-winged doves. Nothing about the appearance of this specimen indicates that it had been caged; its plumage is not soiled, nor are feathers broken or fault-barred. The date, May 20, 1889, was within the breeding season. It is comparable in size and color to specimens of *collina* from the Pacific coast and piedmont from Guatemala to Costa Rica. According to Alexander Wetmore, with whom this specimen was discussed, the collectors Heyde and Lux obtained a large number of "trade skins," many of them from Guatemala. There are several instances in which Guatemalan birds in their collections were mislabeled "Panama." For the present it seems inadvisable to accept this specimen as proof that *collina* occurs there. *Collina* breeds and winters as far south as the Guanacaste region of Costa Rica, so a few of them may have populated arid woodlands of southwestern Panamá, but if so it is strange that no specimens of this race have been collected or reported there since 1889.

SPECIMENS EXAMINED

México: OAXACA: La Ventosa; CHIAPAS: Berriozabal, Chicomuselo, Cd. Cuauhtemoc, Entronque Santa Isabel, Esperanza, Hacienda Monserrate, Mazapa, Pinuela, Rezo de Oro, San Bartolo, San José (near Comitán), Tuxtla Gutiérrez. **Guatemala:** Antigua, Chanquejelve, Chiquimula, El Rancho, Lake Atescatempa, Progreso, Sacapulas, San José de Arada, Usumatlán, Zacapa. **El Salvador:** Laguna de las Ranas, Puerto El Triunfo, Río Goascorán, Río Lempa (near Puente Cuscatlán), San Miguel, Sonsonate. **Honduras:** Comayagua, Coyoles, El Hatillo, La Hor Archaga, Monte Redondo, Río Hondo, Siguatepeque, Subirana. **Nicaragua:** Calabasas, San Rafael del Norte. **Costa Rica:** Hacienda El Pelón, Las Cañas, La Palma de Nicoya, Miravalles, Punta Piedra, Tenorio. All seasons are represented by these specimens, but the majority are of spring and winter months.

Only 11 specimens of white-winged doves from Panamá were available for this study. A twelfth specimen was not sufficiently authenticated to be considered a satisfactory record. The 11 birds were from the coastal mangrove swamps of southwestern Panamá, and eight of the nine males were collected during the breeding season. They are different from other resident populations farther north in Central America and are described as a distinct subspecies which may be called:

***Zenaida asiatica panamensis*, new subspecies**
Panamanian White-winged Dove

CHARACTERS

Smaller than *collina*, especially in wing and tail length, and averaging paler brown on the back and breast. Its undertail coverts are paler than those of *collina* which average darker gray. It lacks the rich cinnamon brown tones of the back and breast characteristic of most specimens of *australis*.

DESCRIPTION

Type, U. S. Nat. Mus. No. 476630, adult male, breeding, Río Pocrí, Puerto Aguadulce, Coclé, Panamá, March 12, 1962, collected by A. Wetmore. Crown dark vinaceous drab; hindneck vinaceous drab; back and tertiaries buffy brown; middle rectrices mummy brown; throat slightly paler than sayal brown; breast drab; abdomen pearl gray; and flanks pale quaker drab.

Several of the males from Aguadulce are slightly paler on the breast and upper parts than the type specimen. Five of the eight have the middle pair of rectrices marked with a more or less visible terminal band of grayer or paler brown.

The female, No. 477593, is slightly paler and less vinaceous brown on the breast, and slightly grayer brown on the upper parts. Her crown and nape are a paler vinaceous drab than those of the males.

Compared with *collina*, most specimens of *panamensis* are paler and grayer, especially on the back and tertiaries; the chin is grayer and less brownish; the middle rectrices are lighter brown or grayer and often show a paler terminal bar, whereas in *collina* they are usually more uniformly brown.

Z. a. australis is darker, with a cinnamon brown tone to the breast, and this color usually extends farther down on the under parts than in *panamensis*. The back, scapulars, tertiaries, wing coverts, and middle rectrices are a darker brown in *australis*, and its middle rectrices usually are uniformly colored and lack the paler terminal band so common in *panamensis*. Both male and female *panamensis* have significantly shorter wings than *collina* and *australis*.

MEASUREMENTS

Males (9 specimens): wing 150.0–158.0 mm. (av. 154.8), tail 106.5–114.0 (110.3), tarsus 23.5–26.0 (24.7), and culmen 19.0–20.5 (19.8).
Females (2 specimens): wing 150.0–151.5 mm. (av. 150.8), tail 104.0–105.0 (104.5), tarsus 23.8–24.0 (23.0), and culmen 20.0.

RANGE

Resident and fairly common in the mangrove swamps around the shores of the Gulf of Parita on the northeastern coast of the Azuero Peninsula, from the lower Río Parita (Monagrillo), Herrera, to the

Río Pocrí and the Río Antón, Coclé. This race is believed to be non-migratory.

The breeding habitat in the mangrove swamp woodland apparently is characteristic of this race. None of these birds was observed in other habitat types in the localities visited.

SPECIMENS EXAMINED

Panamá: La Isleta and Río Pocrí in Aquadulce, Province of Coclé; and Río Parita in Monagrillo, Province of Herrera.

DISCUSSION

Of the 12 subspecies mentioned, their grouping in the following table, map, and figures is based on their breeding distribution in three zones, (1) the Gulf and Caribbean, (2) the interior highlands, and (3) the Pacific Coast. Within these groups the arrangement is from north to south. Those of group 1 breed in lowlands of the eastern coast of México and Central America and in the West Indies, and include *asiatica*, *peninsulae*, and *australis*. They are of medium to small sizes for this species, have shorter wings and tail, and live chiefly in tropical and subtropical lowlands.

Group 2 of the interior highlands includes *grandis*, *monticola*, and *alticola*. They are large for whitewings, have longer wings and tail, and do not occur in lowland localities.

Group 3, Pacific Coast, includes *mearnsi*, *palustris*, *insularis*, *collina*, *panamensis*, and *meloda*. The races in this last group are of medium to large size, and the ranges of several extend from the lowlands inland to higher elevations. Their wings and tail are of medium length to long except in the mangrove-dwelling race *panamensis*, in which these dimensions are smaller.

Figure 1 shows the tentative boundaries of the breeding ranges of the various subspecies, but further information will undoubtedly result in many changes in this map. In the case of *australis*, for example, the breeding range is without doubt more extensive than shown, but in the series of birds examined, only the localities in northern Honduras were represented by breeding specimens. Their wintering ranges are not mapped because the overlapping of *asiatica* and *mearnsi* on the ranges of resident races is so complex. In some places three different races may be wintering in the same locality.

There are many unanswered questions in white-winged dove taxonomy and distribution, especially in areas where insufficient field work and collecting have been done. To determine the ecological distribution of distinct populations, additional specimens should be taken during the breeding season from México south to Costa Rica. Likewise, there are considerable gaps in our knowledge of the distribution and taxonomy of this species in South America and the West Indies.

TABLE.—Measurements of 12 subspecies of white-winged doves
[In millimeters]

Subspecies and sex	Number in sample	Range	Standard deviation	Standard error	Mean \pm Confidence limits .05
Wing measurements:					
<i>asiatica:</i>					
males	32	151.0–164.0	2.93	0.52	157.3 \pm 1.1
females	20	146.0–158.9	3.13	0.70	153.5 \pm 1.5
<i>peninsulæ:</i>					
males	14	148.5–156.3	2.75	0.76	151.5 \pm 1.6
females	18	143.0–155.0	3.80	0.90	148.6 \pm 1.9
<i>australis:</i>					
males	10	154.0–161.0	2.08	0.66	158.5 \pm 1.5
females	11	150.8–158.2	2.59	0.78	154.1 \pm 1.7
<i>grandis:</i>					
males	10	166.0–175.0	2.90	0.92	172.0 \pm 2.1
females	5	162.0–164.9	1.37	0.61	163.5 \pm 1.7
<i>monticola:</i>					
males	44	161.3–177.0	3.41	0.51	167.2 \pm 1.0
females	22	156.0–171.0	4.12	0.85	162.8 \pm 1.8
<i>alticola:</i>					
males	8	164.5–173.0	2.70	0.95	167.9 \pm 2.3
females	6	153.0–162.0	3.83	1.56	156.7 \pm 4.0
<i>mearnsi:</i>					
males	38	155.0–170.4	3.08	0.50	161.6 \pm 1.0
females	27	148.0–164.0	3.65	0.70	157.9 \pm 1.4
<i>palustris:</i>					
males	22	158.0–169.0	2.74	0.58	163.2 \pm 1.2
females	20	153.5–166.0	0.74	0.74	159.5 \pm 1.6
<i>insularis:</i>					
males	9	163.0–176.0	4.33	1.44	170.3 \pm 3.3
females	4	161.8 165.0	1.45	0.73	163.3 \pm 2.3
<i>collina:</i>					
males	52	158.0–169.9	2.38	0.33	162.6 \pm 0.7
females	22	151.0–165.6	3.65	0.78	157.4 \pm 1.6
<i>panamensis:</i>					
males	9	150.5–158.0	2.58	0.86	154.8 \pm 2.0
females	2	150.0–151.5	1.06	0.75	150.8 \pm —
<i>meloda:</i>					
males	11	164.0–175.5	4.14	1.25	168.3 \pm 2.8
females	10	159.4–169.0	3.86	1.22	164.5 \pm 2.8
Tail measurements:					
<i>asiatica:</i>					
males	32	100.7–115.0	3.30	0.58	108.8 \pm 1.2
females	20	101.0–112.6	2.68	0.60	107.2 \pm 1.2
<i>peninsulæ:</i>					
males	14	97.1–108.0	2.72	0.72	103.5 \pm 1.5
females	18	93.0–104.0	3.22	0.76	99.6 \pm 1.6
<i>australis:</i>					
males	10	108.0–114.0	2.43	0.77	111.3 \pm 1.7
females	11	103.0–112.0	2.29	0.69	106.2 \pm 1.5
<i>grandis:</i>					
males	9	120.5–133.0	3.60	1.2	126.6 \pm 2.8
females	5	112.9–121.3	3.87	1.7	116.5 \pm 4.7
<i>monticola:</i>					
males	44	114.0–127.5	3.52	0.55	120.4 \pm 1.1
females	22	111.0–124.4	3.67	0.71	116.2 \pm 1.5
<i>alticola:</i>					
males	8	116.6–129.5	3.89	1.37	122.0 \pm 3.3
females	6	104.0–113.3	3.58	1.46	109.9 \pm 3.8

TABLE.—Measurements of 12 subspecies of white-winged doves—Continued
[In millimeters]

Subspecies and sex	Number in sample	Range	Standard deviation	Standard error	Mean \pm Confidence limits .05
Tail measurements—Cont.					
<i>mearnsi</i> :					
males	38	106.7–123.5	3.80	0.63	116.3 \pm 1.3
females	27	103.8–116.0	2.69	0.52	110.1 \pm 1.1
<i>palustris</i> :					
males	22	109.0–123.6	3.75	0.79	117.2 \pm 1.6
females	20	107.0–117.0	3.42	0.72	112.2 \pm 1.5
<i>insularis</i> :					
males	8	114.0–126.0	3.47	1.24	121.4 \pm 2.9
females	4	108.0–113.0	2.16	1.08	110.0 \pm 3.4
<i>collina</i> :					
males	52	108.0–121.9	2.63	0.36	113.0 \pm 0.7
females	22	103.7–111.0	2.53	0.54	107.0 \pm 1.1
<i>panamensis</i> :					
males	9	106.5–114.0	2.82	0.94	110.3 \pm 2.2
females	2	104.0–105.0	0.71	0.50	104.5 \pm —
<i>meloda</i> :					
males	10	120.0–133.0	3.95	1.19	125.2 \pm 2.7
females	10	113.3–125.0	4.69	1.48	118.9 \pm 3.4
Culmen measurements:					
<i>asiatica</i> :					
males	21	19.0–21.3	0.50	0.11	20.1 \pm 0.2
females	19	17.0–21.2	1.16	0.27	19.5 \pm 0.6
<i>peninsulæ</i> :					
males	13	18.0–21.3	1.04	0.29	20.2 \pm 0.6
females	18	18.4–21.7	0.97	0.22	20.0 \pm 0.5
<i>australis</i> :					
males	10	18.0–20.9	1.12	0.35	19.4 \pm 0.8
females	10	18.8–21.0	0.85	0.27	19.9 \pm 0.6
<i>grandis</i> :					
males	10	20.0–23.0	0.85	0.26	21.5 \pm 0.6
females	5	20.7–22.3	0.67	0.3	21.5 \pm 0.8
<i>monticola</i> :					
males	41	18.9–22.9	0.91	0.17	21.1 \pm 0.3
females	21	19.2–23.0	1.07	0.24	21.0 \pm 0.5
<i>alticola</i> :					
males	8	19.0–21.9	1.23	0.43	20.2 \pm 1.0
females	6	18.5–20.0	0.51	0.21	19.2 \pm 0.5
<i>mearnsi</i> :					
males	35	20.8–24.8	0.96	0.16	22.5 \pm 0.3
females	23	20.7–25.4	1.16	0.24	22.1 \pm 0.5
<i>palustris</i> :					
males	22	19.0–23.0	1.15	0.25	20.7 \pm 0.5
females	20	19.8–23.0	1.02	0.23	21.4 \pm 0.5
<i>insularis</i> :					
males	9	19.2–21.0	0.64	0.21	20.5 \pm 0.5
females	3	20.0–22.0	1.16	0.58	20.6 \pm 2.5
<i>collina</i> :					
males	49	17.5–22.2	0.98	0.14	20.0 \pm 0.3
females	18	18.1–22.1	1.32	0.31	20.1 \pm 0.7
<i>panamensis</i> :					
males	9	19.0–20.5	0.52	0.17	19.8 \pm 0.4
females	2	20.0–20.0	0.00	—	20.0 \pm —
<i>meloda</i> :					
males	11	20.5–23.2	1.00	0.30	21.6 \pm 0.7
females	10	20.5–22.5	0.66	0.21	21.4 \pm 0.5

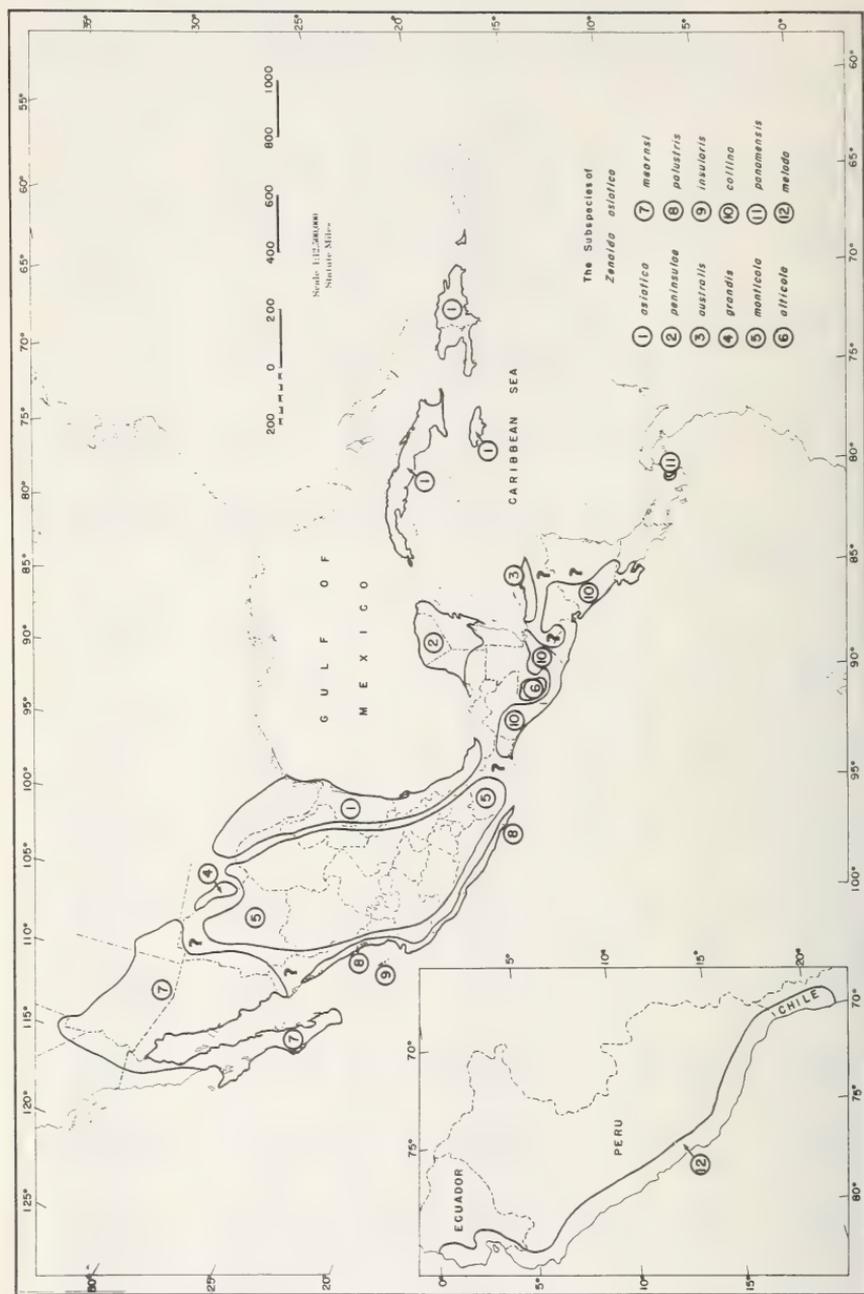


Figure 1.—Breeding ranges of the subspecies of white-winged doves.

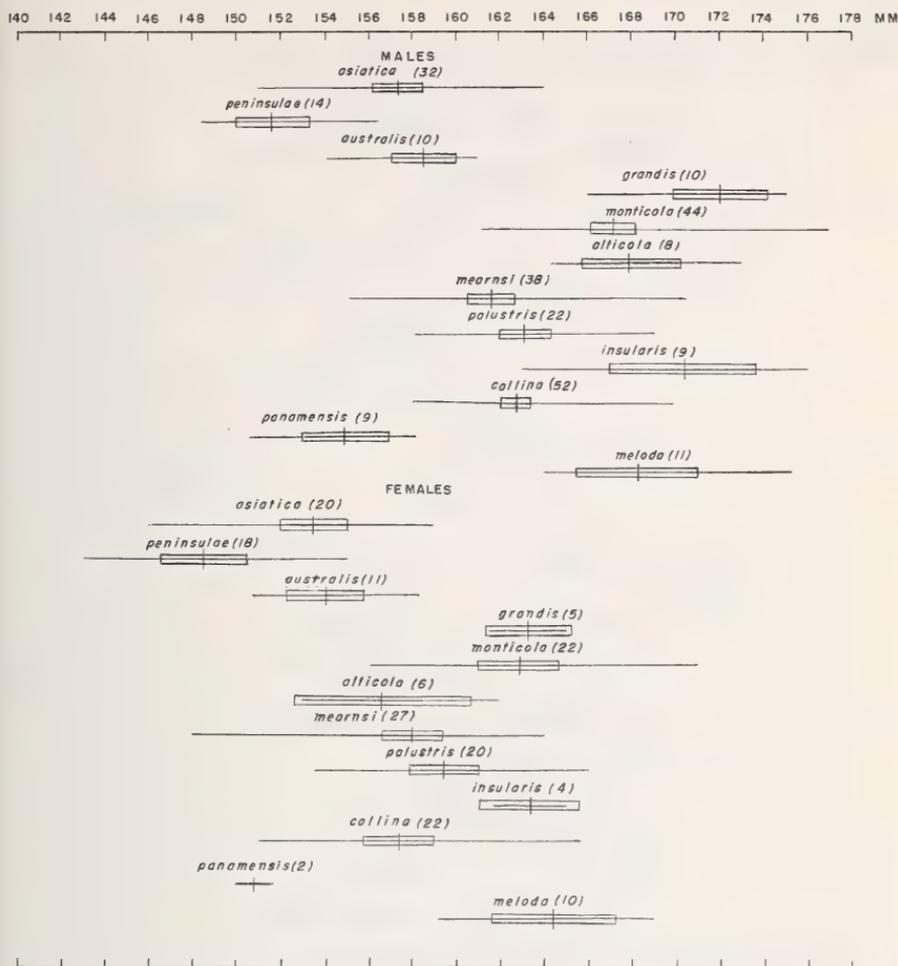


Figure 2.—Statistical comparison of wing measurements of subspecies of white-winged doves.

The present studies indicate that *asiatica* does not occur as a breeder anywhere on the mainland south of the Isthmus of Tehuantepec, and *mearnsi* may not breed south of northern Sinaloa.

Morphological differences between populations are not great, and in several races the general trends do not conform to the classical rules of morphological variation correlated with climate. In general, long-winged birds are characteristic of the higher altitudes and more temperate areas, and short-winged birds are typical of the tropical lowlands of the Gulf and Caribbean. However, some of the subspecies having the longest wings and tails are those in tropical lowlands of some Pacific coastal localities from México south to northern Chile.

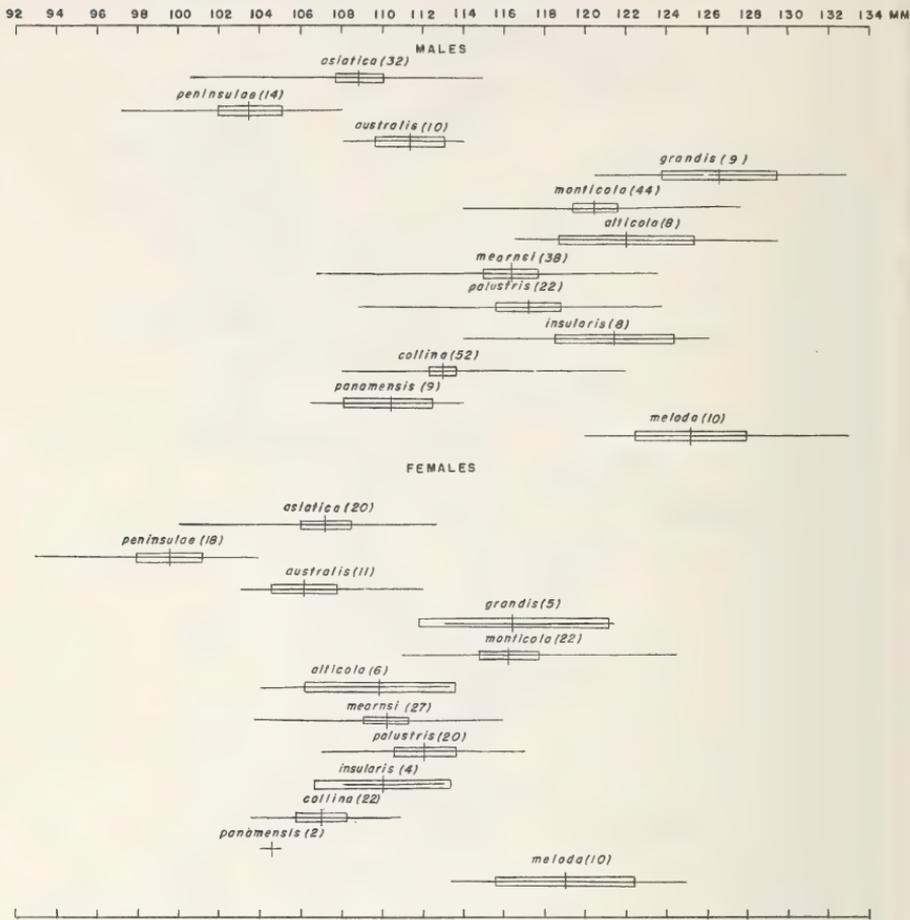


Figure 3.—Statistical comparison of tail measurements of subspecies of white-winged doves.

The various subspecies of white-winged doves do not seem to follow Allen's rules in terms of bill length. All of the races in the hottest year-round habitats, in the tropical lowlands of Central America, and on the Pacific coast of México have short bills. The race with the longest bill is *mearnsi*, yet its Arizona range is at the greatest latitude of any of the whitewings. Although Arizona desert summers are hot, the more tropical habitats in Latin America are hotter.

The subspecies of whitewings show more agreement with Bergman's rule, but there are exceptions. The largest birds in body size are those in the highlands of México and Central America. They live at

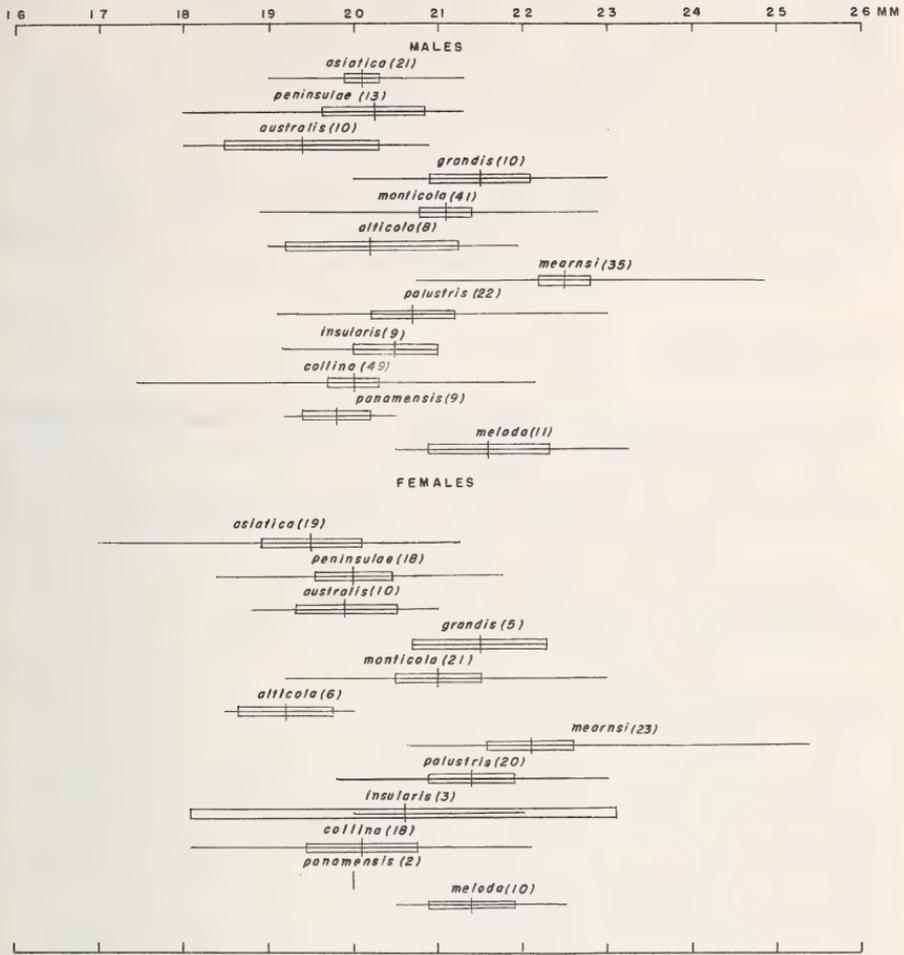


Figure 4.—Statistical comparison of culmen measurements of subspecies of white-winged doves.

higher altitudes where the climate is cooler, but *meloda*, which also is large, lives in Pacific coastal and piedmont areas of tropical western South America. The climate of the range of *meloda* is modified somewhat by the proximity of the Humboldt Current. The smallest whitewings in body size are those in the hot, tropical lowlands of Yucatán and Panamá.

In conformance with Gloger's rule, dark pigmentation appears to be associated with the more humid habitats and paler hues with the more arid areas. The darkest are those of the wooded highlands of Guatemala and of the mangrove swamps of the Pacific lowlands of México from southern Sinaloa to Guerrero. The palest are those of

the deserts of Arizona, Baja California, the highlands of México, and the Pacific coast of South America, especially if breeding specimens are compared. The summer (breeding) plumage shows the greatest contrast between some of the subspecies as birds of arid, rocky habitats show much more fading and wear of plumage than those in more moist woodlands. The plumage of most white-winged doves is darkest and richest in color when in fresh condition after the postnuptial molt. Combinations of these environmentally related characters of dimensions and plumage color are the basis for the differences found in the several races described in this paper.

SUMMARY

In a study of the distribution and taxonomy of the white-winged dove, *Zenaida asiatica*, it was found that the subspecies *Z. a. asiatica* of Texas and northeastern México and *Z. a. mearnsi* of Arizona are strongly migratory. The former winters chiefly in Central America and the latter in western México. With the clarification of their ranges and the study of breeding populations in México and Central America it became apparent that several undescribed races were resident in these countries. Systematic collecting in many localities, the review of museum specimens, and field studies of ecological differences among populations indicated the presence of at least seven undescribed subspecies which are described in this paper.

These subspecies are *Z. a. peninsulae* of the Yucatán peninsula, *Z. a. grandis* of central western Texas, *Z. a. monticola* of the Mexican highlands, *Z. a. palustris* of the central and southern Pacific coastal plain of México, *Z. a. insularis* of the Tres Mariás Islands, Nayarit, México, *Z. a. collina* of Central America, chiefly on the Pacific piedmont and coastal plain from Chiapas, México, to Costa Rica, and *Z. a. panamensis* of the northeast coast of the Azuero peninsula, Panamá. Measurements of specimens, with figures presenting a statistical analysis of these measurements, are given, together with a map showing the breeding ranges.

LITERATURE CITED

- BOND, JAMES, and R. M. DE SCHAUENSEE.
1944. Results of the Fifth George Vanderbilt Expedition. The Birds. Academy of Natural Sciences of Philadelphia, Monograph 6, p. 7-56.
- CARRIKER, M. A., Jr.
1910. An annotated list of the birds of Costa Rica including Cocos Island. Carnegie Institute, Annals of the Carnegie Museum, Vol. 6, p. 314-915.
- CHAPMAN, F. M.
1896. Notes on birds observed in Yucatan. American Museum of Natural History, Bulletin 8, p. 271-290.
- COLE, LEON J.
1906. Aves from Yucatan. Harvard University, Museum of Comparative Zoology, Bulletin 50, p. 109-146.
- DICKEY, DONALD R., and A. J. VAN ROSSEM.
1938. The birds of El Salvador. Field Museum of Natural History, Zoological Series 23, Publication No. 406. 609 p.
- FRIEDMANN, HERBERT, LUDLOW GRISCOM, and ROBERT T. MOORE.
1950. Distributional check-list of the birds of Mexico, Part 1. Cooper Ornithological Club, Pacific Coast Avifauna No. 29. 202 p.
- GRANT, P. R.
1965. A systematic study of the terrestrial birds of the Tres Marias Islands, Mexico. Yale University, Peabody Museum of Natural History, Postilla, No. 90. 106 p.
- GRISCOM, LUDLOW.
1932. The distribution of bird-life in Guatemala. American Museum of Natural History, Bulletin 64. 425 p.
- HELLMAYR, C. E., and B. CONOVER.
1942. Catalogue of birds of the Americas. Field Museum of Natural History, Zoological Series 13, Publication No. 514. 636 p.
- LAWRENCE, GEORGE N.
1874. Birds of western and northwestern Mexico, based upon collections made by Col. A. J. Grayson, Capt. J. Xantus and Ferd. Bischoff, now in the Museum of the Smithsonian Inst. at Washington, D. C. Boston Society of Natural History, Memoirs, Vol. 2, No. 30, p. 265-319.
- MAYR, E., E. G. LINSLEY, and R. L. USINGER.
1953. Methods and principles of systematic zoology. McGraw-Hill, New York. 797 p.
- MCLELLAN, M. E.
1927. Notes on the birds of Sinaloa and Nayarit, Mexico, in the fall of 1925. California Academy of Science, Proceedings, Vol. 16, No. 1, p. 1-51.
- NELSON, E. W.
1899. Birds of the Tres Marias Islands, western Mexico. U. S. Biological Survey, North American Fauna, No. 14, p. 7-62.
- PAYNTER, RAYMOND A., Jr.
1955. The ornithogeography of the Yucatan Peninsula. Yale University, Peabody Museum of Natural History, Bulletin 9. 347 p.
- PETERS, JAMES L.
1913. List of birds collected in the Territory of Quintana Roo. Auk, Vol. 30, p. 367-380.
1937. Check-list of the birds of the world. Harvard University Press, Cambridge. Vol. 3, 311 p.

PITELKA, FRANK A.

1948. Notes on the distribution and taxonomy of Mexican game birds. *Condor*, Vol. 50, p. 121-122.

RIDGWAY, ROBERT.

1912. Color standards and color nomenclature. Published by the author, Washington, D. C., 43 p., 53 color plates.
 1915. Descriptions of some new forms of American cuckoos, parrots, and pigeons. *Biological Society of Washington, Proceedings*, Vol. 28, p. 105-107.
 1916. Birds of North and Middle America. *U. S. National Museum Bulletin* 50, Part 7. 543 p.

SALVIN, OSBERT.

1889. A list of the birds of the islands of the coast of Yucatan and of the Bay of Honduras. *Ibis*, Vol. 31, p. 377.

_____ and F. D. GODMAN.

1902. *Biologia Centrali-Americana. Aves*, Vol. 3, p. 245-247.

SAUNDERS, GEORGE B.

1951. A new white-winged dove from Guatemala. *Biological Society of Washington, Proceedings*, Vol. 64, P. 83-87.
 1959. La paloma de alas blancas en las Americas. *Memoria de la Segunda Convencion Nacional Forestal, Departamento de Divulgacion y Propaganda de la Subsecretaria de Recursos Forestales, Mexico, D. F., 1959*, p. 414-422.
 1962. The white-winged doves of the Americas. *U. S. Fish and Wildlife Service*, mimeographed, 10 p. (Based on a translation of the paper, "La paloma de alas blancas en las Americas," *Memoria de la Segunda Convencion Nacional Forestal, Mexico, 1959*.)

_____, C. O. HANDLEY, Jr., and A. D. HOLLOWAY.

1950. A fish and wildlife survey of Guatemala. *U. S. Fish and Wildlife Service, Special Scientific Report—Wildlife*, No. 5. 162 p.

SCHALDACH, W. J., Jr.

1963. The avifauna of Colima and adjacent Jalisco, Mexico. *Western Foundation of Vertebrate Zoology, Proceedings*, Vol. 1, No. 1. 100 p.

SKUTCH, ALEXANDER F.

1964. Life histories of Central American pigeons. *Wilson Bulletin*, Vol. 76, No. 3, p. 211-247.

STAGER, KENNETH E.

1957. The avifauna of the Tres Marias Islands, Mexico. *Auk*, Vol. 74, No. 4, p. 413-432.

STORER, ROBERT W.

1961. Two collections of birds from Campeche, Mexico. *Occasional Papers of the Museum of Zoology, University of Michigan*, No. 621, p. 1-20.

VAN ROSSEM, A. J.

1947. Comment on certain birds of Baja California, including descriptions of three new races. *Biological Society of Washington, Proceedings*, Vol. 60, p. 51-56.

VAN TYNE, JOSSELYN, and GEORGE M. SUTTON.

1937. The birds of Brewster County, Texas. *Miscellaneous Publications of the Museum of Zoology, University of Michigan*, No. 37, 119 p.

The Department of the Interior, created in 1849, is a Department of Conservation, concerned with management, conservation, and development of the Nation's water, wildlife, fish, mineral, forest, and park and recreational resources. It has major responsibilities also for Indian and Territorial affairs.

As America's principal conservation agency, the Department works to assure that nonrenewable resources are developed and used wisely, that park and recreational resources are conserved for the future, and that renewable resources make their full contribution to the progress, prosperity, and security of the United States, now and in the future.

QL
151
N864
NH

MAMMALS OF MARYLAND



NUMBER 66

UNITED STATES
DEPARTMENT OF THE INTERIOR
BUREAU OF SPORT FISHERIES AND WILDLIFE



NORTH AMERICAN FAUNA

This publication series includes monographs and other reports of scientific investigations relating to birds, mammals, reptiles, and amphibians, for professional readers. It is a continuation by the Bureau of Sport Fisheries and Wildlife of the series begun in 1889 by the Division of Ornithology and Mammalogy (Department of Agriculture) and continued by succeeding bureaus—Biological Survey and Fish and Wildlife Service. The Bureau distributes these reports to official agencies, to libraries, and to researchers in fields related to the Bureau's work; additional copies may usually be purchased from the Division of Public Documents, U.S. Government Printing Office.

Reports in NORTH AMERICAN FAUNA since 1950 are as follows (an asterisk indicates that sale stock is exhausted):

- *60. Raccoons of North and Middle America, by Edward A. Goldman. 1950. 153 p.
- *61. Fauna of the Aleutian Islands and Alaska Peninsula, by Olaus J. Murie; Invertebrates and Fishes Collected in the Aleutians, 1936-38, by Victor B. Scheffer. 1959. 406 p.
- *62. Birds of Maryland and the District of Columbia, by Robert E. Stewart and Chandler S. Robbins. 1958. 401 p.
- *63. The Trumpeter Swan; Its history, habits, and population in the United States, by Winston E. Banko. 1960. 214 p.
- *64. Pelage and Surface Topography of the Northern Fur Seal, by Victor B. Scheffer. 1961. 206 p.
- 65. Seven New White-winged Doves From Mexico, Central America, and Southwestern United States, by George B. Saunders. 1968. 30 p.

MAMMALS OF MARYLAND

By
John L. Paradiso



NUMBER 66

UNITED STATES
DEPARTMENT OF THE INTERIOR

Walter J. Hickel, *Secretary*

BUREAU OF SPORT FISHERIES AND WILDLIFE

John S. Gottschalk, *Director*



North American Fauna, Number 66

Published by
Bureau of Sport Fisheries and Wildlife
April 1969

UNITED STATES GOVERNMENT PRINTING OFFICE • WASHINGTON • 1969

CONTENTS

	Page
Introduction.....	1
Location and area of Maryland.....	2
Temperature.....	3
Average annual precipitation.....	3
Effects of civilization.....	4
Principal biotic or natural areas in Maryland.....	4
Eastern Shore section.....	5
Western Shore section.....	6
Piedmont section.....	7
Ridge and Valley section.....	7
Allegheny Mountain section.....	7
Maryland's mammalian fauna.....	8
Keys.....	9
Accounts of species.....	14
Order Marsupialia (pouched mammals).....	14
Order Insectivora (shrews, moles, etc.).....	15
Order Chiroptera (bats).....	41
Order Lagomorpha (rabbits, hares, etc.).....	61
Order Rodentia (gnawing mammals).....	67
Order Carnivora (flesh-eating mammals).....	130
Order Artiodactyla (even-toed hoofed mammals).....	167
Marine mammals of Maryland.....	173
Extirpated Recent mammals of Maryland.....	181
References.....	184

MAPS

	Page
FIGURE 1. Map of Maryland showing the 23 counties, Baltimore City, and the District of Columbia.....	3
2. Physiographic provinces of Maryland.....	5
3. Biotic sections of Maryland.....	6
4. Distribution of <i>Sorex cinereus fontinalis</i> and <i>S. c. cinereus</i>	17
5. Distribution of <i>Sorex longirostris longirostris</i>	21
6. Distribution of <i>Sorex fumeus fumeus</i>	24
7. Distribution of <i>Sorex dispar dispar</i>	26
8. Distribution of <i>Microsorex hoyi winnemana</i>	27
9. Distribution of <i>Blarina brevicauda kirtlandi</i>	29
10. Distribution of <i>Cryptotis parva parva</i>	33
11. Distribution of <i>Parascalops breweri</i>	35
12. Distribution of <i>Scalopus aquaticus aquaticus</i>	37
13. Distribution of <i>Condylura cristata cristata</i>	40
14. Distribution of <i>Myotis lucifugus lucifugus</i>	42
15. Distribution of <i>Myotis keenii septentrionalis</i>	44
16. Distribution of <i>Myotis sodalis</i>	45

	Page
FIGURE 17. Distribution of <i>Myotis subulatus leibii</i>	47
18. Distribution of <i>Lasionycteris noctivagans</i>	49
19. Distribution of <i>Pipistrellus subflavus subflavus</i>	51
20. Distribution of <i>Eptesicus fuscus fuscus</i>	52
21. Distribution of <i>Lasiurus borealis borealis</i>	55
22. Distribution of <i>Lasiurus cinereus cinereus</i>	57
23. Distribution of <i>Nycticeius humeralis humeralis</i>	59
24. Distribution of <i>Sylvilagus floridanus mallurus</i>	62
25. Distribution of <i>Lepus americanus virginianus</i>	65
26. Distribution of <i>Tamias striatus fisheri</i> and <i>T. s. lysteri</i>	69
27. Distribution of <i>Marmota monax monax</i>	71
28. Distribution of <i>Sciurus carolinensis pennsylvanicus</i>	73
29. Distribution of <i>Sciurus niger cinereus</i> and <i>S. n. vulpinus</i>	79
30. Distribution of <i>Tamiasciurus hudsonicus loquax</i>	81
31. Distribution of <i>Glaucomys volans volans</i>	84
32. Distribution of <i>Oryzomys palustris palustris</i>	88
33. Distribution of <i>Reithrodontomys humulis virginianus</i>	91
34. Distribution of <i>Peromyscus maniculatus nubiterrae</i> and <i>P. m. bairdii</i>	94
35. Distribution of <i>Peromyscus leucopus noveboracensis</i>	96
36. Distribution of <i>Neotoma floridana magister</i>	100
37. Distribution of <i>Clethrionomys gapperi gapperi</i>	102
38. Distribution of <i>Microtus pennsylvanicus pennsylvanicus</i> and <i>M. p. nigrans</i>	106
39. Distribution of <i>Pitymys pinetorum scalopsoides</i>	108
40. Distribution of <i>Ondatra zibethicus</i>	110
41. Distribution of <i>Synaptomys cooperi stonei</i>	115
42. Distribution of <i>Zapus hudsonius americanus</i>	127
43. Distribution of <i>Napaeozapus insignis insignis</i>	129
44. Distribution of <i>Canis latrans</i>	131
45. Distribution of <i>Vulpes vulpes fulva</i>	135
46. Distribution of <i>Urocyon cinereoargenteus cinereoargenteus</i>	140
47. Distribution of <i>Procyon lotor lotor</i>	144
48. Distribution of <i>Mustela erminea cicognanii</i>	147
49. Distribution of <i>Mustela frenata noveboracensis</i>	149
50. Distribution of <i>Mustela vison</i>	153
51. Distribution of <i>Mephitis mephitis nigra</i>	156
52. Distribution of <i>Spilogale putorius putorius</i>	159
53. Distribution of <i>Lutra canadensis</i>	161
54. Distribution of <i>Lynx rufus rufus</i>	165

INTRODUCTION

In 1950, Marshall C. Gardner (1950a, 1950b) began the first comprehensive listing of Maryland mammals, but he completed only the sections dealing with marsupials, insectivores, and bats. This has been the only statewide study of Maryland mammals ever undertaken, although a number of sectional accounts have appeared, including those by Goldman and Jackson (1939), Bures (1948), Hampe (1939), and Bailey (1923). In addition, Mansueti (1950) treated in detail the extinct and vanishing species of the State.

The present survey originated in the mid-1950's, but intensive work on it was not begun until 1962. During the course of the study, field work was conducted in all parts of the State except the Allegheny Mountain section. Specimens collected during this field work, and the large series of Maryland mammal specimens available in the national collections, form the basis for the present survey. In the "specimens examined" sections of the following accounts, the specimens are in the collections housed in the U.S. National Museum unless otherwise noted. Abbreviations used in the text for other institutions from which material has been examined are K.U. for Museum of Natural History, University of Kansas, U. Mich. for Museum of Zoology, University of Michigan, and U. Md. for University of Maryland. All measurements given in the accounts are in millimeters.

Several species are included in the body of the text for which there are as yet no valid records for the State. These have been indicated by placing the common names in parentheses. They are included because of the virtual certainty that they are a part of Maryland's mammal fauna. Of one of these species, a specimen was taken in West Virginia only a few feet from the Maryland state line; as for the others, Maryland contains abundant suitable habitat and they are known to occur both north and south of the State.

Distribution maps have been prepared for all land species except introduced forms and certain ones that have been restocked or are so widespread in distribution that they have been recorded from every county in the State. On the maps, crosshatched areas represent probable distribution, shaded symbols indicate specimens examined, unshaded symbols indicate published records or other reports that appear to be valid, and an unshaded symbol with a dot in the center indicates a type

locality. When more than one species or subspecies is represented on a single map, circles and triangles are used to distinguish them, and the crosshatchings representing their probable distributions run in different directions.

I want to express my thanks to Theodore A. Bookhout and Vagn Flyger of the University of Maryland's Natural Resources Institute for contributing a number of Maryland mammal records. I also want to acknowledge my gratitude to the late Romeo Mansueti of the Chesapeake Biological Laboratory, Solomons, Md., for his encouragement and advice on a number of distributional problems.

LOCATION AND AREA OF MARYLAND

Maryland lies between the parallels of $35^{\circ} 53'$ and $39^{\circ} 44'$ north latitude and the meridians $75^{\circ} 4'$ and $79^{\circ} 29'$ west longitude. It is bounded on the north by the State of Pennsylvania and on the east by the State of Delaware and the Atlantic Ocean. The southern boundary of the State is the Potomac River which separates it from Virginia and West Virginia. West Virginia also borders Maryland on the west. The District of Columbia is a political entity on the Potomac, between Prince Georges and Montgomery counties, Maryland. It is not physiographically distinct from Maryland in any way, and herein is regarded as a part of Maryland.

The Maryland Geological Survey lists the total area of the State as 12,300.21 square miles, of which 2,437 square miles are water. Thus the total land area of Maryland is 9,863.21 square miles, making the State the eighth smallest in the Union. The area of the District of Columbia is some 70 square miles, of which 8 are water.

Maryland extends in a general ESE-WNW direction for about 320 miles; the greatest north-south distance is approximately 150 miles. The State is actually a narrow cross section of the Coastal Plain, the Piedmont Plateau, and the Appalachian ridges. Elevations pass gradually from sea level to 3,342 feet on Backbone Mountain in Garrett County.

Geologically, Maryland varies greatly. Formations range from the most ancient granite and gneiss, through rocks of every age and great mineralogical diversity down to the coastal deposits of Recent times. Overlying these rock formations are a great diversity of soils. In contrast to its more northern neighbors, Maryland has never been glaciated.

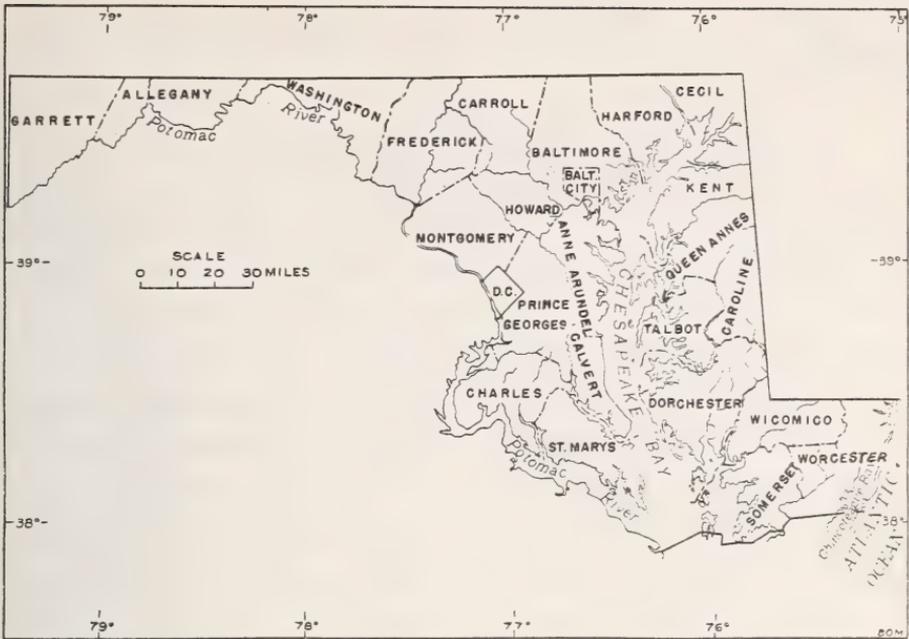


FIGURE 1.—Map of Maryland showing the 23 counties, Baltimore City, and the District of Columbia.

TEMPERATURE

The mean annual temperature for Maryland is 53 to 54 degrees. It varies from area to area, the greatest difference being between Worcester County on the Eastern Shore and Garrett County in the Allegheny Mountains: according to Shreve et al. (1910), the average annual temperature at Sunnyside in Garrett County is 47.1 degrees, whereas at Pocomoke City in Worcester County it is 58, a difference of 11 degrees. At intermediate points the average annual temperatures are also intermediate; the differences that exist are due to such factors as elevation and proximity to the ocean and Chesapeake Bay. The average date for the last killing frost in spring in western Maryland is the first week in May; farther east it is the last 10 days of April. In western Maryland the average time for the first killing frost in autumn is late September; in the eastern part of the State it is early November.

AVERAGE ANNUAL PRECIPITATION

Precipitation is distributed throughout the year, but with a somewhat greater amount in the warmer months than in the cold season. The heaviest rainfall, from 38 to 46 inches, occurs in western Maryland.

The Coastal Plain receives between 40 and 44 inches each year. Calvert County is one of the driest areas of the State and receives only about 36 inches yearly.

EFFECTS OF CIVILIZATION

Maryland, like most other eastern States, has no truly virgin areas. Even in the remotest regions of the western part of the State, logging has been conducted, and fields and pastures range well up onto the sides of the mountains. Some of the wildest parts of the State, until quite recently, were the marshes that lined both the eastern and the western sides of Chesapeake Bay and those along the Atlantic Ocean. With the expanding populations of both Washington and Baltimore seeking areas for summer recreation, many of these marshes are being drained and "improved" for human habitation. In addition, easy access is now available to the outer barrier beach on Assateague Island. The suburban communities of all the larger cities of the State are spreading farther and farther into the countryside and have eliminated some fine woods, swamps, and meadows. This is particularly true of Baltimore and Washington, the suburbs of which now extend 25 miles or more into the surrounding country. As a result, the site where the only specimen of the rare pigmy shrew, *Microsorex hoyi winnemana*, has ever been taken in Maryland is now part of a housing project, and the southeasternmost Coastal Plain locality for the southern bog lemming, *Synaptomys cooperi*, has met the same fate. Nevertheless, a number of areas remain in Maryland which are relatively isolated and which support a varied and abundant mammal fauna. Some species, such as the white-tailed deer and the cottontail rabbit, have actually profited by the changes man has brought to the State.

PRINCIPAL BIOTIC OR NATURAL AREAS IN MARYLAND

Maryland lies in 5 major physiographic provinces (Fenneman, 1938): Coastal Plain, Piedmont, Blue Ridge, Ridge and Valley, and Appalachian Plateaus.

There are three major forest regions (as described by Braun, 1950) in Maryland which correspond roughly to these physiographic provinces. They are the Oak-Pine Forest, the Oak-Chestnut Forest, and the Mixed Mesophytic Forest. Stewart and Robbins (1958) divide these major forest regions of Maryland into biotic or natural sections that represent areas showing floral or faunal differences of a secondary nature. They divide the Oak-Pine Forest region into an Eastern Shore section, an Upper Chesapeake Bay section, and a Western Shore sec-

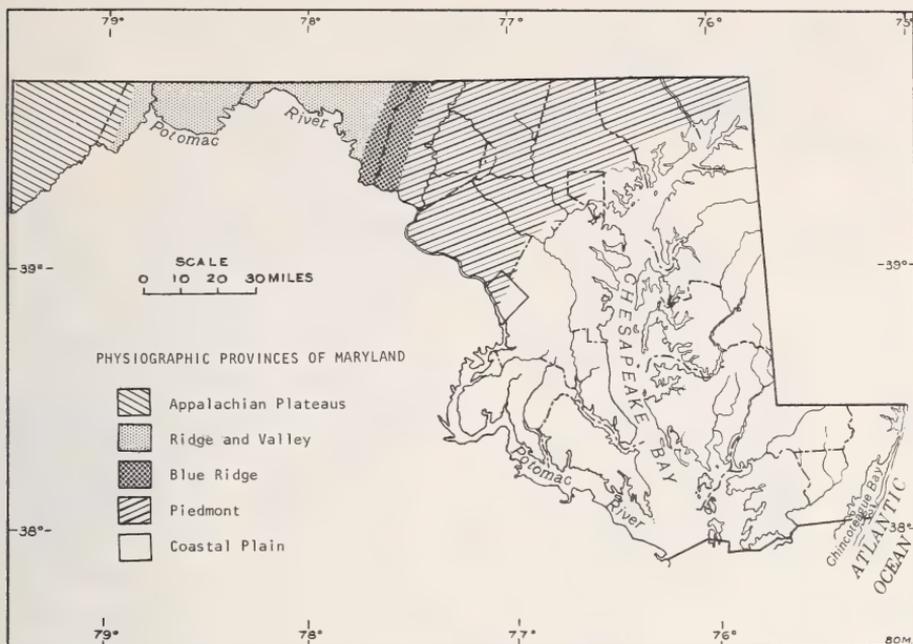


FIGURE 2.—Physiographic provinces of Maryland.

tion. The Oak-Chestnut Forest region is split into a Piedmont section and a Ridge and Valley section, while the Allegheny Mountain section comprises the Mixed Mesophytic Forest region in Maryland.

In general, mammal distribution in Maryland correlates well with these natural areas or sections, and reference is made to them throughout the text. An exception is that of the Upper Chesapeake Bay section (comprising the northern portion of the Eastern Shore, and the Coastal Plain of Baltimore and Harford counties) which seems to be too weakly differentiated as a biotic area from adjacent sections to have any relevance with regard to mammal distribution. This section has been deleted herein, the northern portion of the Eastern Shore being assigned to the Eastern Shore section, and the Coastal Plain of Baltimore and Harford counties being treated as part of the Western Shore section.

The following is primarily a condensation of Stewart and Robbins' description of Maryland's biotic sections.

Eastern Shore Section

The upland forests of this section are composed chiefly of loblolly pine (*Pinus taeda*) stands and oak-hickory forests or a mixture of the two. Along the tidal marshes, loblolly pine is found generally without deciduous associates. The Eastern Shore section is poorly drained and

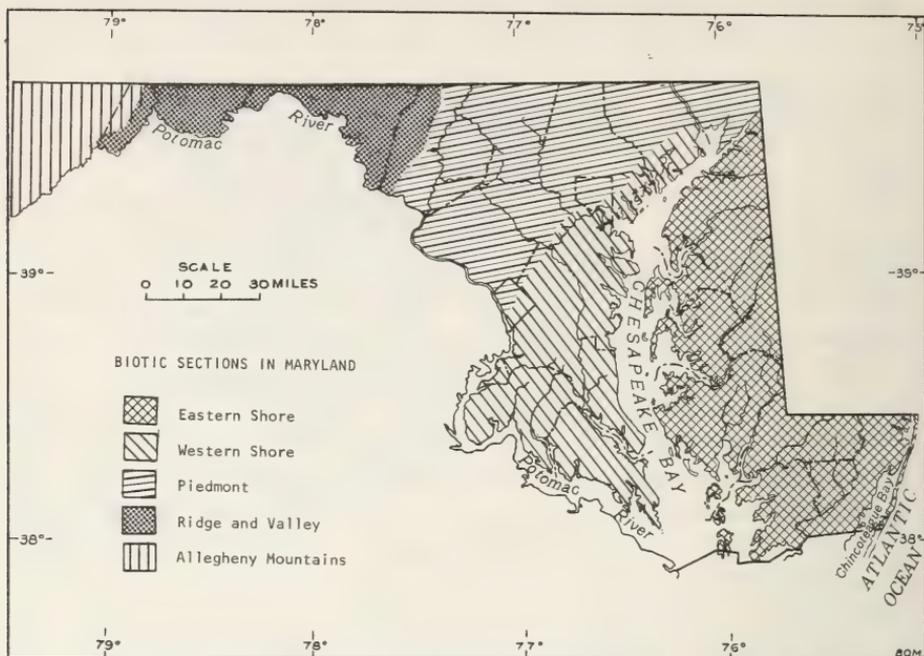


FIGURE 3.—Biotic sections of Maryland.

there are many upland and lowland swamps in which occur sweetgum (*Liquidambar styraciflua*), blackgum (*Nyssa sylvatica*), red maple (*Acer rubrum*), pin oak (*Quercus palustris*), and American holly (*Ilex opaca*). Along the Pocomoke River there are many plants with southern affinities such as bald cypress (*Taxodium distichum*), red bay (*Persea borbonia*), horse-sugar (*Symplocos tinctoria*), water oak (*Quercus nigra*), cross vine (*Bignonia capreolata*), and laurel-leaved greenbriar (*Smilax laurifolia*). In the northern part of this section the upland forests are almost entirely deciduous and of the oak-hickory type. In addition there are such habitats as barrier beaches, salt marshes, and brackish marshes. Elevation is under 100 feet, and the topography is flat.

Western Shore Section

The upland forests of the Western Shore section are composed of scrub pine (*Pinus virginiana*) stands, oak-hickory forests, or a mixture of the two. In the southern part loblolly pine is common, and in the sandy soil of the northern part pitch pine (*Pinus rigida*) frequently predominates. Rich moist upland forests of white oak (*Quercus alba*) and tulip poplar (*Liriodendron tulipifera*) occur locally throughout the section. Small seepage areas are frequent and usually support an upland swamp forest type that contains a well-

developed understory. Flood-plain forests are particularly luxuriant in the Western Shore section. Tidal marshes are commonly found around the numerous estuaries. Elevation is from 100 to 300 feet, and the topography is rolling.

Piedmont Section

The Piedmont section occupies the area of the Piedmont physiological province (Fenneman, 1938) and a small part of the Coastal Plain known as Elk Neck in Cecil County. The forests in this section consist mostly of white oak, black oak (*Quercus velutina*), tulip poplar, smoothbarked hickories (*Carya* sp.), and flowering dogwood (*Cornus florida*). In some areas chestnut oak (*Quercus prinus*) or scarlet oak (*Quercus coccinea*) is common, and occasionally stands of scrub pine or pitch pine are found. Beech (*Fagus grandifolia*) is often encountered on ravine slopes, and mixed mesophytic forest communities occur in some of the larger valleys with steep north slopes. These communities contain a mixture of central and northern hardwoods and sometimes hemlock (*Tsuga canadensis*). Elevations in this section range between 300 and 800 feet, and the topography is gently rolling. Much of the land has been cleared for farming.

Ridge and Valley Section

Chestnut oak is the common tree throughout most of the section, and in the higher elevations it is often found in nearly pure stands. In dry areas and on slopes with southern or western exposure there is scarlet oak, interspersed with occasional stands of scrub pine, pitch pine, or Table Mountain pine (*Pinus pungens*). Most of the ravines and steep northern slopes are occupied by mixed mesophytic forest communities in which the common species are hemlock, white pine (*Pinus strobus*), beech, sweet birch (*Betula lenta*), basswood (*Tilia americana*), sugar maple (*Acer saccharum*), tulip poplar, white oak, and northern red oak (*Quercus rubra*). On the valley floors, white oak, black oak, tulip poplar, and flowering dogwood communities occur. Groves of red cedar (*Juniperus virginiana*) are found in the limestone areas of the Hagerstown Valley. The section consists of a series of parallel ridges that range up to 2,000 feet in elevation.

Allegheny Mountain Section

This area is a high, undulating plateau, averaging about 2,500 feet above sea level. Several ridges, some 500 feet high, cross this plateau diagonally from northeast to southwest. The highest point in the State, Backbone Mountain (3,342 feet), is in this section. Hemlock

and white pine are occasionally encountered on the slopes and in the valleys, but deciduous trees predominate. These include sweet birch, sugar maple, red maple, black cherry (*Prunus serotina*), basswood, beech, shagbark hickory (*Carya ovata*), white oak, and northern red oak. On higher ridges, northern red oak and red maple predominate, with chestnut oaks, black oak, and yellow birch (*Betula lutea*) interspersed. Scattered red spruce (*Picea rubens*) is sometimes also found. In valleys above 2,400 feet, there are some relict bogs consisting of sedge meadows and bog heaths interspersed with patches of alder (*Alnus* sp.), great laurel (*Rhododendron maximum*), red spruce, hemlock, yellow birch, and red maple.

MARYLAND'S MAMMALIAN FAUNA

These biotic sections of Maryland are not sufficiently differentiated to support widely divergent mammalian populations. Some forms are confined to one or two sections of the State, but in general the mammalian fauna does not differ greatly from section to section. The average-fauna formula (Long, 1963) discussed below, reveals that the most significant division in the State is between the Piedmont section and the Ridge and Valley section. The most diversified mammalian fauna is in the Allegheny Mountain section, the most impoverished in the Eastern Shore section.

Long (1963, p. 139) recommends the average-fauna formula, $2C(100)/(N_1 + N_2)$, for deriving a numerical expression of the faunal resemblance of one area to another (in this formula, C = number of kinds common to both faunas, N_1 = number of kinds in smaller fauna, N_2 = number of kinds in larger fauna). Using this formula, and substituting the number of species and subspecies for each section of Maryland, the following comparisons were obtained:

	Western Shore	Piedmont	Ridge and Valley	Allegheny Mountain
Eastern Shore.....	90	83	73	62
Western Shore.....		92	77	67
Piedmont.....			83	68
Ridge and Valley.....				87

These percentages show, as is to be expected in an area of this small size, that the mammal fauna of all the sections of Maryland rather closely resemble one another. Naturally, the most distant sections of the State geographically and ecologically, the Allegheny Mountain and the Eastern Shore, differ the most faunistically. Nevertheless 75 percent of the species and subspecies are common to both sections. The

closest resemblance between two sections is that between the Western Shore and the Piedmont. Surprisingly, the two Coastal Plain sections, the Western Shore and the Eastern Shore, show slightly less resemblance to each other. This is probably due to the isolating effect of the Chesapeake Bay on the Eastern Shore.

The percentages show clearly that the Allegheny Mountain and Ridge and Valley sections have close faunal resemblance, and that as a unit they stand somewhat apart from the three eastern sections. Thus, while the resemblance ratio of the Eastern Shore to the Western Shore is 90 percent, and that of the Western Shore to the Piedmont is 92 percent, the Piedmont has a resemblance to the neighboring Ridge and Valley section of only 83 percent. The resemblance of the Ridge and Valley to its neighboring Allegheny Mountain section returns to 87 percent, indicating that these two sections differ to some extent from the three eastern sections, which in turn appear to form a closely allied mammalian fauna unit. Therefore, the most strongly marked division with regard to mammal distribution in Maryland is that between the gently rolling Piedmont of Montgomery, Howard, Baltimore, Harford, Carroll, and eastern Frederick Counties and the upland Blue Ridge Mountains (Ridge and Valley section) to the west in Washington and western Frederick Counties.

Taken as a whole, Maryland's mammal fauna seems to be more northern than southern in origin. Only a few distinctly southern species (represented usually by small numbers of individuals) reach Maryland. Some of these are *Reithrodontomys humulis*, *Sorex longirostris*, and *Spilogale putorius*. On the other hand, a number of distinctly northern species reach south to Maryland (*Sorex cinereus*, *Mustela erminea*, *Lepus americanus*, *Tamiasciurus hudsonicus*, and a number of others) and extend even farther south, particularly in the Appalachian Mountains, where many of them range as far south as North Carolina and Tennessee.

KEYS

The following keys employ external and easily observable or measurable characters when possible. In a few instances it has been necessary to resort to dental characters when external ones were not sufficiently marked to separate forms. The keys are designed for use on adult animals only.

Key to the Orders of Maryland Land Mammals

- | | | |
|---|--|---|
| 1a. Forelimbs modified as wings..... | <i>Chiroptera</i> (bats) | |
| b. Forelimbs not modified as wings..... | | 2 |
| 2a. Feet provided with hoofs..... | <i>Artiodactyla</i> (even-toed hoofed mammals) | |
| b. Feet provided with claws..... | | 3 |

- 3a. Canine teeth absent; incisors chisel-like----- 4
 b. Canine teeth present; incisors not chisel-like----- 5
 4a. Upper incisors 2-2----- *Lagomorpha* (rabbits, hares, etc.)
 b. Upper incisors 1-1----- *Rodentia* (gnawing mammals)
 5a. Canine teeth similar in appearance to other teeth; eyes inconspicuous-----
 Insectivora (moles, shrews, etc.)
 b. Canine teeth well developed; eyes not rudimentary----- 6
 6a. Tail prehensile; first digit on fore and hind limbs opposable; abdominal
 pouch present in female----- *Marsupialia* (pouched mammals)
 b. Tail not prehensile; first digit not opposable; no abdominal pouch pres-
 ent----- *Carnivora* (flesh eating mammals)

Key to the Order Insectivora in Maryland

- 1a. Forefeet greatly enlarged and adapted for digging----- 9
 b. Forefeet similar in size to hind feet and not adapted for digging----- 2
 2a. Tail short, less than 25 percent of total length of animal----- 3
 b. Tail long, more than 30 percent of total length of animal----- 4
 3a. Coloration grayish; size more than 100 mm.; 32 teeth in mouth
 Blarina brevicauda (short-tailed shrew)
 b. Coloration brownish; size small, less than 100 mm.; 30 teeth in mouth
 Cryptotis parva (least shrew)
 4a. Third and fifth upper unicuspid teeth minute so that only three of the
 five upper unicuspids are visible when skull is viewed laterally
 Microsorex hoyi (pigmy shrew)
 b. Only fifth unicuspid tooth in upper jaw minute so that four unicuspids
 are visible when skull is viewed laterally----- 5
 5a. Total length 145 mm. or more; hind feet large and fringed with stiff
 hairs; third and fourth toes of hind feet thinly webbed for about half
 their length----- *Sorex palustris* (water shrew)
 b. Total length 135 mm. or less; hind feet not conspicuously large and not
 fringed with stiff hairs; no webbing on any toes----- 6
 6a. Tail more than 55 mm. in length; coloration uniform dark gray through-
 out----- *Sorex dispar* (long-tailed shrew)
 b. Tail less than 55 mm. in total length; coloration not uniformly dark
 gray----- 7
 7a. Total length greater than 110 mm----- *Sorex fumeus* (smoky shrew)
 b. Total length under 100 mm----- 8
 8a. Coloration reddish brown----- *Sorex longirostris* (southeastern shrew)
 b. Coloration dull brown or grayish brown----- *Sorex cinereus* (masked shrew)
 9a. Snout fringed with fleshy projections; tail long, more than 50 mm. in
 length----- *Condylura cristata* (star-nosed mole)
 b. Snout not fringed with fleshy projections; tail less than 40 mm. in
 length----- 10
 10a. Tail thin, flesh-colored and scantily haired
 Scalopus aquaticus (eastern mole)
 b. Tail thick, blackish and well haired
 Parascalops breweri (hairy-tailed mole)

Key to the Order Chiroptera in Maryland

- 1a. Interfemoral membrane wholly or partially furred on upper surface----- 2
 b. Interfemoral membrane not furred on upper surface----- 4

- 4a. Coloration of sides orange; tail often tipped with white
Napaeozapus insignis (woodland jumping mouse)
- b. Coloration of sides yellowish; tail never tipped with white
Zapus hudsonius (meadow jumping mouse)
- 5a. Tail bushy..... 6
- b. Tail not bushy..... 10
- 6a. Fore and hind limbs connected by a loose fold of skin; adapting the animal for gliding..... *Glaucomys volans* (southern flying squirrel)
- b. Fore and hind limbs not connected by a loose fold of skin..... 7
- 7a. Tail less than one-quarter of the total length... *Marmota monax* (woodchuck)
- b. Tail greater than one-third of the total length..... 8
- 8a. Coloration reddish-brown above; under 325 mm. in total length
Tamiasciurus hudsonicus (red squirrel)
- b. Coloration not reddish-brown; over 325 mm. in total length..... 9
- 9a. Coloration of upper parts gray, darker along middle of back; under 550 mm. in total length; upper premolars 2-2
Sciurus carolinensis (gray squirrel)
- b. Coloration of upper parts variable-grayish, reddish, or buffy, but sides not noticeably paler than back; over 550 mm. in total length; upper premolars 1-1..... *Sciurus niger* (fox squirrel)
- 10a. Coloration on back reddish, marked with several longitudinal black and white stripes..... *Tamias striatus* (eastern chipmunk)
- b. Back not striped..... 11
- 11a. Tail flattened horizontally, paddle-like..... *Castor canadensis* (beaver)
- b. Tail not horizontally flattened..... 12
- 12a. Tail compressed laterally..... *Ondatra zibethicus* (muskrat)
- b. Tail not compressed laterally..... 13
- 13a. Total length over 325 mm..... 14
- b. Total length less than 275 mm..... 17
- 14a. Total length over 500 mm.; aquatic in habits... *Myocastor coypus* (nutria)
- b. Total length less than 500 mm..... 15
- 15a. Tail length equal to, or more than, half total length of animal
Rattus rattus (black rat)
- b. Tail length less than half total length..... 16
- 16a. Tail well haired, and not conspicuously scaly
Neotoma floridana (eastern woodrat)
- b. Tail scantily haired and noticeably scaly... *Rattus norvegicus* (Norway rat)
- 17a. Tail very short, equal to about one-sixth of total length
Pitymys pinetorum (pine vole)
- b. Tail longer than one-sixth of total length..... 18
- 18a. Tail only moderately short, equal to about one-third of the total length... 19
- b. Tail longer than one-third of total length..... 20
- 19a. Back marked with a wide band of dull red from forehead to rump
Clethrionomys gapperi (red-backed vole)
- b. Back dark brown to nearly black... *Microtus pennsylvanicus* (meadow vole)
- 20a. Line of demarcation between coloration of back and abdomen indistinct; coloration often uniform gray throughout... *Mus musculus* (house mouse)
- b. Sharp line of demarcation between coloration of back and abdomen; abdomen always white..... 21
- 21a. Total length over 225 mm..... *Oryzomys palustris* (rice rat)
- b. Total length under 200 mm..... 22

22a. Coloration on back chestnut brown

Peromyscus leucopus (white-footed mouse)

b. Coloration on back grayish brown-- *Peromyscus maniculatus* (deer mouse)

Key to the Order Carnivora in Maryland

- 1a. Coloration black, or black and white----- 2
 b. Coloration not black----- 4
- 2a. Size large, over 1,200 mm. in total length; tail short and not bushy
Euarctos americanus (black bear)
- b. Under 800 mm. in total length; tail long and bushy----- 3
- 3a. Upper parts marked with no more than two white stripes
Mephitis mephitis (striped skunk)
- b. Upper parts marked with four or more white stripes
Spilogale putorius (spotted skunk)
- 4a. Black facial mask; tail ringed----- *Procyon lotor* (raccoon)
 b. No black facial mask; tail not ringed----- 5
- 5a. Total length under 700 mm----- 6
 b. Total length over 900 mm----- 9
- 6a. Underparts brown except for white spots on chin and throat
Mustela vison (mink)
- b. Underparts whitish or yellowish----- 7
- 7a. No black tail tip; tail less than one-quarter of total length
Mustela nivalis (least weasel)
- b. Black tail tip; tail more than one-quarter of total length----- 8
- 8a. Black tail tip nearly 50 percent of tail vertebrae length
Mustela erminea (ermine)
- b. Black tail tip 40 percent or less of tail vertebrae length
Mustela frenata (long-tailed weasel)
- 9a. Claws retractile; pupils of eyes elliptical; tail short, less than 165 mm
Lynx rufus (bobcat)
- b. Claws not retractile; pupils of eyes not elliptical; tail long, over 300
 mm----- 10
- 10a. Toes of fore and hind feet webbed; tail thick and heavy; aquatic in
 habits----- *Lutra canadensis* (otter)
- b. Toes not webbed; tail not thick and heavy; not aquatic in habits----- 11
- 11a. Coloration reddish; tail tip white----- *Vulpes vulpes* (red fox)
 b. Coloration grizzled grayish; no white tail tip----- 12
- 12a. Total length over 1,050 mm----- *Canis latrans* (coyote)
 b. Total length under 1,050 mm----- *Urocyon cinereoargenteus* (gray fox)

Key to the Order Artiodactyla in Maryland

- 1a. Back brownish, or reddish-olive in coloration, speckled with indistinct
 white blotches; antlers narrow and standing erect above head; small
 canine teeth in upper jaws----- *Cervus nippon* (Sika deer)
- b. Back reddish-brown (summer) or grayish (winter) in coloration, not
 speckled; antlers heavy, and curving forward over head; no canine
 teeth present in upper jaws----- *Odocoileus virginianus* (Virginia deer)

ACCOUNTS OF SPECIES

Order MARSUPIALIA (pouched mammals)

Family DIDELPHIDAE (opossums)

OPOSSUM

Didelphis marsupialis virginiana Kerr

Didelphis virginiana Kerr, The animal kingdom . . . , p. 193, 1792.

Type locality.—Virginia.

General distribution.—In the eastern United States from Vermont, New York, central Michigan, Wisconsin, and Minnesota, south to central Georgia, Alabama, Mississippi, Louisiana, and Texas.

Distribution in Maryland.—Occurs abundantly in all sections of the State.

Distinguishing characteristics.—Teeth 5/4, 1/1, 3/3, 4/4, = 50; tail naked and prehensile; five toes on each foot, the first on each hind foot clawless and thumblike; outer hair long and coarse, underfur short and soft; general coloration grizzled-grayish.

Measurements.—Three adults from Cabin John, Montgomery County, measure: Total length 780, 737, 795; tail vertebrae 298, 325, 333; hind foot 70, 63, 70; greatest length of skull 117.7, 98.6, 111; zygomatic breadth 63.5, 53.5, 54.7.

Habitat and habits.—The opossum prefers densely forested areas. Llewellyn and Dale (1964, pp. 120–121) found that at the Patuxent Research Center, near Laurel, Prince Georges County, this species was primarily an animal of the low, dense woodland, favoring sections near water. They found that well-drained upland woods were less desirable, and the open cleared or cultivated lands seemed to be of slight value for the opossum. Nevertheless, it will frequently wander into meadows and cultivated fields in search of food. The prehensile tail and opposable first toe on the hind foot make this animal almost as much at home in trees as on the ground.

The opossum apparently does not favor the pine woods and salt marshes along the Atlantic coast. One specimen was taken on the Virginia portion of Assateague Island in the early 1930's, but local residents report that none have been seen there in a number of years.

The species is abundant in the Rock Creek Park area of the District of Columbia, often wandering into nearby regions of the city at night, searching for food and sometimes rummaging in garbage pails in residential areas considerably distant from the wooded areas. One such wanderer recently made his abode in the backyard of a row-house near the center of the city where he remained for many weeks,

visiting a nearby porch in the evenings to eat the pet food set out by the owner for her cat.

The opossum is a marsupial, distantly related to such animals as the kangaroo and the koala of Australia. It gives birth to live young, but the young are born in a premature condition and are nursed in the pouch or marsupium of the mother. When born, they are naked or grublike in appearance, but the forelimbs are well enough developed to be used for crawling into the pouch. Development is rapid in the pouch, and within 4 to 5 weeks the young are ready to leave for short periods. Llewellyn and Dale (1964, pp. 118-121) found that in Maryland the opossum begins to breed in early February, and young are found in the pouch until August. Hartman (1952, p. 73) estimates the gestation period as slightly under 13 days. Evidently two litters are produced during a breeding season, but the first litter accounts for the majority of young. Llewellyn and Dale found that the average number of young for 57 litters in pouch was 7.74.

The opossum makes its home in almost any shelter where it can be dry and safe from enemies. This may be under sheds or buildings, in brush piles, or in holes in trees. In its eating habits the opossum is as unselective as it is in finding a shelter. Hartman (1952, p. 62) lists the frequency of foods taken in the following order: insects, fruits, invertebrates (other than insects), mammals, reptiles, grains, birds, and eggs. It also eats carrion.

Specimens examined.—*Montgomery County*: Bethesda, 2; Boyds, 1; Cabin John, 3; Plummers Island, 2; no exact locality, 2. *Prince Georges County*: Beltsville, 2; Bladensburg, 1; Branchville, 4; Greenbelt, 2; Laurel, 36; Patuxent Research Center, 2; T.B., 1. *District of Columbia*: 25.

Other records and reports.—Opossums have been killed in every Maryland county (LeCompte, 1942).

Remarks.—As noted by Gardner (1950, p. 65), Maryland opossums are indistinguishable from Virginia topotypes of *virginiana*.

Order INSECTIVORA (shrews, moles, etc.)

Family SORICIDAE (shrews)

MASKED SHREW

Sorex cinereus Kerr

This species closely resembles the southeastern shrew (*Sorex longirostris*) and the pigmy shrew (*Microsorex hoyi*). The differences between the masked shrew and these other species are discussed under the species accounts of the other two.

There are two subspecies of *Sorex cinereus* in Maryland. These are:

Sorex cinereus cinereus Kerr

Sorex arcticus cinereus Kerr, The animal kingdom . . ., p. 206, 1792.

Type locality.—Fort Severn, Ontario, Canada.

General distribution.—This is a wide-ranging subspecies, distributed over much of the northern part of North America. In the eastern United States it ranges throughout New England, New York, and western Pennsylvania, and south in the Appalachian Mountains to North Carolina.

Distribution in Maryland.—Ridge and Valley, and Allegheny Mountain sections. (See fig. 4.)

Distinguishing characteristics.—Teeth 3/1, 1/1, 3/1, 3/3, = 32; third unicuspid usually larger than, or equal in size to, fourth unicuspid; size very small; snout elongated and pointed; tail long, slightly less than half the total length of the animal; ears short and hidden in fur; coloration in winter pelage dark brown to almost black on upper parts, lighter brown or grayish on underparts; in summer, coloration is somewhat lighter and more brownish.

Measurements.—An adult female from 9 miles east of Oldtown, Allegany County, measures: Total length 88; tail 40; hind foot 11; ear 7; condylobasal length of skull 15.7; cranial breadth 7.4; interorbital breadth 2.3; maxillary breadth 3.9; crown length of upper toothrow (exclusive of first incisors) 5.4.

Habitat and habits.—This shrew is most common around rocks in moist or damp coniferous or deciduous woods. Sometimes it lives in grassy bogs and swamps, but rarely if ever in dry fields or woods.

The nest is located on or near the surface of the ground, in a cavity under a log, rock, or other object. It is composed mainly of leaves, and in shape resembles a flattened sphere some 3 inches in diameter. In its ramblings this shrew utilizes surface runways that it constructs itself and subterranean runways that have been dug by mice.

The masked shrew is a voracious eater and consumes a wide variety of foods. These include beetles, moths, caterpillars, bugs, flies, crickets, spiders, worms, and the flesh of mice and other shrews. It also eats some vegetable matter such as moss and seeds.

Little is known of the breeding habits of the masked shrew. The breeding season may extend from March to September, and as many as three litters may be produced in a single season. The gestation period is probably about 18 days, and from 4 to 10 young are produced per litter, the usual number being 7. The male stays with the female before and after pregnancy and during the early development of the young. A young shrew is able to shift for itself within 20 to 25 days after its birth.

The shrew is physically strong for its size, but being extremely active it seems to burn itself out at an early age. Its longevity is probably not over 2 years if it is allowed to live its full life span.

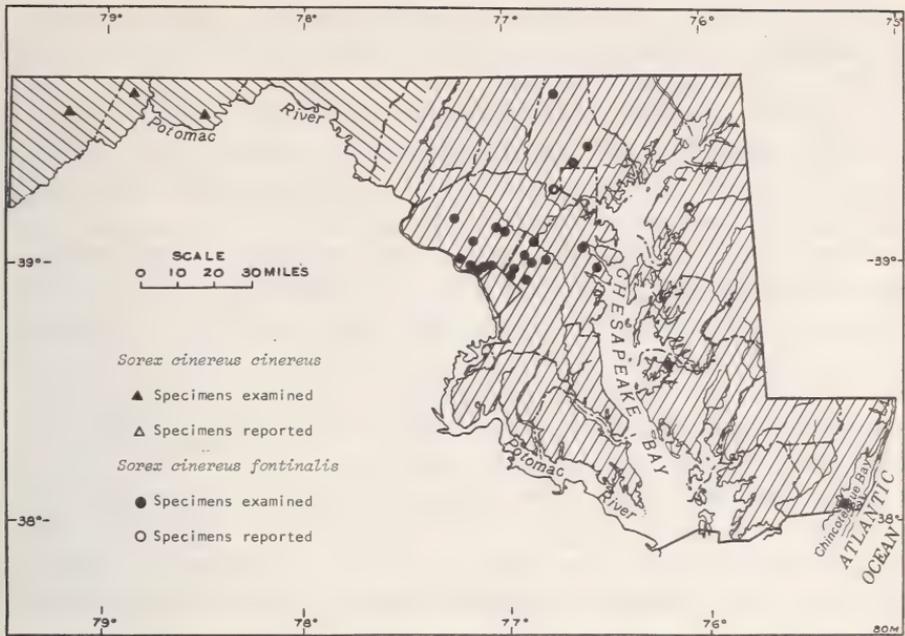


FIGURE 4.—Distribution of *Sorex cinereus fontinalis* and *S. c. cinereus*.

Specimens examined.—*Allegany County*: Mount Savage, 1; Oldtown, 3 miles E, 1; Oldtown, 9 miles E, 1. *Garrett County*: Bittinger, 2; Cunningham Swamp, 4 (Coll. U. Md.).

Sorex cinereus fontinalis Hollister

Sorex fontinalis Hollister, Proc. U.S. National Museum, 40: 378, 17 April 1911.

Type locality.—Cold Spring Swamp, near Beltsville, Prince Georges County, Maryland.

General distribution.—Piedmont and Coastal Plain of Pennsylvania, Maryland, and northern Virginia.

Distribution in Maryland.—Piedmont, Western Shore, and Eastern Shore sections.

The characters of this race seem to be best developed in the lower Piedmont section near Washington, D.C. (near the type locality). Specimens from the Coastal Plain sections of the Eastern Shore and upper Western Shore are less typical and apparently represent intergrades with *S. c. cinereus*, which is distributed to the northeast in New Jersey. In the upper Piedmont the subspecies intergrades with *S. c. cinereus*. No specimens of masked shrew have been taken in the southern part of the Western Shore section (Calvert, St. Marys, and Charles Counties) and perhaps the species does not range this far south in the State.

Distinguishing characteristics.—This subspecies is very similar to *S. c. cinereus* and differs from it only in minor details which are most evident on the skull. Externally, the only apparent differences are somewhat smaller size and shorter tail. The skull is smaller, with a narrower braincase and a shorter, relatively wider rostrum. The unicuspid toothrow is shorter than in *S. c. cinereus*, and the teeth in the unicuspid row are more crowded.

This subspecies of masked shrew closely resembles the southeastern shrew (*Sorex longirostris*), which in the eastern United States reaches the northern limits of its range in Maryland. Differences between the two are discussed under the species account for *Sorex longirostris*.

Measurements.—External measurements of eight adults from the vicinity of Rockville, Montgomery County, are as follows: Total length 81.7 (76–89); tail vertebrae 33.7 (30–35); hind foot 10.6 (10–11). Cranial measurements of five adults from the vicinity of Rockville are: Condylbasal length 14.9 (14.7–15.2); cranial breadth 7.0 (6.7–7.1); least interorbital breadth 2.7 (2.6–2.8); maxillary breadth 4.1 (4.0–4.2); crown length of upper toothrow (exclusive of first incisors) 5.5 (5.3–5.7).

Habitat and habits.—Bures (1948, p. 62) collected 14 masked shrews (which he incorrectly believed to be *Sorex longirostris*) near Lake Roland, Baltimore County. He says that, with two exceptions, all of these shrews were taken in a mixed deciduous woods bordering a railroad siding. Of the two exceptions, one was trapped in a dense tangle of sumac and honeysuckle bordering a marsh, and the other in similar habitat along a small stream paralleling Falls Road. He states that systematic trapping throughout the area confirmed his opinion that this shrew does not wander far from deciduous woods. Hampe (1939, p. 5), however, trapped this shrew in the Patapsco State Park in the marshy pastures near Glenartney, and the type specimen of the subspecies was collected in a cold spring swamp in Prince Georges County.

This shrew apparently does not occur on the outer barrier beaches of the Atlantic Coast. Many weeks of trapping there failed to produce a single specimen. It does inhabit the adjacent mainland, and the skull of one was found in an owl pellet on Mills Island in Chincoteague Bay, Worcester County. The shrew had undoubtedly been captured by the owl on the nearby mainland.

Regarding the nesting habits and young of this species, Hampe (1936) writes that he examined the nest of one which was under a discarded trash-filled box among the leaves about 6 feet from the road between Glenartney and Vineyard, Baltimore County. It was composed of a small bundle of dried and broken leaves loosely packed in a small depression in the ground. It was fairly dry, but the surrounding ground was very damp. This nest was found on 18 October 1936

and contained six blind and hairless young. At the time of this discovery the young were probably a week old, and one of them measured 43 mm. in total length with tail and hind foot measurements of 12 and 6 mm. respectively. The nest was visited again in about 2 weeks, and the young had developed to a size of 77 mm. in total length with tail and hind foot measurements of 33 and 10 mm. They were well furred and quite active. When the nest was visited for the final time on 8 November, only 3 young could be found, and they quickly scampered away into the surrounding brush. The mother was seen in the nest only when it was first investigated on 18 October, and she scurried away very rapidly when the nest was opened.

With regard to feeding and breeding habits of this race not much is known, but they probably are similar to those of *Sorex c. cinereus*. As with *cinereus*, this subspecies appears to be cyclical as far as abundance in particular areas is concerned; some years they are scarce, in others numerous. An example of how abundant these shrews may be in some years is provided by Kyle Barbehenn who collected 60 of them near Germantown, Montgomery County, between November 1958 and January 1959, and more than 150 near Rockville, Montgomery County, from February to April 1959.

Specimens examined.—*Anne Arundel County*: Annapolis, 3 miles NW, 1; Severn Run, 1. *Baltimore County*: Lake Roland, 11; Lock Raven, 5; Pretty Boy Reservoir (near Middletown), 1. *Dorchester County*: Cambridge, 1. *Montgomery County*: Ashton, 1; Bethesda, 1; Cabin John, 1; Chevy Chase, 1; Germantown, 60; Glen Echo Heights, 1; Great Falls, 1; Rockville (near), 153; Sandy Spring, 1. *Prince Georges County*: Beltsville, 1; Bowie, 1; Hollywood, 1; Hyattsville, 5; Landover, 1; Laurel, 3; Patuxent Wildlife Research Center, 3; Tuxedo, 1. *Worcester County*: Mills Island, 1 (from owl pellet).

Other records and reports.—*Kent County*: Chestertown (U.S. Fish and Wildlife Service files). *Baltimore County*: Patapsco State Park (Hampe, 1936).

Remarks.—This shrew was for many years considered a distinct species. Poole (1937, p. 96), however, showed that in Pennsylvania there is an unbroken gradation between this form and *Sorex cinereus* and that the two are only subspecifically separable. In Maryland, the most typical specimens of *fontinalis* are found in the vicinity of the type locality. Farther to the northwest, near Rockville and Germantown, Montgomery County, specimens, although still referable to *fontinalis*, are somewhat larger than typical of the race, and are approaching *cinereus*. The real dividing line for the 2 subspecies in Maryland is that between the Piedmont and the Ridge and Valley sections, those to the west being referable to *cinereus*, those to the east to *fontinalis*. Specimens from north of Baltimore and from the Eastern Shore sec-

tion also appear to be intergrading with *S. c. cinereus*. *S. c. fontinalis* appears to represent the end of a cline with regard to small size, shortening of the rostrum, crowding of the unicuspid toothrow, and short tail.

Maryland represents the southern terminus for the distribution of the species *Sorex cinereus* east of the Appalachian Mountains.

SOUTHEASTERN SHREW

Sorex longirostris longirostris Bachman

Sorex longirostris Bachman, Journal Acad. Nat. Science, Philadelphia, ser. 1, 7 (2) : 370, 1837.

Type locality.—Hume Plantations, swamps of the Santee River (= Cat Island, mouth of Santee River), South Carolina.

General distribution.—The southeastern United States from southern Maryland and the District of Columbia to central Florida, and westward, around the southern end of the Appalachian Mountains to Kentucky, central Indiana, and Illinois.

Distribution in Maryland.—The southern portion of the Western Shore section, and perhaps extending into the lower Piedmont section. Maryland is the northernmost limit of the distribution of the species in the eastern United States.

Distinguishing characteristics.—This shrew may be easily confused with *Sorex cinereus*, particularly the race *fontinalis*, and with *Microsorex hoyi*. It is distinguished from *Sorex cinereus* by the following: size smaller; tail shorter; coloration more reddish in winter pelage; feet smaller; rostrum shorter and blunter; unicuspid toothrow more crowded; and a greater tendency for the fourth unicuspid to exceed the third in size. From *Microsorex hoyi* it differs in a major dental character. In *Microsorex* the third upper unicuspid is minute and disk-like, and not visible when the jaw is seen in side view. The fifth unicuspid is also minute and not visible in side view, so that only 3 unicuspids are visible laterally in the upper jaw, the first, second, and fourth. In *Sorex longirostris* (and *Sorex cinereus*) 4 or 5 unicuspids are always visible when the skull is viewed laterally. In addition, *Sorex longirostris* is somewhat larger, more reddish in coloration, and has a longer tail than *Microsorex hoyi*.

Measurements.—One specimen from Chesapeake Beach, Calvert County, has the following cranial measurements: Condylbasal length 14.3; cranial breadth 6.6; least interorbital breadth 2.9; maxillary breadth 4.1; crown length of upper toothrow (exclusive of first incisor) 5.1.

Three specimens from Raleigh, N.C., average 82.6 mm. in total length and have an average tail length of 30.2 mm.

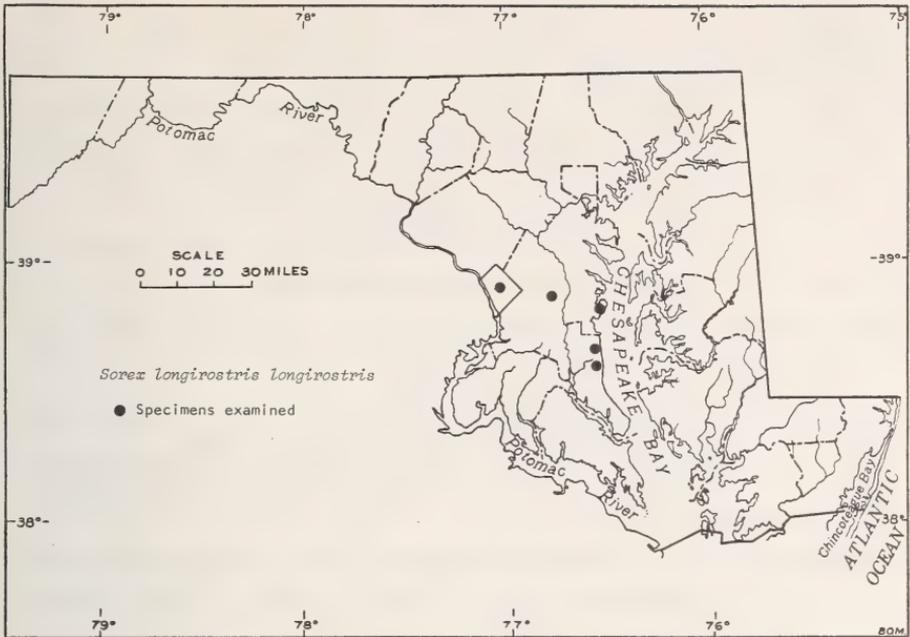


FIGURE 5.—Distribution of *Sorex longirostris longirostris*.

Habitat and habits.—Although this shrew prefers moist situations such as bogs and damp woods, it has on occasion been taken on comparatively high ground. It is a rare species, and little is known of its habits, although they probably do not differ much from those of *S. cinereus*. An interesting sidelight on the specimen from Chesapeake Beach, Calvert County, is a notation on the original label that says “fell over cliffs to bayshore.”

Specimens examined.—*Anne Arundel County*: Shadyside, 1. *Calvert County*: Camp Roosevelt, 2; Chesapeake Beach, 1. *Prince Georges County*: Hall, 1. *District of Columbia*: 1.

Remarks.—It is interesting to note that, in the eastern United States at least, the ranges of *Sorex cinereus* and *Sorex longirostris* do not at present seem to overlap anywhere. North of a certain line (in Maryland this line lies in the Western Shore section between Washington, D.C., and Shadyside, Anne Arundel County) all specimens collected have been *S. cinereus*, whereas south of this line *S. longirostris* only has been taken. There does not appear, however, to be any evidence of intergradation between the species. Specimens of *S. longirostris* from Calvert and Anne Arundel Counties, Md., are just as typical of that species as are those from farther south in North and South Carolina, whereas specimens from Rockville, only a few miles away, are clearly *S. cinereus*. That the two are distinct species is further demonstrated

by the fact that both have been taken in the same field in central Indiana.

In all probability *Sorex cinereus* will eventually be found to be a resident of the southern portion of the Western Shore section, and *S. longirostris* may be distributed through more of the Piedmont and northern Western Shore section than is currently indicated.

(WATER SHREW)

Sorex palustris punctulatus Hooper

Sorex palustris punctulatus Hooper, Occas. Papers Mus. Zool. Univ. Mich., 463 : 1, 15 September 1942.

Type locality.—West Virginia, Randolph County, 6 miles northwest of Durbin, Shavers Fork of the Cheat River, 3,600 feet elevation.

General distribution.—"Allegheny Mountains of eastern West Virginia, and probably also of southwestern Pennsylvania, western Maryland, and northwestern Virginia." (Hooper, 1942, p. 1).

Distribution in Maryland.—Not recorded for the State, but undoubtedly occurs in the higher elevations of the Allegheny Mountain section.

Distinguishing characteristics.—Largest of all the eastern long-tailed shrews; hind feet large, and with a fringe of stiff hairs; third and fourth hind toes joined by thin web at the base for slightly more than half their length; grizzled coloration on upper parts, and pale gray underparts in winter pelage; tail markedly bicolored. Tooth formula as in *Sorex cinereus*, but third unicuspid smaller than fourth. This is an amphibious species, well adapted for an aquatic life.

Measurements.—Hooper (1942) gives some measurements of the type and two paratypes (from Randolph and Preston Counties, W. Va.) as follows: Total length 152, 153, 155; tail 64, 70, 71; hind foot 19, 20, 20; condylobasal length of skull 21.1, 21.2,—, cranial breadth 10.6, 10.3,—; interorbital breadth 3.9, 3.8, 3.9; maxillary breadth 6.5, 6.4, 6.5; maxillary toothrow 7.9, 8.0, 8.1.

Habitat and habits.—This species prefers very wet areas along the borders of streams, lakes, and ponds. Often it is found in marshes and bogs, and in beaver and muskrat houses, particularly in winter. It favors heavily wooded areas and is rarely found in marshes that are devoid of bushes or trees. According to Hooper (1942), the type specimen of the subspecies *punctulatus* was collected under a log at the base of a yellow birch sapling, in a forest of spruce, hemlock, yellow birch, maple, and beech, about 100 yards from Shavers Fork, the nearest body of water. The paratypes were taken at the edge of streams feeding or draining spruce swamps, one specimen among bracken, rhododendron, and hemlock, the other among sedges, rushes, willow, and spruce. There are many areas similar to this in Garret County

which the water shrew may inhabit, and one of the specimens mentioned by Hooper was taken one mile south-southeast of Cranesville, Preston County, W. Va., at an altitude of 2,600 feet, only a few yards from the Maryland State line.

This shrew does not hibernate and is active all winter. It is primarily nocturnal in habits, but occasionally is abroad during daylight hours. It is well adapted to an aquatic life and is one of the best swimmers of the nonmarine mammals. It can swim, dive, float, run along the bottom of a pond or creek, and actually run upon the surface of the water for some distance. Jackson (1961, p. 38) says that he once saw a water shrew run a distance of more than 5 feet across the surface of a pool. The body and head of the animal were entirely out of the water, the surface tension of the water supporting the shrew, and at each step the animal took there appeared to be a little globule of air held by the hair fringe on the hind feet.

Conaway (1952), writing of the western subspecies *navigator*, says that it apparently has an extensive breeding season since pregnant females have been collected in March, suckling females the first week in June, half grown young early in July, a female with five small embryos on August 2, and a male with enlarged testes on 9 August. The number of embryos varies from 4 to 8, and the gestation period is probably about 21 days. These shrews do not live long; Conaway estimates that the maximum age of any specimen obtained would not be in excess of 18 months.

The food of the water shrew consists largely of insect matter, chiefly beetles and their larvae, flies, caddisflies, and mayflies. Snails, leeches, small fish, and fish eggs are also consumed. Vegetable matter probably supplies only a small part of the diet.

SMOKY SHREW

Sorex fumeus fumeus Miller

Sorex fumeus Miller. North American Fauna, 10: 50, 31 December 1895.

Type locality.—Peterboro, Madison County, N.Y.

General distribution.—Eastern North America, from southeastern Ontario and central New England to the Smoky Mountains and northern Georgia. It has also been reported from central Kentucky (Barbour, 1951, p. 102) and southeastern Wisconsin (Jackson, 1928, p. 65).

Distribution in Maryland.—Higher elevations (above 2,000 feet) in the Allegheny Mountain section; may also occur at higher elevations in the Ridge and Valley section. It is not a common species in Maryland.

Distinguishing characteristics.—In summer pelage resembles *Sorex cinereus*, but is larger, has a longer tail, bigger feet, and somewhat

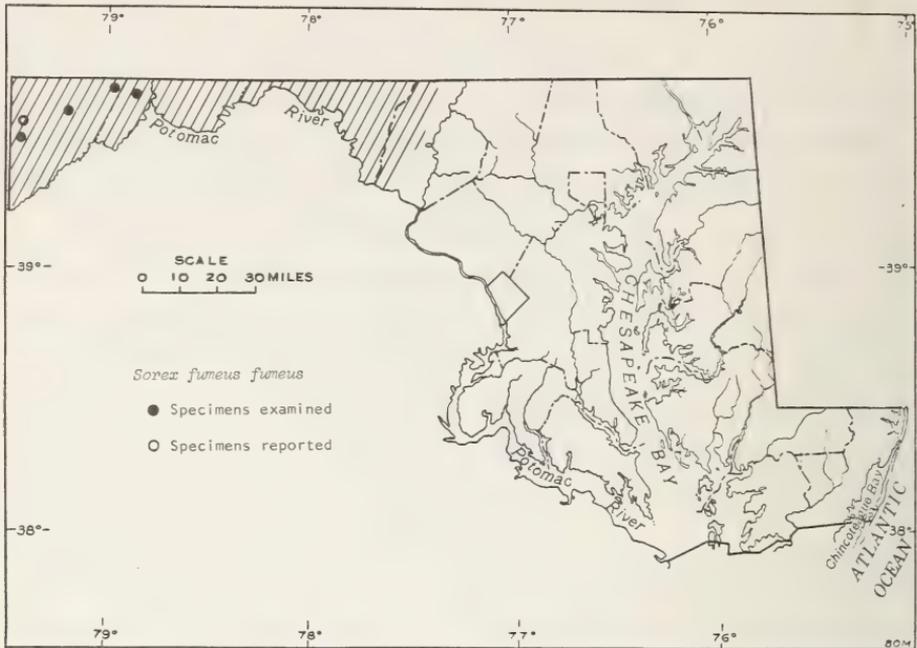


FIGURE 6.—Distribution of *Sorex fumeus fumeus*.

paler coloration. In winter pelage, coloration is grayish, and this shrew resembles *Sorex dispar*, but has a shorter tail. Tooth formula as in *Sorex cinereus*; third unicuspid larger than fourth.

Measurements.—Six adults from Finzel, Garrett County, 6 miles north of Frostburg, average as follows: Total length 110.8 (104–118); tail 44.5 (42–50); hind foot 13.2 (13–14); condylobasal length of skull (average of 3) 17.9 (17.7–18.2); cranial breadth (average of 4) 8.7 (8.6–8.9); least interorbital breadth 3.7 (3.6–3.9); maxillary breadth 5.0 (4.8–5.3); length of maxillary toothrow (average of 5) 6.7 (6.5–6.8).

Habitat and habits.—The smoky shrew is essentially a northern and mountain species and reaches its greatest abundance in the cool forested regions of New England, New York, and Pennsylvania. Most of Maryland apparently does not provide suitable habitat, for it is not a common species in the State. It prefers damp woods and bogs at the higher altitudes, where it lives under moss-covered logs and rocks. E. A. Preble's field notes report that the specimens collected at Finzel were taken in a hemlock and rhododendron swamp, and those at Bittinger, Garrett County, deep in a hemlock forest.

This shrew does not hibernate, and in general is active at all hours of the day and night. Its weak feet are not adapted for digging burrows, and it occupies those made by larger mammals such as the hairy-tailed mole, short-tailed shrew, red-backed mouse, and pine mouse. The

nests are located at various places in these tunnels, a favorite being under a log or stump. These nests, usually made of shredded leaves, are roughly spherical in shape and about the size of a baseball. They generally are situated some 4 to 19 inches below the surface of the ground.

Breeding in this species may begin in late March and the earlier litters appear in early May. As many as three litters may be produced each season, the last appearing in late August. The gestation period is about 20 days, and the young number from 3 to 10, 5 or 6 being the most common.

Hamilton (1940, p. 480) lists the foods of the smoky shrew as the following: insects, earthworms, vegetables, centipedes, snails, salamanders, mammals, sowbugs, spiders, and birds.

Hamilton (1943, p. 486) believes that adults, after completing their reproductive duties, die of old age when 14 to 17 months of age.

Specimens examined.—*Allegheny County*: Mount Savage, 4 (Coll. U. Md.). *Garrett County*: Bittinger, 3; Finzel, 6; Swallow Falls State Forest, 3.

Other records and reports.—*Garrett County*: Cranesville Swamp, one mile SE (Coll. U. Mich.); Sang Run (Coll. Maryland Nat. Hist. Soc.).

LONG-TAILED SHREW

Sorex dispar dispar Batchelder

Sorex macrurus Batchelder, Proc. Biol. Soc. Washington, 10: 133, 8 December 1896. Not *S. macrourus* Lehmann, 1822.

Sorex dispar Batchelder, Proc. Biol. Soc. Washington, 24: 97, 15 May 1911. (A renaming of *S. macrurus* Batchelder.)

Type locality.—Beede's (sometimes called Lenne Heights), in township of Keene, Essex County, N.Y.

General distribution.—Mountainous regions of the eastern United States, from Maine south into North Carolina and Tennessee.

Distribution in Maryland.—Allegheny Mountain section; may occur at higher elevations in Ridge and Valley section. It has been taken in Maryland only at Muddy Creek Falls, in Swallow Falls State Forest, Garrett County (Mansueti and Flyger, 1952, p. 250). It is one of the rarest shrews in Maryland.

Distinguishing characteristics.—Similar to *Sorex fumeus*, but with a longer tail, somewhat smaller size, and a uniform slate-gray coloration in all pelages. Tooth formula as in *Sorex cinereus*, with third unicuspid equal to fourth in size.

Measurements.—External measurements of the type as given in the original description are: Total length 130; tail 60; hind foot 15; ear 10.

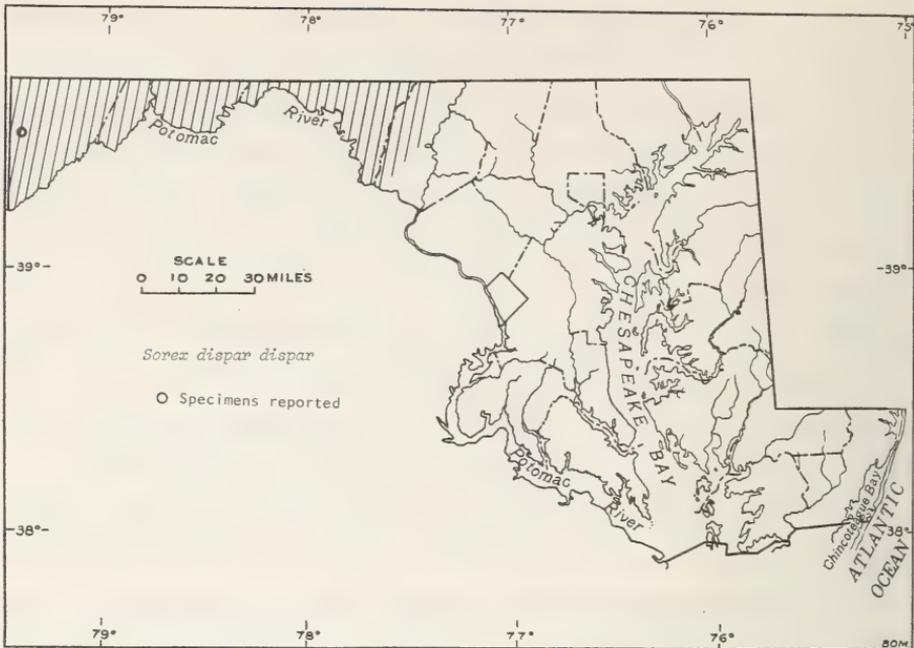


FIGURE 7.—Distribution of *Sorex dispar dispar*.

Some cranial measurements of the type as given by Jackson (1928, p. 90) are: Condylbasal length of skull 18.2; cranial breadth 8.1; interorbital breadth 3.5; maxillary toothrow 6.1.

Habitat and habits.—This shrew prefers moist rocky areas and the crevices between boulders, and large masses of rocks. It has also been taken under moss-covered logs in damp coniferous forests. Mansueti and Flyger (1952, p. 250) report that the three specimens they collected on 6 September 1950, at Muddy Creek Falls, in Swallow Falls State Forest, Garrett County, at an altitude of 2,200 feet, were taken in snap traps placed on ledges in crevices of outcropping sandstone 2 or 3 feet above a small stream's level in a relatively cool moist hemlock and rhododendron forest. Charles O. Handley, Jr. (1956, p. 435) says that the Virginia specimen he took on Big Mountain, Giles County, in September of 1955 was secured in a trap set about 12 inches below the surface in a patch of talus.

Very little is known of the habits of this species, but in all probability it differs little from other long-tailed shrews. Hamilton (1943, p. 39) says that G. H. H. Tate collected a female with 2 embryos in late August in the Adirondack Mountains of New York.

Records and reports.—*Garrett County:* Swallow Falls State Forest, at Muddy Creek Falls (Mansueti and Flyger, 1952).

PIGMY SHREW

Microsorex hoyi winnemana Preble

Microsorex winnemana Preble, Proc. Biol. Soc. Washington, 23: 101, 24 June 1910.

Type locality.—Bank of Potomac River near Stubblefield Falls, Fairfax County, Va.

General distribution.—Maryland, south into western North Carolina.

Distribution in Maryland.—May occur in all sections, but is rare. It has been taken in Maryland only at Berwyn, Prince Georges County.

Distinguishing characteristics.—This is the smallest mammal in North America and possibly the smallest in the world with respect to weight. Externally it resembles *Sorex cinereus* and *Sorex longirostris*, but is smaller and darker (less reddish) and has a shorter tail. Although the tooth formula is the same as that of the genus *Sorex*, there are certain peculiarities in the upper unicuspid toothrow which distinguish it. The third upper unicuspid is minute and disklike, compressed anteroposteriorly between the second and fourth unicuspids, and is not visible when the jaw is viewed laterally. The fifth unicuspid is minute and peglike, and is also not visible in side view, so that only three unicuspids can be seen in the side view of the upper jaw (first,

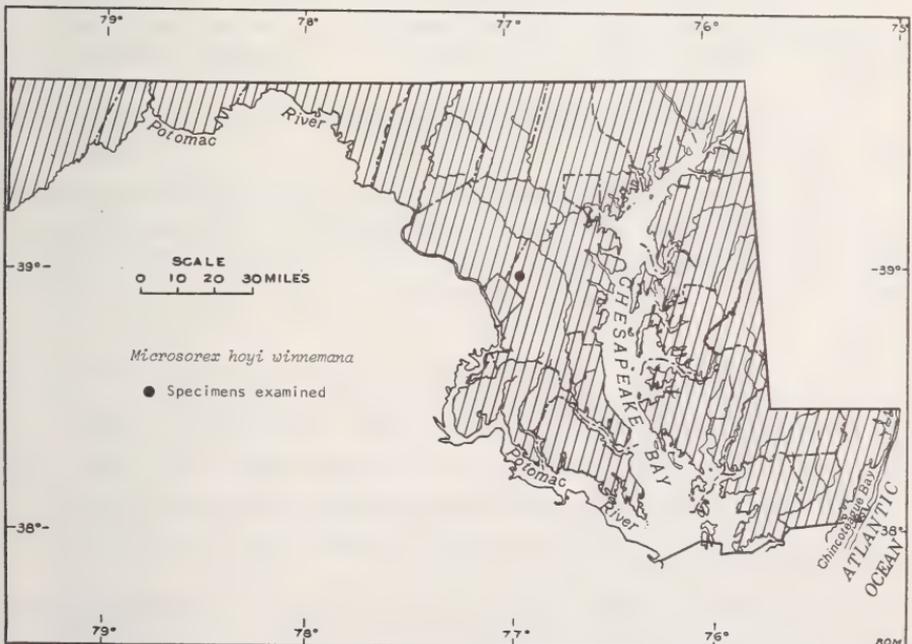


FIGURE 8.—Distribution of *Microsorex hoyi winnemana*.

second, and fourth). This differs from the genus *Sorex* in which four or five unicuspid are always visible when the skull is viewed laterally.

Measurements.—External measurements of the Berwyn specimen are as follows: Total length 86; tail 29; hind foot 9.5. The skull of this specimen is crushed, but some cranial measurements of the type, as given by Jackson (1928, p. 210) are: Condylbasal length of skull 13.0; cranial breadth 6.1; interorbital breadth 2.7; maxillary tooththrow 4.1.

Habitat and habits.—These rare shrews are little known. The type specimen was dislodged from the decayed interior of a large fallen log, and the specimen from Berwyn was found in the decayed heart of a dead chestnut tree, cut from a dry hillside at some distance from water.

Specimens examined.—*Prince Georges County*: Berwyn, 1.

SHORT-TAILED SHREW

Blarina brevicauda kirtlandi Bole and Moulthrop

Blarina brevicauda kirtlandi Bole and Moulthrop, Sci. Publ. Cleveland Mus. Nat. Hist., 5: 99, 11 September 1942.

Type locality.—The Holden Arboretum, Kirtland Township, Lake County, and Chardon Township, Geauga County, Ohio. (The county line bisects the type locality.)

General distribution.—Ranges from northwestern Michigan, eastern Wisconsin, and Illinois, east throughout most of Pennsylvania to central New Jersey and southward through Delaware, Maryland, and West Virginia to southwestern Virginia.

Distribution in Maryland.—Abundant in suitable habitat in all sections of the State.

Distinguishing characteristics.—A large, short-tailed, slate-colored shrew, with a shorter blunter muzzle than any of the shrews previously discussed. The tooth formula is as in *Sorex*, with the fifth unicuspid being minute. The teeth are generally darkly tinged with reddish brown.

Measurements.—Thirty-seven adults from the vicinity of Annapolis, Anne Arundel County, average as follows: Total length 115.2 (107–122); tail 23.3 (19–27); hind foot 14.4 (13–15). Seventeen adults from the vicinity of Annapolis have the following cranial measurements: Condylbasal length 21.9 (20.8–22.7); mastoidal breadth 12.1 (11.4–12.8); interorbital breadth 5.8 (5.3–6.1); maxillary breadth 7.7 (7.3–8.0); unicuspid tooththrow 8.6 (7.9–8.9).

Measurements of eight adults from Cambridge, Dorchester County (Coll. K.U.), are: Total length 103.6 (101–107); tail vertebrae 23.1 (20–25.5); hind foot 13.6 (13–14.5); condylbasal length of skull 21.0

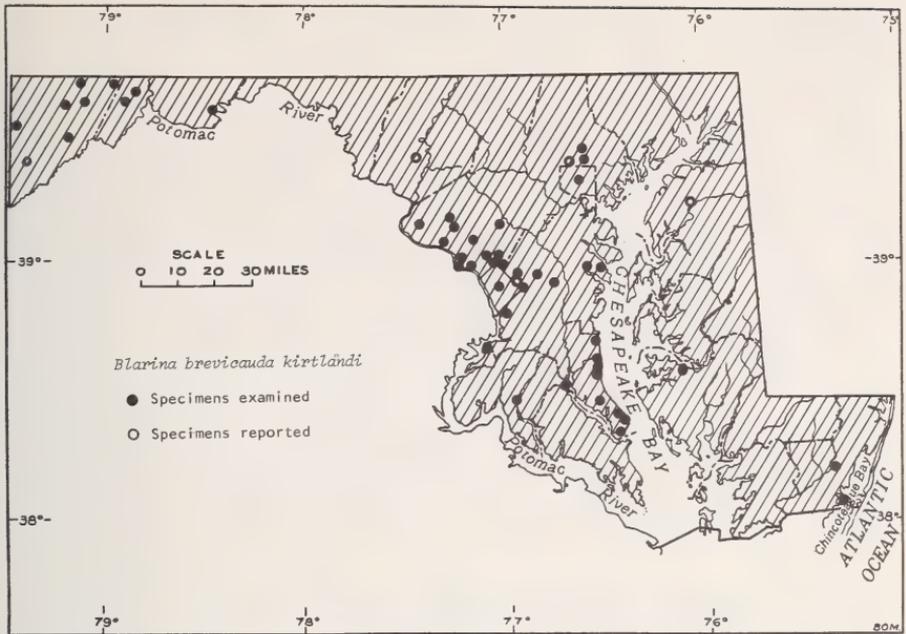


FIGURE 9.—Distribution of *Blarina brevicauda kirtlandi*.

(20.5–21.7); mastoidal breadth 11.3 (11.0–11.7); interorbital breadth 5.4 (5.3–5.6); maxillary breadth 7.3 (7.1–7.6); unicuspid toothrow 7.6 (7.2–8.2).

Habitat and habits.—This is one of the most abundant mammals in Maryland. It is found in a wide variety of habitats, but is most numerous in damp woods where there is a thick understory. It is also encountered in meadows and old fields, but not on the Atlantic barrier beaches of the Delmarva Peninsula, where many weeks of trapping on Assateague Island failed to uncover a single specimen. Elsewhere in the State, this shrew vies with the meadow mouse and the white-footed mouse in abundance, but does appear to be cyclical as regards numbers, and in some years is more plentiful than in others.

The short-tailed shrew, like other Maryland shrews, is active the year around, neither hibernating nor migrating. It is abroad both during daylight hours and at night. It is quick and energetic in its actions, and appears to be constantly on the go during its periods of activity. Its runways zigzag in all directions and lie on the surface of the ground just beneath the vegetation or litter. In these runways, the short-tailed shrew constructs two types of nests. One of these is a small resting nest, and the other a much larger breeding nest. The latter may be some 6 to 10 inches long and averages about 4 inches in diameter. The nests are made of leaves, shredded grasses, and other

vegetable fibers. In general, these nests are not as finely made as most mouse nests.

The breeding season for this species extends from March to September, and usually two or three broods of young are reared each season. The gestation period is from 21 to 22 days, and between 3 and 10 young may be produced, although the average number is slightly below 7. These young leave the nest in 18 to 20 days, and by the time they are 3 months of age they are essentially mature animals. This shrew may live up to 3 years, but the life span is usually less than this, probably not more than 18 or 20 months.

This species has a voracious appetite. Hamilton (1930, p. 30) found that an examination of 244 intestinal tracts from New York State *Blarina* yielded the following food percentages: Insects 47.8, arachnids 2, millipedes 1.7, vertebrates 4.1, crustaceans 6.7, mollusks 5.4, annelids 7.2, centipedes 3.8, plant matter 11.4, inorganic matter 2.3, and undeterminable material 5.2. Only 1.7 percent of the stomachs examined were empty.

The bite of this shrew is poisonous. Pearson (1942) found that a poisonous extract could be prepared from the submaxillary salivary glands of this species and that a toxic material is also present in the saliva and may be introduced into wounds made by the teeth, but because of the small size of the animal its bite probably would have little if any effect on man. There have been reports, however, of distress following the bite of a shrew. Maynard (1889) says that when he was bitten by one of them he experienced considerable pain and swelling in the vicinity of the wound which persisted for a week or longer. Others have been bitten repeatedly by shrews of this species and have experienced no after effects whatsoever other than the distress accompanying the actual breaking of the skin by the sharp teeth.

These shrews appear to be somewhat more gregarious than most other species of shrews. It is not uncommon to capture a specimen each night for 4 or 5 consecutive nights in a trap set in the same place, indicating that the animals are using the same runways if not actually associating with each other. It may be stated, however, that in general this shrew is solitary and pugnacious both to its own kind and to any other creature it may encounter.

Specimens examined.—*Alleghany County*: Frostburg, 1 (Coll. Frostburg State College); Mount Savage, 42; Oldtown (near), 7. *Anne Arundel County*: Annapolis (near), 40; South River and U.S. Route 50 (junction of), 1. *Baltimore City*: 1. *Baltimore County*: Dulaney Valley, 1; Loch Raven, 1. *Calvert County*: Breezy Point, 2; Chesapeake Beach, 1; Cypress Swamp along Battle Creek, 2; Hungerford Creek, 3½ miles N of Solomons, 1; Marine Training Base, ¾ mile N of Solomons, 13; Plum Point, 1; Scientist Cliffs, 2; Solomons, 2. *Charles*

County: Benedict, 1; Marshall Hall, 1; Newport, 7. *Dorchester County*: Cambridge, 15 (14 in Coll. K.U.). *Garrett County*: Bittinger, 5; Cranberry Swamp, 1; Finzel, 13; Grantsville, 5; Mountain Lake Park, 2; Swallow Falls State Forest, 2; Swanton, 4; Wolf Swamp, 2. *Montgomery County*: Burnt Mills, 2; Cabin John, 1; Cropley, 2; Germantown, 1; Kensington, 1 mile N, 2; Plummers Island, 3; Poolesville, 1; Rockville, 17; Rockville, 2.3 miles NE, 6; Sandy Spring, 6; Seneca, 3; Sececa Creek at Clopper Road (Route 117), 1; Silver Spring, 6; Takoma Park, 1. *Prince Georges County*: Northwest Branch Anacostia River, 1; Hyattsville, 5; Lanham, 1; Laurel, 4; Mitchellsville, 1 mile W., 2; Oxon Hill, 12; Prince Georges County Sphagnum Bog, 1. *Worcester County*: Mills Island, 2 (skulls from owl pellets); Snow Hill, 5 miles NE, 1. *District of Columbia*: 107.

Other records and reports.—*Baltimore County*: Lake Roland (Bures, 1948, p. 62); Towson (Gentile, 1949, p. 11). *Frederick County*: Locust Grove (Merriam, 1895, p. 13). *Kent County*: Chestertown (U.S. Fish and Wildlife Service files). *Prince Georges County*: Bladensburg (Bailey, 1896, p. 100).

Remarks.—This species is in need of revision throughout its range. Pending this, only tentative conclusions may be reached regarding the various races and their distribution. At present it appears that three subspecies are distributed along the northeastern coast of the United States. The most northerly race, *talpoides*, ranges throughout most of New England, New York, extreme northern Pennsylvania, and northern New Jersey. It is a large pale race, with an elevated cranium and a long slender rostrum. Distributed along the east coast to the south of *talpoides* is *kirtlandi* from northeastern Ohio, ranging throughout most of Pennsylvania, central and southern New Jersey, Delaware, Maryland, and West Virginia into southwestern Virginia. It is somewhat smaller and darker than *talpoides* and has a shorter, broader rostrum. Distributed to the south of *kirtlandi* is the very small dark southern race *carolinensis*. Several authorities have considered the range of *carolinensis* to extend north to Cambridge, Dorchester County, Md. (Bole and Moulthrop, 1942, p. 108; Gardner, 1950a, p. 67; Jones and Findley, 1954, p. 210). I have examined a number of specimens from this locality (as well as series from farther south on the Delmarva Peninsula) and consider them to be intergrades between *carolinensis* and *kirtlandi*, but closer to *kirtlandi* and referable to that race. The intergrading character of this population is reflected primarily in smaller size, particularly as regards external measurements. The average total length of eight specimens from Cambridge is 103.6 mm. as contrasted with 97.4 mm. for eight specimens from South Carolina (near the type locality of *carolinensis*) and 116 for the type specimen

of *kirtlandi* from northeastern Ohio. Cranially, eight adults from Cambridge average closer in size to *kirtlandi* and have an average condylobasal length of 21.0 and a mastoidal breadth of 11.3, contrasted with an average condylobasal length of 18.4 and mastoidal breadth of 10.1 in typical *carolinensis* (25 specimens from Raleigh, N.C.) and 21.0 and 11.9 in the type specimen of *kirtlandi*. Apparently the entire southern portion of the Delmarva Peninsula is an area of intergradation between *kirtlandi* and *carolinensis*. Specimens I have examined from near Wattsville, Accomack County, Va., and Cape Charles at the southern tip of the Delmarva Peninsula in Northampton County, Va., although still decidedly referable to *kirtlandi*, are smaller in size both externally and cranially than typical *kirtlandi* and appear to be approaching *carolinensis*.

LEAST SHREW

Cryptotis parva (Say)

Sorex parvus Say, in Long, Account of an expedition from Pittsburg to the Rocky Mountains, . . . 1: 163, 1823.

Type locality.—West bank of Missouri River, near Blair, formerly Engineer Cantonment, Washington County, Nebr.

General distribution.—The species is distributed over most of the eastern and midwestern United States, from central New York, Michigan, Wisconsin, Minnesota, and South Dakota, south to Florida in the east, and northeastern Mexico in the west.

Distribution in Maryland.—Occurs in all sections of the State.

Distinguishing characteristics.—Teeth 3/1, 1/1, 2/1, 3/1, = 30; small size; brownish coloration; short tail. Most closely resembles *Blarina brevicauda* but is smaller, more brownish, and has 30 teeth instead of 32. It may be distinguished from all other shrews in Maryland by its short tail.

Measurements.—Six adults from 3/4 mile N of Solomons Island, Calvert County, measure as follows: Total length 76.3 (74–80); tail 15.2 (14–16); hind foot 10 (10–11); condylobasal length of skull 15.2 (15.0–15.6); palatal length 6.5 (6.4–6.9); cranial breadth 7.7 (7.6–8.0); interorbital constriction 3.6 (3.5–3.7); maxillary breadth 5.0 (5.0–5.1); molar toothrow 5.4 (5.2–5.6).

Habitat and habits.—Most commonly found in dry fallow fields and stubble in the uplands, and in the marshes in the coastal areas. This shrew appears to be abundant in some places, and scarce or absent in almost identical habitat elsewhere. Along with *Microtus pennsylvanicus*, it is the most frequently taken small mammal on Assateague Island, where it occurs everywhere except on the sparsely vegetated beach dunes. Another area of abundance for the species is the dry fallow fields of southern Maryland. In such a field, three-fourth mile

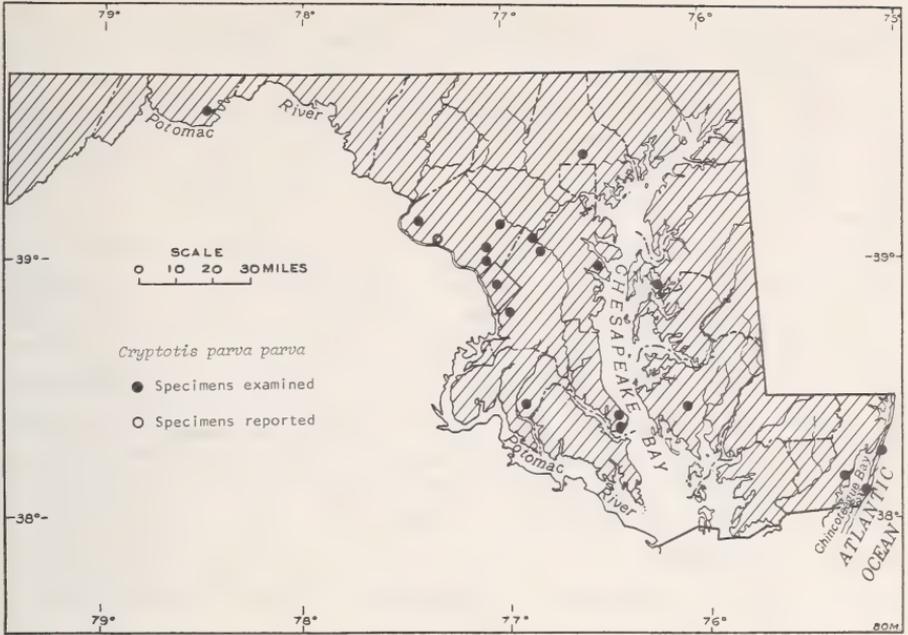


FIGURE 10.—Distribution of *Cryptotis parva parva*.

N of Solomons, Calvert County, this shrew was taken in traps as often as the short-tailed shrew and the house mouse.

This small shrew generally follows the runways of larger mice and shrews, but it also constructs runways of its own. In soft ground it sometimes uses its snout to push dirt away, and by worming its way along may make a tunnel. These small burrows are not much different from those made by certain large beetles or other insects and are difficult to identify. The nest of this species is usually placed in a slight hollow on the surface of the ground, or under a rock or log. Rarely is it located beneath the ground and then only at a depth of 4 or 5 inches or less. Sometimes it will utilize artificial objects such as tin cans in which to nest. The structure of the nest is globular, and composed of dry grass and leaves.

The breeding season for this species is from March to November, and young, born early in the spring, usually breed within the year. The gestation period is about 16 days, and between four and five broods may be produced during a season. The number of young per litter varies from three to nine, with the usual number being four to six.

The food of this species, like that of other shrews, consists primarily of insects and other animal matter. It is known to eat beetles, bugs, grasshoppers, earthworms, millipedes, and snails. It is also said to be fond of salamanders, frogs, and broods of young honeybees.

Unlike most other shrews, the least shrew is gregarious, and may be said to be almost colonial in habits. Jackson (1961, p. 58) says that often when a log, slab, or rock is overturned four to eight or more of these little shrews may be found living together underneath. Maurice K. Brady of Washington, D.C., told Jackson that in Virginia near Washington in 1925 he uncovered a nest of this species which contained 25 *Cryptotis*, all in a pile.

Specimens examined.—*Allegany County*: Oldtown, 9 miles E, 1. *Anne Arundel County*: Annapolis (vicinity), 2. *Baltimore County*: Lock Raven Reservoir, 1. *Calvert County*: Solomons, 1; Solomons, $\frac{3}{4}$ mile N, 7. *Charles County*: Newport, 1. *Dorchester County*: Blackwater National Wildlife Refuge, 1. *Montgomery County*: Bethesda, 1; Kensington, 13; Poolesville, 1; Sandy Spring, 19. *Prince Georges County*: Laurel, 6; Oxon Hill, 1; Patuxent Research Center, 5. *Queen Annes County*: Parson Island, 1. *Worcester County*: Ocean City, 4 and 5 miles S, 7; Ocean City, 15 miles S, 1; Chincoteague Bay, 2. *District of Columbia*: 8.

Other records and reports.—*Montgomery County*: Seneca (Kilham, 1954, p. 252).

Remarks.—This species is in need of revision over its entire range. Until this revision is completed, all specimens from Maryland are provisionally referred to *Cryptotis parva parva*.

Family TALPIDAE (moles)

HAIRY-TAILED MOLE

Parascalops breweri (Bachman)

Scalops breweri Bachman, Boston Jour. Nat. Hist., 4: 32, 1842.

Type locality.—Martha's Vineyard, Massachusetts (there is some question, however, whether this species ever occurred on Martha's Vineyard Island).

General distribution.—Northeastern United States and adjacent Canada, south in the Appalachians to western North Carolina.

Distribution in Maryland.—Occurs at higher elevations in the Allegheny Mountain and Ridge and Valley sections.

Distinguishing characteristics.—Teeth $3/3$, $1/1$, $4/4$, $3/3$, = 44; tail short and hairy; coloration dark slate to black dorsally, slightly paler below; pelage soft and thick, but somewhat coarser than in the eastern mole (*Scalopus aquaticus*); palms enlarged and nearly circular in outline; toes not webbed.

This species can readily be distinguished from the eastern mole by its hairy tail, and from the star-nosed mole (*Condylura cristata*) by the absence of nasal projections.

Measurements.—Jackson (1915: 80) gives external measurements of eight males from Magnetic City, N.C., as follows: Total length 149.5

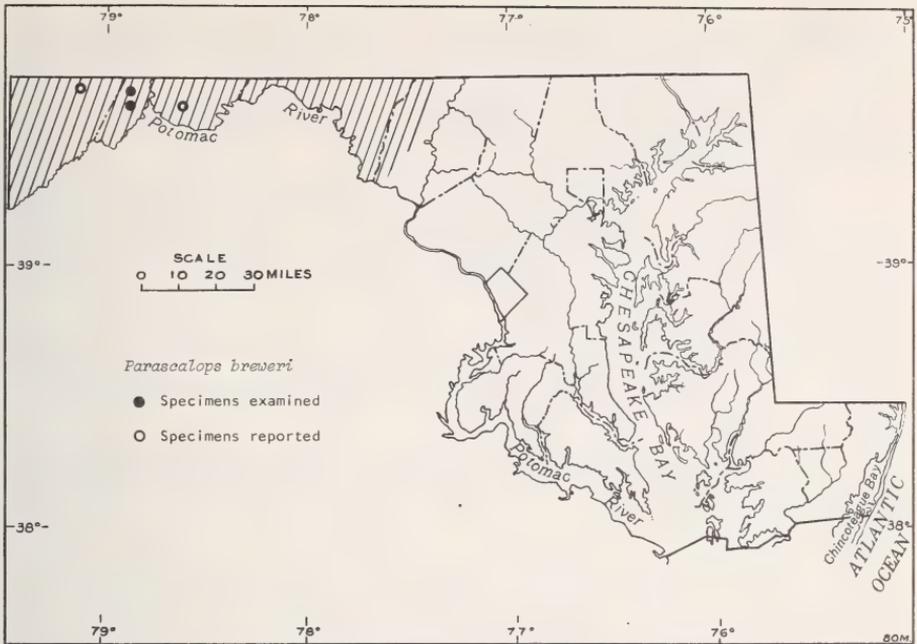


FIGURE 11.—Distribution of *Parascalops breweri*.

(139–152); tail vertebrae 30 (23–36); hind foot 19.5 (18–20). He gives some measurements of the skulls of 10 adult males from Magnetic City as follows: Greatest length 32.4 (31–33.8); mastoidal breadth 14.5 (13.9–15); interorbital breadth 7.3 (7.1–7.5); maxillary toothrow 9.9 (9.2–10.2). Females average smaller than males.

A male (probably immature) from Vale Summit Road, between Clarysville and Vale Summit, Allegany County, has the following external measurements: total length 136; tail 22; hind foot 16. This animal weighed 35.7 grams.

Habitat and habits.—In Maryland this mole is found only at high elevations in the western part of the State, where it lives in loose well-drained light soils. It may be found in pastureland, as well as in the deep woods, but is seldom encountered in damp areas or in clay soils. Although the eastern mole (*Scalopus aquaticus*) also occurs in western Maryland, it appears to be ecologically or at least altitudinally separated from the hairy-tailed mole. The eastern mole has been taken in the lowlands; the hairy-tail only at higher elevations.

This species makes irregular subsurface runways which form an elaborate network. In the winter these tunnels are deep so as to avoid the freezing temperatures of the upper layers of earth. Nests are constructed in these deep burrows, some 10 to 20 inches below the surface of the ground. These are made of dried grasses and leaves, and are some 6 inches in circumference.

Mating occurs in March or April, and four to five young are produced in late April or May after a gestation period of probably a month. The young moles develop rapidly and are able to shift for themselves within a month. They are sexually mature and able to breed the following spring.

The primary foods of this species are earthworms, insects, insect larvae, and other arthropods. They are very voracious eaters, and Hamilton (1943, p. 27) reports that a captive mole of this species weighing 50 grams consumed 66 grams of earthworms and insect larvae within a 24-hour period.

Specimens examined.—*Allegheny County*: Mount Savage, 1. (Coll. U. Md.); Vale Summit Road, between Clarysville and Vale Summit, 1 (Coll. U. Md.).

Other records and reports.—*Allegheny County*: Warrior Mountain (U.S. Fish and Wildlife Service files). *Garrett County*: Grantsville, near (Coll. U. Mich.).

Remarks.—Two specimens of this species from Grantsville, Garrett County, collected 28–29 August 1949 by J. A. King, and now stored in the Museum of Zoology, University of Michigan, are the first actually taken in this State. The species, however, is probably not as rare in western Maryland as the few trapping records and reports would indicate.

EASTERN MOLE

Scalopus aquaticus aquaticus (Linnaeus)

(*Sorex*) *aquaticus* Linnaeus, Syst. Nat., ed. 10, 1: 53, 1758.

Type locality.—Philadelphia, Pa. (Fixed by Jackson, N. Amer. Fauna 38, p. 33, 30 September 1915).

General distribution.—Eastern United States, from southern New England, and New York State, south to Virginia, and in the Appalachian Mountains south to Tennessee, North Carolina, and South Carolina.

Distribution in Maryland.—Eastern Shore, Western Shore, and Piedmont sections and at lower elevations in the Ridge and Valley and Allegheny Mountain sections. Rare or absent apparently in the Ridge and Valley, and Allegheny Mountain sections at elevations over 2,000 feet.

Distinguishing characteristics.—Teeth 3/2, 1/0, 3/3, 3/3, = 36; forefeet broad and greatly enlarged, adapted for digging; body stout and cylindrical; pelage soft and velvety, black to brownish black in coloration; tail short and naked; eyes and ears small and not visible on superficial examination.

Differs from the hairy-tailed mole (*Parascalops breweri*) in that the tail is short and naked, and from the star-nosed mole (*Condylura cristata*) in that the snout is without fleshy projections.

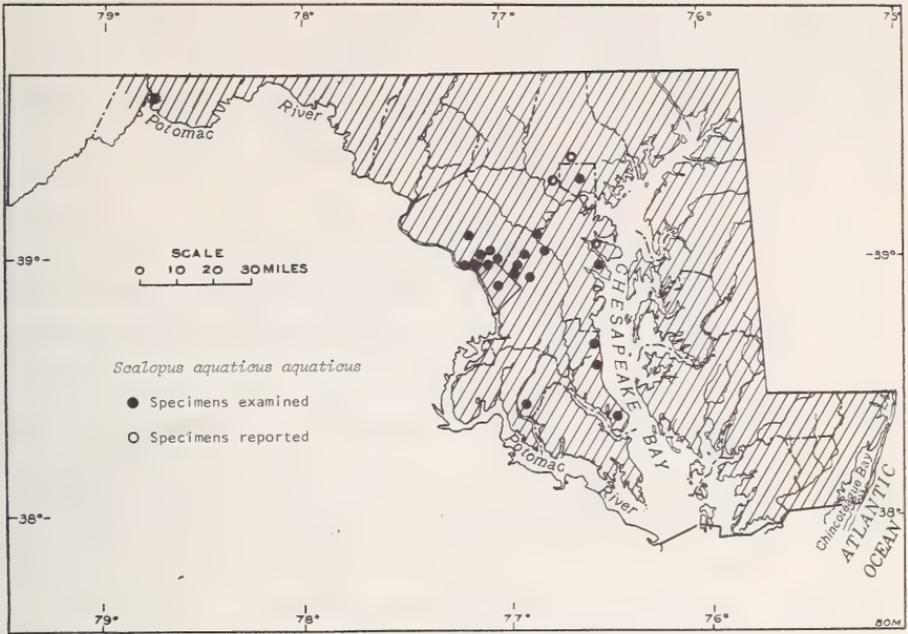


FIGURE 12.—Distribution of *Scalopus aquaticus aquaticus*.

Measurements.—Jackson (1915, p. 34) gives external measurements of 15 adult males from Washington, D.C., as follows: Total length 163.4 (154–175); tail vertebrae 26.5 (22–29); hind foot 19.8 (18–21).

Cranial measurements for 21 adult males from Washington and vicinity are: Greatest length 34.3 (33.2–35.6); mastoidal breadth 17.7 (17–18.3); interorbital breadth 7.4 (7.2–7.8); maxillary toothrow 10.8 (10.4–11.3). Females average smaller than males in size.

Habitat and habits.—The eastern mole normally lives in sandy soils and light loams in meadows, pastures, cultivated fields, gardens, lawns, and thin woods. Rocky areas and swamps are generally avoided since they are barriers to the mole's burrowing activity. It does, however, prefer moist situations to dry ones. Very sandy regions, such as the barrier beaches that line Maryland's ocean front, are apparently unfavorable to the eastern mole, and many weeks of searching for their signs near Ocean City, Worcester County, and on Assateague Island to the south proved fruitless. Bures (1948, pp. 61–62), found moles in the Bare Hills–Lake Roland area of Baltimore County to be restricted to the moist or wet soil bordering the Lake and along the two streams that empty into Jones' Falls. He says that numerous individuals were observed at work on the lawns of property fronting Falls Road. In the Ridge and Valley and Allegheny Mountain sections, there is evidence that this species occurs only in the lowlands, whereas higher up on the

mountains it is replaced by the hairy-tailed mole. In Mason County, W. Va., McKeever et al. (1952, p. 25) found an eastern mole inhabiting the sandy soil of the Ohio River bottomland and a hairy-tailed mole in the nearby forest-covered hills. This distribution occurs in the Appalachians in general, including the Ridge and Valley and Allegheny Mountain sections of Maryland.

The eastern mole does not hibernate, but is active the year round. It constructs a series of burrows just beneath the surface of the ground during wet weather to facilitate the capture of earthworms which form a major part of its diet. In dry and cold weather this species digs deeper permanent burrows some 10 or more inches below the surface. Rarely does the eastern mole emerge from its subterranean burrows and prowl about above ground. A nest is built in one of the permanent burrows, which may be from 5 to 18 inches down, usually under the roots of shrubs or stumps. It is most often made from grass and rootlets, but occasionally leaves are employed. This nest is placed on the bottom of a flattened ellipsoidal enlargement of the tunnel, the length of which is about 8 inches and the diameter about 5.

Mating in this species takes place in March and continues into April. The young are born in the latter part of April or in May. The gestation period is about 45 days, and from two to five young are born each season. By the time a young mole is 5 weeks of age it is more than half the size of the mother.

Eighty percent of the diet of the eastern mole is animal matter, consisting primarily of worms, insects, and insect larvae. Some of the favorite foods are beetles, earthworms, wireworms, white grubs, spiders, centipedes, millipedes, slugs, and insect and mollusk eggs. Some of the plant matter consumed are corn, potatoes, grass, tomatoes, apples and occasionally wheat and oats. The eastern mole is a voracious eater and in 24 hours may consume a quantity of food equal to its weight.

Moles are harmful when they disfigure lawns and provide highways in gardens for field and pine mice. Their destruction of insects places them in a more favorable light. A friend once told me that these moles had almost eliminated the larvae of Japanese beetles on his grounds. Tunneling activities of moles aid in the formation of soil. (Hamilton, 1943, pp. 23-24).

Specimens examined.—*Allegheny County*: Cumberland, 3 (Coll. U. Md.). *Anne Arundel County*: Annapolis, 3 miles NW, 1; no exact locality, 2. *Baltimore City*: 2. *Calvert County*: Chesapeake Beach, 1; Plum Point, 1; Solomons, 4 miles N, 1. *Charles County*: Newport, 3. *Howard County*: no exact locality, 1 (embryo in alcohol). *Montgomery County*: Cabin John, 2; Capitol View, 1; Chevy Chase, 1; Plummers Island, 5; Rockville, 2; Seven Locks, 1; Silver Spring, 4; Woodside, 4. *Prince Georges County*: Beltsville, 2; Berwyn, 1; Branchville,

4; Brookland, 1; Highland, 1; Landover, 2; Laurel, 13; Mount Rainier, 1; Patuxent Research Center, 1. *District of Columbia*: 83.

Other records and reports.—*Anne Arundel County*: Severna Park (Cooper, 1953, p. 79). *Baltimore County*: Lake Roland (Bures, 1948, p. 61); Patapsco State Park (Hampe, 1939, p. 5). *Montgomery County*: Forest Glen (Bailey, 1896, p. 100).

STAR-NOSED MOLE

Condylura cristata cristata (Linnaeus)

(*Sorex*) *cristatus* Linnaeus, Syst. nat., ed. 10, 1: 53, 1758.

Type locality.—Eastern Pennsylvania.

General distribution.—Southeastern Canada, and northeastern United States, south to central Minnesota, Wisconsin, Indiana, Ohio, eastern West Virginia, and northern Virginia.

Distribution in Maryland.—Locally abundant in all sections of the State although apparently rare or absent in some areas with suitable habitat.

Distinguishing characteristics.—Teeth 3/3, 1/1, 4/4, 3/3, = 44; body form mole-like, but more slender; forefeet broad and enlarged for digging, but not to the same extent as in *Scalopus*; pelage black in coloration, somewhat harsher in texture than that of *Scalopus*; tail long, and at certain times of the year enlarged. The most distinctive feature of this mole is the snout, which is fringed with 22 pink projections, or tentacles, and is responsible for the popular name of the animal.

Measurements.—Two adults from the District of Columbia measure as follows: Total length 183, 185; tail vertebrae 65, 66; hind foot 28, 28; greatest length of skull 33.9, 33.4; mastoidal breadth 12.8, 12.8; interorbital breadth 6.8, 6.7; maxillary toothrow 6.6, 6.3.

Habitat and habits.—The star-nosed mole prefers damp habitat in meadows, fields, woods, or swamps, but is sometimes taken in the leaf mold of dense forests, or in relatively dry fields in which there are a few damp spots from which its tunnels radiate. Occasionally it is found at a considerable distance from any water. One specimen was captured in June 1958 in the lower Eastern Shore section near Watts-ville, Accomack County, Va., a few miles from the Maryland boundary. It was taken in a museum special mouse trap set in a surface runway in dry meadow at least a fourth of a mile from the nearest water. Generally, however, the star-nosed mole will be encountered in very wet situations, and its tunnels frequently lead directly into a stream or pool. This animal is an efficient swimmer, using its broad forefeet as oars and its tail as a scull.

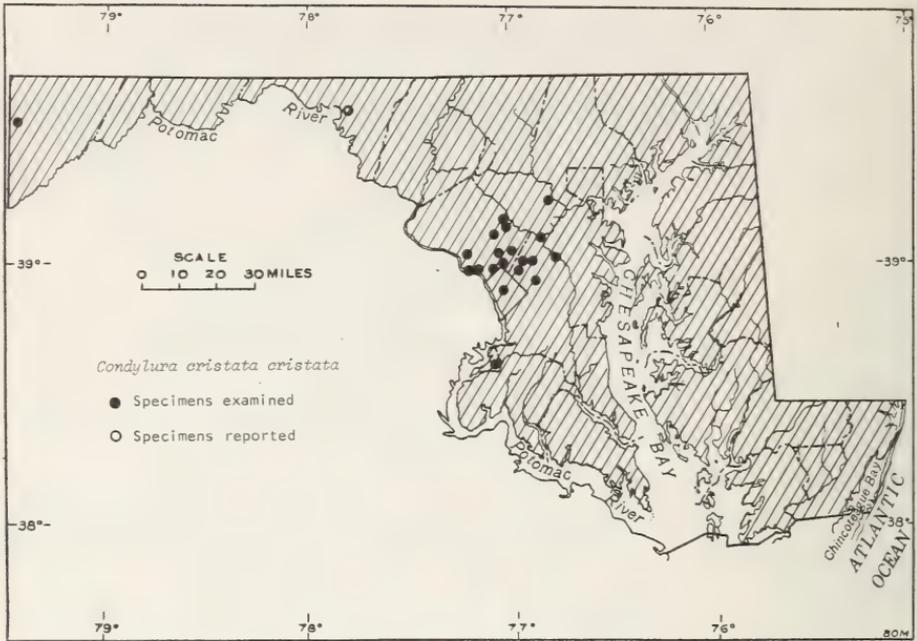


FIGURE 13.—Distribution of *Condylura cristata cristata*.

The star-nosed mole is less fossorial than the eastern or hairy-tailed moles; it is active both day and night, summer and winter. It often uses surface runways, and sometimes in the winter it will burrow in the snow, or even run across it. The tunnels that this species digs are more irregular in pattern than those of other Maryland moles. These burrows are deep in places, and then abruptly rise to near the surface. Frequently the tunnels enter the bank of a stream a foot or more below the water line. The nest of the star-nosed mole is constructed of leaves and grass and is located in a flattened spherical chamber about 5 or 6 inches in diameter and some 4 or 5 inches high. It is usually placed 3 or 4 inches below the surface of the ground, but may be as much as 10 inches down. It is always, however, above the high water level.

It is believed that star-nosed moles pair in the autumn and remain together until the young are born. Breeding occurs in the spring, and birth is from April to June, the gestation period being about 45 days. There is only a single litter per year, and the size of the litter varies from three to seven, six being the usual number. The young mature rapidly and are ready to leave the nest within about a month's time. Star-nosed moles are more gregarious than other eastern moles, and may perhaps, be colonial, although colonies are probably formed through family lineage.

Star-nosed moles are amphibious, and spend a good deal of time in water. They are excellent swimmers and divers, and a large portion of their food consists of aquatic insects and worms, only about one fourth of the diet being composed of terrestrial forms.

Specimens examined.—*Charles County*: Marshall Hall, 1. *Garrett County*: Cranesville Swamp, 1. *Howard County*: Ellicott City, 1. *Montgomery County*: Brookeville, 1; Burnt Mills, 1; Cabin John, 1; Chevy Chase, 1; Chevy Chase Lake, 1; Oakdale, 1; Plummers Island, 1; Potomac P.O., 1; Sandy Spring, 1; Silver Spring, 1; Woodside, 2. *Prince Georges County*: Beltsville, 1; College Park, 2; Glenndale, 1; Lanham, 1; Laurel, 2; Patuxent River Marsh, 1; no exact locality, 1. *District of Columbia*: 10.

Other records and reports.—*Prince Georges County*: Branchville (U.S. Fish and Wildlife Service files). *Washington County*: Williamsport (Jackson, 1915, p. 91).

Remarks.—Maryland specimens average somewhat smaller in size, both externally and cranially than typical *C. c. cristata*, and are tending in this character toward the smaller southern subspecies *C. c. parva*.

Order CHIROPTERA (bats)

Family VESPERTILIONIDAE (vespertilionid bats)

LITTLE BROWN MYOTIS

Myotis lucifugus lucifugus (Le Conte)

V[*espertilio*]. *lucifugus* Le Conte, in McMurtrie, The animal kingdom . . . by the Baron Cuvier, vol. 1, App., p. 431, 1831.

Type locality.—Georgia; probably the Le Conte plantation near Riceboro, Liberty County.

General distribution.—Eastern and northern North American from Alaska and Labrador south in the Appalachians to Georgia, and west into Arkansas.

Distribution in Maryland.—Abundant in all sections of the State.

Distinguishing characteristics.—Teeth 2/3, 1/1, 3/3, 3/3, = 38; face covered with fur except for lips and nostrils; ears moderately long, not extending beyond nostrils when laid forward; tragus slender and pointed; wing membrane between humerus and knee sparsely furred; interfemoral membrane not furred; coloration rich brown, almost bronze; young animals much darker in coloration; sagittal crest usually lacking on skull.

Measurements.—Eight adults from the District of Columbia have external measurements as follows: Total length 85.6 (80–95); tail vertebrae 38.5 (36–42); hind foot 8.9 (8.0–10.5). Some cranial measurements of seven adults from Washington, D.C., are as follows:

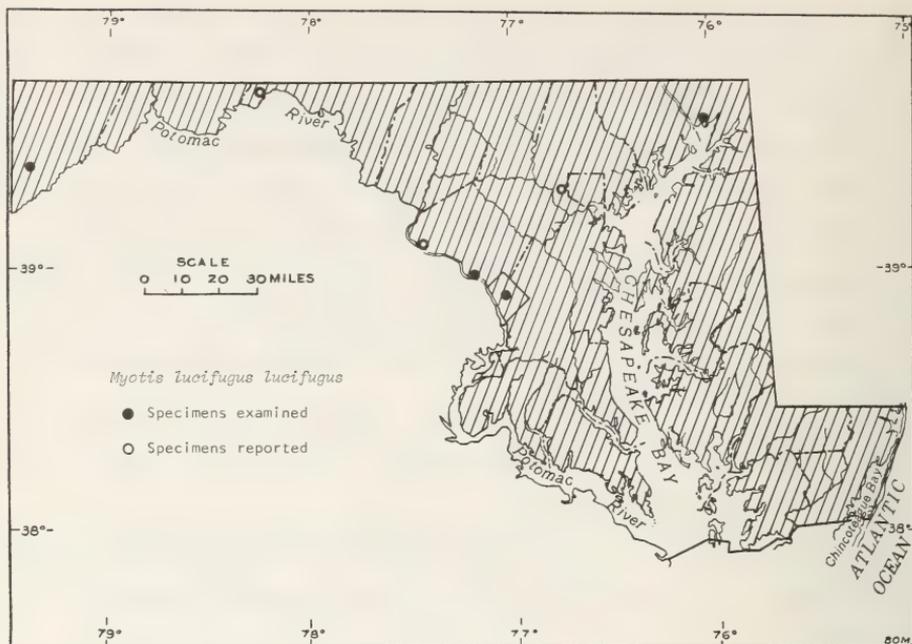


FIGURE 14.—Distribution of *Myotis lucifugus lucifugus*.

Greatest length 14.0 (13.7–14.2); zygomatic breadth 8.4 (8.0–9.1); interorbital breadth 4.0 (3.9–4.2); length of maxillary toothrow 5.1 (5.0–5.2).

Habitat and habits.—This species occurs almost everywhere, roosting in the attics of houses, in hollow trees, or in caves. It is gregarious by nature; in the attic of one house near Seneca Point, Cecil County, over 9,000 were found roosting at one time.

The little brown myotis hibernates in winter and, in some areas at least, is migratory in habits, traveling “flyway” routes from winter hibernating quarters to summering areas. During these migrations they may travel as far as 100 to 150 miles or more, returning by similar routes to their winter quarters. The migratory patterns of Maryland’s little brown myotis have not been studied, but the files of the Bat Banding Office, U.S. Fish and Wildlife Service, contain two records of movements of this species into the State. In both instances, the little brown myotis were banded in Hellhole Cave, Pendleton County, W. Va., in March 1964 and were picked up in the vicinity of Deep Creek Lake in Garrett County in June and July of 1964. Perhaps some of Maryland’s *Myotis lucifugus* population winters in caves in West Virginia and Virginia, and travels north to forage in Maryland during the summer. Others that winter in Maryland may venture further north into Pennsylvania in the summer months.

Mating in this species usually occurs in the autumn, before the bats enter hibernation. Normally the spermatozoa survive in the uterus throughout the winter, and fertilization occurs the following spring. Copulation, however, may occur during the winter or in the spring. The gestation period probably is about 80 days, and the young are born in late May or early June. Usually only a single offspring comprises a litter, but occasionally two are produced. In about 4 weeks after their birth, the young are flying and foraging for their own food. Sexual maturity is achieved at about 8 months. There is only one litter per season.

The food of the little brown myotis appears to be composed entirely of insects, particularly nocturnal species of moths, beetles, and bugs. It has a voracious appetite, consuming large numbers of insects nightly.

This bat is long-lived; there are records of banded animals recovered in good health as much as 20 years after banding.

Specimens examined.—*Cecil County*: Seneca Point, 1. *Garrett County*: Oakland, 1. *Montgomery County*: Plummers Island, 1. *District of Columbia*: 29.

Other records and reports.—*Baltimore County*: Patapsco State Park (Bull. Nat. Hist. Soc. Maryland 10 (1), p. 5, 1939). *Garrett County*: Deep Creek Lake (banding recovery record). *Montgomery County*: Edwards Ferry (banding recovery record). *Washington County*: Round Top Mountain, near Hancock (banding record).

Remarks.—This bat is far more common than the few locality records above would indicate. It is probably the most abundant bat in Maryland.

KEEN'S MYOTIS

Myotis keenii septentrionalis (Trouessart)

[*Vespertilio gryphus*] var. *septentrionalis* Trouessart, *Catalogus mammalium* . . . , fasc. 1, p. 131, 1897.

Type locality.—Halifax, Nova Scotia, Canada.

General distribution.—Eastern North America, from Newfoundland, Nova Scotia, Quebec, and Ontario, south to northern Florida and west to Manitoba, North and South Dakota, Nebraska, Kansas, and Arkansas.

Distribution in Maryland.—Occurs in all sections of the State, and is common.

Distinguishing characteristics.—This bat is similar in size and color to the little brown myotis (*Myotis lucifugus*), but may be distinguished from that species by its long ears, which extend some 4 to 5 millimeters beyond the tip of the nose when laid forward. The skull is narrower in proportion to its length than that of the little brown myotis.

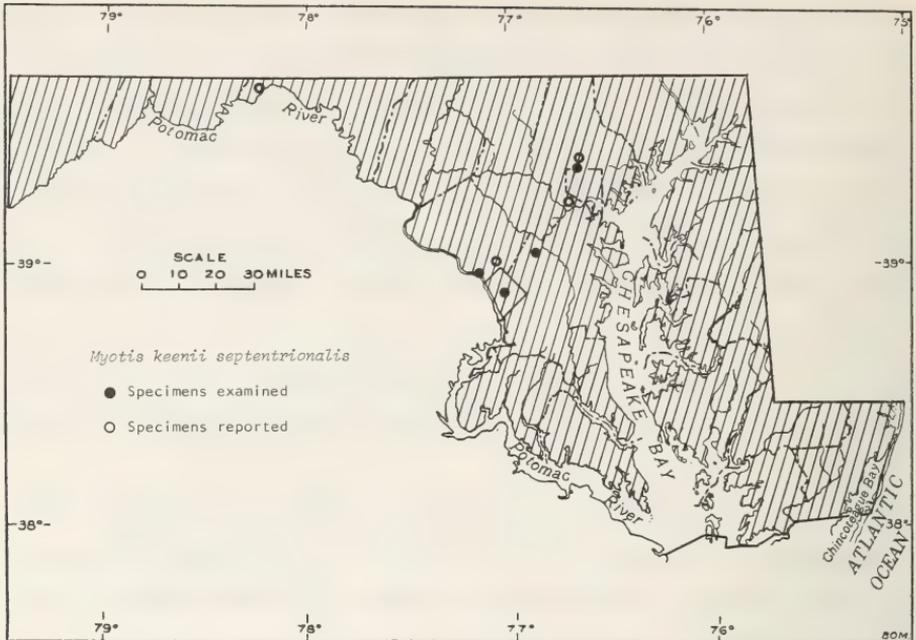


FIGURE 15.—Distribution of *Myotis keenii septentrionalis*.

Measurements.—External measurements of three adults from Plummers Island, Montgomery County, are as follows: Total length 81, 87, 75; tail vertebrae 38, 35, 35; hind foot 9, 9, 10. Some cranial measurements of four adults from Plummers Island are: Greatest length 14.5 (14.4–14.7); zygomatic breadth 8.9 (8.8–9.0); interorbital breadth 3.6 (3.6–3.7); length of maxillary toothrow 5.9 (5.7–6.0).

Habitat and habits.—This species roosts in small colonies in caves, and under loose bark on trees. Frequently it is found in association with the little brown myotis, from which it differs little in habitat selection or habits, except that it seems to be more solitary. Mansueti (1941, pp. 56–57) found one sleeping under the bark of a dead standing tree near Arbutus, Baltimore County. When he peeled the bark away, the bat flew to a nearby tree and crawled up under some loose bark on it. This species is more abundant than the few Maryland records indicate.

Specimens examined.—*Baltimore County*: Bare Hills, 1. *Montgomery County*: Cabin John Bridge, 1; Plummers Island, 5. *Prince Georges County*: Muirkirk, 1. *District of Columbia*: 4.

Other records and reports.—*Baltimore County*: Arbutus (Mansueti, 1941); Lake Roland (Bures, 1948: 63). *Montgomery County*: Forest Glen (Miller, 1897: 76). *Washington County*: Round Top Mountain, near Hancock (bat banding record, U.S. Fish and Wildlife Service).

INDIANA MYOTIS

Myotis sodalis Miller and G. M. Allen

Myotis sodalis Miller and G. M. Allen, Bull. U.S. Nat. Mus., 144: 130, 25 May 1928.

Type locality.—Wyandotte Cave, Crawford County, Indiana.

General distribution.—Eastern United States from central New England west to Wisconsin, Missouri, and Arkansas, south into northern Florida. It occurs on the Atlantic Coastal Plain, however, only in the New England area.

Distribution in Maryland.—Apparently very rare in the State. Its distribution is probably limited to limestone caves in the Ridge and Valley and Allegheny Mountain sections.

Distinguishing characteristics.—Resembles *Myotis lucifugus*, but differs in coloration, the fur being a dull grayish chestnut rather than bronze, with the basal portion of the hairs of the back dull lead colored; coloration of underparts pinkish to cinnamon; hind feet smaller and more delicate than in *M. lucifugus*; slight, but well-defined sagittal crest usually present on skull.

Measurements.—Two adults from the type locality in Indiana have measurements as follows: Total length 86, 87; tail vertebrae 35, 38; hind foot 9, 9; greatest length of skull 14.1, 13.9; zygomatic breadth 8.7, 8.3; interorbital breadth 3.8, 3.7; length of maxillary toothrow 5.5, 5.3.

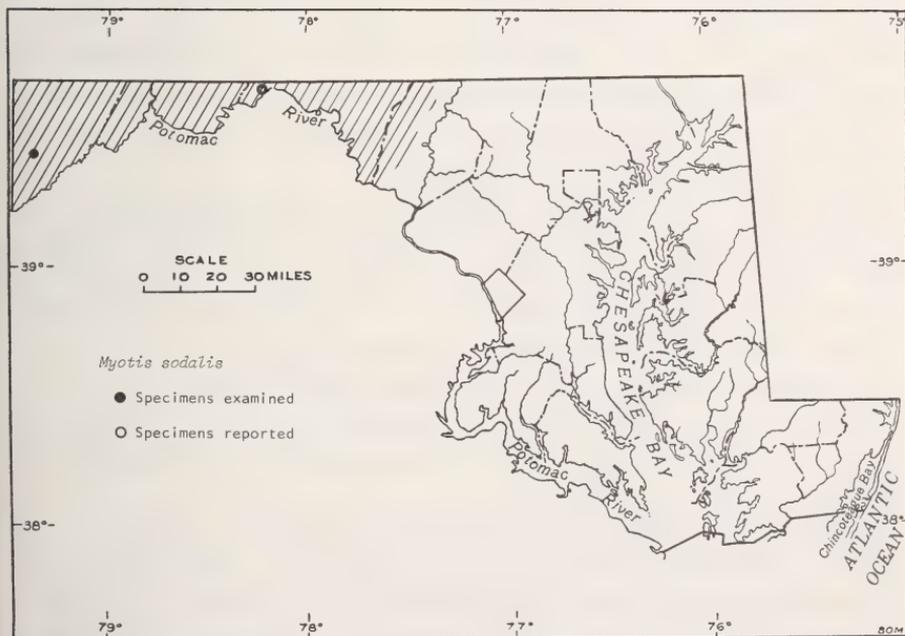


FIGURE 16.—Distribution of *Myotis sodalis*.

The skull of an adult from Oakland, Garrett County, measures: Greatest length 13.7; zygomatic breadth 8.1; interorbital breadth 3.7; length of maxillary toothrow 5.0.

Habitat and habits.—This bat roosts almost exclusively in limestone caves, preferring those in which there are considerable bodies of water. It forms large colonies and is often found in association with *M. lucifugus*. It is known from only 2 localities in Maryland.

Hall (1962) has thoroughly studied the life history of this bat. He found that at Blackball Mine, La Salle County, Ill., the earliest date for entrance into hibernation was 14 September. The major buildup of the hibernating colony was during October and the first part of November. The hibernating colony starts diminishing in early April, and by the first week of June no *sodalis* are in hibernation. He estimates that the average hibernation period for this species would be from 15 October to 20 April, or 187 days. He found that large numbers of Indiana myotis accumulate in a few caves to hibernate, and that for five consecutive winters the species was found in the same seven caves and in no others in Edmondson County, Kentucky. This species also occupies caves during the nonhibernating summer months, and may be considered a true cave species.

As far as movements and migrations are concerned, Hall says that the same individual may be present in one area winter and summer whereas others may move as much as 250 miles between seasons. He says that the few band recoveries indicate that certain movement areas exist for certain populations. For instance, he found that one such population range includes Kentucky, Indiana, Illinois, and southern Ohio, and that no movement takes place between this area and the Ozark area of Arkansas and Missouri.

Little is known regarding the feeding and breeding habits of *M. sodalis*, but probably they are quite similar to those of *M. lucifugus*. Like that species, *M. sodalis* is long-lived. One specimen banded in Carter County, Ky., on 12 March 1950, was recovered in good health 14 years later on 8 January 1964, in the same cave.

Specimens examined.—*Garrett County*: Near Oakland, 1.

Other records and reports.—*Washington County*: Round Top Mountain, near Hancock (bat banding record, U.S. Fish and Wildlife Service).

Remarks.—The skull of the Maryland specimen is small in all measures, but otherwise appears to be typical *M. sodalis*. It has the slight but perfectly defined sagittal crest which is generally present in this species and lacking in *M. lucifugus*. Unfortunately, the skin is missing from the National Museum collections.

SMALL-FOOTED MYOTIS

Myotis subulatus leibii (Audubon and Bachman)

Vespertilio leibii Audubon and Bachman, Jour. Acad. Nat. Sci. Philadelphia, ser. 1, 8: 284, 1842.

Myotis winnemana Nelson, Proc. Biol. Soc. Wash., XXVI: 183, 8 August 1913. (Type from Plummers Island, Maryland.)

Type locality.—Erie County, Ohio.

General distribution.—Ontario and southwestern Quebec, south to western North Carolina, and west to southern Iowa, eastern Kansas, and northeastern Oklahoma.

Distribution in Maryland.—Recorded from Plummers Island, Montgomery County, and Round Top Mountain near Hancock, Washington County. This species probably hibernates in caves in the Allegheny Mountain section, and passes through the rest of the State during migrations.

Distinguishing characteristics.—Similar to *Myotis lucifugus*, but differs in its smaller size, golden tinted fur, black ears, black facial mask, and shorter forearm. The skull is much flatter than that of *M. lucifugus*, and the braincase narrower.

Measurements.—Two adults from Plummers Island, Montgomery County (the first the type of *M. winnemana* Nelson) measure as follows: Total length 82, 80; tail vertebrae 39, 35; hind foot 8, 7; greatest

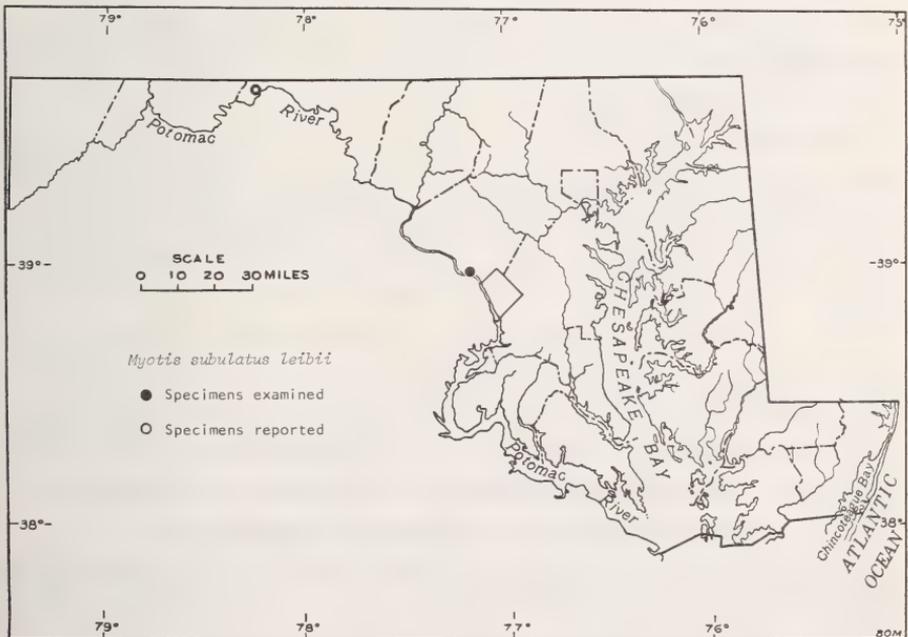


FIGURE 17.—Distribution of *Myotis subulatus leibii*.

length of skull 13.7, 13.1; interorbital breadth 3.4, 3.3; length of maxillary tooththrow 5.1, 5.0.

Habitat and habits.—These bats probably hibernate in caves in the wild forested regions of the Allegheny Mountains and migrate elsewhere in the State during late winter and early spring. Most specimens have been taken in caves located in hemlock forests. The position of these bats as they hang on the walls or ceilings of the caves is a definite means of identification. The arms, instead of hanging parallel to the body, as generally found in *M. lucifugus* and other bats, are extended about 30 degrees from the vertical. Little is known of the feeding and breeding habits, but they are presumed to be similar to *M. lucifugus*.

Specimens examined.—*Montgomery County*: Plummers Island, 2.

Other records and reports.—*Washington County*: Round Top Mountain, near Hancock (bat banding record, U.S. Fish and Wildlife Service).

SILVER-HAIRED BAT

Lasionycteris noctivagans (Le Conte)

V[espertilio]. noctivagans Le Conte, in McMurtrie, The animal kingdom . . . by the Baron Cuvier, vol. 1, App., p. 431, 1831.

Type locality.—Eastern United States.

General distribution.—Nearly all of North America, from the tree line in northern Canada, south to Georgia, Texas, New Mexico, and California.

Distribution in Maryland.—Probably breeds only in the Allegheny Mountain section, but occurs in all sections of the State as a migrant in the spring and the fall.

Distinguishing characteristics.—Teeth 2/3, 1/1, 2/3, 3/3, = 36; pelage dark brownish-black, the ends of the hairs tipped with silver, giving a somewhat frosted effect, particularly along the middle of the back; fur extends onto dorsal surface of interfemoral membrane; ears short and rounded with broad, blunt tragus; skull flattened, and rostrum broad.

Measurements.—An adult male from Plummers Island, Montgomery County has the following external measurements: Total length 116; tail vertebrae 47; hind foot 10. Some cranial measurements of four adults from Washington, D.C. are: Greatest length 15.8 (15.6–16.2); zygomatic breadth (2 specimens) 9.9, 9.1; interorbital breadth 4.1 (4.0–4.3); length of maxillary tooththrow 5.7 (5.6–5.8).

Habitat and habits.—This bat is found most frequently flying about ponds and streams in wooded areas. It roosts in hollow trees, in dense foliage, and occasionally in buildings. It is sociable and often encountered in large groups. As in many species of bats, there is a marked

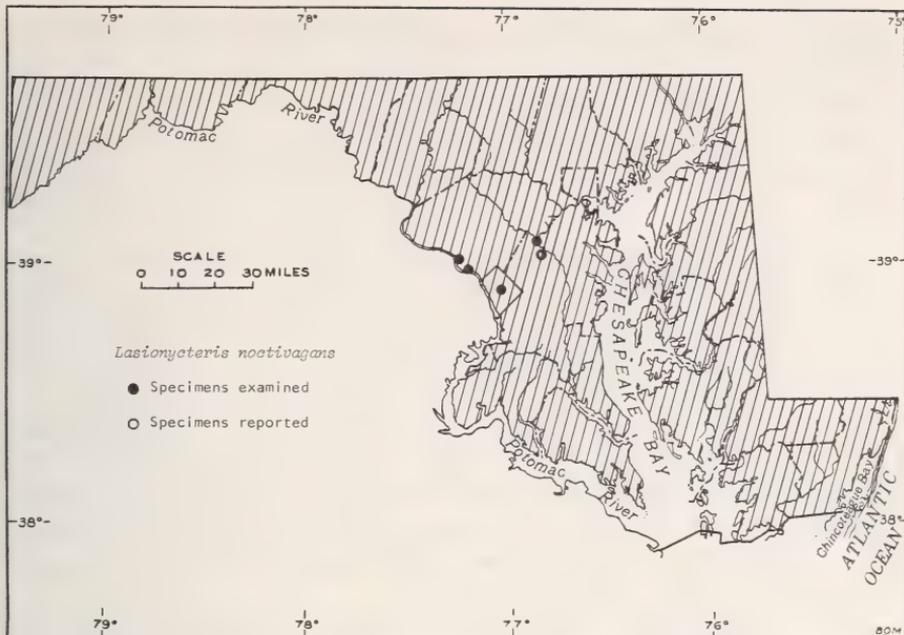


FIGURE 18.—Distribution of *Lasionycteris noctivagans*.

segregation of the sexes and the large colonies seem to be composed primarily of females. Solitary animals are usually males.

The breeding habits of this species are not well known, but according to Jackson (1961, p. 86) it usually has two young, born blind and nearly naked, the last part of June or early in July. The young remain clinging to the breast of the mother until they are about 3 weeks old, when they are able to fly and shift for themselves. A single litter is produced each year.

The silver-haired bat feeds entirely on nocturnal insects, particularly those that fly high in the woodlands or over the borders of watercourses with wooded banks.

Specimens examined.—*Montgomery County*: Great Falls, 1; Plummers Island, 1. *Prince Georges County*: Laurel, 1. *District of Columbia*: 5.

Other records and reports.—*Prince Georges County*: Patuxent Research Center (Gardner, 1950*b*, p. 112).

EASTERN PIPISTRELLE

Pipistrellus subflavus subflavus (F. Cuvier)

V[*espertilio*]. *subflavus* F. Cuvier, Nouv. Ann. Mus. Hist. Nat. Paris, 1: 17, 1832.

Type locality.—Georgia, restricted to the LeConte Plantation, 3 miles SW Riceboro, Liberty County, by Davis (1959, p. 522).

General distribution.—From central Minnesota and southern Quebec south into Georgia and western Florida; west to Oklahoma, Texas, and Tamaulipas. The center of its abundance is the Ohio River Valley; north of this it occurs locally in summer (Davis and Mumford, 1962, p. 396).

Distribution in Maryland.—Probably ranges throughout all sections of the State, although there are no records of it from the Eastern Shore section.

Distinguishing characteristics.—Teeth $2/3$, $1/1$, $2/2$, $3/3$, = 34; smallest bat in Maryland; coloration of dorsum grayish to reddish-brown, each hair tricolored, plumbeous at base, dark brown at tip, with central portion yellowish-brown; flight weak and erratic, giving the animal somewhat the appearance of a large fluttering moth.

Measurements.—External measurements of 11 adults from Washington, D.C., are as follows: Total length 81.6 (75–90); tail 39.5 (37–42); hind foot 8.5 (8.0–9.0). Some cranial measurements of 10 adults from Washington are as follows: Greatest length 12.8 (12.4–13.1); zygomatic breadth 7.9 (7.7–8.2); interorbital breadth 3.5 (3.4–3.6); length of maxillary toothrow 4.3 (4.2–4.4).

Habitat and habits.—This is a wide-ranging species that hibernates in caves, mine shafts, and rock crevices. During the summer months it probably spends the daylight hours in trees, although it is sometimes found in buildings. It is most frequently encountered in wooded areas near water. The pipistrelle is believed to have a feeding range of at least 5 or 6 miles, and a homing instinct has been demonstrated by tracing banded bats for distances up to 80 miles. Individuals roost year after year in the same cave.

Mating occurs in November, and young are born the last part of June or early July. Usually two constitute a litter, but there are occasionally triplets, and sometimes only a single offspring. By the time they are about a month old they are able to fly, and shortly thereafter begin to shift for themselves. Since pipistrelles are so small their food is probably restricted to insects such as flies, moths, and the smaller bugs and beetles.

Despite their diminutive size, pipistrelles apparently have a long life span. Banded individuals have been recovered in good health as long as 10 years after they were originally tagged.

Specimens examined.—*Anne Arundel County*: Magatha R. (= Magothy River?), 2. *Charles County*: Marshall Hall, 13. *Garrett County*: Near Oakland, 1. *Montgomery County*: Capitol View, 1; Glen Echo, 1; Great Falls, 1; Plummers Island, 2. *Prince Georges County*: Hyattsville, 1; Laurel, 1; near D. C. line, 6. *St. Marys County*: St. George Island, 4; *District of Columbia*: 40.

Other records and reports.—*Baltimore County*: Bare Hills (Bures, 1948: 64); Orange Grove (Hampe, 1939: 5). *Washington County*:

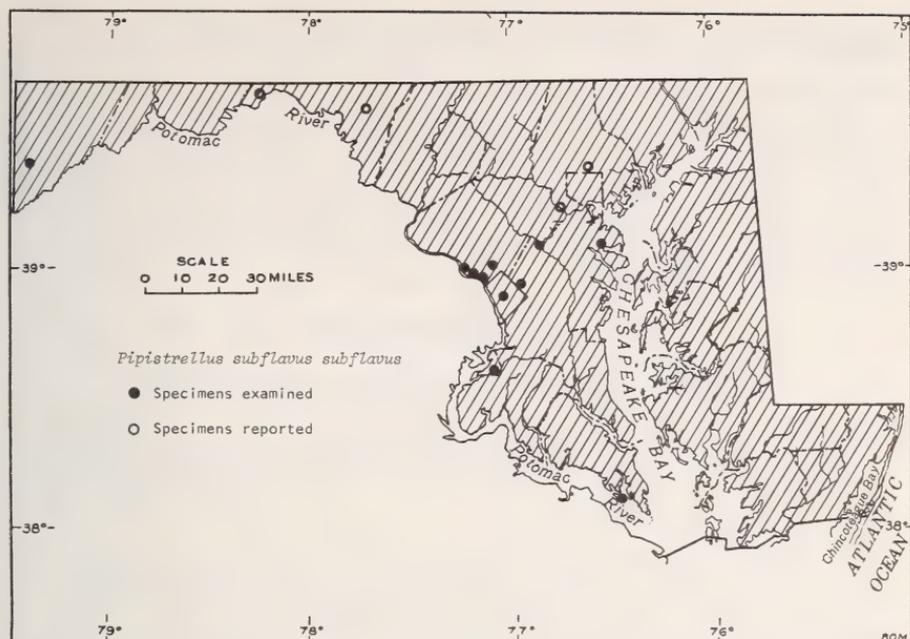


FIGURE 19.—Distribution of *Pipistrellus subflavus subflavus*.

Keedysville, Snively's Cave No. 1 (bat banding record, U.S. Fish and Wildlife Service); Round Top Mountain (bat banding record, U.S. Fish and Wildlife Service).

Remarks.—Two subspecies of *Pipistrellus subflavus* have been named from the eastern United States, *P. s. subflavus*, the typical form as described above, and *P. s. obscurus* Miller (Type locality: Lake George, Warren County, New York). Miller (1897, p. 93) described *obscurus* as differing from *subflavus* only in coloration, being somewhat darker, duller, and more yellowish. Several specimens from the vicinity of Washington, D.C., in the national collections, are darker than typical *P. s. subflavus* and were referred by Bailey (1923, p. 136) and Gardner (1950b, p. 112) to *obscurus*. Bailey (1923, p. 137) says that "They may have migrated from their northern habitat, or merely wandered out of their regular range after the breeding season was over." As pointed out by W. H. Davis (1959, p. 523), who has synonymized *P. s. obscurus* with *P. s. subflavus*, there is a wide range of individual variation in color in this species, and dark specimens are found throughout the entire range of *P. s. subflavus*. The dark specimens from the vicinity of Washington, referred to *obscurus* by both Bailey and Gardner, fall within the range of individual variation of color in the subspecies *subflavus*.

Another Maryland specimen which exhibits atypical coloration is from St. George Island, St. Marys County. It is similar to *P. s. florid-*

anus Davis, which is distributed over peninsular Florida and southeastern Georgia. W. H. Davis (1957, p. 215) speculated that perhaps this animal actually was a *floridanus* that had wandered northward. In a later publication (1959, p. 524), however, he says that unless it can be shown that this actually happened it is best to refer this specimen to *P. s. subflavus*. The specimen has been in the National collections for many years (collected 20 August 1887), and the unusual coloration is perhaps due to fading.

BIG BROWN BAT

Eptesicus fuscus fuscus (Palisot de Beauvois)

Vespertilio fuscus Palisot de Beauvois, Catalogue Raisonné du Muséum de Mr. C. W. Peale, Philadelphia, p. 18 (p. 14 of English ed. by Peale and Beauvois), 1796.

Type locality.—Philadelphia, Pa.

General distribution.—Eastern North America, from Quebec, Ontario, and Manitoba, south into Florida and Nuevo León, México.

Distribution in Maryland.—Abundant in the lower Piedmont and upper Western Shore sections in the vicinity of the fall line. Uncommon in the Allegheny Mountain, Ridge and Valley, and Eastern Shore sections.

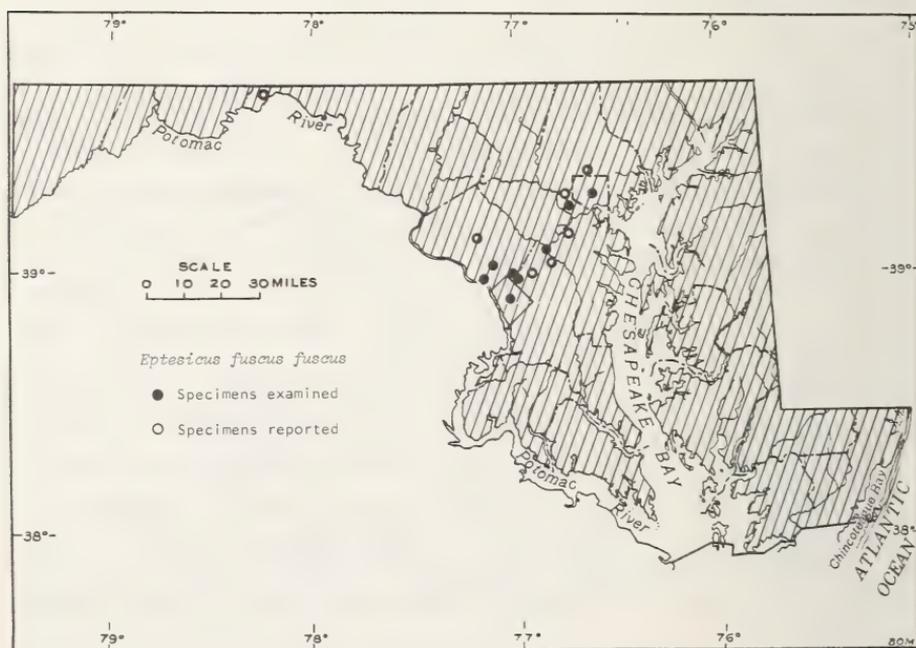


FIGURE 20.—Distribution of *Eptesicus fuscus fuscus*.

Distinguishing characteristics.—Teeth 2/3, 1/1, 1/2, 3/3, = 32; size large, exceeded in Maryland only by the hoary bat; coloration uniformly dark brown; ears thick and heavy, somewhat rounded and medium in size, naked except for some fur at the base; wings and interfemoral membrane lacking fur; skull larger and heavier than any other local bat except *Lasiurus cinereus*, from which it differs in being noticeably narrower. Both *Eptesicus* and *Lasiurus* have 32 teeth, but in *Eptesicus* there are 2 upper incisors and 1 upper premolar, while in *Lasiurus* there are 2 upper premolars and 1 upper incisor on each side.

Measurements.—External and cranial measurements of 15 adults from Washington, D.C., are as follows: Total length 113.2 (110–122); tail 43.6 (40–48); hind foot (average of 9) 12 (10–13); greatest length of skull 18.5 (17.5–19.6); zygomatic breadth (average of 10) 12.6 (12.1–13.4); interorbital breadth 4.2 (3.9–4.5); length of maxillary tooththrow 7.1 (6.9–7.4).

Habitat and habits.—This bat usually occurs around buildings and dwellings where it roosts in the daytime under windowsills, in the eaves of roofs, in cracks or crevices, or behind doors, blinds, and awnings. It is sometimes found in hollow trees, under loose bark, and occasionally in caves or crevices in cliffs. This species is common in parts of Maryland; it is an unusual year when at least one specimen is not captured in the Natural History building of the National Museum and added to the study collection. The big brown bat does not form large colonies as do some species of bats. Probably it is in part migratory, but does not engage in extensive seasonal migrations, other than to find a suitable place for hibernation. This is one of the last bats to hibernate in the fall, and it is on wing again in early March. During mild spells of winter it may be seen flying in the sun at midday (Hamilton, 1943, p. 90). These bats are long-lived; records of banded animals recovered 10 to 15 years later are numerous.

The homing instinct seems to be developed to some degree. Cohen (1944) found several adults behind the shutter of a house in Berwyn, Prince Georges County, and after banding them released them on 4 October 1941, in Baltimore City. Twelve days later, on 15 October 1941, one of these bats was found hanging on the same shutter from which it had been removed in Berwyn. It had travelled a distance of 26.56 miles, over the congested city of Baltimore, and heavily travelled highways, to return to its home roost.

The mating season for the big brown bat is September, and young are born the following June. Normally two comprise a litter, although there may occasionally be only one. The young grow rapidly and 3 or 4 weeks after birth are able to shift for themselves.

This species, like all Maryland bats, is primarily insectivorous. Hamilton (1933a) examined 2,200 summer fecal pellets from northern

West Virginia and concluded that the most common insects consumed by the big brown bat in summer are (in order of abundance of remains): Coleoptera, Hymenoptera, Diptera, Plecotera, Ephemirida, Hemiptera, Tricoptera, Neuroptera, Mecotera and Northoptera. No lepidopterous remains were discovered by Hamilton in the pellets.

Specimens examined.—*Baltimore City*: 1. *Baltimore County*: Catonsville, 1. *Montgomery County*: Kensington, 1; Plummerville Island, 2; Silver Spring, 1; Takoma Park, 2. *Prince Georges County*: Laurel, 3. *District of Columbia*: 86.

Other records and reports.—*Anne Arundel County*: Jessup (Silver, 1928, p. 149). *Baltimore County*: Bare Hills (Cohen, 1942, p. 96); Patapsco State Park (Hampe, 1939, p. 5). *Montgomery County*: Washington Grove (Christian, 1956, p. 66). *Prince Georges County*: Berwyn (Cohen, 1944, p. 65); Patuxent Research Center (Gardner, 1950b, p. 112). *Washington County*: Round Top Mountain, near Hancock (banding record).

RED BAT

Lasiurus borealis borealis (Müller)

Vespertilio borealis Müller, Des Ritters Carl von Linne . . . vollständiges Natursystem nach der zwölften lateinischen Ausgabe. . . Suppl. (Mammalia), p. 20, 1776.

Type locality.—*New York*

General distribution.—Eastern North America, from southern New Brunswick, Quebec, Ontario, Manitoba, Saskatchewan, and Alberta, south to Florida and Texas.

Distribution in Maryland.—Abundant in all sections of the State.

Distinguishing characteristics.—Teeth 1/3, 1/1, 2/2, 3/3, = 32; size medium; color bright rufous or fulvous, hairs plumbeous at base and whitish at tips, producing a slight frosted effect; ears broad and blunt, rounded at tip, reaching about halfway from the angle of the mouth to the nostril when laid forward; tail moderately long; interfemoral membrane thickly furred on upper surface.

This bat is easily distinguished from all other bats in Maryland by its bright rufous coloration and the furred interfemoral membrane. Males generally are darker and more reddish than females.

Measurements.—An adult male from Doubs, Frederick County, and an adult female from 3 miles NW of Annapolis, Anne Arundel County, measure respectively: Total length 109, 113; tail 49, 50; hind foot 10, 7; greatest length of skull 13.0, 12.6; zygomatic breadth 9.5, 9.5; interorbital breadth 4.4, 4.2; length of maxillary toothrow 4.5, 4.4.

Habitat and habits.—This bat shows a preference for deciduous woodlands, orchards, and city parks with trees and tall shrubs. It generally chooses the branch of a shady tree in which to roost, some-

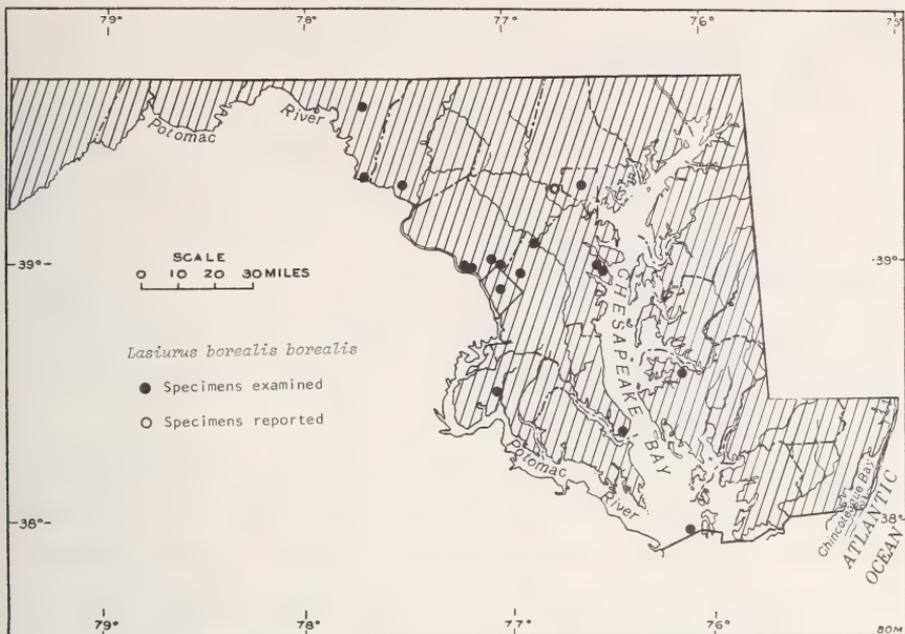


FIGURE 21.—Distribution of *Lasiurus borealis borealis*.

times within a few feet of the ground, and conceals itself in the foliage.

It is well known that the red bat is migratory in habits, spending summers in northern areas and flying south in the autumn. They are not found in the winter in the more northern areas, while their numbers appear to increase in the south. In Maryland they apparently occur the year round, specimens having been taken in all months from April through December, and in nearby Arlington, Va., on 1 March. Whether the same population occurs here in the summer as in the winter is not known. Perhaps the summer population migrates farther south and its place is taken by a more northern population which has migrated in.

It appears that this bat migrates southward in the fall behind an advancing cold front. David Bridge, a Maryland bird bander, tells me that he often takes red bats in the autumn in his bird nets at Kent Point on Kent Island, Queen Annes County, for several days following the movement of a cold front through the area.

The red bat is a strong swift flyer. Jackson (1961, p. 96) states that observational timing he made of it would indicate an ordinary straightaway flying speed of near 40 miles per hour. It has sometimes been observed flying far out to sea as much as 500 miles from the nearest land. Usually it migrates at night, but occasionally it is observed during the day. A. H. Howell (1908, p. 36) observed over a

hundred bats, most of which were probably of this species, passing over a part of Washington, D.C., between 9 and 10 a.m. on the cloudy mild morning of 28 September 1907.

Red bats mate during early August; copulation occurs while the bats are in flight. The female apparently stores the sperm, and the young are not born until the following June after a gestation period of 80 to 90 days. Three are the usual number of young per litter, although there are occasionally two or four.

Like other Maryland bats, the red bat is insectivorous and catches most of its prey while on wing. Some insects, however, are probably taken from the foliage or even near the ground, since remains of crickets have been found in stomachs. Additional items of diet are flies, bugs, beetles, cicadas, and other insects.

Specimens examined.—*Anne Arundel County*: Annapolis, 1; Annapolis, 3 miles NW, 1; no exact locality, 2. *Baltimore City*: 1. *Calvert County*: Solomons, 1. *Charles County*: Port Tobacco, 1½ miles SW, 2. *Dorchester County*: Cambridge, 1. *Frederick County*: Doubs, 1. *Montgomery County*: Forest Glen, 6; Glen Echo, 1; Plummers Island, 7; Silver Spring, 2. *Prince Georges County*: College Park, 1; Laurel, 14. *Somerset County*: off Tangier Island, Virginia, 1; *Washington County*: Hagerstown, 2; Sandy Hook, 1. *District of Columbia*: 83.

Other records and reports.—*Baltimore County*: Patapsco State Park (Hampe, 1939, p. 5). *Queen Annes County*: Kent Point (bird bander David Bridge in verbis, 16 September 1964).

Remarks.—A closely related species, the seminole bat, *Lasiurus seminolus* (Rhoads), which normally is found in Florida, southern Georgia, Alabama, Mississippi, and Louisiana, has been reported twice from southeastern Pennsylvania (Poole, 1932, p. 162; 1949, p. 80) and once from central New York (Layne, 1955, p. 453). Layne suggests that individuals of this species may wander northward far out of the normal range in summer, and if this is so, the seminole bat may eventually be taken in Maryland. This species is distinguished from the red bat by its much darker coloration, a rich mahogany brown slightly frosted with white.

HOARY BAT

Lasiurus cinereus cinereus (Palisot de Beauvois)

Vespertilio cinereus (misspelled *linereus*) Palisot de Beauvois, Catalogue raisonné du muséum de Mr. C. W. Peale, Philadelphia, p. 18, 1796.

Type locality.—Philadelphia, Pa.

General distribution.—Most of North America, from the Atlantic to the Pacific, north into Canada, and south into Mexico. Breeds in the northern part of its range, mostly north of the United States.

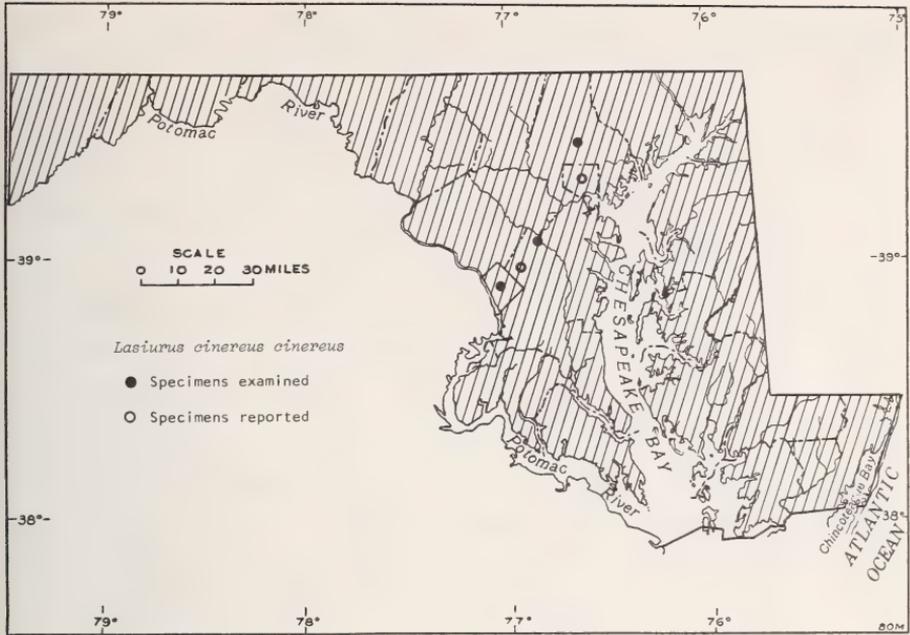


FIGURE 22.—Distribution of *Lasiurus cinereus cinereus*.

Distribution in Maryland.—Occurs as a migrant in all sections of the State; may breed in the higher portions of the Allegheny Mountain section.

Distinguishing characteristics.—Teeth as in *L. borealis*; size large (averaging 135 mm in total length); wingspread averaging around 14 inches; coloration a mixture of grayish umber and chocolate brown, heavily tinged with white, so as to produce a hoary effect, especially on the back; head blunt, with ears large and rounded, conspicuously rimmed with black or dark brown; tail medium length, about 40 percent of total length of the animal; interfemoral membrane thickly furred on upper surface nearly to the edge; anterior edge of underside of wing furred for about half its length. This bat is easily distinguished from all other Maryland bats by its large size and unique coloration.

Measurements.—Measurements of an adult male from Washington, D.C., are as follows: Total length 135.5; tail 61.5; hind foot 13; greatest length of skull 16.1; zygomatic breadth 12.0; interorbital breadth 4.9; length of maxillary toothrow 6.2.

An adult female from Washington, D.C., has the following cranial measurements: Greatest length of skull 16.9; zygomatic breadth 12.7; interorbital breadth 5.5; length of maxillary toothrow 6.2.

Habitat and habits.—This is a migratory species. It breeds and spends the summer in the northern part of its range, from southeast-

ern Pennsylvania and possibly the higher mountains of the Appalachians, north into Canada. It migrates southward quite late in the season. It prefers to roost in coniferous forests, but may also be found in farmyards, city parks, and yards, particularly where coniferous trees are growing. The hoary bat has an extensive home range and may fly a mile or more from its roosting site in search of food. It is a strong and rapid flyer, and Jackson (1961, p. 100) estimates that it can achieve speeds of up to 60 miles an hour. The scarcity of records and specimens from Maryland indicates that it is rare here. In the summer, it occurs in the higher mountains of the Allegheny Mountain section. In other seasons, it may be encountered throughout Maryland.

Little is known of the breeding habits of this bat. Jackson (1961, pp. 100-101) says that mating probably occurs in September or October and the young are born in May or June, thus giving an apparent gestation period of about 8 months. It seems probable, however, that as in some other species of bats spermatozoa survive in the uterus through the winter, and that fertilization takes place early in the spring, giving an actual gestation period of about 90 days. Usually, two young comprise a litter, although it is possible that as many as four may be produced.

The hoary bat is primarily an insect feeder, but occasionally preys on smaller bats.

Specimens examined.—*Baltimore County*: Cockeysville, 1. *Prince Georges County*: Laurel, 1. *District of Columbia*: 3.

Other records and reports.—*Baltimore City* (Merriam, 1887, p. 86). *Prince Georges County*: Berwyn (Tromba, 1954, p. 253).

EVENING BAT

Nycticeius humeralis humeralis (Rafinesque)

Vespertilio humeralis Rafinesque, American Monthly Mag., 3 (6) : 445, October 1818.

Type locality.—Kentucky.

General distribution.—From Pennsylvania, Michigan, and Illinois, south into Florida and Texas, and west into eastern Oklahoma and Kansas.

Distribution in Maryland.—Probably absent in the higher mountains of the Allegheny Mountain and Ridge and Valley sections, but elsewhere it may occur sparingly as a summer resident.

Distinguishing characteristics.—Teeth 1/3, 1/1, 1/2, 3/3, = 30; superficially resembles *Myotis* but can be easily distinguished by the reduced number of teeth and the short sparse brown fur which is dull umber above and plumbeous at the base; fur on abdomen paler than on dorsum; ears small and thick. The young of this species are considerably darker than the adults.

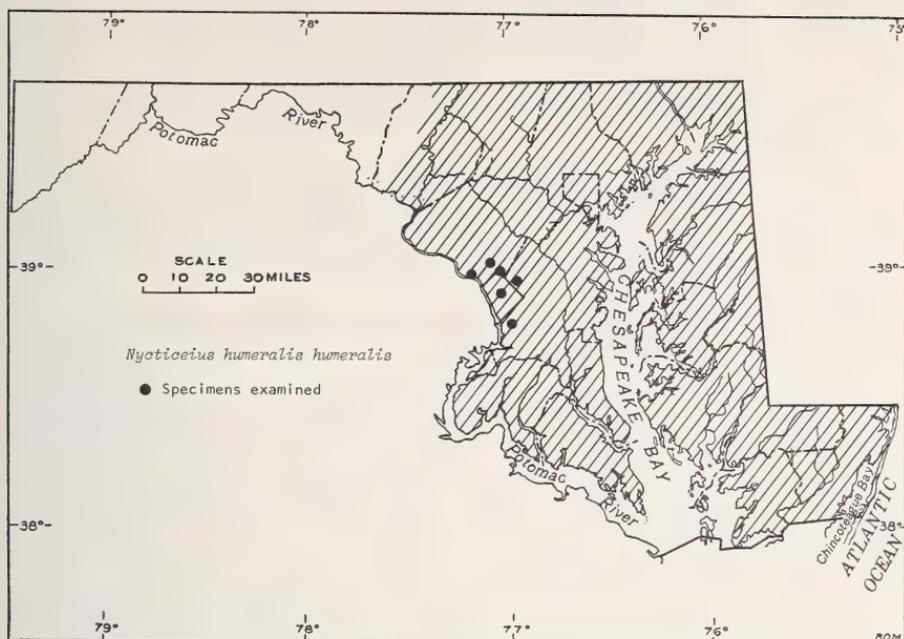


FIGURE 23.—Distribution of *Nycticeius humeralis humeralis*.

Measurements.—Three adults from the vicinity of Washington, D.C., have external measurements as follows: Total length 90, 95, 94; tail 39, 35, 35; hind foot 10, 9, 8. Six adults from the vicinity of Washington have the following cranial measurements: Greatest length 14.2 (13.7–15.5); zygomatic breadth 9.7 (9.6–10.0); interorbital breadth 3.9 (3.8–4.0); maxillary tooththrow 5.2 (5.0–5.4).

Habitat and habits.—This is essentially a southern species that wanders north in summer sometimes as far as Pennsylvania, Michigan, and Illinois. It prefers to roost in hollow trees, flying out with a slow and steady flight as darkness falls. It gives birth to two young, generally in late May. Little else is known of its habits or life history.

Specimens examined.—*Montgomery County*: Linden, 1; Plummers Island, 1; Silver Spring, 1. *Prince Georges County*: Hyattsville, 2; Oxon Hill, 1; near D.C. line, 1. *District of Columbia*: 6.

(BIG-EARED BAT)

Plecotus townsendii virginianus (Handley)

Corynorhynchus virginianus Handley, Jour. Washington Acad. Sci., 45 (2): 148, 23 May 1955.

Type locality.—Schoolhouse Cave, 4.4 miles NE of Riverton, 2,205 feet, Pendleton County, W. Va.

General distribution.—Central part of the Appalachian highlands in eastern Kentucky, western Virginia, and eastern West Virginia.

Distribution in Maryland.—Not as yet recorded, but should be looked for in the higher portions of the Allegheny Mountain section. To date it has not been found resident in any Maryland caves, but it probably enters the State on feeding forays from caves in nearby West Virginia and Virginia.

Distinguishing characteristics.—Teeth 2/3, 1/1, 2/3, 3/3, = 36, ears very long; glandular masses on nose appear as lumps; fur long and limp; colored a dark brown above, and pinkish buff on belly, inter-femoral membrane naked.

The very large ears serve to distinguish this bat from any others that may be encountered within Maryland.

Measurements.—Handley (1959, p. 233) gives some measurements of a series of adults from West Virginia as follows: Total length 101 (98–103); tail vertebrae 50 (48–52); hind foot 11 (10–12); ear from notch 34 (31–38); greatest length of skull 16.5 (16.2–16.8); zygomatic breadth 8.8 (8.6–9.0); interorbital breadth 3.7 (3.6–3.9); length of maxillary toothrow 5.3 (5.2–5.4).

Habitat and habits.—This is a true cave bat usually roosting in small groups and emerging at dusk to fly at considerable heights. After dusk it descends nearer the ground, sometimes at an elevation of only several feet, searching for insect prey. When roosting in the caves during the day, the long ears are spirally coiled and flattened against the neck. It is a shy bat, quick to take alarm. With its large ears, it can detect the least sound and seems to be more wary than other species.

Although Pearson et al. (1952) have made a detailed study of the life history of the western subspecies of *Plecotus townsendii*, little is known concerning the habits of the eastern race. Since the two are widely separated geographically, much of Pearson's findings may not be applicable to the eastern form. Hamilton (1943, pp. 102–103) says that the eastern race bears its young during late June and that the mother carries the single offspring until it becomes too heavy. As with other vespertilionid bats, the spermatozoa are probably stored over winter in the uteri of the females and are capable of fertilizing in the spring.

This species is insectivorous, and Hamilton (1943, p. 104) says that those examined for a clue to their feeding habits contained only the remains of Lepidoptera in their stomachs.

Remarks.—This bat has never been taken within Maryland, but has been found in several caves very close to the border of the western part of the State, in Grant, Preston, and Tucker Counties, W. Va.

During the Pleistocene, a bat very similar to this species did inhabit Maryland caves. Gidley and Gazin (1933, p. 345) described *Corynorhynchus alleganiensis* (= *Plecotus alleganiensis*) from Pleistocene deposits in Cumberland Cave, Allegany County, Md. Handley (1959, p.

210) states that *P. alleganiensis* was similar in many respects to (and possibly directly ancestral to) *P. townsendii*.

Order LAGOMORPHA (rabbits, hares, etc.)

Family LEPORIDAE (rabbits, hares)

EASTERN COTTONTAIL

Sylvilagus floridanus mallurus (Thomas)

L[epus]. n[uttalli]. mallurus Thomas, Ann. Mag. Nat. Hist., ser. 7, 2: 320, October 1898.

Type locality.—Raleigh, N.C.

General distribution.—Primarily east of the Appalachian Mountains, from Massachusetts, south into central Florida, west to Tennessee and Alabama.

Distribution in Maryland.—Occurs abundantly in all sections of the State. Cottontails have been introduced into parts of Maryland from areas outside the range of *mallurus*, and hence all population in the State may not be referable to that race.

Distinguishing characteristics.—Teeth 2/1, 0/0, 3/2, 3/3, = 28; size small; ears large, pelage long and coarse, reddish brown, mixed with black on the dorsum; underparts white, including the underside of the tail; nape and legs cinnamon-rufous. This species differs from the New England cottontail (*S. transitionalis*), which has not yet been taken in Maryland but which probably occurs in the mountains of the western part of the State, in several external and cranial characters which are described under that species.

Measurements.—External measurements of three adults from the three adults from Washington, D.C., are: Basilar length 57.5, 57.0, 45.8; tail 60, 64, 75; hind foot 99, 84, —. Cranial measurements of three adults from Washington D.C., are: Basilar length 57.5, 57.0, 56.5; zygomatic breadth 36.9, 36.5, 36.3; interorbital breadth 19.1, 18.5, 17.9; length of maxillary toothrow 14.1, 14.0, 13.2.

Habitat and habits.—This rabbit occupies a variety of habitats from the marshes of the Delmarva Peninsula to the fields and meadows of western Maryland. It is seldom encountered in heavy woods. It occurs on Assateague Island, off the Atlantic coast of Maryland, where it is particularly abundant in the wooded thickets and dry sandy areas adjacent to the marshes. These rabbits are found in the tall grass and thickets in villages and towns and even in the large cities such as Baltimore and Washington. The summer food consists of almost any type of green vegetation, but it seems to be especially fond of legumes, dandelions, plantains, and lettuce. During winter it eats tender parts of many shrubs and trees and will gnaw away the bark of some species of

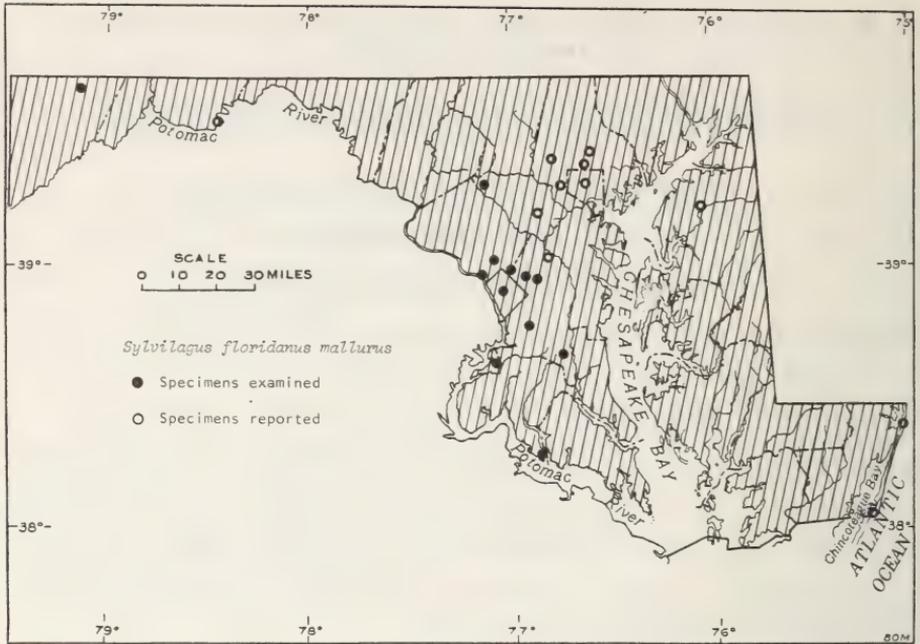


FIGURE 24.—Distribution of *Sylvilagus floridanus mallurus*.

trees. With the deforestation of much of Maryland since Colonial times the cottontail has found more suitable habitat and today is abundant throughout the State.

The cottontail is both diurnal and nocturnal, but is most active during the first 3 or 4 hours after daylight and from 2 to 3 hours before sunset to about 1 hour after sunset. It does not hibernate, but is active yearlong. Cottontails are solitary and seldom are two or more found together except in the case of mother and young.

The female builds a brood nest of grass combined with fur plucked from her own abdomen. The nest, placed in a depression in the ground, is about 4 or 5 inches in diameter and depth. It is usually well concealed in grass, weeds, thickets, or scrubby woods. In addition to the brood nest, the cottontail makes forms that are used as hiding or resting places. These forms are made by scratching or trampling a shallow oval hollow in the ground and sometimes lining it with grass, leaves, or fur.

Cottontails in Maryland mate in late winter. The gestation period varies from 28 to 32 days, and the first litter of the year appears by mid-March. Two or three litters are produced each season, and the number of young per litter varies from three to six, with five being the most frequent.

Specimens examined.—*Charles County*: Marshall Hall, 1; Rock Point, 1. *Garrett County*: Grantsville, 1. *Howard County*: Long Cor-

ner, 2. *Montgomery County*: Kensington, 1; Plummers Island, 2; Takoma Park, 1; no exact locality, 1. *Prince Georges County*: Clinton, 1; East Riverdale, 1; Lanham, 1; Westwood, 1; no exact locality, 3. *District of Columbia*: 24 (many of these are labeled "purchased in Washington Market" and were probably taken outside the District of Columbia area).

Other records and reports.—*Allegheny County*: Oldtown, 9 miles E (personal observation). *Baltimore City*: (personal observation). *Baltimore County*: Bare Hills–Lake Roland area (Bures, 1948, p. 68); Loch Raven (Kolb, 1938); Gwynnbrook State Game Farm (Sheffer, 1957, p. 90); Patapsco State Park (Hampe, 1939, p. 7). *Howard County*: Atholton (personal observation). *Kent County*: Chestertown (U.S. Fish and Wildlife Service files). *Prince Georges County*: Patuxent Research Center (Herman and Warbach, 1956, p. 85). *Worcester County*: Assateague Island, near the Virginia border (personal observation); Ocean City, 1 mile N (personal observation).

Remarks.—Nelson (1909, p. 168) considers the specimen from Grantsville in the extreme western Allegheny Mountain section to be a distinct intergrade with *S. f. mearnsi*, nearly pale enough to be classified with *mearnsi*.

(NEW ENGLAND COTTONTAIL)

Sylvilagus transitionalis (Bangs)

Lepus sylvaticus transitionalis Bangs, Proc. Boston Soc. Nat. Hist., XXVI, pp. 405–407, 31 January 1895.

Type locality.—Liberty Hill, New London County, Conn.

General distribution.—Distributed from southeastern Maine, southern New Hampshire, and Vermont, south through eastern New York, New Jersey, and eastern Pennsylvania and along the Allegheny Mountains through West Virginia to northern Georgia and northeastern Alabama.

Distribution in Maryland.—There are no valid records of the New England cottontail from Maryland, but it almost certainly occurs in the Allegheny Mountain section at higher elevations.

Distinguishing characteristics.—Similar in coloration to the eastern cottontail, except that the underfur is a much darker gray. The back is ochraceous buff, overlaid with a wash of black-tipped guard hairs which give it a dark appearance. The ears are short and round and have a black margin on the outside edge, making a distinct black line which does not blend gradually into the browner color of the ear as in the eastern cottontail. A definite black patch is between and just in front of the ears.

Cranially this species differs from the eastern cottontail in that the skull is lighter and slenderer, the interorbital breadth narrower, and

the rostrum thinner. The supraorbital process is very slender, narrowing anteriorly so that the notch is absent, or virtually so. The posterior portion of the process is very narrow and in some instances is free of the skull, leaving a distinct foramen. The auditory bullae are noticeably smaller in this species than in *S. floridanus*.

Measurements.—Nelson (1909, p. 168) gives average measurements of five adults from Wilmington, Mass., as follows: Total length 388; tail vertebrae 39; hind foot 96; basilar length of skull 54.8; interorbital breadth 17.1.

Since geographic variation appears to be slight in this species, Maryland specimens, if taken, probably would not differ greatly in size from the Massachusetts series.

Habitat and habits.—Llewellyn and Handley (1945, p. 384) say that in Virginia

All specimens examined were taken at elevations above 3,000 feet in the Allegheny Mountains. Signs indicate that these cottontails occupy the woods and brush along most of the higher crests and ridges of the state.

They believe that the species will be found in Virginia only at elevations above 3,000 feet. Since the species occurs in the Alleghenies to the north and south of Maryland, and since there are several mountains in western Maryland that exceed 3,000 feet in altitude, it is almost certain that the New England cottontail is resident in Maryland and will eventually be taken there.

This species is similar to *Sylvilagus floridanus* with regard to breeding habits and food preferences.

Remarks.—The records of Nelson (1909, p. 199) for the occurrence of the New England cottontail in Washington, D.C., and in nearby Alexandria, Va., have been shown by Bailey (1923, pp. 120–121) to be erroneous. He says:

They have been recorded from the District . . . and from Alexandria, but the record based on 2 young taken in a nest in the Soldiers Home grounds by Dr. C. W. Richmond on 20 June 1886 was erroneously included under this species, and a specimen which I bought on 1 January 1904 of a colored man on the street who said he killed it at Alexandria, probably came from West Virginia where they are common and are often included in shipments of rabbits to market.

SNOWSHOE RABBIT

Lepus americanus virginianus Harlan

Lepus virginianus Harlan, Fauna Americana, p. 196, 1825.

Type locality.—Blue Mountains, near Harrisburg, Pa.

General distribution.—Southern Ontario, and northeastern United States, from southern Maine, south in the Appalachian Mountains to North Carolina and Tennessee.

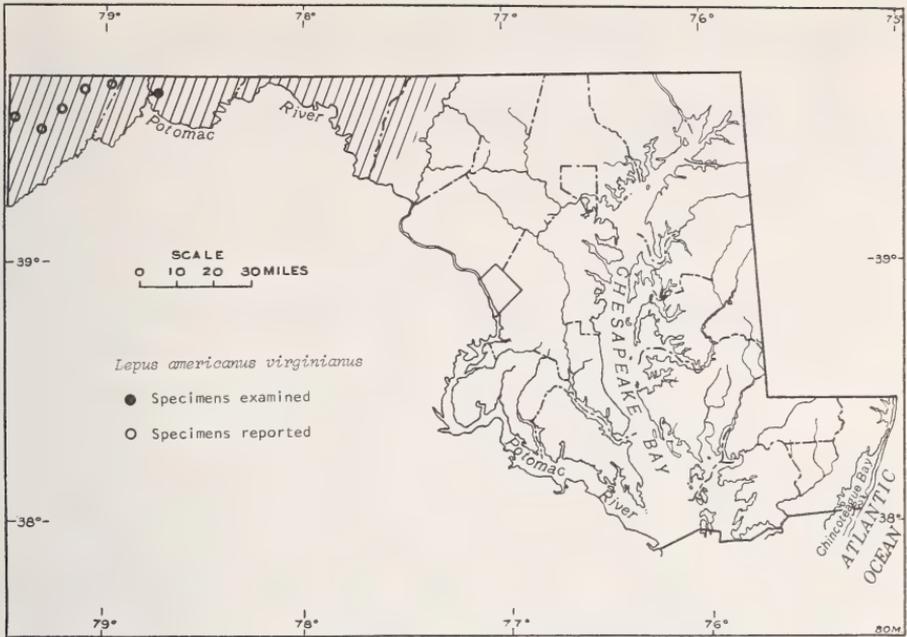


FIGURE 25.—Distribution of *Lepus americanus virginianus*.

Distribution in Maryland.—Occurs in the Allegheny Mountain and Ridge and Valley sections where it is now uncommon.

Distinguishing characteristics.—A medium-sized rabbit with large hind feet and thick fur. Coloration in summer pelage, dull rusty brown varying to buffy brown, always more or less darkened by a wash of black. In winter, coloration is sometimes pure white with a little dusky around tips of ears; but frequently a dull brownish wash is present on the feet and terminal half of the ears.

Cranially, this species differs from *Sylvilagus floridanus* and *S. transitionalis* in its larger size and heavier build, with much stronger development of the supraorbitals which are subtriangular and stand out broadly winglike with a broad open notch between the posterior process and the skull.

Measurements.—Nelson (1909, p. 86) gives average measurements of five adults from Pennsylvania as follows: Total length 518; tail vertebrae 49; hind foot 414; basilar length of skull 65.0; interorbital breadth 22.0.

Habitat and habits.—This rabbit prefers areas of spruce in the highest regions of the Allegheny Mountain and Ridge and Valley sections, where it has been observed in open woods and thickets. Spruce areas are small and scattered districts in the upland swamps and on some of the mountain tops.

Mansueti (1953, pp. 72–73) says that

The varying hare seems to be destined to permanent extirpation in Maryland. It is a species with specialized habitat requirements and one of limited distribution. Its environment is being encroached upon by civilization gradually in some and swiftly in other places. . . . The optimum habitat is forest of the high intermountain Allegheny Plateau which has at least a moderate understory of small trees and shrubs to provide food and cover. These areas are gradually being destroyed by an increasing deer herd as well as human expansion in Garrett County.

The last reliable reports of snowshoe rabbits in Maryland were by John Hamlet, formerly with the U.S. Fish and Wildlife Service, who reported that in 1945 he observed a female in Garret County but did not record the exact locality, and by John Smith of Mountain Lake who shot one near the Holy Cross Camp, Deep Creek Lake, Garrett County, in March 1957. This latter animal was probably one of 18 that had been shipped into the country from the Adirondacks of New York and released in March 1952. (Maryland Conservationist 34 (2), p. 25, March 1957.)

The snowshoe rabbit is active in the summer and winter, primarily early in the morning and late in the evening. Although it constructs no nests, it returns to the same spot regularly so that a form is eventually hollowed out. This form is nearly always concealed under grass, brush, shrubbery, or a fallen log.

This species breeds promiscuously. Mating begins early in March and may continue well into April. The first litter appears in April after a gestation period of about 36 days; as many as four litters a year are possible during a breeding season, although there are usually only two. The number of young may range from one to five or more, but most frequently three or four.

Food of the snowshoe rabbit in summer consists of dandelion, grasses, clover, ferns, and the tender parts of certain shrubs and trees. In winter, when many summer foods are not available, it feeds on bark and shoots of woody plants.

Specimens examined.—*Allegheny County*: Cumberland, 1.

Other records and reports.—*Garrett County*: Cranesville Swamp area (Mansueti, 1953, p. 72); Deep Creek Lake (Maryland Conservationist 34(2), p. 25, March 1957); Finzel (Mansueti, 1953, p. 72, says that a specimen from this locality is in the collections of the U.S. National Museum and lists it among his specimens examined. There is no record, however, that a specimen from Finzel has ever been in the National Museum collections. Rhodes (1903, pp. 119–120) quotes Merriam as saying that Preble was told of the occurrence of *Lepus virginianus* at Finzel, Md., only half a mile from the Pennsylvania line. Mansueti may have confused this record with the specimen of *Lepus a. virginianus* from Cumberland, Md., which is in the National Museum collections, and which is probably the one he examined.);

Little Crossings, headwaters of North Branch of Castleman River (Browning, 1928, p. 242) ; Wolf Swamp, SE of Grantsville (Mansueti, 1953, p. 72).

Remarks.—Several hundred snowshoe rabbits have been stocked at various times in several localities in western Maryland. None of these introductions appear to have been very successful, although the specimen taken by John Smith at Deep Creek Lake in March 1957 seems to be one of those stocked in 1952.

Order RODENTIA (gnawing mammals)

Family SCIURIDAE (squirrels)

EASTERN CHIPMUNK

Tamias striatus (Linnaeus)

[*Sciurus*] *striatus* Linnaeus, Syst. nat., ed. 10, 1: 64, 1758.

The eastern chipmunk is distributed from Quebec, New Brunswick, and Nova Scotia, south into Georgia and Louisiana, west to eastern Oklahoma, Kansas, Nebraska, North and South Dakota, and Saskatchewan. In Maryland, two subspecies are recognizable. They are—

Tamias striatus fisheri A. H. Howell

Tamias striatus fisheri A. H. Howell, J. Mammal., 6(1) : 51, 9 February 1925.

Type locality.—Merritts Corners, 4 miles E of Ossining (Sing Sing), Westchester County, N.Y.

This type locality has been the source of some confusion in the literature. It has been listed by various authorities as "Merritt's Corners, four miles W of Sing Sing [= Ossining] New York," (Howell, 1925, p. 51) ; "Merritts Corners, 4 miles E of Ossining (Sing Sing), N.Y.," (Howell, 1929, p. 16) ; "Merritts Corners, 4 miles W of Sing Sing (Ossining), Westchester County, N.Y.," (Poole and Schantz, 1942, p. 560) ; "Merritts Corners, 4 miles E of Ossining (Sing Sing), Westchester County, N.Y." (Miller and Kellogg, 1955, p. 218) : "Merritts Corners, 4 miles W Ossining (Sing Sing), Westchester County, N.Y.," (Hall and Kelson, 1959, p. 294).

The confusion involves whether Merritts Corners, a small New York State village not found on current maps of the region, actually lies west or east of Ossining, N.Y., and hence west of the Hudson River in Rockland County or east of the Hudson in Westchester County.

The locality as listed on the original label of the type specimen (U.S.N.M. Cat. No. 193370, collected on 23 August 1884, by A. K. Fisher) reads: "Sing Sing, N.Y." and on the back is written "Merritts Corners 4 miles E of Sing Sing." U.S. Geological Survey maps of the region (1893 edition, reprinted 1897) reveal that Merritts Corners, the type locality of *T. s. fisheri*, is located east of the Hudson River, in Westchester County, N.Y., at 41°11'27" N lat., and 73°47'51" W long., and is approximately 3¾ miles E and 1¾ miles N of Ossining, N.Y.

General distribution.—Middle Atlantic States, from the lower Hudson River Valley in New York, south to Virginia and West Virginia.

Distribution in Maryland.—Uncommon in the Eastern Shore and Western Shore sections; abundant locally in the Piedmont and Ridge and Valley sections. In the Allegheny Mountain section it is replaced by the subspecies *T. s. lysteri*. (see fig. 26.)

Distinguishing characteristics.—Teeth 1/1, 0/0, 1/1, 3/3, = 20; a small, heavyset ground squirrel with dense, moderately fine fur; pelage marked by two pale and three dark stripes on sides of face and five blackish and four pale stripes extending down the back; rump rusty in coloration; top of head and dark facial stripes near russet, light facial stripes pale buffy; dark stripes on back nearly black in color, paler stripes near smoke-gray shading posteriorly into russet; center or inner pale stripe is the broadest and always gray in coloration; tail moderately long, grayish red and not bushy. This species may be distinguished from any other in Maryland by the striping pattern of the pelage.

Measurements.—Four adults from the District of Columbia have the following external measurements: Total length 243.2 (234–255); tail 90.2 (83–99); hind foot 34.1 (33–35). Cranial measurements of nine adults from the vicinity of Washington, D.C., are as follows: Greatest length 39.5 (38.9–40.3); zygomatic breadth 22.0 (21.3–22.8); postorbital breadth 11.2 (10.6–12.2); length of nasals 13.2 (12.5–14.0).

Habitat and habits.—The chipmunk is largely a ground dweller, only rarely climbing trees. It prefers to live on wooded hillsides or mountain slopes, but is also fond of stone walls and rail fences. Though usually favoring dry situations, it is occasionally found in moist bottom land woods. It spends a good deal of time in burrows which it digs beneath a rock, stone wall, tree roots, or a building. The burrow is sometimes as much as 20 feet in length and 1 to 3 feet below the surface of the ground. The chipmunk in Maryland remains more or less active during the winter. All summer long, and especially in the autumn, it is busily engaged in storing food, primarily seeds and nuts for winter use. This food is kept in a "storeroom" adjoining the rooms where the animal is spending the winter. The food of the chipmunk consists of small seeds, berries, fruits, and nuts, and occasionally small birds, mice, snakes, snails, slug, insects, and other small animal life. Chipmunks are polyestrous and breed from March onward. The number of young is three to five, and the gestation period 31 days. Puberty is reached at the age of 2½ to 3 months.

Specimens examined.—*Anne Arundel County*: Epping Forest (near Annapolis), 2. *Frederick County*: Catoctin State Park, 1. *Harford County*: Fallston, 3. *Howard County*: Long Corner, 2. *Montgomery County*: Bethesda, 1; Chevy Chase, 2; Dickerson, 1; Rockville, 3; Takoma, 1; Washington Grove, 2; Linden, 1. *Prince Georges County*: Laurel, 5. *District of Columbia*: 42.

Other records and reports.—*Baltimore County*: Bare Hills–Lake Roland Area (Bures, 1948, p. 67); Lock Raven (Kolb, 1938); Patapsco State Park (Hampe, 1939, p. 6). *Montgomery County*: Sligo; Piney Branch; Silver Spring; Sandy Spring (all from Bailey, 1896, p. 95); Plummers Island (Goldman and Jackson, 1939, p. 133). *Prince Georges County*: Patuxent Research Center (Herman and Warbach, 1956, p. 87). *Worcester County*: near Milburn Landing (Vagn Flyger, personal communication, 22 June 1964).

Tamias striatus lysteri (Richardson)

Sciurus (Tamias) lysteri Richardson, Fauna Boreali-Americana, 1: 181, pl. 15, June 1829.

Type locality.—Penetanguishene, Ontario.

General distribution.—Nova Scotia, New Brunswick, and southeastern Ontario, south into Connecticut and Pennsylvania and in the Appalachian Mountains to western Maryland.

Distribution in Maryland.—Occurs in the higher mountains (above 2,000 feet altitude) of the Allegheny Mountain section where it is abundant.

Distinguishing characteristics.—This subspecies is similar to *T. s. fisheri*, but has paler upper parts, especially the rump and the median grayish bands. This paler coloration is most marked in the northern

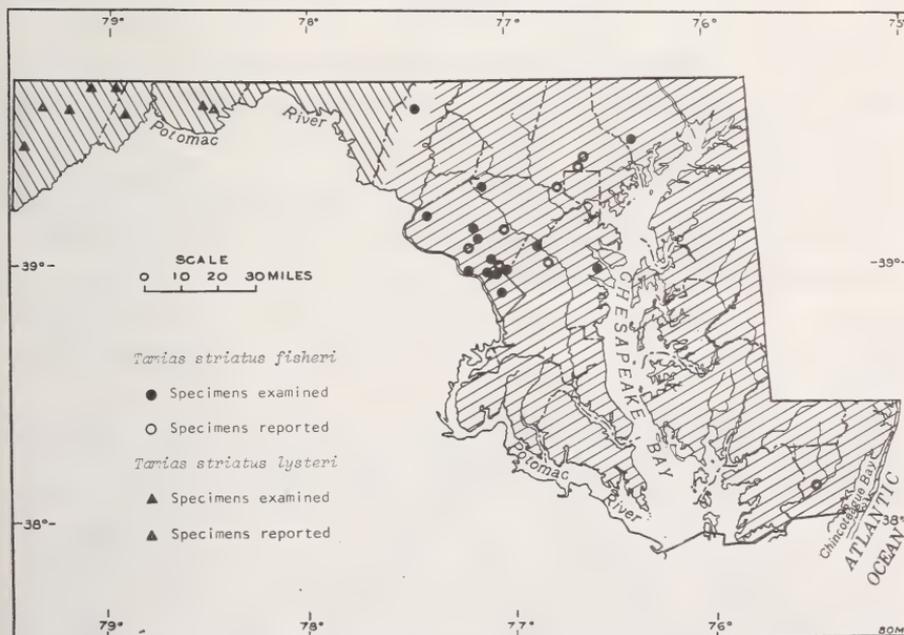


FIGURE 26.—Distribution of *Tamias striatus fisheri* and *T. s. lysteri*.

part of the range of the subspecies in the vicinity of the type locality. Maryland specimens are not so pale as typical *lysteri*.

Cranially the differences between the two subspecies are very slight. *T. s. lysteri* averages somewhat smaller, and has relatively longer nasal bones.

Measurements.—External measurements of five adults and cranial measurements of four adults from Garrett and Allegany Counties, Md., are as follows: Total length 233.4 (220–247); tail 87.8 (81–100); zygomatic breadth 21.2 (19.9–22.2); postorbital breadth 10.9 (10.5–11.2); length of nasals 13.5 (12.7–14.0).

Habitat and habits.—Similar to *T. s. fisheri*.

Specimens examined.—*Allegany County*: Dans Mountain (4 miles northwest of Rawlings), 1. *Garrett County*: Bittinger, 1; Cunningham Swamp, 1 (Coll. U. Md.); Finzel, 4; Grantsville, 1; Herrington Manor, 1.

Other records and reports.—*Allegany County*: Accident (Howell, 1929, p. 19).

Remarks.—All Maryland specimens assigned to this subspecies represent intergrades between *T. s. lysteri* and *T. s. fisheri* in coloration, size, and relative length of nasals, and assigning them to *lysteri* is somewhat arbitrary. Specimens from Fallston, Harford County, are also intergrades but are closer to *fisheri* and have been assigned herein to that subspecies.

WOODCHUCK

Marmota monax monax (Linnaeus)

[*Mus*] *monax* Linnaeus, Syst. nat., ed. 10, 1: 60, 1758.

Type locality.—Maryland.

General distribution.—Middle eastern United States from Pennsylvania, New Jersey, Ohio, Indiana, Illinois, Lower Peninsula of Michigan, and Iowa, south to Arkansas and the northern parts of Alabama, Georgia, and South Carolina.

Distribution in Maryland.—Abundant in all sections except the Eastern Shore, where it has until lately been unknown. There is recent evidence, however, that the species is extending its range into that section.

Distinguishing characteristics.—Teeth 1/1, 0/0, 2/1, 3/3, = 22; the heaviest member of the squirrel family found within the State (weight 5 to 12 lbs.); tail short and somewhat bushy; fur thick and coarse; coloration above grizzled brown, with top of head, face, legs, and tail dark brown to blackish brown; under parts lighter in coloration, and pelage not so thick; incisor teeth white; ears short and rounded.

The large size, grizzled brownish coloration, and short bushy tail readily distinguish this animal from any other rodent in Maryland.

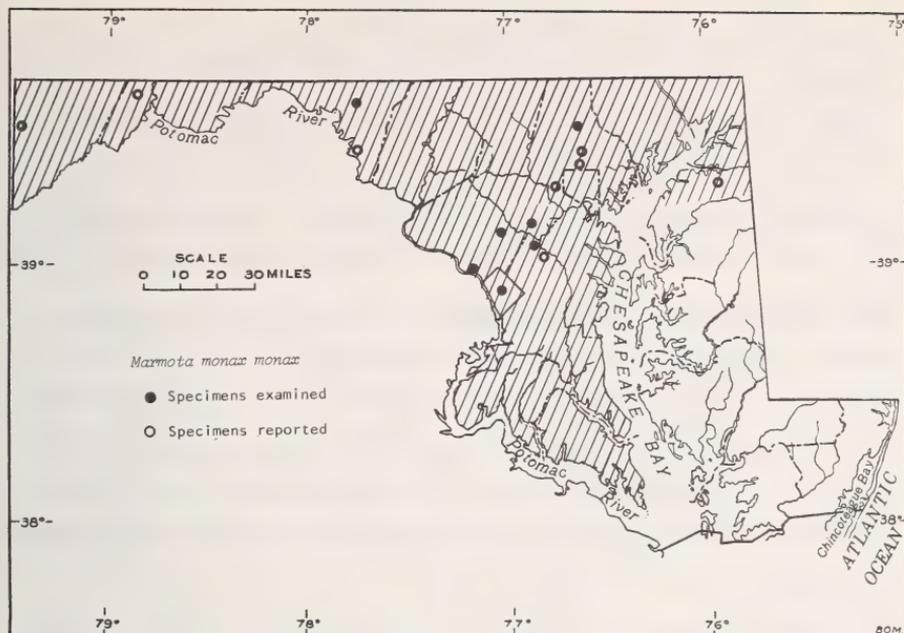


FIGURE 27.—Distribution of *Marmota monax monax*.

Measurements.—Males average larger than females in overall size. Two adult females, one from Sparks, Baltimore County, and the other from Washington, D.C., have external measurements as follows: Total length 628, 615; tail 157, 148; hind foot 88, 86. Cranial measurements of three adult males from the District of Columbia and nearby Maryland are as follows: Condylobasal length 102.6, 97.5, 95.7; palatal length 59.3, 56.2, 55.3; zygomatic breadth 69.3, 65.8, 65.9; least interorbital breadth 27.3, 25.9, 27.2; maxillary tooththrow 21.7, 21.6, 22.0. Cranial measurements of five adult females average: Condylobasal length 91.3 (89.0–94.2); palatal length 53.5 (51.0–56.0); zygomatic breadth 62.5 (59.6–64.8); least interorbital breadth 24.6 (23.3–26.3); maxillary tooththrow 21.1 (20.4–21.8).

Habitat and habits.—This is primarily a forest border and open field mammal, seldom found in heavy dense woods. It prefers the edges of brushy woodlands, and particularly open fields along streams. Woodchucks are found along poorly cleared fence lines, in meadows, cow pastures, and grainfields, especially where rocky outcroppings or old stumps occur. They are common on the bluffs that line the Maryland side of the Potomac River, and occur in great numbers in the farming country of Montgomery and Frederick Counties. Hampe (1939, p. 6) reports that they are very abundant throughout the Patapsco State Park, and that numerous burrows are found in the hill-sides along the river. In the Bare Hills–Lake Roland region of Balti-

more County, Bures (1948, p. 67) found that they were not very common, their range being limited to areas of cultivation and the region between the deciduous woods and the marsh. Woodchucks abound in Garrett County, particularly in the vicinity of Deep Creek Lake.

This species is active both day and night and is frequently seen in grassy shoulders and rocky outcroppings that border Maryland highways. On many occasions it falls victim to modern high-speed traffic and is one of the most frequently encountered road-kills in the State.

The woodchuck inhabits an extensive burrow which sometimes extends to a depth of 5 feet and may be some 30 feet in length. The burrow usually has several entrances, which may be located beneath a wall or tree stump. Within the burrow, there is usually one chamber in which a bulky grass nest is situated. In this chamber the female gives birth to four or five young in April or May after a gestation period of about 4 weeks. The babies remain in the den for about a month, after which their eyes open, and they become completely independent of the mother by early July.

Principal food of the woodchuck consists of grasses and succulents such as clover, alfalfa, plaintain, and various perennials, in addition to beans, peas, corn, and apples; seldom does the woodchuck consume flesh, although it has been known to pursue poultry and eat insects and snails. During the summer it becomes fat on these foods, and early in the autumn when the first frost is on the ground it descends into its burrow and goes into hibernation. It usually emerges again in late February or early March.

Specimens examined.—*Baltimore County*: Sparks, 1. *Howard County*: Simpsonville, 1. *Montgomery County*: Plummers Island, 4; Sandy Spring, 1. *Prince Georges County*: Laurel, 5; near Washington, D.C., 1. *Washington County*: Hagerstown, 1. *District of Columbia*: 6.

Other records and reports.—*Allegany County*: Mount Savage (Coll. U. Md.). *Baltimore County*: Bare Hills—Lake Roland area (Bures, 1948, p. 67); Lock Raven (Kolb, 1938); Patapsco State Park (Hampe, 1939, p. 6). *Garrett County*: Cranesville Pine Swamp (Mansueti, 1958, p. 83). *Kent County*: Galena (Allen, 1950, p. 28). *Prince Georges County*: Patuxent Research Center (Grizzell, 1949, p. 74). *Washington County*: Sharpsburg, 1 mile W (personal observation).

Remarks.—Allen (1950, p. 28) says that the Eastern Shore is one of those regions that has been invaded by the woodchuck in the last 50 years. It first appeared on the Prettyman Farm near Galena in Kent County around 1900. Evidently it is spreading southward around the Chesapeake Bay from Pennsylvania.

GRAY SQUIRREL

Sciurus carolinensis pennsylvanicus Ord

Sciurus pennsylvanicus Ord, in [Guthrie], a new geographical, historical and commercial grammar; . . . , Philadelphia, ed. 2, 2: 292, 1815.

Type locality.—Pennsylvania, west of the Allegheny Ridge.

General distribution.—From southern New Brunswick, Quebec, and Ontario, south into Virginia and in the Appalachians to Tennessee, west into eastern Iowa and southern Minnesota.

Distribution in Maryland.—Abundant in all sections of the State.

Distinguishing characteristics.—Teeth 1/1, 0/0, 2/1, 3/3, = 22; size large; tail bushy and flattened; coloration variable both in summer and winter; upper parts usually yellowish brown in summer, with a slightly grayish cast to the sides of the neck, the shoulders, and thighs; face clay colored to cinnamon buff; forelegs gray above, hind legs reddish; tail brown at base, hairs blackish near middle and tipped with gray; in winter pelage, paler and more grayish.

A melanistic color phase occurs frequently in this species, particularly in *S. c. pennsylvanicus*. Albinistic animals are also often encountered.

Measurements.—External and cranial measurements of three adult males from Cambridge, Dorchester County, are as follows: Total length 462, 486, 465; tail vertebrae 201, 216, 190; hind foot 64, 64, 61;

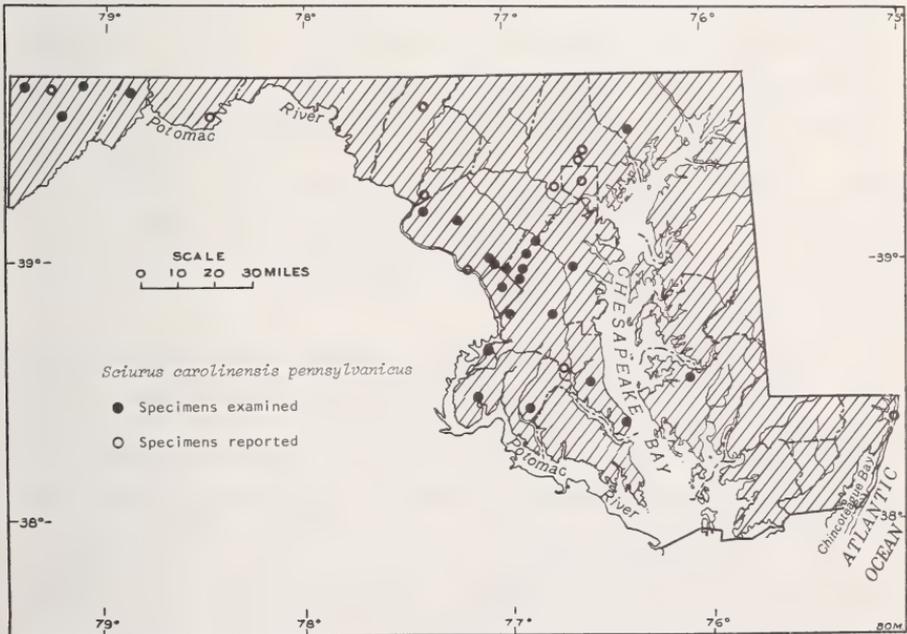


FIGURE 28.—Distribution of *Sciurus carolinensis pennsylvanicus*.

greatest length of skull 62.6, 62.4, 62.8; zygomatic breadth 33.4, 33.4, 33.6; least interorbital breadth 16.9, 19.2, 18.2; length of maxillary toothrow 10.9, 11.6, 11.2.

Habitat and habits.—This is a squirrel of the hardwood and mixed coniferous-hardwood forests, particularly those with nut-bearing trees and bushy undergrowth. It is quite common in the parks of Washington, D.C., particularly Rock Creek Park. Most of these are descended from introduced stock. Bailey (1923, p. 108) says:

The late Dr. William L. Ralph purchased many gray squirrels and liberated them in the Smithsonian grounds, where up to the time of his death in 1907 he fed and cared for them . . . They soon became common in the Mall . . . and spread to the White House grounds, LaFayette Square, and other city parks.

Melanistics squirrels were introduced and liberated into the National Zoological Park and are still frequently seen there. Of these, Bailey (1923, p. 109) says:

The first shipment of 10 (black squirrels) was from Rondeau Provincial Park, Morpeth, Ontario, 18 May 1906; and these squirrels were immediately liberated in the northwestern part of the zoo where they were very much at home. They have since been constantly in the park, especially from the vicinity of the great flight cage to the Klinge Valley and they have spread northward to Cleveland Park and nearly to Chevy Chase.

Five of the 31 skins of gray squirrels in the National Museum collections from the District of Columbia show melanistic tendencies.

The gray squirrel is common throughout Maryland. Hampe (1939, p. 6) says that it is the most common squirrel in the Patapsco State Park and has been observed in the Park every month of the year; young squirrels are numerous there after the first of July. Bures (1948, p. 67) says the gray squirrel is quite common in the Bare Hills-Lake Roland area. I found them numerous on the Delmarva Peninsula; in southern Maryland; in the Piedmont region, particularly in the vicinity of Sugar Loaf Mountain; and in the mountains of the western part of the State. Gray squirrels do not occur on Assateague Island, but I have seen them in the thickets back of the dunes several miles north of Ocean City.

The gray squirrel is most at home in trees and descends to the ground only when necessary to obtain food and bury nuts. It does not hibernate, even in the coldest northern portions of its range. This squirrel is diurnal and is most active in the early morning and late afternoon.

Its bulky nest is generally constructed in an enlarged natural cavity of an old oak tree, but sometimes an outdoor nest of firmly woven leaves is constructed among the branches or in the crotch of a tree.

Squirrels mate during midwinter, and the gestation period is about 40 days. A second mating usually occurs sometime in May or June. The young are two to five (generally four) in number. When 2 months

of age, they are weaned, but remain with the mother until she has her second litter.

The gray squirrel is generally vegetarian in habits, its food consisting of many kinds of nuts (including acorns), seeds, fruits, buds, fungi, inner bark of certain trees, and occasionally corn and other grains, and fleshy parts of plants. Sometimes it eats small amounts of animal food such as insects or an occasional bird's egg or small bird.

Specimens examined.—*Allegheny County*: Mount Savage, 1 (Coll. U. Md.). *Anne Arundel County*: Priest Bridge, 1. *Calvert County*: Little Cove Point Area, 2; Prince Frederick, 1. *Charles County*: Marshall Hall, 1; Newport, 1; Port Tobacco, 2. *Dorchester County*: Cambridge, 3. *Garrett County*: Friendsville, ¼ mile NW, 1 (Coll. U. Md.); Grantsville, 2; Meadow Mountain, 1 (Coll. U. Md.). *Harford County*: Fallston, 5. *Montgomery County*: Dickerson, 1; Germantown, 2; Kensington, 1; Takoma Park, 2; Woodside, 1. *Prince Georges County*: Beltsville, 1; Bladensburg, 2; Branchville, 1; College Park, 1; Fort Washington, 1; Laurel, 22; (Upper) Marlboro, 2; Muirkirk, 1; Oxon Hill, 1; Patuxent River (fork), 2; Piscataway Creek, 2; Scagg's Swamp, 1. *District of Columbia*: 40.

Other records and reports.—*Allegheny County*: South end of Town Hill Mountain (personal observation). *Baltimore City* (Flyger, 1960b, p. 366). *Baltimore County*: Bare Hills-Lake Roland area (Bures, 1948, p. 67); Loch Raven (Kolb, 1938); Patapsco State Park (Hampe, 1939, p. 6). *Frederick County*: Thurmont (Coll. U. Md.); Sugar Loaf Mountain (personal observation). *Garrett County*: Keyser's Ridge (Coll. U. Md.); *Montgomery County*: Plummers Island (Goldman and Jackson, 1939, p. 133). *Prince Georges County*: Aquasco (Herman, and Reilly, 1955, p. 402). *Worcester County*: Ocean City, 2 miles N (personal observation).

Remarks.—All of Maryland was formerly included within the range of the southern subspecies of gray squirrel, *Sciurus carolinensis carolinensis* Gmelin (see Bangs, 1896, p. 153, and Miller, 1924, p. 223). Patton (1939, pp. 75-76), however, in a study of the distribution of the gray squirrel in Virginia, concluded that *S. c. carolinensis* occupies the southern half of the Piedmont Plateau and the entire Coastal Plain region in that State. He says that in Virginia the area of intergradation between *S. c. carolinensis* and *S. c. leucotis* (= *pennsylvanicus*) lies along a line drawn from central King George County to southeastern Patrick County, and he assigned a specimen from Eastville, on the Virginia portion of the Delmarva Peninsula, to *S. c. carolinensis*. This suggests that, although most of Maryland lies within the range of *S. c. pennsylvanicus*, the southern portions of the Western Shore and Eastern Shore sections are within the range of *S. c. carolinensis*, and the range of the species in Maryland has been mapped in this way by

Hall and Kelson (1959, p. 371). However, a careful comparison of specimens from Calvert and Charles Counties in the Western Shore Section and Cambridge in the Eastern Shore section with specimens of typical *pennsylvanicus* from central Pennsylvania and New York show that they differ in no essential respect from that subspecies, whereas they are considerably larger and paler than typical *carolinensis*. I have also examined the specimen from Eastville, Va., assigned by Patton (1939) to *carolinensis*, and consider it to be referable to *pennsylvanicus*. It is somewhat darker than typical *pennsylvanicus*, but can be matched in coloration by many specimens in similar prelude from the northern portion of the range of *pennsylvanicus*. In size it is indistinguishable from typical *pennsylvanicus* and considerably larger than *carolinensis*. Consequently, all of Maryland falls within the range of *S. c. pennsylvanicus*, and this range extends at least as far south as Eastville on the Virginia portion of the Delmarva Peninsula and probably as far as the tip of that peninsula.

FOX SQUIRREL

Sciurus niger Linnaeus

[*Sciurus*] *niger* Linnaeus, Syst. nat. ed. 10, 1: 64, 1758.

This is our largest tree squirrel and one of the most spectacular rodents in Maryland. It resembles the gray squirrel but is considerably bigger and heavier, and less often observed. Mansueti (1952, p. 31) comments that a ratio of 40 grays to one fox squirrel may be high, but that few fox squirrels have been reported in recent years and the species appears to be becoming scarce in all the Atlantic Coast States.

The distribution of fox squirrels in Maryland has been reviewed by Mansueti (1952, pp. 31-41), and most of the following is based upon his records or records cited by him.

Two subspecies occur within Maryland. They are:

Sciurus niger cinereus Linnaeus

[*Sciurus*] *cinereus* Linnaeus, Syst. nat., ed. 10, 1: 64, 1758.

Sciurus niger bryanti H. H. Bailey, Bailey Mus. Libr. Nat. Hist., Newport News, Virginia, Bull. No. 1 [p. 1], 1 August 1920. (Type locality: Dorchester County, Md.)

Type locality.—Restricted to Cambridge, Dorchester County, Maryland, by Barkalow (1956, p. 13).

General distribution.—Formerly from Northampton County in Virginia to southeastern Pennsylvania, but now confined to the Eastern Shore section of Maryland. It has been listed by the Department of the Interior as an endangered form.

Distribution in Maryland.—Occurs in limited numbers in Dorchester, Queen Annes, Talbot, Wicomico, Somerset, and Worcester

Counties. The present center of population appears to be in the vicinity of Blackwater National Wildlife Refuge where it is still common. (See fig. 29.)

Distinguishing characteristics.—Teeth 1/1, 0/0, 1/1, 3/3, = 20; coloration uniform light grizzled-gray above with a steel blue cast; belly and feet white; tail with a pronounced black stripe on outer edges. A melanistic form occurs in which the belly and back are blackish. May be readily distinguished from the gray squirrel, which it resembles somewhat in coloration, by its much larger size and reduced dentition.

Measurements.—Five adults from Dorchester County have external measurements as follows: Total length 579 (560–605); tail 273 (263–285); hind foot 77 (73–81). Cranial measurements of four adults from Dorchester County are: Greatest length 68.5 (67.7–69.8); zygomatic breadth 38.8 (37.9–39.8); least interorbital breadth 20.8 (19.4–22.3); length of maxillary toothrow 11.9 (11.8–12.0).

Habitat and habits.—This subspecies prefers mature forests of mixed hardwoods and conifers in which mast-producing trees such as oaks, hickories, and pines are present. It is particularly partial to old-growth loblolly pine forests, many of which, however, have been cut over or burned through forest fires.

This squirrel spends much time on the ground but generally doesn't stray far from the home roost. It lies close to the body of a tree or limb, seldom leaping from tree to tree as does the gray squirrel. Nests, which serve as home during summer and winter, are placed near the tips of branches in old pines, generally from 30 to 50 feet above the ground. Mating may occur at any time throughout the year, but is most frequent during the latter part of February or early March. Usually, four young comprise a litter and are born in April.

Fox squirrels feed more on the ground than do gray squirrels. Food consists primarily of acorns, hickory nuts, walnuts, and particularly the seeds of loblolly pine. They seldom, if ever, cause damage to corn or other domestic crops.

This squirrel has become greatly reduced in numbers and has entirely disappeared from some areas of its former range. One of these areas is the northern portion of the Eastern Shore section; this is the area where this subspecies would be expected to intergrade with *Sciurus niger vulpinus*, the form inhabiting the Western Shore of Maryland.

Specimens examined.—*Dorchester County*: Airey (near), 1; Blackwater Refuge, 1; Bucktown, 1; Cambridge, 9. *Kent County*: East Neck Island, 3. Eastern Shore (no exact locality), 3.

Other records and reports (with dates of capture or sighting when available).—*Dorchester County*: Big Blackwater Section, 1932,

(Dozier and Hall, 1944, p. 5); Gibbs Marsh, between Golden Hill and Church Creek, near Blackwater River (Mansueti, 1952, p. 33); Grif-fins Neck (Dozier and Hall, 1944, p. 10); Milton (Dozier and Hall, 1944, p. 10); Salem Woods, 14 Miles from Cambridge on road to Salisbury, 1933, (Dozier and Hall, 1944, p. 5); Secretary (Dozier and Hall, 1944, p. 10); Taylors Island, 1963, (James B. Trefethen in correspondence to Bureau of Sport Fisheries and Wildlife, 12 November 1964). *Queen Annes County*: Church Hill (near), 4 miles below Chestertown, 1943, (Dozier and Hall, 1944, p. 3). *Somerset County*: Big Swamp, 2 miles E of Kings Creek, 1922, (Dozier and Hall, 1944, p. 3); Westover, due west of, 1940, (Dozier and Hall, 1944, p. 3); Loretto, near, 1944, (Dozier and Hall, 1944, p. 3). *Talbot County*: Trappe, near, 1948, (Mansueti, 1952, p. 33). *Worcester County*: Newark, 1951, (Mansueti, 1952, p. 33); Pocomoke City, near, (Dozier and Hall, 1944, p. 3).

Sciurus niger vulpinus Gmelin

[*Sciurus*] *vulpinus* Gmelin, Syst. nat., ed. 13, p. 147, 1788 (based on specimens from the eastern United States, including the Blue Mountains of Pennsylvania).

General distribution.—Formerly occurred from central New York, south through south-central Pennsylvania, western Maryland, eastern West Virginia, western Virginia, and in the Appalachian Mountains to western North Carolina. Distribution presently reduced to south-central Pennsylvania, Maryland, western Virginia, and eastern West Virginia.

Distribution in Maryland.—Found locally in heavily forested regions in the Western Shore, Piedmont, Ridge and Valley, and Allegheny Mountain sections.

Distinguishing characteristics.—Similar in size and general characteristics to *S. n. cinereus*, but differs in coloration. The body is generally buffy brown above, in contrast to the bluish grizzled gray of *cinereus*; tail grayish white above, rufous below; feet and ears rufous; top of head more blackish than the back. May be distinguished from the gray squirrel by its larger size.

Measurements.—No external measurements are available for any of the Maryland adults in the National Museum collections. Two adults from White Sulphur Springs, West Virginia, which are typical of this subspecies have the following measurements: Total length 615, 603; tail 299, 298; hind foot 77, 79. Four Maryland specimens (two from Laurel, Prince Georges County; one from Priest Bridge, Anne Arundel County; and one from North Chesapeake Beach, Calvert County) have the following cranial measurements: Greatest length 67.7 (66.6–68.2); zygomatic breadth 38.6 (38.2–39.4); least interor-

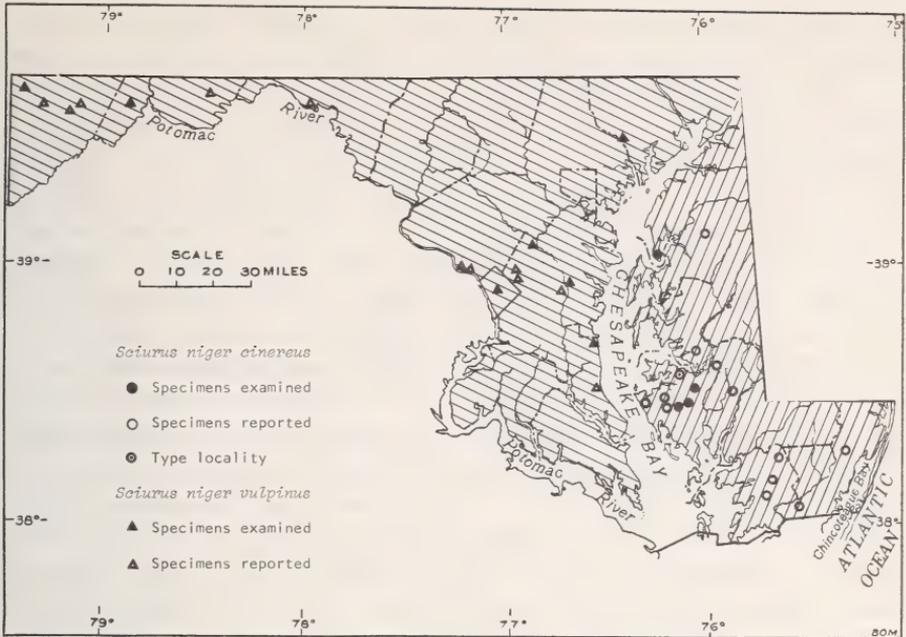


FIGURE 29.—Distribution of *Sciurus niger cinereus* and *S. n. vulpinus*.

bital breadth 20.3 (20.1–20.5); length of maxillary toothrow 11.9 (11.0–12.3).

Habitat and habits.—Not much has been published concerning the habitat and habits of this subspecies. It is said to prefer open deciduous woods, wood borders, and orchards, but as noted by Bailey (1923, p. 110) it is skillful in keeping out of sight. Mansueti (1952, p. 35) states that the subspecies has been considerably decimated in recent years, and the remaining fox squirrels are strictly local in distribution and are more or less relic populations where they occur.

Bailey (1923, p. 110) reported that at various times fox squirrels were released in the National Zoological Park in Washington, D.C. These apparently never flourished, since none have been observed in the park in years.

Specimens examined.—*Allegany County*: Between Clarysville and Red Hill, 1 (Coll. U. Md.). *Anne Arundel County*: Patuxent River at Priest Bridge, 10. *Calvert County*: North Chesapeake Beach, 1. *Garret County*: Friendsville, 1/4 mile NW, 2 (Coll. U. Md.). *Harford County*: Fallston, 1. *Prince Georges County*: Laurel, 4. *District of Columbia*: 4 (these were either purchased at the Central Market or trapped in the National Zoological Park, and probably are not actually from the District of Columbia area).

Other records and reports (from Mansueti, 1952, except where otherwise noted).—*Allegany County*: Green Ridge State Forest, 1935.

Calvert County: Governors Run, 1948 (?). *Garrett County*: Accident 1945 and 1951; Bittinger, 1948; Meadow Mountain, 1947. *Montgomery County*: Great Falls, 1916; Plummers Island (Goldman and Jackson, 1939, p. 133). *Prince Georges County*: Bladensburg (near), 1949 (?). College Park, 1948; 1/2 mile east of intersection of Highways 214 and 301, 1940. *Washington County*: Fort Frederick State Park, 1950.

Remarks.—Mansueti (1952, p. 35) lists on a provisional basis a third subspecies of the fox squirrel in Maryland, the more western *Sciurus n. rufiventer*. He and Vagn Flyger in 1950 examined the tail of a fox squirrel shot on a hill near Storey's Landing, Deep Creek Lake, Garrett County, several years before, and found that its coloration was similar to that of *rufiventer*. This subspecies normally occurs west of the Allegheny Mountains and prefers open or parklike upland woods rather than heavily forested sections. It commonly occurs along fence rows in cultivated fields or in pastures where there are only scattered trees. Mansueti claims that these conditions are found in many parts of Garrett County, particularly around Deep Creek Lake and that *rufiventer* may be moving into this area from further west. He states that possibly as the heavily forested areas are cut, and *S. n. vulpinus* vacates, *S. n. rufiventer* invades the area vacated. On the other hand, he notes that numbers of *S. n. rufiventer* have been released in southwestern Pennsylvania in an effort to restock the area and some of these may have migrated south into Maryland. The two specimens from Garrett County that I have examined, however, are typical *S. n. vulpinus* and exhibit none of the characters of *rufiventer*.

RED SQUIRREL

Tamiasciurus hudsonicus loquax (Bangs)

Sciurus hudsonicus loquax Bangs, Proc. Biol. Soc. Washington, 10: 161, 28 December 1896.

Type locality.—Liberty Hill, Conn.

General distribution.—Southern Ontario, southern Vermont and New Hampshire, south to northern Virginia and West Virginia, west to eastern Iowa and southeastern Minnesota.

Distribution in Maryland.—Occurs locally in the Piedmont, Ridge and Valley, and Allegheny Mountain sections; scarce or absent over most of the Western Shore section; apparently absent in the Eastern Shore section.

Distinguishing characteristics.—Teeth 1/1, 0/0, 2/1, 3/3, = 22; anterior upper premolar frequently lacking, and when present so reduced as to be easily overlooked; size small, the smallest of our local tree squirrels; tail relatively short and bushy; general coloration in winter bright rufous above, white below; ears tufted with black; in summer, coloration more olive dorsally, with ears untufted.

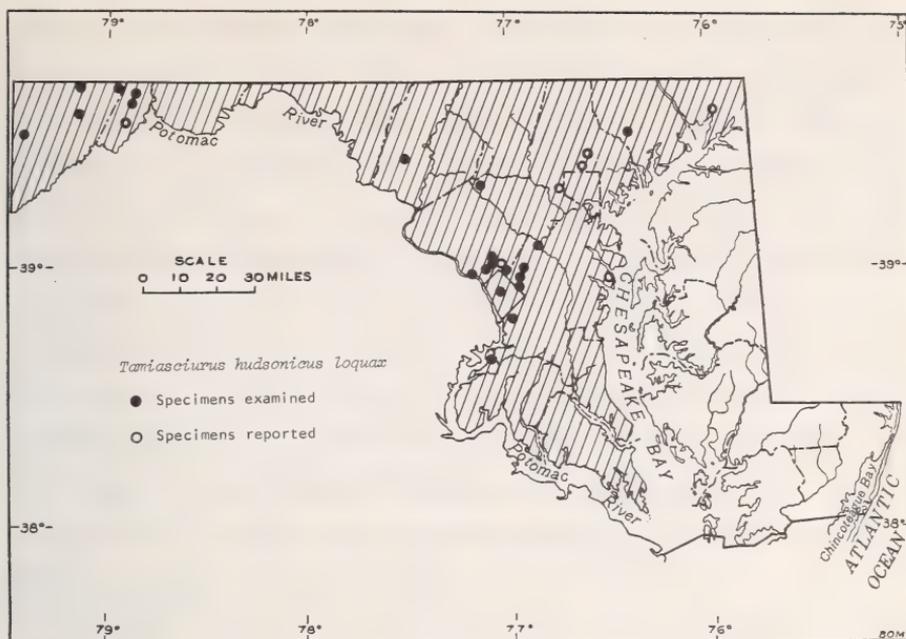


FIGURE 30.—Distribution of *Tamiasciurus hudsonicus loquax*.

This squirrel is differentiated from all others in Maryland by its small size and reddish coloration.

Measurements.—Two adults from the vicinity of Bethesda, Montgomery County, have external measurements as follows: Total length 310, 303; tail 130, 130; hind foot 50, 51; ear 22, 27. Cranial measurements of 10 adults from Laurel, Prince Georges County are: Greatest length 45.2 (44.4–46.0); zygomatic breadth 26.2 (26.0–27.2); least interorbital breadth 13.9 (13.1–14.6); length of maxillary toothrow 7.2 (6.6–7.8).

Habitat and habits.—This squirrel prefers spruce and hemlock forests, but is often found in deciduous woods and in rural areas in the northern hardwoods region where it sometimes builds nests in the attics of houses. It is more terrestrial than the gray squirrel, spending a great deal of time on the ground searching for food. It is also more omnivorous than the gray squirrel, eating almost any kind of seed, nut, or berry. Various kinds of fungi are consumed and even an occasional egg when the nest of a songbird is raided. Hamilton (1943, p. 224) says that it has been known to kill and partially devour young cottontail rabbits.

The bulky nest of the red squirrel, made of grass and moss, is usually placed high in the branches of a tree and can be distinguished from that of the gray squirrel by its smaller size and the finer material used in its construction. The red squirrel is active throughout the year.

It produces litters of from three to six young early in the spring and often a second litter in late summer.

The center of Maryland's red squirrel population is the spruce and hemlock forests of the Allegheny Mountain section of the State. It is scarce or absent over most of the Western Shore section and apparently lacking in the Eastern Shore section. David H. Johnson, formerly Curator of Mammals, U.S. National Museum, tells me that he is very familiar with pine woods near Greenbelt, Prince Georges County, and never observed a red squirrel there. J. C. Lingeback, Division of Mammals, U.S. National Museum, advises me that in his many years of field experience in the Annapolis area of Anne Arundel County he never observed a red squirrel. Flyger (1957, p. 1), however, reports that he trapped a red squirrel on 23 February 1957 near the Naval Academy in Annapolis and that there had been a colony there for several years. This is probably an artificially introduced population. Red squirrels have, however, been taken at such Western Shore section localities as Laurel, Bladensburg, Oxon Hill, Riverdale, and College Park, in Prince Georges County, and Marshall Hall in Charles County. These localities are not very distant from the fall line and the beginning of the Piedmont section, and elsewhere in the Western Shore section the red squirrel appears to be exceedingly scarce.

Even in the Piedmont section the species is only locally abundant, being completely absent over large areas. At one time it was numerous in Rock Creek Park in Washington, D.C., but none have been seen there in recent years. It is still plentiful in some suburban areas northwest of Washington. A lactating female was found dead by David H. Johnson on a road adjacent to a pine woods a few miles northwest of Bethesda, Montgomery County, in October 1955, and another near this general area in September 1957. Johnson tells me that it is the common squirrel in some of the pine woods in the Bethesda area, being more often seen there than gray squirrels. In the Piedmont section of Baltimore County, Hampe (1939, p. 6) reported red squirrels uncommon in the pine woods of the Patapasco State Park, but Bures (1948, p. 67) found that it was a common resident of the Bare Hills-Lake Roland area a few miles to the northeast. Evidently, the red squirrel has a scattered distribution in Maryland and is only abundant locally.

Specimens examined.—*Allegheny County*: Frostburg, 1; Mount Savage, 2 (Coll. U. Md.). *Charles County*: Marshall Hall, 1. *Frederick County*: Middletown, 6. *Garrett County*: Bittinger, 1; Finzel, 2; Grantsville, 1; Swallow Falls State Park, 1. *Harford County*: Fallston, 1. *Howard County*: Long Corner, 1. *Montgomery County*: Bethesda, 3½ miles NW, 1; Bethesda, 5 miles NW, 1; Kensington, 8; Linden, 2; Plummers Island, 1; Takoma Park, 3. *Prince Georges*

County: Bladensburg, 2; College Park (near), 1; Laurel, 16; Oxon Hill, 1; Riverdale, 1. *District of Columbia*: 25.

Other records and reports.—*Allegheny County*: Dans Mountain (Coll. U. Md.). *Anne Arundel County*: Annapolis (Flyger, 1957, p. 1). *Baltimore County*: Bare Hills—Lake Roland area (Bures, 1948, p. 67); Loch Raven (Kolb, 1938); Patapsco State Park (Hampe, 1939, p. 6). *Cecil County*: Northeast (Coll. Acad. Nat. Sci. Philadelphia). *Montgomery County*: Silver Spring (files of U.S. Fish and Wildlife Service). *Prince Georges County*: Hyattsville (Bailey, 1923, p. 107).

Remarks.—Specimens from Garrett County and Allegheny County appear somewhat darker in summer and winter pelage than specimens from farther east in the State and may represent intergrades with the southern Appalachian subspecies *T. h. abieticola*.

SOUTHERN FLYING SQUIRREL

Glaucomys volans volans (Linnaeus)

[*Mus*] *volans* Linnaeus, Syst. Nat., ed. 10, 1: 63, 1758.

Type locality.—Virginia (fixed by Elliot, Field Columb. Mus., Zool. Ser., 2: 109, 1901).

General distribution.—From central Minnesota, Upper and Lower Peninsulas of Michigan, southeastern Ontario, New York, and southern New Hampshire, south to North Carolina and Tennessee, west to eastern Kansas and Nebraska.

Distribution in Maryland.—Probably abundant in all sections of the State where there is suitable habitat. No specimens or records are available, however, from the Eastern Shore, Ridge and Valley, and Allegheny Mountain sections, but this probably indicates that these sections have not been systematically trapped for the species rather than a scarcity of the animals themselves. Flying squirrels are nocturnal, shy, and seldom observed.

Distinguishing characteristics.—Teeth 1/1, 0/0, 2/1, 3/3, = 22; a small squirrel that is characterized by a "flying membrane", a loose fold of fully furred skin connecting the fore and hind limbs from wrists to ankles. The tail is broad, flattened, and almost parallel-sided, with the tip rounded; pelage extremely soft and dense; coloration of upper parts varies with season and age, but is generally grayish brown; under parts usually white or creamy white in coloration, with the white extending from the base of the hairs to the tip; dark brown streak extending along side edge of "flying membrane"; tail grayish above, cinnamon below; forefeet white, hind feet brown except for some white on toes.

This species may be distinguished from all other squirrels in Maryland by the distinctive "flying membrane." The northern flying squirrel, *Glaucomys sabrinus*, has not as yet been reported from Maryland,

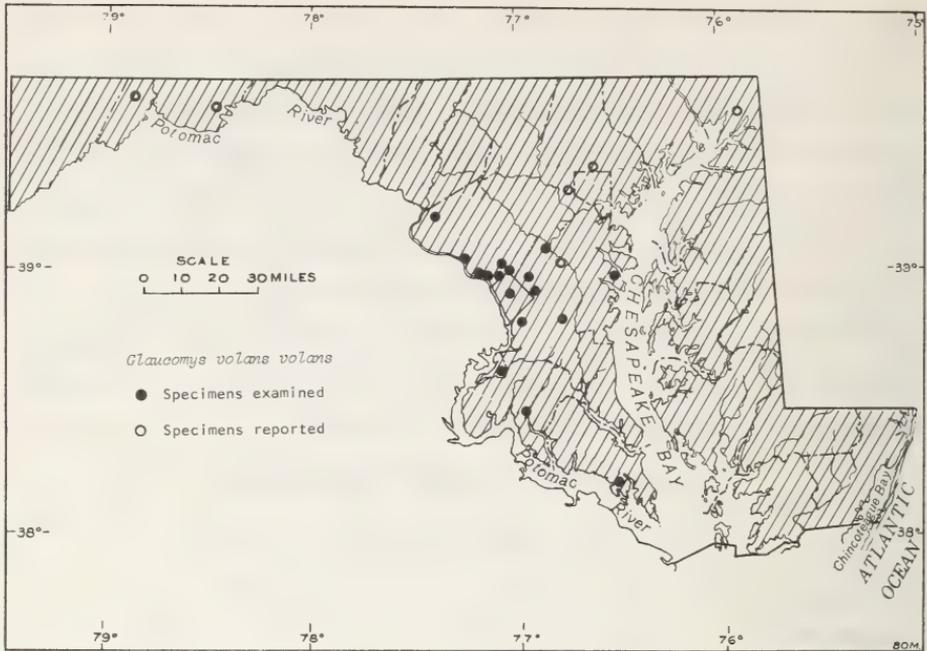


FIGURE 31.—Distribution of *Glaucomyx volans volans*.

but may occur in spruce and fir forests in the highest elevations of the Allegheny Mountain section. It differs from the present species primarily in that it is much larger in size and the basal portion of the white hairs of the belly are colored grayish.

Measurements.—External and cranial measurements of eight adults from Newport, Charles County, are as follows: Total length 221.9 (211–240); tail vertebrae 97.9 (90–110); hind foot 26.6 (21–30); greatest length of skull 34.6 (33.5–35.6); zygomatic breadth 20.5 (19.7–21.3); interorbital breadth 6.9 (6.5–7.5); length of maxillary tooth row 6.4 (6.2–6.5).

Habitat and habits.—This is essentially a species of the heavy timber and is never found at any great distance from water. It prefers forests of deciduous trees, but is sometimes encountered in woodlands of mixed conifers and hardwoods. Occasionally it may occupy an old orchard.

The species is probably abundant in all sections of the State where there is suitable habitat, but because of its secretive habits it is seldom noticed. Bures (1948, p. 67) says that in the Bare Hills–Lake Roland area of Baltimore County it is as common as the chipmunk, but because of its nocturnal habits is less often observed. Hampe (1939, p. 6) found that it was fairly common in the Patapsco State Park. He observed one at twilight on 22 May 1936. Bailey (1923, p. 112) found the species common in the woods of the District of Columbia, right up to the edge of the city.

The flying squirrel is one of the most nocturnal mammals in Maryland, rarely leaving its nest before the sun is well down. It remains active throughout the night, foraging for hickory nuts, beechnuts, acorns, maple and wild cherry seeds, apples, and buds and blossoms of some trees. It is carnivorous to some extent and occasionally feeds on insects, young birds, and birds' eggs. This squirrel is highly social.

The favorite nesting site for the flying squirrel is a hole in a dead or dying tree. A cavity made by a woodpecker is often preferred, although occasionally a natural one will be utilized and artificial bird nest boxes are sometimes used. The nest is composed of finely shredded leaves and inner bark.

This species probably does not hibernate in Maryland, although farther north it becomes inactive during colder weather (Sollberger, 1940, p. 285). Mating may occur in late February or early March and the gestation period is about 40 days. Three young usually comprise a litter, and a second mating sometimes occurs in July (Sollberger, 1943, p. 163).

Specimens examined.—*Anne Arundel County*: Annapolis, 3 miles NW, 1. *Charles County*: Marshall Hall, 2; Newport, 10. *Montgomery County*: Cabin John Creek, 1; Capitol View, 1; Chevy Chase, 1; Dickerson, 1; Garrett Park, 1; Glen Echo Heights, 1; Great Falls, 1; Kensington, 2; Plummerville Island (near), 1; Silver Spring, 4. *Prince Georges County*: Anacostia River, NW Branch, 1; Branchville, 1; Laurel, 2; Upper Marlboro, 1; no exact locality, 3. *St. Marys County*: Tall Timbers, 1.

Other records and reports.—*Allegany County*: Mount Savage (Coll. U. Md.); Town Hill (Coll. U. Md.). *Baltimore County*: Bare Hills—Lake Roland area (Bures, 1948, p. 67); Patapsco State Park (Hampe, 1939, p. 6). *Cecil County*: Bacon Hill (3 specimens in Phila. Acad. Nat. Sci.). *Montgomery County*: Forest Glen (Bangs, 1896, p. 166). *Prince Georges County*: Patuxent Research Center (Herman and Warbach, 1956, p. 87).

Family CASTORIDAE (beavers)

BEAVER

Castor canadensis Kuhl

Castor canadensis Kuhl, Beitr. z. zool. u. vergleich. Anat., Abth. 1, p. 64, 1820.

Type locality.—Hudson Bay.

General distribution.—Formerly ranged over most of the forested regions of North America, north of Mexico. It was exterminated in many areas of its range and later successfully reintroduced into some sections.

Distribution in Maryland.—Formerly occurred in all sections of the State, but was exterminated around the turn of the century or earlier. It has been deliberately restocked in some areas and naturally invaded others from neighboring States where animals were stocked or remnant populations survived.

Distinguishing characteristics.—Teeth 1/1, 0/0, 1/1, 3/3, = 20; largest rodent in Maryland; body thickset and compact; legs short; ears small; hind feet large with the toes webbed; tail broad, flat, nearly hairless, and covered with large scales; pelage with very soft dense underfur, overlaid with long coarse guard hairs; coloration dark rich brown above, lighter below.

Measurements.—“Nine adults from the Allegheny National Forest, Pennsylvania, average: Total length, 1,031 mm. (970–1,090 mm.); tail vertebrae, 358 mm. (260–440 mm.); greatest width of tail, 129 mm. (112–150 mm.); hind foot, 169 mm. (156–183).” (Handley and Patton, 1947, p. 158).

“The skull is large and massive, that of the adult more than 120 mm. long and 85 mm. broad; . . . length of upper molar series about 28 to 30 mm.” (Jackson, 1961, p. 192).

Habitat and habits.—This species prefers forested areas wherever there are suitable watercourses for the construction of dams and lodges. The sluggish fresh-water streams of the Eastern Shore section are especially suited to their needs.

The beaver feeds on a wide range of plants. These may be sedges, rushes, water grasses, various roots and tubers, and bark, leaves, and twigs of bushes and trees. In winter it feeds primarily on green branches that it stores under water near the lodge. In Maryland its favorite trees appear to be sweetgum, pine, ash, dogwood, oak, and maple.

These animals are monogamous, and it is believed that they mate for life. Breeding begins about mid-January and extends to the end of February. The gestation period is approximately 120 days, and a single litter of from one to eight kits is produced a year (the most frequent number being four or five).

The beaver's most important activity is felling trees for dams and lodges. A large beaver lodge is about 5 to 6 feet high and 15 or 20 feet wide at the water level. More often, however, smaller lodges are built, some 3 to 4 feet in height and 8 to 10 feet in diameter. The inside of a lodge consists of one room about 2 to 3 feet in height, and as many as 8 to 10 beaver may occupy it. The opening to the lodge is always under water. Many beavers, however, that inhabit lakes or deep streams live in bank dens rather than constructing lodges and dams.

The beaver is active throughout the year, but is seldom active during daylight hours. Its routine workday begins at dusk and ends at dawn.

Young beavers in their second year leave the parental colonies and emigrate to establish themselves in new colonies by pairs. Sometimes they may move as much as 30 miles to a new home. Most of this movement is accomplished in the water, because the animal is quite clumsy and slow moving on land.

According to Mansueti (1950, p. 33) no one knows when Maryland's native beavers were finally exterminated. He judges that on the basis of when they disappeared in Pennsylvania and New Jersey, they probably were gone from the Maryland lowlands about 150 years ago and that there were probably some native beavers left in western Maryland less than 100 years ago. Their extirpation was due to a number of reasons, the primary ones being heavy trapping pressure for their pelts, and elimination of suitable habitat. Beaver have reappeared in Maryland in recent years either through deliberate introductions or as a result of their natural migrations from other states where they had not been entirely extirpated or had been stocked. They are flourishing now in certain areas, presumably because low pelt value makes trapping unprofitable in the State.

Recent records and reports.—Bonwill and Owens (1939, pp. 36–37) mention 3 areas of Maryland where these animals were thriving in 1939. One was on the Upper Potomac River near Gorman, Garrett County; the second on Town Creek in Allegany County; and the third at a point where the Andover and Sewell Creeks meet at the head of the Chester River in Kent County. They believe that the first two colonies were the result of migrations from colonies in Pennsylvania or West Virginia that had escaped extermination in those States or had been reintroduced there. The Kent County colony was a result of migration from a colony in Delaware which had been stocked with animals from Maine by the Delaware Board of Game and Fish Commissioners in 1935.

Arner (1949, p. 23) says that the beaver migrated into the western Maryland Counties of Garrett and Allegany from colonies in West Virginia and are firmly established in eight streams in Garrett County and three streams in Allegany. They may be found in Garrett County in the Youghiogheny River, Laurel Run, Harrington Creek, and Broad Ford Run. In Allegany County they inhabit Evitts Creek and Town Creek; and beaver cuttings have been found on Sideling Hill in Washington County. He estimates that in 1949 there were 150 beavers in western Maryland.

Remarks.—Authorities are in agreement that Maryland's native beaver population probably represented the subspecies *C. c. canadensis*. It is impossible to assign subspecific rank to Maryland's present beaver population since they come from so many different sources, and even some of the areas from which they have been stocked were

themselves stocked at an earlier period with animals from elsewhere. No specimens of the native population or the present population of beavers have been available to me for examination.

Family CRICETIDAE (deer mice, harvest mice, voles, etc.)

MARSH RICE RAT

Oryzomys palustris palustris (Harlan)

Mus palustris Harlan, Silliman's Amer. Jour. Sci., 31 : 385, 1837.

Type locality.—"Fast Land" near Salem, Salem County, N.J.

General distribution.—In the Coastal Plain from southeastern Pennsylvania and southern New Jersey, south to northern Florida, west to the Mississippi River and north in the Mississippi Valley to southeastern Missouri, southern Illinois, and central Kentucky.

Distribution in Maryland.—Recorded only from the Eastern Shore and Western Shore sections.

Distinguishing characteristics.—Teeth 1/1, 0/0, 0/0, 3/3, = 16; ratlike in general appearance, but considerably smaller than adult Norway rat; tail long, nearly half the total length; fur long and coarse; color of upper parts grizzled grayish brown, mixed with blackish, sides paler with less blackish; underparts white to pale buff; tail sparsely haired and scaly, brownish above and whitish below. Young animals are more grayish than adults.

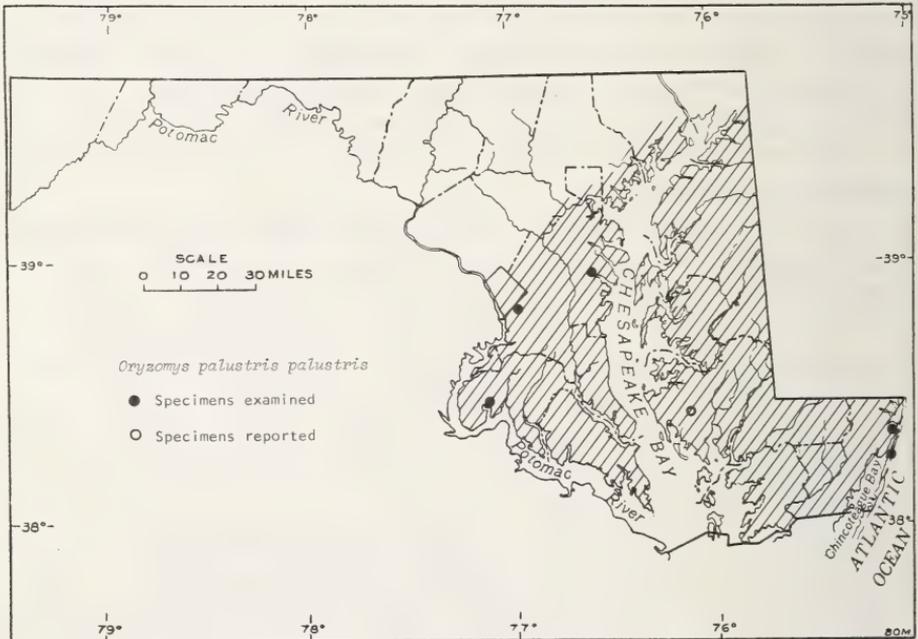


FIGURE 32.—Distribution of *Oryzomys palustris palustris*.

Marsh rice rats superficially resemble young Norway rats from which they may be distinguished by the upper cheek teeth. These teeth have two longitudinal rows of tubercles in rice rats; in Norway rats there are three such rows.

Measurements.—An average-sized female from West Ocean City, Worcester County, has measurements as follows: Total length 247; tail 120; hind foot 30; ear 10; greatest length of skull 30.4; zygomatic breadth 16.4; interorbital breadth 4.9; length of upper molar toothrow 4.4.

An adult female from Nanjemoy Creek, Charles County, has the following external measurements: Total length 262; tail 127; hind foot 30.

There is a peculiar size variation often encountered in this species. Males and females generally average about the same size, but often an apparently adult female may be strikingly smaller than the average.

Habitat and habits.—This species is partially amphibious and shows a great preference for wet meadows, marshy areas, watercourses, cane breaks, and swamps, and is only rarely encountered in dry fields.

Marsh rice rats are polyestrous and breed from March to November in Maryland (Harris, 1953, p. 485). The gestation period is 25 days and the female mates again immediately after parturition. Litter size varies from one to five with the average being three.

This species is an accomplished swimmer and does not hesitate to dive and swim under water for great distances when alarmed. It makes nests of grasses and weeds which may be placed under a mass of tangled debris or woven into the rushes a foot or more above the high water level. Its presence may usually be detected by the extensive and well-defined runways it makes and by the mats of cut vegetation floating at irregular intervals in the tidal waters. Sometimes, however, there may be little evidence of rice rats in an area. Harris (1953, p. 481) says that in the Blackwater National Wildlife Refuge in Dorchester County 40 percent of the 86 rice rat captures were made at trap stations showing no signs of small mammals, but some were taken at muskrat houses. Also, he was never able to locate any rice rat nests in this area, and noted that only a few of the runways found might have been made by this species. Rice rats are primarily nocturnal, and Harris states that only rarely was this species observed in the daytime.

In Maryland, rice rats are confined in distribution to the fresh and salt water marshes of the Western Shore and Eastern Shore sections. They seem to be particularly numerous in the fresh, brackish, and salt water marshes of the lower Eastern Shore section and occur in great numbers on Assateague Island, where they occupy the wetter portions of these marshes.

Specimens examined.—*Anne Arundel County*: South River, at U.S. Route 50, 1. *Charles County*: Nanjemoy Creek, 5. *Prince Georges County*: Oxon Hill, 2 miles NW, 2. *Worcester County*: Ocean City, 4 and 5 miles S (Assateague Island), 2; West Ocean City, 4.

Other records and reports.—*Dorchester County*: Blackwater National Wildlife Refuge (Harris, 1953).

EASTERN HARVEST MOUSE

Reithrodontomys humulis virginianus A. H. Howell

Reithrodontomys humulis virginianus A. H. Howell, Jour. Mammal., 21 (3) : 346, 13 August 1940.

Type locality.—Amelia, Va.

General distribution.—Known from central Virginia north to Maryland. Exact northern limits of range unknown.

Distribution in Maryland.—Rare in Maryland; probably occurs only in the Western Shore and southern Piedmont sections.

Distinguishing characteristics.—Teeth 1/1, 0/0, 0/0, 3/3, = 16; upper incisors with conspicuous grooves; mouselike in form; tail about half total length; coloration grayish-brown above with a distinct band of blackish along the median line; sides of head and body paler, more or less washed with light pinkish cinnamon, this color forming a definite lateral line next to the belly; underparts grayish white; tail bicolored, fuscous above, grayish white below; ears fuscous, feet white.

This species closely resembles the house mouse (*Mus musculus*) in general appearance, but may readily be distinguished from that species by the deeply grooved upper incisors. In the eastern United States the harvest mouse is the only long-tailed cricetine rodent with grooved incisors.

Measurements.—An adult female from Takoma Park (near Riggs Mill), Prince Georges County, measures as follows: Total length 132; tail 59; hind foot 15.5; ear 12; greatest length of skull 20.0; zygomatic breadth 10.1; least interorbital breadth 2.9; upper molar toothrow 2.5.

Howell (1940, p. 346) gives external measurements of 10 specimens from the type locality as follows: Total length 117.2 (110–125); tail vertebrae 51.8 (45–56); hind foot 16.2. The greatest length of skull of these 10 specimens is 18.7 (18.3–19.1). It can be seen that the Maryland specimen is considerably larger both externally and in the greatest length of the skull than topotypes of the subspecies from Amelia, Va.

Habitat and habits.—The harvest mouse prefers nonforested land, particularly cultivated fields where grain crops are growing. It seems to be equally at home in dry fields or in bogs, provided there is thick growth of tall grasses or sedges.

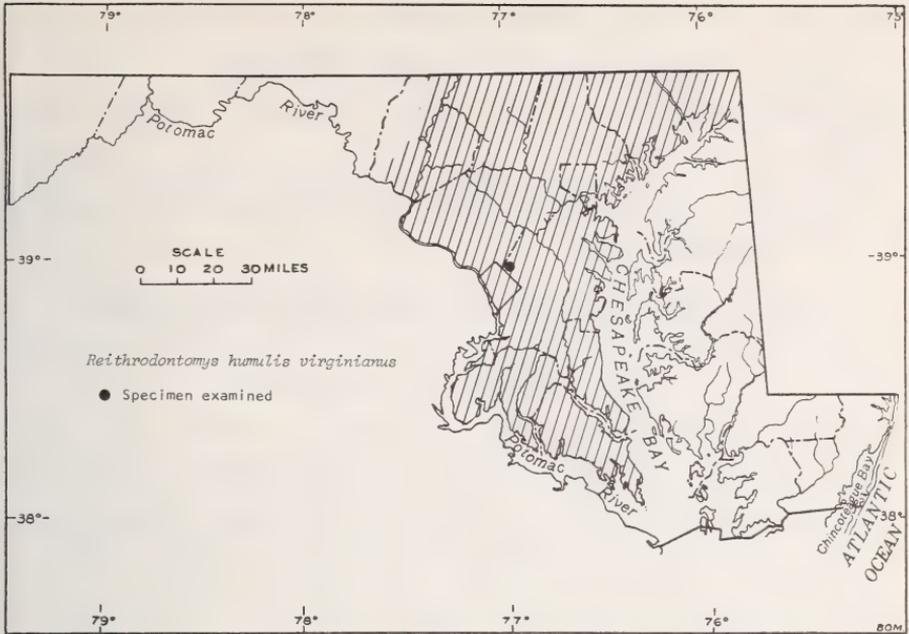


FIGURE 33.—Distribution of *Reithrodontomys humulis virginianus*.

Little is known of the habits of this species. It lives in the cover of grass, weeds, and grains where it makes little runways over the surface of the ground. According to Lewis (1940, p. 426), in Amelia County, Va., it generally makes nests of fine grass blades on top of the ground in tall grass or sedges. These nests are globular and average larger than a croquet ball.

The breeding season is from May to November; the number of young from one to five; the gestation period is about 23 days.

The food of the eastern harvest mouse consists largely of seeds and grains with considerable green vegetation and occasionally fruit (Howell, 1914, p. 11).

According to Bailey (1923, p. 118), many skulls of harvest mice were found in owl pellets in the Smithsonian tower in Washington, D.C. The owl, or owls, however, may have been feeding in nearby Virginia and thus the skulls may not represent District of Columbia or Maryland records. This rodent species has been trapped at only one locality in Maryland.

Specimens examined.—*Prince Georges County*: Takoma Park (near Riggs Mill), 1. Howell (1940, p. 346), reported examining two specimens from Riggs Mill, and records in the files of the U.S. Fish and Wildlife Service indicate that Ray Greenfield actually took three specimens in that same area on 26 January 1934. Only one specimen from that locality, however, is now in the National collections.

DEER MOUSE

Peromyscus maniculatus (Wagner)

Hesperomys maniculatus Wagner, Arch. Naturgesch., Jahrg. 11, 1: 148, 1845.

This is a wide-ranging species that occurs over much of North America. Numerous subspecies have been described; of these, two are known to occur in Maryland. They are:

Peromyscus maniculatus bairdii (Hoy and Kennicott)

Mus bairdii Hoy and Kennicott, in Kennicott, Agricultural Report, U.S. Commissioners Patents, 1856, p. 92, 1897.

Type locality.—Bloomington, McLean County, Ill.

General distribution.—Prairie region of the upper Mississippi Valley, from eastern Kansas and Missouri; north to southwestern Manitoba, Canada; eastward through southern Minnesota, Wisconsin, and Michigan to the man-made prairie of central New York, Pennsylvania, Maryland, and northern Virginia.

Distribution in Maryland.—The distribution of this subspecies within the State is unknown. It has been taken in Maryland only at the Patuxent Research Center, Prince Georges County. (See fig. 34.)

Distinguishing characteristics.—Teeth 1/1, 0/0, 0/0, 3/3, = 16; coloration of upperparts brownish gray, mixed with darker hairs; underparts white, the basal gray of the underfur often conspicuous; tail short and distinctly bicolored, upperparts brownish black, white beneath; feet white. Immature animals are more grayish dorsally.

This subspecies is readily distinguished from *Peromyscus maniculatus nubiterrae* by its much shorter tail. It is easily confused with *Peromyscus leucopus*, but may be distinguished by several characters which are discussed under that species.

Measurements.—External measurements of two adults from the Patuxent Research Center, Prince Georges County, (a wild-caught female and one of her laboratory-raised offspring) are as follows: Total length 152, 149; tail 63, 59; hind foot 18, 19; ear 13.5, 14.0. Cranial measurements of three adults from the Patuxent Research Center (the wild-caught female and two of her laboratory-raised offspring) are: Greatest length 23.1, 23.3, 23.0; zygomatic breadth 11.5, 12.1, 11.9; interorbital breadth 3.7, 3.9, 3.9; length of maxillary tooth-row 3.0, 3.3, 3.3.

Habitat and habits.—This subspecies inhabits prairies, open fields, and arable land and is entirely absent from dense forests. It was unknown in Maryland until 1949, when Lucille F. Stickel and Oscar Warbach live-trapped several in crop fields at the Patuxent Research Center. These fields are about 1.9 miles north of Bowie and are situated on a wide bench of sandy clay near the Patuxent River. From May

1949 to June 1950, 23 of these mice were captured by Stickel and Warbach.

According to W. H. Stickel (1951, p. 26) the Maryland specimens of this race were most often caught in corn and in young wheat; only occasionally were they found in hay or tall wheat. He says that the subspecies seems to be precariously established at the Patuxent Research Center and was not common, nor did the numbers appear to increase, during the year the area was extensively studied.

Peromyscus m. bairdii is essentially a subspecies of the prairie region of the upper Mississippi Valley. In recent years it appears to have been extending its range eastward consequent with the deforestation of wide areas of land in the eastern United States. In 1909, Osgood (1909, p. 79) knew it only from as far east as Ohio. In 1934, Mitchell (1934, p. 71) recorded it from Meadville, Pa., and in 1938, Moulthrop (1938, p. 503) listed it from Elba, Genesee County, N.Y. Hamilton (1950, p. 100) recorded the first appearance of *bairdii* in 1947 at Ithaca, N.Y., an area that had been heavily trapped for the previous 20 years, and mentioned the capture of the subspecies at North Harrisburg, Dauphin County, Pa., the first record from east of the Appalachian Mountains. More recently, Peacock and Peacock (1962, p. 98) have taken specimens from the area being developed into Dulles Airport, near Chantilly, Fairfax County, Va.

Stickel (1951, p. 26) states that no doubt the animal is expanding its range by natural means in consequence of artificially created habitats, but the possibility of accidental transportation is considerable. It may be that the mouse has succeeded in crossing the heavily forested Appalachian Mountains by following the grass-lined banks and shoulders that line the roads in that area. It would in this way remain ecologically separated from *Peromyscus m. nubiterrae*, the race inhabiting the dense forests of the Appalachians.

Just how widely *bairdii* is distributed in Maryland is unknown. No additional specimens have been taken since Stickel and Warbach collected those at the Patuxent Research Center in 1939. I have trapped many cultivated fields in central Maryland and grassy roadsides in the western part of the State with the hope of obtaining additional records, but without success. The recent records from nearby Chantilly, Va., however, lead me to believe that the subspecies is probably widely distributed, although perhaps scarce as regards total numbers, in open fields throughout Maryland.

These mice feed largely on seeds, grain, and the ripe heads of grasses; berries and numerous insects are also consumed. The nest is built slightly underground, or on the surface, and usually placed under some object, such as a board, fallen tree limb, rock, or old pasteboard carton. The breeding season generally begins in early March and ex-

tends through November. A female may breed three or four times yearly, and a litter may contain from two to nine young, although four to six is the most common number.

Specimens examined.—*Prince Georges County*: Patuxent Research Center, 3.

Peromyscus maniculatus nubiterrae Rhoads

Peromyscus leucopus nubiterrae Rhoads, Proc. Acad. Nat. Sci. Philadelphia, 48: 187, April 1896.

Type locality.—Summit of Roan Mountain, Mitchell County, North Carolina. Altitude 6,370 feet.

General distribution.—Allegheny and Blue Ridge Mountains and adjacent ranges from western Pennsylvania and New York, south to western North Carolina and northeastern Georgia.

Distribution in Maryland.—Found in the Allegheny Mountain section at elevations usually above 2,500 feet.

Distinguishing characteristics.—Similar in coloration and size to *P. m. bairdii*, but is readily distinguished from that subspecies by its much longer tail, which is more than half the total length of the animal. Usually *nubiterrae* has larger ears and feet than *bairdii*.

In general, *nubiterrae* can be distinguished from *Peromyscus leucopus* by certain subtle differences in coloration. Some specimens of *nubiterrae*, however, are confusingly similar to *Peromyscus leucopus*,

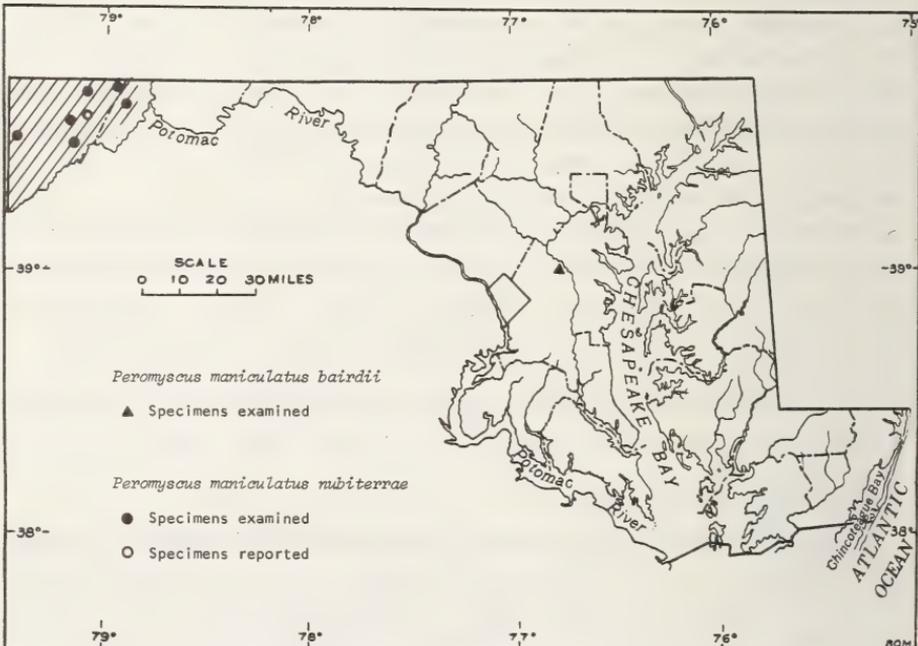


FIGURE 34.—Distribution of *Peromyscus maniculatus nubiterrae* and *P. m. bairdii*.

and their distinguishing characteristics are discussed in more detail under that species.

Measurements.—Thirteen adults from Finzel, Garrett County, have external measurements as follows: Total length 179.3 (172–190); tail 93.1 (82–102); hind foot 20.5 (20–22). Eleven adults from Finzel have the following cranial measurements: Greatest length 24.6 (24.3–25.3); zygomatic breadth 12.3 (11.7–13.3); interorbital breadth 3.7 (3.5–3.9); maxillary toothrow 3.3 (3.2–3.5).

Habitat and habits.—This subspecies prefers dense woods and is most abundant among mossy boulders and logs in moist spruce and fir forests at higher elevations. E. A. Preble (in field notes) gives information about where he took specimens in Garrett County. He says that they were common in a tract of hemlock woods about 3 miles east of Grantsville. One specimen was taken in a small strip of deciduous trees and shrubs adjoining a field where *Peromyscus leucopus* was also taken. At Finzel, at an elevation of about 2,600 feet, he found that these mice were abundant and inhabiting all sorts of situations from the dry hillsides and edges of fields to the deep hemlock swamps, while at Bittinger (elevation about 2,600 feet) they were abundant only in the deep woods.

This mouse nests in burrows under rocks and logs and sometimes in hollow trees. It is somewhat arboreal and may build tree nests as high as 50 feet above the ground (J. W. Bailey, 1946, p. 216). Two or three litters, of from two to seven young, are produced each season. Food consists of seeds, nuts, and berries, supplemented with insects, snails, and occasionally dead birds and other mice.

Specimens examined.—*Allegheny County*: Frostburg, 1. *Garrett County*: Bittinger, 6; Finzel, 18; Grantsville, 16; Swallow Falls State Forest (near Muddy Creek Falls), 1.

Other records and reports.—*Garrett County*: New Germany (Coll. Nat. Hist. Soc. Maryland).

WHITE-FOOTED MOUSE

Peromyscus leucopus noveboracensis (Fisher)

[*Mus. sylvaticus*] *noveboracensis* Fisher, Synopsis Mammalium, p. 318, 1829.

Type locality.—New York.

General distribution.—From eastern and southern Ontario, east to Maine, south along the Atlantic coast into Virginia, West Virginia, and northern Kentucky, westward, south of Great Lakes, to eastern North Dakota, South Dakota, Nebraska, northeastern Oklahoma, and northwestern Arkansas.

Distribution in Maryland.—Occurs abundantly in all sections of the State.

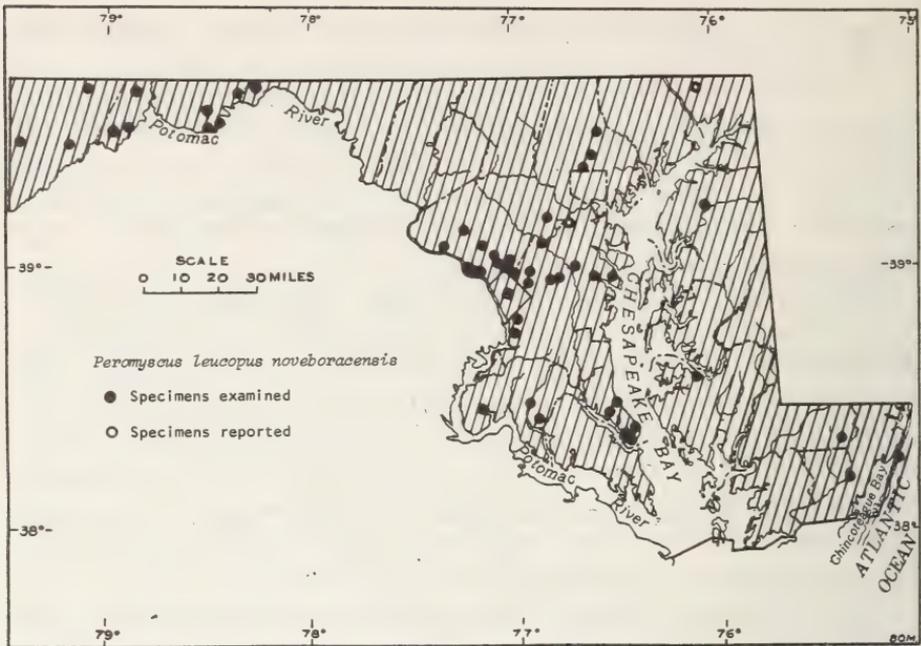


FIGURE 35.—Distribution of *Peromyscus leucopus noveboracensis*.

Distinguishing characteristics.—The white-footed mouse closely resembles the deer mouse (*Peromyscus maniculatus*), from which it may be distinguished as follows:

From *Peromyscus m. bairdii* it differs in being larger, longer tailed, lighter and more brightly colored with more reddish on sides and back, and in having noticeably larger ears and feet; the tail is less distinctly bicolored.

Cranially, *P. l. noveboracensis* is larger than *P. m. bairdii*, and the incisive foramina are differently shaped. These foramina are anteriorly constricted in *noveboracensis*, and open and evenly curved in *bairdii*. A detailed comparison of these two forms is given by Stickel (1951, p. 25-32).

From *Peromyscus m. nubiterrae*, *P. l. noveboracensis* differs in being larger, shorter tailed, (tail less than half the total length of the animal) and more brightly colored, with more reddish on sides and back. This color difference is subtle in individual specimens but becomes apparent when large series of both species are examined. The tail in *noveboracensis* is less distinctly bicolored than in *nubiterrae*.

Some specimens of *nubiterrae* and *leucopus* are so similar in external characteristics that only by a detailed examination of the skull can they be separated. The skull of *nubiterrae* is slender and elongated, the braincase considerably flattened, whereas cranially *noveboracensis* is broader and heavier with the braincase more inflated. As in *P. m.*

bairdii, the incisive foramina of *nubiterrae* are open and evenly curved, while in *noveboracensis* they are anteriorly constricted. The teeth in the latter form, even in juvenile animals, are noticeably larger and more robust than in *nubiterrae*.

Measurements.—External measurements of eight adults from Allegany County (Dans Mountain State Park, and vicinity of Oldtown) are as follows: Total length 174.4 (170–188); tail 76.2 (70–92); hind foot 21.1 (20–22); ear 15.7 (13–18). Nine adults from the same localities have the following cranial measurements: Greatest length 26.2 (26.0–26.7); zygomatic breadth 13.4 (12.7–14.0); interorbital breadth 4.1 (3.9–4.3); maxillary toothrow 3.6 (3.4–3.8).

Habitat and habits.—This species is primarily a woodland inhabitant, but is often found in brushy regions and sometimes in grassy areas that border woodlands. It is one of the most abundant mammals in Maryland. On Assateague Island their tracks have been observed even on the bare sand dunes a few yards from the ocean beach. Usually, however, this mouse will be found not more than 50 feet from woods or forests, of which it seems to prefer the deciduous woods, especially oak-hickory forest.

Nests are built almost anywhere. Although it apparently does not dig its own burrow, or make a trail, this mouse will utilize burrows or trails of other small mammals. Jackson (1961, p. 218) says that it seems to prefer a tree site for its nest, usually about 6 to 8 feet from the ground, but that he has found them in abandoned squirrel nests as high as 20 feet above ground. He says that often the nest is built in a hollow tree or limb, and that another favorite site is under an old stump or log. The nest itself is composed of soft material such as grass, leaves, or other vegetation. It is usually about 10 or 12 inches in diameter and 6 or 8 inches deep.

Breeding takes place in late February or early March, and the first litter is born in April. The gestation period is variable, but is usually between 23 and 25 days, and the litter size varies from one to seven, usually three to six, with four the most frequent number. Each female may produce as many as four litters during the breeding season.

The principal food for the species is seeds of various grasses, weeds, clover, small fruits, and grain as well as acorns and hickory nuts. Insects form a small portion of the diet as does green herbage. This mouse sometimes occupies houses, where it may be bothersome. On Assateague Island in 1957 and 1958, white-footed mice were inhabiting the houses and outbuildings, while house mice (*Mus musculus*) occurred in the woods and marshes, but apparently not in the houses.

Specimens examined.—*Allegany County*: Dans Mountain State Park, 13; Green Ridge, 4; Mount Savage, 11; Oldtown, 4 miles E,

31; Oldtown, 9 miles E, 12; Rawlings, 2; Sideling Hill Creek, 8. *Anne Arundel County*: Annapolis, 3 miles NW, 12; Priest Bridge, 4; South River (at U.S. Route 50), 10. *Baltimore County*: Lake Roland, 5; Loch Raven, 7; Notch Cliff, 1. *Calvert County*: Battle Creek (Cypress Swamp), 4; Cove Point, 3; Drum Point, 2; Scientist Cliffs, 1; Solomons, 2; Solomons, 3½ miles N, 17. *Charles County*: Nanjemoy Creek, 2; Newport, 6; Zekiah Swamp, 4. *Dorchester County*: Cambridge, 5. *Garrett County*: Cranberry Swamp, 7; Grantsville, 4; Swallow Falls, 2 miles S, 2; Swanton, 3. *Howard County*: Atholton, 6. *Montgomery County*: Burnt Mills, 2; Cabin John (vicinity of), 4; Cupids Bower Island (vicinity of), 5; Forest Glen, 1; Great Falls, 1; Kensington, 5; Linden, 2; Plummers Island, 4; Rockville (vicinity of), 6; Seneca Creek (at Clopper Road), 5; Silver Spring, 26; Takoma Park, 1; Woodside, 1. *Prince Georges County*: Anacostia River, NW Branch, 3; Bladensburg, 7; Branchville, 2; Broad Creek (Indian Head Bluff), 4; Collingwood (= Collington?) 1 mile S, 2; Hyattsville, 4; Lanham, 4; Laurel, 10; Oxon Hill, 12; Riggs Mill, 1; Riverdale, 3. *Washington County*: Bear Creek, just N of U.S. Route 40, 2. *Wicomico County*: Powellsville, 1. *Worcester County*: Snow Hill, 1 mile NE, 1; Ocean City, 5 miles S, 1. *District of Columbia*: 62.

Other records and reports.—*Allegany County*: LaVale (Coll. U. Md.). *Anne Arundel County*: Dorsey (U.S. Fish and Wildlife Service files). *Cecil County*: Rising Sun (U.S. Fish and Wildlife Service files). *Garrett County*: Muddy Creek Falls (Mansueti and Flyger, 1952, p. 250). *Kent County*: Chestertown (U.S. Fish and Wildlife Service files). *Prince Georges County*: Bowie (Lucille F. Stickel, 1946, p. 301).

Remarks.—Specimens from the Eastern Shore section (Cambridge, Powellsville, Snow Hill, and Assateague Island), as well as Virginia specimens from Accomack and Northampton Counties on the lower Delmarva Peninsula, are not typical *noveboracensis* but are somewhat darker in coloration, and smaller in size, and appear to be intergrades with *P. l. leucopus* (Rafinesque). The type locality of *P. l. leucopus* is in western Kentucky, which is also an area of intergradation. Maryland specimens from the Eastern Shore section are only slightly larger and paler than specimens from western Kentucky near the type locality of *P. l. leucopus*. Nevertheless, they are considerably different from *P. l. leucopus* from southern Louisiana (where the subspecies is best characterized) both in size and coloration, and are more closely related to *P. l. noveboracensis* from central New England where *noveboracensis* is best characterized) than to Louisianan *P. l. leucopus*.

EASTERN WOOD RAT

Neotoma floridana magister Baird

N[eotoma]. magister Baird, Mammals, in Repts. Expl. Surv. . . ,
8 (1) : 498, 14 July 1858.

Type locality.—Cave near Carlisle, Cumberland County, or near Harrisburg, Dauphin County, Pa.

General distribution.—Appalachian Mountain region, from extreme western Connecticut and southern New York, south through western Virginia and Tennessee to the Tennessee River in northern Alabama, west to central Kentucky and northward to extreme southern Indiana.

Distribution in Maryland.—The Allegheny Mountain and Ridge and Valley sections; occurs east of the Blue Ridge Mountains in the Piedmont section along the cliffs and bluffs of the Potomac River to the vicinity of Washington, D.C. It may occur among the cliffs and bluffs of river valleys elsewhere in the Piedmont section.

Distinguishing characteristics.—Teeth 1/1, 0/0, 0/0, 3/3, = 16; size large; coloration grizzled grayish dorsally, with some buffy intermixture, paler and more buffy on sides; underparts and feet white; ears large and naked; tail long, hairy, and distinctly bicolored, black dorsally and white underneath; vibrissae very long, and black or white in coloration. The young are similar to the adults, but are grayer.

This species may be confused with the Norway rat, which it resembles superficially. It may be distinguished from that species by its larger naked ears, its much longer vibrissae, its longer, more hairy, and bicolored tail, and its softer, more grizzled grayish coloration. In addition, the molar teeth of the two species differ. In the eastern wood rat the crowns are flat, with the enamel thrown into prismatic folds; in the Norway rat the molars are tuberculate.

Measurements.—An adult male from 9 miles E of Oldtown, Allegany County, measures as follows: Total length 430; tail 188; hind foot 42; ear 30; greatest length of skull 56.2; interorbital breadth 6.8; length of nasals 21.5; length of molar toothrow 9.3.

Hamilton (1943, p. 306) gives the following external measurements for 10 adults from New York, Pennsylvania, and West Virginia: Total length 423 (405–441); tail 186 (170–200); hind foot 43.5 (40–46).

Habitat and habits.—The eastern wood rat prefers cliffs, rock slides, caves, and bare patches in the mountainous regions of the State. It ranges into the Piedmont section at least in the Potomac River Valley, where it lives in the cliffs and rocks that border the river. It may occur in the bluffs that border other rivers in the Piedmont section, and has been reported from Woodside, Montgomery County (Wetmore, 1923, p. 187). In the Potomac River Valley, it has been found as far south

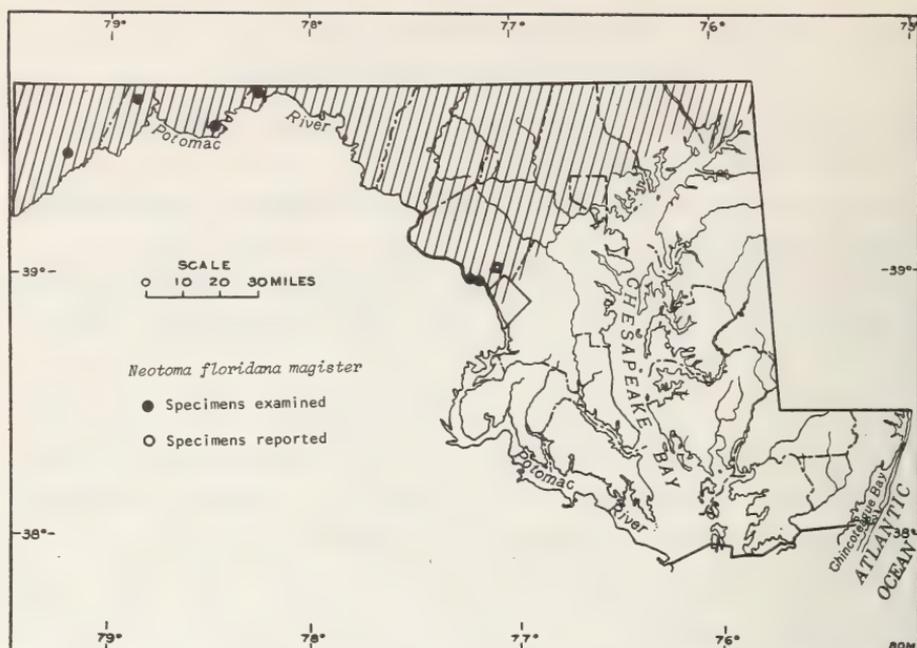


FIGURE 36.—Distribution of *Neotoma floridana magister*.

as Plummerville, Montgomery County, and on the Virginia side of the river at Chain Bridge.

Wood rats were particularly abundant in the vicinity of Oldtown, Allegany County, in the fall of 1961, where virtually every rocky outcropping contained signs of them. They had taken up residence under the front porch of a hunting cabin 9 miles east of Oldtown, and the sounds of their activity could be heard all night. They are inquisitive animals, and one had thoroughly explored an automobile that was parked nearby, even crawling into the engine compartment, leaving tracks everywhere in the dust.

The eastern wood rat appears to have moved into Maryland's Piedmont section only within recent years. Wetmore (1923, p. 187) reports that although Plummerville had been under observation by Washington naturalists since 1902, it wasn't until 1921 that the species was discovered to be resident there. It was known, however, to inhabit the cliffs along the Virginia side of the Potomac River as far south as Chain Bridge for many years before it was first reported from Plummerville Island, and it seems probable that the Plummerville Island population crossed over from Virginia during a winter when the Potomac was frozen over. Wetmore (1923) says that one was killed on Plummerville Island on 25 June 1921, by Mr. W. R. Maxon, but was not preserved. On 26 September and 15 October 1921, two specimens were collected and preserved in the Biological Survey collection. In the

same year, five nests of this species were discovered beneath the cabin on the island.

Wetmore (1923) describes the nests of the eastern wood rat on Plummers Island as being composed of bits of finely shredded cedar bark and similar materials that formed a flattened mass 12 to 15 inches across with a small depression in the center. As it was warm weather the cavities were open above, but the walls were so arranged that they could be pulled out to form a domed covering if the need for greater warmth arose.

Wood rats eat practically any vegetation they can obtain, including fruits and berries, fungi, ferns, rhododendron, and a host of others. The species breeds from spring until fall, and as many as three broods may be raised annually. The gestation period is 30 to 36 days, and one to three young are usually born.

Specimens examined.—*Allegheny County*: Mount Savage, 1 (Coll. U. Md.); Oldtown, 9 miles E, 1. *Garrett County*: Backbone Mountain, Savage River Dam Site, 2 (Coll. U. Md.). *Montgomery County*: Plummers Island, 2. *Washington County*: Bear Creek, just north of U.S. 40, 1 (Coll. U. Md.).

Other records and reports.—*Montgomery County*: Perry's Island (Wetmore, 1923: 187); Woodside (Wetmore, 1923: 187).

RED-BACKED MOUSE

Clethrionomys gapperi gapperi (Vigors)

Arvicola gapperi Vigors, Zool. Jour., 5: 204, 1830.

Type locality.—Between York [Toronto] and Lake Simcoe, Ontario, Canada.

General distribution.—Massachusetts south in the Appalachians to western Virginia and west through New York, northern Michigan, and southern Ontario to eastern Minnesota.

Distribution in Maryland.—Occurs on the cooler forested slopes in the Ridge and Valley and Allegheny Mountain sections.

Distinguishing characteristics.—Teeth 1/1, 0/0, 0/0, 3/3, = 16; cheek teeth rooted in adults; size medium; coloration of upper parts rusty red, becoming buffy on the sides and around the face; underparts buffy white; tail less than a third of total length of animal, and bicolored, blackish above, paler below.

This mouse may be distinguished from most other Maryland mice by its reddish coloration and short tail. It resembles the pine mouse, however, in both these characters, but differs in that the reddish coloration is confined to the dorsum, whereas in the pine mouse the reddish coloration extends onto the sides. In addition, the ears of the red-backed mouse are larger, the tail is considerably longer, and the fur is longer, coarser, and less mole-like.

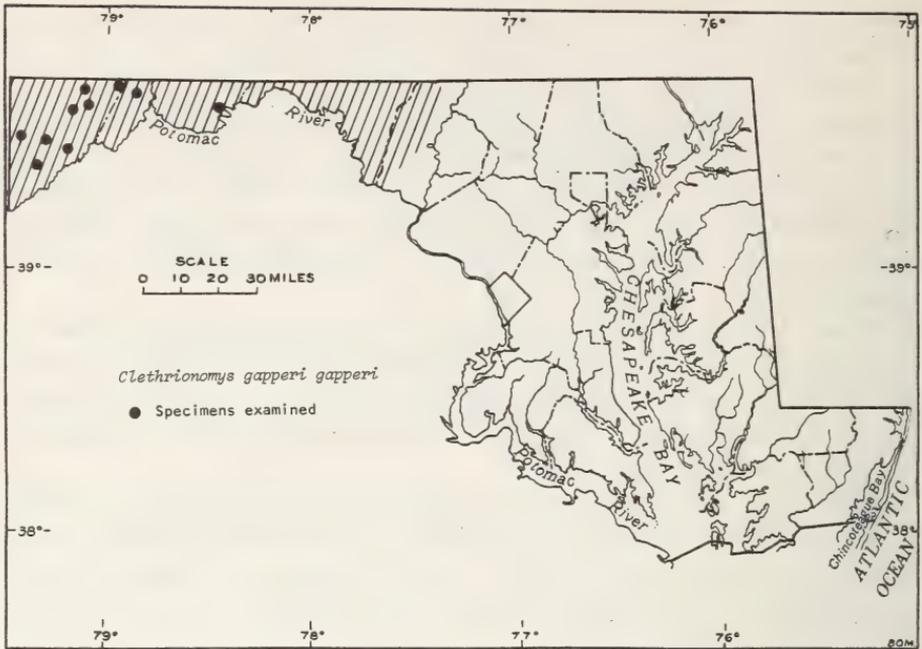


FIGURE 37.—Distribution of *Clethrionomys gapperi gapperi*.

Measurements.—Ten adults from Garrett County have the following external and cranial measurements: Total length 147.3 (140–155); tail 42.9 (38–48); hind foot 19.5 (19–20); condylobasal length of skull 24.9 (24.1–25.8); zygomatic breadth 13.3 (13.0–13.7); interorbital breadth 4.0 (3.9–4.2); length of molar toothrow 5.4 (5.2–5.6).

Habitat and habits.—This mouse prefers cool, damp, forested areas where it lives among the mossy rocks and rotten logs. In the northern part of its range it is widely distributed, but in Maryland it is restricted to the higher mountains, where it is locally abundant. Preble (field notes) took the red-backed mouse at Finzel on the border of a hemlock woods, and at Grantsville he found that it was very common in a tract of hemlocks 3 miles east of the town. It was also abundant in the mixed forest covering the steep slopes on the east side of the Castleman River, and in the hemlock woods near Bittering. At Mountain Lake Park, Preble took a specimen among rocks in an oak woods, and at Swanton he trapped a very dark individual in deep hemlock woods. Bookhout tells me that he trapped one in Allegany County in a rock outcrop in a second-growth oak-hickory forest.

This species does not make elaborate tunnels, but will occupy those made by moles and shrews. Jackson (1961, pp. 227–228) has described a nest in detail. It was located among the rootlets of small trees and was some 3 inches in diameter. The nest was merely a small carpet of grass stems and a few particles of dead leaves and moss, the entire

bulk of which would be no larger than a man's thumb. Another nest was located at a depth of about 18 inches under a rotten elm stump. It was situated on top of the soil underneath a root of the stump, and was 4 inches in diameter and about 1 inch in depth, slightly hollow and without cover other than the log above. It was composed of small pieces of dry leaves, bark, hazelnut shells, hemlock cones, twigs, dry sphagnum, and green moss.

According to Hamilton (1941, p. 259), in New York State about three-fourths of the food of this species is composed of green vegetation. In addition, a large part of the diet consists of nuts and seeds. Insects are not as often eaten as they are by white-footed mice.

The red-backed mouse does not hibernate, but it does actively gather stores in the fall in preparation for winter. The breeding season is protracted, beginning in the late winter or early spring and extending well into fall. One litter follows another during the breeding season, and from two to eight young comprise a litter. The gestation period is 17 to 19 days.

Specimens examined.—*Allegheny County*: Mount Savage, 6 (Coll. U. Md.); Town Hill Mountain, near beacon light, 1 (Coll. U. Md.). *Garrett County*: Bittinger, 7; Cranberry Swamp, 4 (Coll. U. Md.); Finzel, 5; Grantsville, 3 miles E, 15; Mountain Lake Park, 1; Swallow Falls State Forest (near Muddy Creek Falls), 1; Swanton, 1; Thayerville Swamp, 2 (Coll. U. Md.); Wolf Swamp, 1.

Remarks.—Maryland *C. g. gapperi* average somewhat darker and slightly larger than specimens of this subspecies from Ontario and central New York. They appear to be intergrades between *C. g. gapperi* and *C. g. carolinensis* but are more closely related to the former. The specimen collected by Preble in the deep hemlock woods at Swanton is as dark and large, however, as typical *carolinensis*.

MEADOW VOLE

Microtus pennsylvanicus (Ord)

Two races of this widespread and abundant small mammal are recognizable in Maryland. They are:

Microtus pennsylvanicus pennsylvanicus (Ord)

Mus pennsylvanicus Ord, in Guthrie, a new geogr., hist., comm. grammar . . . Philadelphia, 2d Amer. ed., 2: 292, 1815.

Type locality.—Meadows below Philadelphia, Pa.

General distribution.—From Quebec and New Brunswick, south into Georgia, and west into Nebraska, South Dakota, and North Dakota.

Distribution in Maryland.—Distributed in the Piedmont, Ridge and Valley, and Allegheny Mountain sections. Intergrades with *Microtus*

p. nigrans in the Eastern Shore and Western Shore sections, and is replaced by that subspecies in the southern Eastern Shore and southeastern Western Shore sections. (See fig. 38.)

Distinguishing characteristics.—Teeth 1/1, 0/0, 0/0, 3/3, = 16; molar teeth rootless and persistently growing; coloration of upperparts dull chestnut brown, darkest along the middle of the back; underparts grayish white, or buffy white; feet grayish brown; tail dusky above, paler below, fur overlaid with coarse guard hairs; tail less than a third of total length of animal.

This vole is similar in appearance to the red-backed mouse (*Clethrionomys gapperi*), but is larger and more brownish in coloration, and lacks the red dorsal band. It is also similar in appearance to the pine vole (*Pitymys pinetorum*) but has coarser pelage, bigger ears, and a longer tail. It differs from the southern bog lemming (*Synaptomys cooperi*) in its coarser, shorter pelage and much longer tail, and in lacking grooved upper incisors.

Measurements.—Eleven adults from the vicinity of Oldtown, Allegany County, have the following external and cranial measurements: Total length 169.2 (161.0–187.0); condylobasal length of skull 28.5 (28.1–29.0); zygomatic breadth 15.4 (14.8–15.9); interorbital breadth 3.6 (3.4–4.0); maxillary toothrow 6.9 (6.5–7.3). Males average somewhat larger than females.

Habitat and habits.—This vole is numerous in fields and meadows throughout the State. It is also common in marshes and similar areas with heavy growth of grass; occasionally it is found in orchards and open woodland if the ground cover is grassy. This is one of the most abundant mammals in Maryland.

Meadow voles construct extensive runways on the surface of the ground. These runways are about 1½ inches in diameter and run in a network under the cover of dead grass. They are sometimes the only sign of the presence of these voles in an area. If the runway is fresh and is being used, there will generally be droppings and cut pieces of grass at various intervals along it. The nest of the meadow vole is usually constructed on the surface of the ground in one of the runways. It is bulky, generally about 5 or 6 inches in diameter and 3 or 4 inches deep, usually covered, but sometimes not.

The meadow vole is active both day and night. It is cyclic in nature and the reproductive habits vary from year to year (Hamilton, 1937). It is polyestrous and may breed the year round, although in Maryland there is a tendency not to breed during the coldest part of winter. The females reach puberty and begin to breed at 25 days of age, and from six to eight young generally comprise a litter. The gestation period in this species is 21 days, or a little less, and as many as 17 litters may be produced in a year.

The food of the meadow vole consists chiefly of fresh grass, sedges, grains, and seeds. Green vegetation comprises the major portion of its diet in the spring and summer, while in the fall, grains and seeds are an important commodity. In winter, bark and roots of shrubs and trees are sometimes consumed.

Hamilton (1943, p. 327) says that the meadow vole is of great economic importance. By girdling fruit trees and nursery stock it causes monetary loss to the horticulturist. The amount of forage crops it consumes, while difficult to measure, is in the aggregate a very great loss to the farmer. It does, however, perform a useful function in providing predatory birds and mammals with an abundant source of food.

Specimens examined.—*Allegany County*: Cumberland, 2; Mount Savage, 8; Oldtown, 4 miles E, 19; Oldtown, 9 miles E, 74; Sideling Hill Creek, 3. *Anne Arundel County*: Annapolis, 1 mile W, 6; Annapolis, 3 miles W, 4; Annapolis, 4 miles W, 2; Lake Shore area, 1. *Baltimore County*: Loch Raven, 2. *Charles County*: Nanjemoy Creek, 2; Newport, 5. *Garrett County*: Finzel, 1; Grantsville, 1; Mountain Lake Park, 2. *Howard County*: Atholton, ½ mile S, 5; Long Corner, 1. *Montgomery County*: Cabin John Bridge, 1 mile N, 1; Kensington, 1; Rockville, 2.3 miles NE, 3; Seneca, 1½ miles NW, 26; Seneca, 2.9 miles W, 52; Silver Spring (vicinity), 5. *Prince Georges County*: Collingwood (=Collington?), ½ mile S, 2; Hyattsville, 10; Lanham, 1; Laurel, 30; Oxon Hill, 11; Riggs Mill, 1. *Queen Annes County*: Parson Island, 2. *District of Columbia*: 91.

Other records and reports.—*Allegany County*: Dans Mountain (Coll. U. Md.); La Vale (Coll. U. Md.); McCoole (Coll. Carnegie Museum). *Anne Arundel County*: Dorsey (U.S. Fish and Wildlife Service files). *Baltimore County*: Bare Hills–Lake Roland area (Bures, 1948, p. 67); Patapsco State Park (Hampe, 1939, p. 6). *Garret County*: Cranberry Swamp (Coll. U. Md.). Cranesville Pine Swamp (Mansueti, 1958, p. 83); Cunningham Swamp (Coll. U. Md.). *Prince Georges County*: Patuxent Research Center (Herman and Warbach, 1956, p. 87).

Remarks.—This subspecies intergrades with *Microtus p. nigrans* in the Eastern Shore and Western Shore sections. Specimens from the northern portion of these sections (Parson Island, Annapolis vicinity, Laurel, Oxon Hill) are, however, clearly referable to *M. p. pennsylvanicus*, as is a small series from Newport, in the south central Western Shore section.

Microtus pennsylvanicus nigrans Rhoads

Microtus pennsylvanicus nigrans Rhoads, Proc. Acad. Nat. Sci. Phila., 49: 307, 18 June 1897.

Type locality.—Currituck, Currituck County, N.C.

General distribution.—Near the coast from southeastern Maryland to north-eastern North Carolina.

Distribution in Maryland.—Southern Eastern Shore section at least as far north as Cambridge, Dorchester County, and southeastern Western Shore section in Calvert and probably St. Marys Counties. This subspecies intergrades with *Microtus p. pennsylvanicus* in the central portion of the Western Shore section and in the northern part of the Eastern Shore section.

Distinguishing characteristics.—Similar to *Microtus p. pennsylvanicus* except that it is somewhat larger and has a darker coloration, almost black in some pelages.

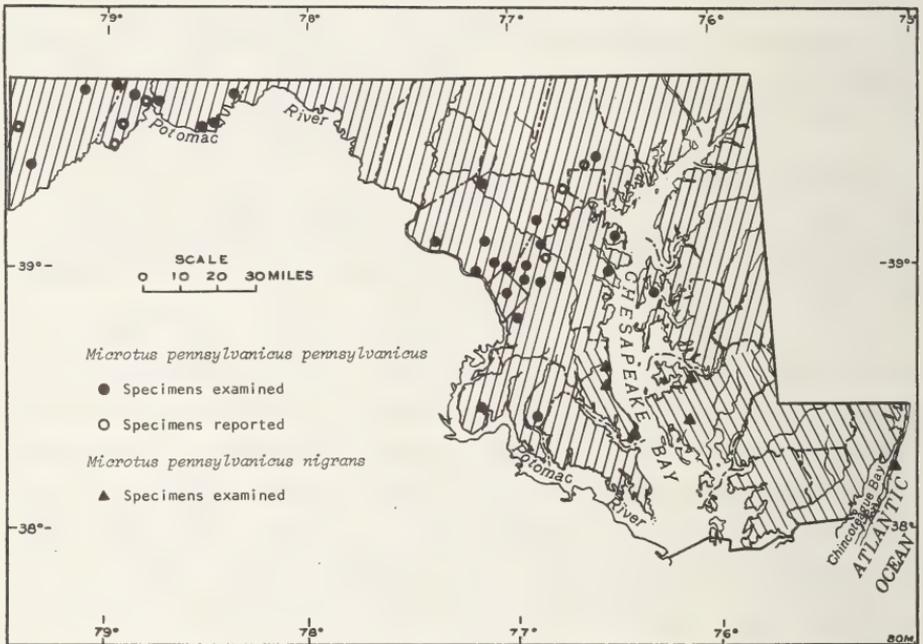


FIGURE 38.—Distribution of *Microtus pennsylvanicus pennsylvanicus* and *M. p. nigrans*.

Measurements.—External and cranial measurements of seven adults from Drum Point, Calvert County, are as follows: Total length 173.1 (168–184); tail 47.8 (42–52); hind foot 22.6 (22–23); ear 14.3 (12–16); condylobasal length of skull 29.1 (28.1–30.5); zygomatic breadth

15.9 (15.4–16.6); interorbital breadth 3.8 (3.5–4.0); maxillary tooth-row 6.8 (6.6–6.9).

Habitat and habits.—In the southern Eastern Shore section, this subspecies abounds in the dryer portions of brackish and salt marshes along the Atlantic seacoast and the Chesapeake Bay. It is probably the most abundant mammal occurring on Assateague Island. As an example of its numbers on this outer barrier island, it may be noted that in a single night in the spring of 1956, 60 specimens were taken in 100 traps set in tall grass and myrtle on the edge of a fresh water impoundment on the Virginia portion of the island a few miles south of the Maryland line. It also lives in the marshes of the Blackwater National Wildlife Refuge in Dorchester County where it builds nests in muskrat houses (Harris, 1953).

In the Western Shore section, in Calvert County, this vole has been taken in dry meadows and brushy fields.

The habits of this subspecies apparently differ in no essential respect from those of *Microtus p. pennsylvanicus*.

Specimens examined.—*Calvert County*: Breezy Point, 1; Drum Point, 12; Scientists Cliffs Road (1 mile E Route 2), 2. *Dorchester County*: Blackwater National Wildlife Refuge, 5; Cambridge, 5. *Worcester County*: Assateague Island, 4 and 5 miles S Ocean City, 10.

PINE VOLE

Pitymys pinetorum scalopsoides (Aud. and Bachman)

Arvicola scalopsoides Audubon and Bachman, Proc. Acad. Nat. Sci. Philadelphia, 1: 97, October 1841.

Type locality.—Long Island, N.Y.

General distribution.—Northeastern United States, from central New England, south to Virginia and western North Carolina, west to Illinois and Wisconsin.

Distribution in Maryland.—Common in all sections of the State.

Distinguishing characteristics.—Teeth 1/1, 0/0, 0/0, 3/3, = 16; molar teeth not rooted, and grow persistently; tail very short, buffy brown above, lighter below; ears very short, and hidden in fur; pelage short, soft and glossy, almost mole-like; coloration russet to chestnut brown on dorsum, becoming lighter on sides; underparts grayish buff; feet grayish brown.

This species resembles the meadow vole (*Microtus pennsylvanicus*) from which it may be distinguished by its shorter tail, shorter ears, and finer, more russet pelage. It differs from the red-backed mouse (*Clethrionomys gapperi*) in that the reddish coloration of the dorsum extends onto the sides and is not confined to a band on the dorsum; smaller ears; shorter tail; fur shorter, softer and more mole-like.

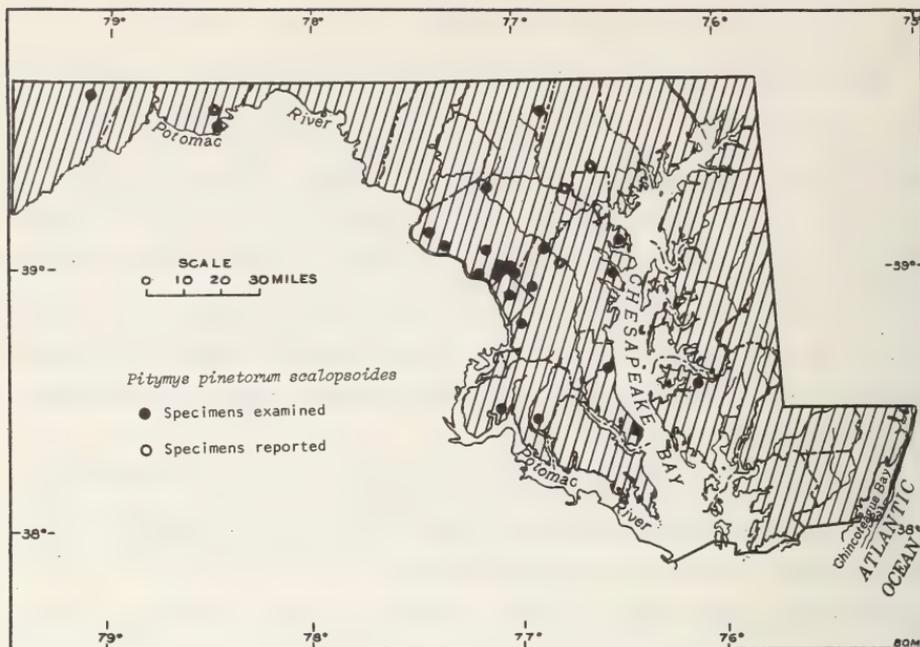


FIGURE 39.—Distribution of *Pitymys pinetorum scalopsoides*.

From the southern bog lemming (*Synaptomys cooperi*) this species may be readily distinguished by the lack of grooves on the upper incisors.

Measurements.—Ten adults from the District of Columbia have the following external measurements: Total length 124.8 (120–131); tail 22.1 (15–25); hind foot 16.6 (16–18). Eleven adults from the District of Columbia have cranial measurements as follows: Condylbasal length 24.9 (24.2–25.9); zygomatic breadth 15.5 (14.2–16.3); interorbital breadth 4.2 (3.9–4.6); length of maxillary toothrow 6.1 (5.8–6.5).

Habitat and habits.—This species is not particular with regard to habitat preference, being found in old fields, wood borders, and cultivated fields, especially in loose sandy soils. It is often found in old apple orchards where the soil is mellow and sandy, and the grass and weeds have been allowed to grow, forming a heavy protective carpet of vegetation. The fallen apples also provide the mice with food in autumn, and the bark of apple roots supply a favorite winter food. Contrary to its name, the pine vole is seldom found in pine woods in Maryland.

Hamilton (1938, pp. 163–170) in his life history study of the species says that the animal threads its way just beneath the thick carpet of leaves which forms a ceiling to its burrow. Rarely the pine vole tunnels to a depth of a foot or more, but by far the greater number

of burrows are shallow, descending to a depth of only 3 or 4 inches. In orchards it tunnels its way to fallen apples, and then burrows up from underneath to feed on the fruit. These mice seldom leave their subterranean burrows.

The nest of the pine vole is globular in shape, and composed of almost any material the animal can procure, generally dead leaves and grasses. The nest may be just below the ground surface, or, occasionally under some shallow-rooted stump. Usually there are three or four exits.

This species feeds largely on roots and tubers, bulbs, and the bark of trees and shrubs. It seldom eats green vegetation, seeds, or most kinds of fruit, although it does relish apples and pears. Generally, considerable quantities of roots and tubers, which presumably are utilized as the bulk of the winter food, are stored in its burrows. Pine voles often are responsible for depredations in orchards, where they frequently girdle apple trees severely.

This species is cyclic, and according to Hamilton (1938, p. 166) its reproductive behavior undoubtedly varies from year to year as does that of *Microtus*. The breeding season is from early March to mid-November, and small litters of from two to four young are produced. The gestation period in all probability approximates the 21 days of *Microtus*.

Specimens examined.—*Allegany County*: Oldtown, 9 miles E, 4. *Anne Arundel County*: Annapolis, 3 miles NW, 2; Lake Shore area, 2. *Calvert County*: Plum Point, 2 miles W, 1; Solomons Island, 3½ miles N, 1. *Carroll County*: Hampstead, 1. *Charles County*: Newport, 3; Port Tobacco, 3 miles SW, 1. *Dorchester County*: Cambridge, 3. *Garrett County*: Grantsville, 1. *Howard County*: Long Corner, 1. *Montgomery County*: Chevy Chase, 1; Kensington, 2; Montgomery Knolls, 1; Plummers Island, 5; Poolesville, 1 mile NE, 1; Rockville, 2.3 miles NE, 10; Seneca, 1.3 miles W, 1; Seneca, 1½ miles NW, 1; Silver Spring, 1; Takoma Park, 1; Woodside, 5. *Prince Georges County*: Bladensburg, 1; Laurel, 9; Oxon Hill, 1. *District of Columbia*: 61.

Other records and reports.—*Allegany County*: Green Ridge (Coll. U. Md.). *Baltimore County*: Bare Hills—Lake Roland area (Bures, 1948: 68); Patapsco State Park (Hampe, 1939: 7). *Prince Georges County*: Patuxent Research Center, along Patuxent River (Stickel, Lucille F., 1948: 506).

MUSKRAT

Ondatra zibethicus macrodon (Merriam)

Fiber macrodon Merriam, Proc. Biol. Soc. Washington, 11: 143, 13 May 1897.

Type locality.—Lake Drummond, Dismal Swamp, Norfolk County, Va.

General distribution.—Reported from Chester County, Pennsylvania, south in the Coastal Plain and Piedmont to the lower Cape Fear drainage of southeastern North Carolina.

Distribution in Maryland.—Eastern Shore, Western Shore, and Piedmont sections.

Muskrats are especially abundant in the fresh-water and brackish marshes of the Eastern Shore section. The subspecies *macrodon* intergrades with *O. z. zibethicus* in the Piedmont section and is probably replaced by that subspecies in the Ridge and Valley and Allegheny Mountain sections.

Distinguishing characteristics.—Teeth 1/1, 0/0, 0/0, 3/3, = 16; tail long and laterally compressed; hind feet partially webbed; ears small and almost hidden in fur; pelage dense, underfur soft and thick, overlaid with long smooth guard hairs; usual coloration a rich brown, with considerable bright russet to red tinge, darker on head, nose, and back; sides grayish brown to russet; underparts considerably lighter, varying from grayish drab to bright cinnamon rufous.

There is a black color phase of this subspecies which in some Maryland marshes runs as high as 65 percent of the population (Dozier, 1948*b*, p. 393). These animals are not uniformly black, but have a modified agouti pattern shown in the lighter ventral surfaces and on the lower side areas where the hairs are subapically banded with

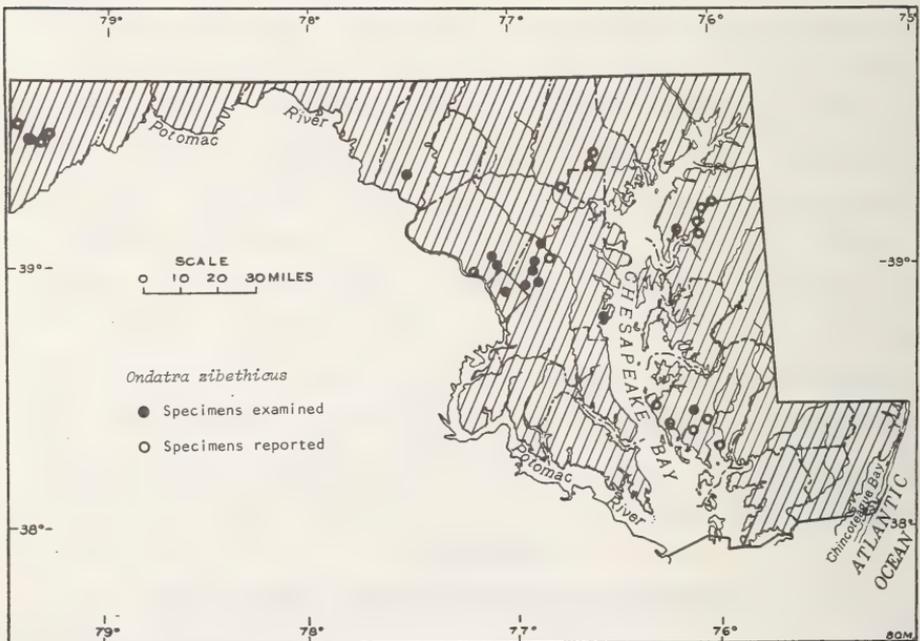


FIGURE 40.—Distribution of *Ondatra zibethicus*.

yellow. The dorsum, however, is a uniform glossy black with no hairs banded with red and yellow. Rarely an albinistic individual is encountered, and Dozier (1948*b*, p. 394) has reported upon a nonalbino white mutation ("Maryland white") occurring in some of the marshes in Dorchester County, and fawn colored mutants from the vicinity of Chestertown, Kent County.

The muskrat is readily distinguished from other Maryland rodents by the combination of its aquatic habits, large size, and laterally compressed tail. The beaver, which the muskrat resembles in aquatic habits, is larger and has a broad, horizontally compressed tail.

Measurements.—External measurements of an old male and two young adult females from Laurel, Prince Georges County, are as follows: Total length 675, 600, 570; tail 280, 275, 266; hind foot 87, 86, 79. Cranial measurements of 11 adults from Laurel are: Condylbasal length 67.6 (63.9–72.2); zygomatic breadth 41.8 (39.8–44.5); least interorbital breadth 5.9 (5.0–6.6); length of maxillary toothrow 16.1 (14.9–17.2).

Dozier et al. (1948, p. 180) found that the average weight of 13,421 male muskrats trapped on the Blackwater National Wildlife Refuge, Dorchester County, was 2 pounds 4 ounces, and the average weight of 10,090 females was 2 pounds 2 ounces. Adult males varied in weight from 6 ounces to 4 pounds, and females from 6 ounces to 3 pounds 12 ounces.

Habitat and habits.—Muskrats are most abundant in the extensive marshes that line the Chesapeake Bay. Elsewhere in Maryland they are found in streams that wind through pastures, and in swamps.

The muskrat is essentially vegetarian, but occasionally will make use of animal food such as fish, mussels, insects, crayfish, and snails. Martin et al. (1951, p. 236) report that at the Patuxent Research Center near Laurel, the most important plant material eaten is burreed, cutgrass, arrowhead, waterlily and panicgrass. Smith (1938, p. 12) found that muskrats in Dorchester County would eat, to some extent, almost any plant found in the marshes there. Certain favorites, however, form their staple diet, and no area lacking these will support a large muskrat population. Three square sedge and broadleaf and narrowleaf cattails constitute four-fifths of the animal's diet, and all parts of these plants are eaten at one time or another during the year. Other foods that are at times utilized by the muskrat in the Dorchester marshes are saltmarsh, wild reed, saltgrass, beak-rush, spikerush, big cordgrass, wild millet, and sweet sedge. Also occasionally eaten are saltmarsh fleabane, marshmallow, waterlily, dodder, iris, waxmyrtle, small pine trees, and poison-ivy. Smith found that Dorchester County muskrats sometimes consumed turtles, blue crabs, fish (chiefly sluggish kinds such as carp), salt-water mussels, and possibly dead birds.

In the Maryland marshes, muskrats are active at all hours, in the spring and throughout the summer.

Muskrat homes are of two general types depending on the topography of the area in which they live. In the uplands they dig burrows into the banks of streams and other bodies of water, while in the marshes they build dome-shaped structures. The entrance hole to a bank burrow is always below the normal level of water. The burrow turns upward above water level and ends in a nest of grass. The dome-shaped structures that they build in the marshes may be as much as 7 or 8 feet in diameter and more than 4 feet high. They are constructed of stalks, roots, and peaty remains of plants and are built on or around a firm foundation such as a stump or the base of a tree. Each house contains one or more nests from which passages lead to plunge holes in the floor. These holes in turn lead to underground tunnels that connect with the surface several feet from the house.

Muskrats are primarily aquatic and construct elaborate canals, 6 inches to a foot wide, and sometimes a foot or more deep, which are not visible when the water is high. Those canals which are used as main arteries of travel are always wider and deeper than those used only as temporary leads made in search of food. In dry areas the muskrats use surface trails concealed in the grass that lead in all directions, and except for size, resemble those made by the meadow mouse.

In addition to surface canals and trails, muskrats construct elaborate systems of underground burrows and tunnels that spread out in all directions and are connected with the surface and the canals by plunge holes scattered at convenient intervals.

Smith (1938, p. 16) found that in Maryland the muskrat may breed in any month with the possible exception of November and December. Most of the young are born from mid-April to mid-September. Most Maryland trappers report that there are three litters a year, but Smith (1938, p. 16) was only able to obtain two a year in pen-raised animals. The number of young is variable; in the Maryland investigations conducted by Smith, the number averaged 4.4, seven being the most found in any one uterus. The gestation period appears to be about 29 or 30 days, and muskrats probably first breed at the age of 1 year.

The population of muskrats in Maryland marshes apparently has been decreasing since 1939. The number of muskrats trapped in the marshes from year to year may not reflect the actual muskrat population since many factors such as food, predation, salinity, and breeding, which are not readily observable, together with the value of pelts, act together to affect muskrat abundance, and may be different from year to year. Furthermore, these factors may cause different reactions on the part of the muskrat populations at different levels of abundance. Nevertheless, trapping records probably give an adequate index of the

larger fluctuations in population level in Maryland. With this in mind, Harris (1952, p. 13) lists the muskrat catch on approximately 600 acres of marsh on the Nanticoke River, Dorchester County. In 1937, the total catch of muskrat on this marsh was 2,417 animals (4.0 animals per acre). By 1950 the catch on this same marsh had dropped to 150 animals, or 0.2 animals per acre. On a Statewide level, the total catch of muskrat was estimated at 2 million in 1938. In 1949, when Maryland first began to keep accurate records of the muskrat catch, only 228,548 animals were reported trapped throughout the State. By 1957 this figure had dropped to a low of 112,348 muskrats. The 1967-68 catch was reported as 139,000.

These figures show that the muskrat population has been experiencing a decline over the past 25 years, and since the muskrat is an economically important animal, there has been considerable speculation and research devoted to the reason, or reasons, for this decline. Hardy (1950, pp. 8-9, 27) records the opinions of the trappers themselves regarding this decline, which includes such ideas as there being a definite ecological relationship between muskrats and domestic hogs. These trappers stated that with the fencing in of property in Dorchester County the hogs were no longer able to root in the marshes and, hence, the ecological relationship of the two species was destroyed and the muskrat population declined. Another theory maintained by some of the trappers is that owing to various causes there has been a great increase in the number of eels in Dorchester County waters and that eels enter the muskrat houses and consume young. Other ideas are that the muskrat decline is due to increased predation by raccoons and foxes; a "dreadful disease"; floristic changes; "trapping under" (placing the trap in underground leads); and high water. Hardy (1950, p. 27) notes that some of these factors may have been operative, but that it can safely be assumed that the diminishing population of the muskrat in Dorchester County has been brought about by a combination of ecological and environmental changes rather than by any single factor. Harris (1952, p. 36) points out that his study on Dorchester County muskrats did not answer the question why there has been a decline in their numbers, but it did show that the combination of predation and a reduced capacity of the marsh to support muskrats may prevent a rapid increase in the muskrat population.

Specimens examined.—*Anne Arundel County*: Broadwater, 1. *Dorchester County*: Blackwater National Wildlife Refuge, 8. *Frederick County*: Jefferson, 1. *Montgomery County*: Forest Glen, 1; Kensington, 1; Sligo Branch, 1. *Prince Georges County*: Beaverdam Creek, 1; Beltsville, 1; Branchville, 3; Lanham, 2; Laurel, 147. *District of Columbia*: 6.

Other records and reports (from Dozier, 1948b, unless otherwise noted).—*Baltimore County*: Bare Hills–Lake Roland area (Bures, 1948, p. 68); Loch Raven (Kirkwood, 1931, p. 317); Patapsco State Park (Hampe, 1939, p. 7). *Dorchester County*: Best Pitch Ferry; Elliotts Island; Fishing Bay; Joe's Point; Robbins, near; Taylors Island; World End Creek, near Golden Hill. *Garrett County*: Piney Run, near Piney Dam (trapping record, Maryland Nat. Res. Inst.); Pawn Run, as it enters Deep Creek (trapping record, Maryland Nat. Res. Inst.). *Kent County*: above and below Chestertown, on the Chester River; Chestertown (specimens in Acad. Nat. Sci. Phila. collection); Fairlee Creek near its Chesapeake Bay Mouth. *Montgomery County*: Mainland across from Plummers Island (Goldman and Jackson, 1939, p. 133). *Prince Georges County*: Patuxent Research Refuge (Uhler & Llewellyn, 1952, p. 81). *Queen Annes County*: Booker's Wharf.

Remarks.—I have not been able to examine specimens from the Ridge and Valley and the Allegheny Mountain sections, but one specimen I examined from Jefferson, Frederick County, just to the east of the Blue Ridge Mountains, is clearly an intergrade with *Ondatra z. zibethicus* in size and coloration, and almost near enough to typical *zibethicus* to be assigned to that subspecies. On the basis of this specimen, and because of the known distribution of *O. z. zibethicus* in Virginia and Pennsylvania, the muskrats of the Ridge and Valley and Allegheny Mountain sections probably are referable to the subspecies *zibethicus*. This subspecies appears to intergrade with the Coastal Plain subspecies *macrodon* throughout most of the upper Piedmont section.

Published reports of this species in western Maryland are by Browning (1928, p. 213) who saw muskrats around 1825 in the vicinity of Deep Creek Lake in Garrett County, and by Mansueti, (1958, p. 83), who observed them in Cranesville Swamp, Garret County, in the 1950's. The species is present in suitable streams and ponds throughout the Ridge and Valley and Allegheny Mountain sections at the present time, and according to Flyger (in verbis, 22 June 1964) trappers report that they are not uncommon.

Ondatra z. zibethicus differs from *O. z. macrodon* in its darker pelage (in normal color phase), and in its smaller size. It is of interest to note that Merriam in his original description of *macrodon* (specimens from Dismal Swamp, Virginia) considered the subspecies to be a much darker form than *zibethicus*. Merriam's specimens, however, were mostly dark phase animals, and as Hollister (1911, p. 18) has shown, *macrodon* (in normal color phase) is actually a lighter and brighter colored subspecies than *zibethicus*.

SOUTHERN BOG LEMMING

Synaptomys cooperi stonei Rhoads

Synaptomys stonei Rhoads, Amer. Nat., 27: 53, January 1893.

Type locality.—May's Landing, Atlantic County, N.J.

General distribution.—Southern Appalachians of eastern Kentucky and Tennessee, western North Carolina and Virginia and western Maryland to the Atlantic Coastal Plain of Maryland, Delaware, and New Jersey, and northward to Connecticut and coastal Massachusetts.

Distribution in Maryland.—Statewide in distribution. The most southeasterly record for the subspecies *stonei* is in Worcester County (Poole, 1943, p. 103).

Distinguishing characteristics.—Teeth 1/1, 0/0, 0/0, 3/3, = 16; size medium; tail short; fur rather long and shaggy; head broad; ears short, rising slightly above the fur; upper incisor teeth grooved. Coloration of upper parts brown to chestnut, grizzled in appearance; underparts silvery, with no sharp line of demarcation on the sides; tail grayish black, not sharply bicolored; feet brownish black.

This is the only short-tailed mouse in Maryland which has grooved upper incisors, and may thus be distinguished from all others. Crani-ally, the southern bog lemming has a shorter rostrum than any other Maryland mouse.

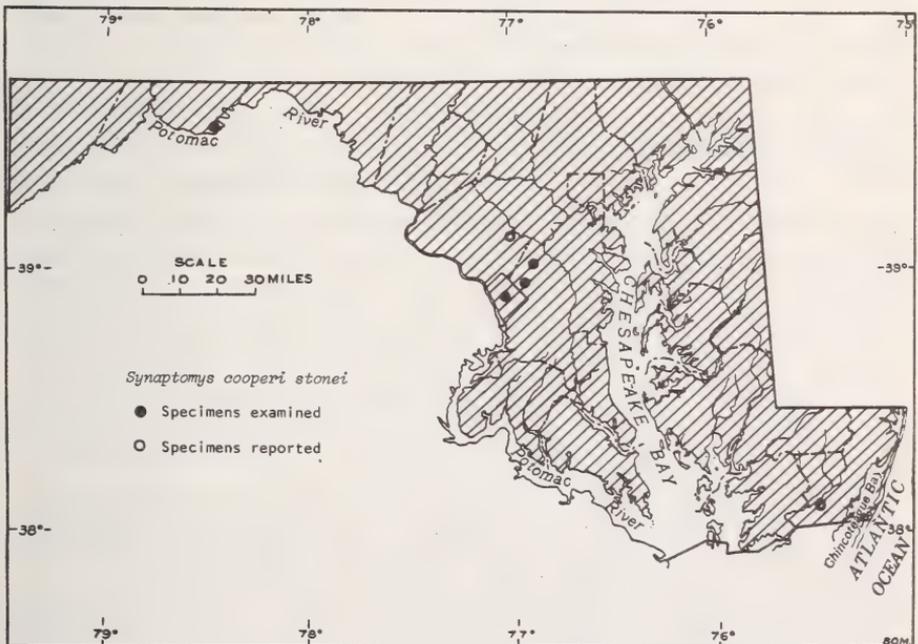


FIGURE 41.—Distribution of *Synaptomys cooperi stonei*.

Measurements.—External measurements of five adults, and cranial measurements of six adults from Laurel, Prince Georges County, are as follows: Total length 127.4 (120–135); tail 21.2 (18–23); hind foot 19 (18–20); greatest length of skull 24.7 (24.3–24.9); zygomatic breadth 17.0 (16.5–17.5); interorbital constriction 2.9 (2.7–3.1); length of maxillary toothrow 7.5 (7.4–7.8).

Habitat and habits.—This species has a preference for sphagnum bogs, and this is where most Maryland specimens have been collected. It is sometimes found, however, in woodland habitats, including beach-maple, oak-hickory, and pine. Specimens have even been taken in grassy areas, orchards, weedy fields, and marshes, and in shocked corn.

According to Conner (1959, p. 171) the chief requirement of *Synaptomys* seems to be the presence of green succulent monocotyledonous plants, primarily sedges and grasses, which are its main source of food.

This species may breed throughout the year, although Conner (p. 203) found that in southern New Jersey there was a spring peak in the breeding cycle, with some breeding continuing through summer and autumn. Poole (1943, p. 103) found a lactating female in Worcester County, Md., in late November. Conner (p. 202) found that litters of from two to five were usual for the species, although a single embryo is not uncommon, and as many as seven young have been reported. His data suggest that in the spring and summer females produce a litter every 67 days.

Wherever the southern bog lemming occurs, it is found in company with other small mammals such as red-backed mice, deer mice, shrews, and moles, and it often occupies the same burrows as these others. The nests are constructed of shredded grasses and sedges and are often concealed some distance beneath the ground. Less often, they are placed directly on the ground where there is sufficient ground cover. Conner (p. 227) found that most of the nests in southern New Jersey were located just under the surface, concealed in either hemlock or moss or in other elevated mounds in the bogs. Most of the nests were balls of dry shredded leaves of sedge, and had two entrances. The diameters ranged from 3½ to 6 inches, and the hollow spaces within the nests averaged about 2½ inches.

Specimens examined.—*Allegheny County*: Oldtown, 9 miles E, 1. *Prince Georges County*: Beltsville, 1; Beltsville, 2½ miles W (sphagnum bog), 5; Hyattsville, 8. *District of Columbia*: 1.

Other records and reports.—*Montgomery County*: Sandy Springs [skull removed from stomach of red-tailed hawk] (Bailey, 1923, p. 118). *Worcester County*: Snow Hill, 6 miles SW (Poole, 1943, p. 103).

Remarks.—The specimen from 9 miles E of Oldtown, Allegany County, is somewhat smaller in size and less grizzled in coloration than those from farther east in the State. This animal may represent an intergrade in these characters with *S. c. cooperi*, the subspecies distributed to the north of *stonei*, or may actually be referable to that form. As Wetzel (1955, p. 12) has pointed out, however, the ranges of all measurements in these two subspecies overlap, and the variation in coloration within only one sample of *cooperi* for one season is much greater than between the various subspecies of *S. cooperi*. This illustrates the difficulty in assigning individual specimens to subspecies. Because of this, the specimen from Allegany County is provisionally assigned to *S. c. stonei*, the range of which is herein considered to encompass the entire State. When more specimens from the Piedmont and the Ridge and Valley sections become available for study, however, it may be found that *S. c. cooperi* is distributed in those sections, and that the specimen from Allegany County should properly be assigned to that race.

Family CAPROMYIDAE (hutias and coypus)

NUTRIA

Myocastor coypus (Molina)

Mus coypus Molina, Sagg. Stor. Natur. Chili, p. 287, 1782.

Type locality.—Rivers of Chile.

General distribution.—Ranges widely over southern South America; introduced into the United States in the 1930's, and now is established in the wild in at least 16 states.

Distribution in Maryland.—A few nutria are established in the Dorchester County marshes.

Distinguishing characteristics.—Teeth 1/1, 0/0, 1/1, 3/3, = 20; size large (sometimes attaining a weight of 21 lbs.); pelage consisting of 2 types of hair, dense underfur, and long glossy overlying guard hairs; coloration rich brown or chestnut on dorsum, paler underneath; tail long and cylindrical; middle toes of hind feet connected by a basal web.

This species superficially resembles the muskrat, from which it may be readily distinguished by its larger size, cylindrical as opposed to laterally compressed tail, and greater number of teeth.

Measurements.—An adult male and female from the Blackwater National Wildlife Refuge, Dorchester County, measure externally as follows: Body length 571, 518; tail 413, —; hind foot 156, 137. Dozier (in correspondence) reports that the heaviest animal he examined at the Fur Animal Experiment Station in Cambridge, Md., weighed 21 pounds.

No skulls of this species are available from Maryland for measurement.

Habitat and habits.—The habitat of the nutria in its South American home is in marshes, swamps, and along the margins of rivers and lakes in fresh-water plant associations. Bednarik (1958, p. 2) says, however, that Randall Rhodes, Curator of Collections at the Cleveland Museum of Natural History, has told him (in personal communication 1954) that in South America he observed that nutria were mostly associated with marine waters. The temperature of the water seems to be of little importance to them, and in the United States they are now found as far north as Michigan and Washington State, where they prosper in the same type of habitat as the muskrat.

The nutria is a vegetarian, consuming a variety of aquatic plants, rushes, reeds, grasses, seeds, cattails, and sedges. In captivity it shows a marked preference for alfalfa and clover and is fond of practically all root crops except Irish potatoes. Because of its voracious appetite it has posed a serious threat to waterfowl marshes in some areas where it has been introduced.

Nutria living in streams or ponds which have steep banks burrow into them close to the water level. Each pair makes its own burrow, which is dug in and upward until well above the water level. The den is lined with grasses, and as the family grows, the burrow is enlarged.

If the nutria are living in a marsh which does not have steep banks, floating nests of aquatic vegetation are built, which resemble those made by the muskrat. Where conditions permit, part of a colony may live in floating nests in the marsh, while other animals will build bank burrows.

The gestation period of this species in Maryland is between 130 and 134 days (Dozier, unpublished data, U.S. Fish and Wildlife Service). The young seem to be born during all seasons, and there are probably two or three litters a year per female. In Louisiana, litter size averages 4.4 young (Harris, 1956).

Nutria apparently became established in the Dorchester County marshes of Maryland sometime in the early 1940's. There are no records of their occurrence there earlier, and Herbert L. Dozier, formerly Director of the U.S. Fur Animal Field Station at the Blackwater National Wildlife Refuge, does not mention their presence in the Maryland marshes in his extensive nutria correspondence in the files of the Fish and Wildlife Service dating back to the period 13 March 1939, to 3 June 1941. It is possible that Maryland's nutria population may have originated as escapees from the U.S. Fur Animal Field Station, although there is no certain proof of this. In the late 1930's and early 1940's Dozier was conducting experiments at the Blackwater Refuge on the feeding, care, and breeding of captive nutria. In one of his let-

ters dated 18 November 1940, now in the files of the U.S. Fish and Wildlife Service, he says:

We have recently completed two new large 100 sq. ft. inclosures in marsh and pond edge and have released a pair of nutria in each to study their reactions to various types of local habitat, etc.

There is no record of what became of the inclosures or animals, and Dozier never published, to my knowledge, the results of his study.

Maryland kept no accurate records of its annual fur catch until 1949. Prior to that, only rough estimates were made each year as to the number of animals trapped in the State, and no mention was ever made of nutria. In 1949, when trappers were first required to report their catches, four nutria were among the animals taken. No further nutria were reported until 1956, when two were trapped in the Dorchester marshes. The following year the catch was 45 and in 1958 the number had risen to 52. Since then the number reported has declined. Thirty-four were reported for 1959, none for 1960, and five in 1961. It appears that nutria in the Maryland marshes are only precariously established.

Specimens examined.—Dorchester County: Blackwater National Wildlife Refuge, 8.

Family MURIDAE (Old World rats and mice)

BLACK RAT

Rattus rattus (Linnaeus)

[*Mus*] *rattus* Linnaeus, Syst. nat., ed. 10, 1: 61, 1758.

Type locality.—Uppsala, Sweden.

General distribution.—This is an introduced species. In the United States, it is well established and abundant in the south Atlantic and Gulf Coast ports. In the northeastern United States it is found in buildings along the docks of some seaports, and at several isolated inland localities.

Distribution in Maryland.—May occur at present in some buildings along the docks in Baltimore City.

Distinguishing characteristics.—Teeth 1/1, 0/0, 0/0, 3/3, = 16; size medium; general build slender; muzzle sharp; ears large, almost naked, reaching or covering the eyes when laid forward; tail slender and long, at least as long as the combined length of the head and body, and sometimes longer; pelage soft, but covered with coarse guard hairs, giving it a harsh appearance.

There are three color phases of this species. Some authorities have considered these as distinct subspecies because of their general association with distinct geographic areas. One of these color phases, known as *R. r. frugivorous*, has a yellowish or reddish brown dorsum, with a white or yellowish abdomen, and is most commonly encountered in the Mediterranean area. Another color variation, *R. r. alexandrinus*, has a

brownish dorsum, similar to that of *frugivorous*, but with a gray venter, and is most abundant in the Middle East and North Africa. The third color phase, known as *R. r. rattus*, has a black dorsum, with a dark gray venter, as in *alexandrinus*, and is mostly associated with the cold temperate countries of northern Europe. In general, *R. r. frugivorous* is a wild-living animal, whereas *alexandrinus* and *rattus* are nearly always associated with man and his habitations. None of these varieties, however, is exclusively limited to any of the geographic or habitational areas mentioned above, and all three forms may occur at any one locality or in any one habitat. Because of this it seems advisable at present to consider them as color phases rather than as distinct subspecies (Caslick, 1956, pp. 255-257). All of the color phases may be encountered in the United States.

Rattus rattus is most easily confused with the Norway rat (*Rattus norvegicus*). It may be distinguished from that species by its smaller size, more slender build, more elongated nose, larger longer ears, and much longer and more slender tail (as long as, or longer than, the combined length of the head and body). Cranially, the two species differ in that the braincase of *R. rattus* is shortened and rounded, whereas that of *R. norvegicus* is narrow and elongated, the well-developed temporal ridges extending parallel to each other for a considerable distance on each side of the cranium.

Measurements.—Two adults from Washington, D.C. (taken on a river boat at the Seventh Street Wharf on 23 April 1923) measure as follows: Total length 405, 423; tail 218, 238; hind foot 37, 39; greatest length of skull 43.6, 43.2; zygomatic breadth 20.8, 20.9; interorbital constriction 6.4, 6.7; length of maxillary toothrow 7.0, 6.9.

Habitat and habits.—This rat is essentially an arboreal animal and seldom inhabits burrows. Where it infests buildings and houses, it is found usually in the walls, ceilings, or roof, but seldom in basements or in sewers. It shuns water and seldom enters it voluntarily. This is, however, the common rat on ships, to which it gains access by climbing the moorings. It is occasionally introduced with shipments of grain or fruit.

In diet, the black rat is omnivorous, consuming a wide variety of grains, fruits, vegetables, and animal matter.

The species is polyestrous all the year round. The duration of gestation is about 21 days, and the average litter size is seven to nine.

Black rats enter into close relations with man wherever they occur, and for this reason they are often involved in the transmission of diseases, principally the bubonic plague.

Specimens examined.—*District of Columbia:* Five (three taken on river boat at Seventh Street Wharf, and two taken in the Central Market in a box of fruit from Egypt in February 1912).

Remarks.—It is generally believed that the black rat was the common rat of the eastern United States before the late 18th century. Around that time, it is said, the Norway rat was introduced, and because it is a larger and more aggressive animal it drove the black rat out except near shipping ports (see Bailey, 1923, p. 114). There is however, no real evidence that the black rat was ever well established in Maryland or in any other Northeastern State. This animal prefers a warm climate and probably found Maryland too cold for its liking. Moreover, it is known that in areas in the South the black rat and the Norway rat live in the same habitations without one species driving away the other. In areas where the two species live together, however, there seems to be an ecological separation in that the black rat usually is found in the upper stories of a building, while the Norway rat inhabits the basement and adjacent sewers and tunnels.

At the present time there are no known colonies of this species in Maryland, although perhaps a few animals inhabit some of the building along the docks in Baltimore City. In 1949 Davis and Fales (1949, p. 248) reported them present in only three Baltimore buildings and estimated the population as not more than 1,000. This rat, however, is the common ship variety and probably has been, and will continue to be, repeatedly introduced into the Baltimore wharf district.

As far as is known, none are established now in Washington, D.C., although here again they may leave boats and take up residence in nearby buildings. Five specimens have been taken in the District of Columbia. Three of these were removed from a boat that had docked at the Seventh Street Wharf in April 1923, and two were trapped in January and February of 1912 at the old Central Market, to which they apparently had been brought in baskets of fruit from Egypt.

NORWAY RAT

Rattus norvegicus (Berkenhout)

Mus norvegicus Berkenhout, Outlines of the natural history of Great Britain and Ireland, 1: 5, 1769.

Type locality.—England.

General Distribution.—This is an introduced form that has become widely established throughout North America.

Distribution in Maryland.—Statewide.

Distinguishing characteristics.—Similar to *R. rattus*, but differs in being larger, heavier, and shorter tailed. In coloration it is grayish or reddish brown on the back, heavily lined with black hairs along the middorsal line. The belly is silvery gray, but in some specimens it may be washed with a dingy yellowish - brown. Cranial differences between this species and *Rattus rattus* are described under the latter species.

Young Norway rats superficially resemble the native American rice rats (*Oryzomys palustris*). They may always be distinguished from this species, and from other cricetines, by the upper molar teeth, which in the genus *Rattus* (and in the other introduced Murid genus *Mus*) are provided with small rounded cusps (tubercles) arranged in three longitudinal rows in contrast to two rows of longitudinal cusps in most cricetines.

Measurements.—An adult from the District of Columbia measures as follows: Total length 470; tail 208; hind foot 43; ear 21; greatest length of skull 52.6; zygomatic breadth 27.6; interorbital breadth 7.4; length of maxillary toothrow 7.3.

Habitat and habits.—This is essentially a water-loving and burrowing animal. In the spring of 1963, large numbers of them were inhabiting burrows in the banks bordering the Loch Raven Reservoir north of Baltimore. They would emerge from the burrows in broad daylight, dive into the reservoir, and swim considerable distances to obtain scraps of bread thrown into the water by visitors who were feeding the numerous carp which swim in the area near the dam. In Washington, D.C., the population of Norway rats has recently risen to alarming proportions. Their burrows may be seen around many of the downtown government buildings and monuments, and at dusk they come into the open and actively forage for food among the refuse and rubble left by tourists during the day.

The city of Baltimore has always had a Norway rat problem, but these animals are not as numerous as was thought at one time. In a careful study of Baltimore's rat population in 1949, Davis and Fales (1950, p. 146) estimated there were approximately 43,000 animals, with a range of from 26,000 to 68,000, of which about 15,000 were in commercial areas. They had estimated that the population in 1947 was 165,000, so that there was a considerable decline in the period 1947 to 1949. With improved sanitation and methods of extermination developed during the intervening years it may be assumed that the rat population of the city at present is no higher, and probably lower, than in 1949. Nevertheless, rats are still a serious economic and public health problem in Washington and Baltimore.

The Norway rat is known to occur throughout the State both in commercial buildings and habitations, and in some places in the wild, particularly in the summer.

The species is extremely adaptable, and about the only factor essential for its success is the presence of water; it drinks freely, and is a good swimmer and diver. It will eat virtually anything, and finds sewers particularly attractive places to live because of the abundant water supply and the offal usually found therein upon which it can

feed. From the sewers it will readily pass into buildings where it may cause considerable damage.

The species is an efficient burrower, and out-of-doors its bank burrows consist of winding galleries furnished with several escape holes. On farms, it frequently makes burrows in manure piles, rubbish mounds, wheat stacks, and hay ricks. Many Norway rats spend the summer months in fields and meadows, and at the approach of cold weather migrate into towns and villages where they seek the warmth of commercial buildings and other habitations.

The gestation period in the Norway rat is 21 days. Studies in England (Hinton, 1931, p. 13) indicate that the average number of young per litter is eight or nine, but that there are records of as many as 23. Usually the number ranges between 6 and 19, and the females may produce five or six litters annually.

It is generally believed that the Norway rat and the black rat are incompatible, and that the larger, more aggressive Norway rat will drive out or kill the smaller, weaker black species wherever they are occupying the same area. There is no proof of this, however, and there are even cases known where the two species have lived together in the confines of a small ship (John Jones, U.S. Fish and Wildlife Service, in verbis). The fact that they only infrequently occur together is probably the result of their preference for different climatic situations. The Norway rat is essentially a northern, cool climate animal and prospers in the temperate regions of northern Europe and North America. The black rat originated in warm, semitropical areas and find its optimum conditions in the warm Mediterranean regions and in the southern portions of the United States. It seems probable that the black rat, although repeatedly introduced, has never been firmly established in the northeastern United States and that the Norway rat has been the common house rat in Maryland since early colonial times.

Specimens examined.—*Anne Arundel County*: Fort Meade, 1. *Baltimore City*: 1. *Calvert County*: Solomons Island, 1. *Montgomery County*: Silver Spring, 1 mile N, 3. *District of Columbia*: 77.

HOUSE MOUSE

Mus musculus Linnaeus

Mus musculus Linnaeus, Syst. nat., ed. 10, Vol. 1, p. 62, 1758.

Type locality.—Uppsala, Sweden.

General distribution.—This is an old world species that has been introduced into the United States and is now found in a commensal and feral state throughout the country.

Distribution in Maryland.—Occurs abundantly as a commensal or as a feral animal in all sections of the State.

Distinguishing characteristics.—This small mouse is well known and needs no extensive description. The upper molar teeth of the house mouse are essentially like those in *Rattus rattus* and *R. norvegicus*, that is, with three rows of longitudinally arranged cusps. This distinguishes the species from all other Maryland mice of small size.

Externally, the house mouse superficially resembles American mice of the genera *Peromyscus* and *Reithrodontomys*. It differs from Maryland *Peromyscus* externally in its smaller size and in coloration. In adult pelage, *Peromyscus* is generally a brownish gray in coloration on the dorsum, with a white venter, the line of demarcation between the two being sharply marked. The tail also is distinctly bicolored, darker above, pale below. In the house mouse, the coloration is more grayish and the abdomen is generally paler than the dorsum, but there is no sharp line of demarcation between the two, the abdomen seldom being pure white as in *Peromyscus*. In addition, the tail of the house mouse is not distinctly bicolored.

The dorsum of the juvenile *Peromyscus* is colored a uniform slaty gray, which is totally unlike the grizzled gray of the house mouse, and the venter is a snowy white as in adults, with a sharp line of demarcation between the two.

Externally, the house mouse is very similar in appearance to the harvest mouse (*Reithrodontomys humulis*). The most certain way of separating the two species is through an examination of the upper incisor teeth. In *Reithrodontomys* there is a longitudinal groove which runs the length of each incisor, while in the house mouse these teeth are smooth. In addition, the biting edges of the upper incisor teeth of the house mouse usually are notched, and the tips of the lower incisors fit into the notches when the jaws are closed.

Measurements.—Seven adults from the vicinity of Ocean City, Worcester County, have the following external measurements: Total length 149.3 (140–167); tail vertebrae 73 (58–88); hind foot 17.4 (16–18). Cranial measurements of five adults from the vicinity of Ocean City are: Greatest length 20.9 (19.8–21.8); zygomatic breadth 11.0 (10.6–11.5); interorbital breadth 3.4 (3.3–3.6); length of maxillary toothrow 3.2 (3.1–3.4).

Habitat and habits.—This is a very plastic animal, and it has adapted itself to a wide variety of habitats. Like the black rat and the Norway rat, it is most often encountered in or near human habitations, but is also found in the wild throughout Maryland.

This species probably is of Asiatic origin. It is efficient at climbing, jumping, and swimming; and it will eat and thrive on practically any food that man consumes. Its nest is made of soft materials and is placed in any convenient location, such as in walls, under floors and steps, in bookcases or furniture, and, in the wild, under logs or stones and other convenient recesses.

The house mouse is very prolific. It attains sexual maturity at the age of 3 months and the breeding season is of long duration. The gestation period is from 19 to 21 days, and the number of young per litter is usually five or six. The young are born blind and naked, but they mature rapidly and are able to leave the mother in about 3 weeks.

When these mice inhabit houses in large numbers, they do considerable damage by eating large quantities of food, or tainting it with their droppings. They will consume linen clothing of all types, gnaw on books, and chew holes in the woodwork. In shops, warehouses, graineries, and on farms, they are usually abundant and destructive.

In Maryland, the house mouse is found everywhere, even on marshes and dunes of the Atlantic outer barrier beaches.

Specimens examined.—*Allegany County*: Green Ridge, 1; Mount Savage, 7. *Anne Arundel County*: Annapolis, 3 miles NW, 1. *Calvert County*: Drum Point, 1; Plum Point, 2; Plum Point, 2 miles W, 6; Scientists Cliffs, 2; Solomons Island, $\frac{3}{4}$ mile N, 11. *Charles County*: Nanjemoy Creek, 1; Port Tobacco, 4. *Howard County*: Long Corner, 2. *Montgomery County*: Cabin John Bridge, 2; Chevy Chase, 3; Forest Glen, 5; Gaithersburg, 5 miles NE, 1; Kensington, 7; Seneca Creek, 1; Silver Spring, 1 mile N, 2. *Prince Georges County*: Beltsville, near, 1; College Park, 1; Lanham, 1; Laurel, 5; Mitchellville, 1 mile W, 9; Oxon Hill, 6; River View, 1; sphagnum bog, near District line, 1. *Queen Annes County*: Parson Island, 1. *Washington County*: Fort Frederick State Park, 2. *Worcester County*: Ocean City, 3; Ocean City, 5 miles S, on Assateague Island, 3; West Ocean City, 4. *District of Columbia*: 83.

Remarks.—Schwarz and Schwarz (1943, pp. 59–72) reviewed the species and suggest that all house mice in the United States are referable to two commensal subspecies *M. m. brevisrostris* and *M. m. domesticus*, the latter being the one that supposedly occurs in Maryland. In all probability, however, house mice have been introduced into Maryland from many different areas and at many different times. The range of variation in size, tail length, and coloration in Maryland specimens is so great that I am unable to assign them a subspecific name.

Family ZAPODIDAE (jumping mice)

MEADOW JUMPING MOUSE

Zapus hudsonius americanus (Barton)

Dipus americanus Barton, Trans. Amer. Philos. Soc., 4: 115, 1799.

Type locality.—Schuylkill River, a few miles from Philadelphia, Pa.

General distribution.—Southeastern United States, east of central Indiana, and south of central New York, southward into northern Georgia.

Distribution in Maryland.—Occurs in all sections of the State.

Distinguishing characteristics.—Teeth 1/1, 0/0, 1/0, 3/3, = 18; upper incisors grooved; tail very long, blackish above, white below (not white tipped); hind legs greatly elongated; pelage short and coarse; coloration yellowish orange, suffused with blackish, the blackish particularly concentrated in the middorsal area and generally forming a rather broad band from nose to tail; coloration of underparts white, sometimes suffused with yellowish orange.

This mouse is readily distinguished from all other Maryland mice, except the woodland jumping mouse (*Napaeozapus insignis*), by its very long tail and powerful elongated hind legs. It is distinguishable from *Napaeozapus* by the presence of a premolar in the upper jaw, the absence of a white tail tip, and the more yellowish coloration (as opposed to orange in *Napaeozapus*) on the flanks.

Measurements.—Measurements of three adults from the vicinity of Seneca, Montgomery County, are as follows: Total length 195, 194, 194; tail 120, 110, 110; hind foot 26, 28, 28; ear 11, 10, 10; greatest length of skull 21.6, 22.0, 22.7; zygomatic breadth 10.5, 10.9, 10.6; interorbital breadth 4.2, 3.9, 4.0; length of maxillary toothrow 3.6, 3.7, 3.5.

Habitat and habits.—Kruttsch (1954, pp. 349–472) revised this genus, and gathered together its natural history data. Most of the following is based on his account.

The meadow jumping mouse inhabits thick vegetation, usually grasses or forbs, or both, in areas near running water. It is found both in woodland and farmland, but is most abundant in open moist areas. In Maryland, the species occurs throughout the State in suitable habitat, although nowhere does it seem particularly abundant, except perhaps on Assateague Island, where it is common in the mixed cord-grass and myrtle back of the ocean dunes.

The species is cyclical in abundance, being more numerous in some years than in others. It is ordinarily a nocturnal animal, appearing in the early dusk and remaining active until predawn. Occasionally, individuals will be active during daylight hours. Meadow jumping mice hibernate in the winter. It appears that it is necessary for this

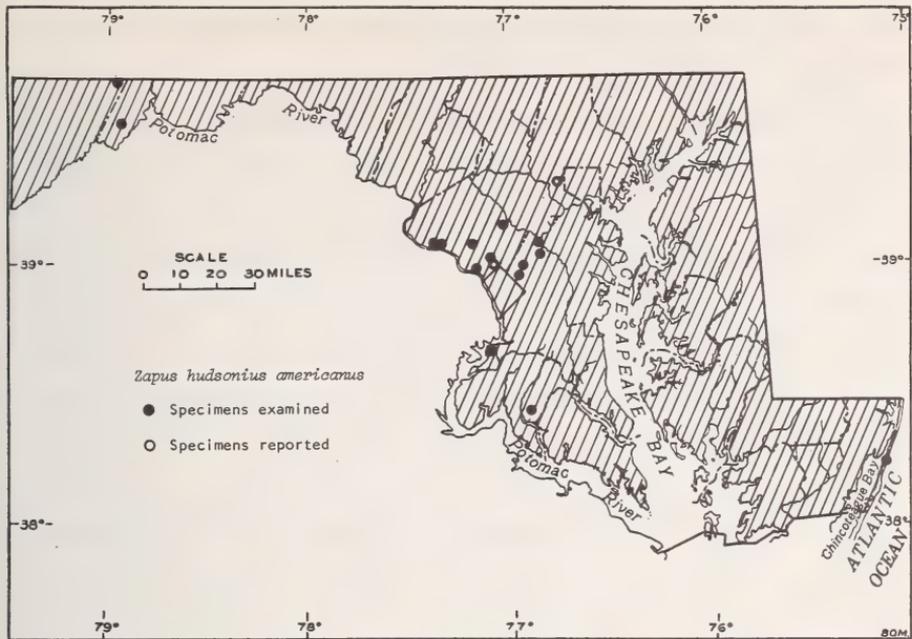


FIGURE 42.—Distribution of *Zapus hudsonius americanus*.

mouse to accumulate a certain amount of fat before it is capable of hibernation (Hamilton 1935, p. 193), and thus those taken in autumn are usually fat.

Almost invariably, meadow jumping mice hibernate in burrows in which nests are constructed of grass, leaves, or other vegetation. Grizzel (1949, pp. 74-75) found two of these animals hibernating in woodchuck dens at the Patuxent Research Center in January 1948. One animal was found 4 feet from the entrance to the burrow and about 40 inches below the surface of the ground. The second was found in another burrow 5 feet from the entrance and 26 inches below the surface. Both animals were curled up in the center of large leaf nests and well insulated from the cold.

In the vicinity of Washington, D.C., these mice remain active well into November, and emerge from hibernation in early April. In the Allegheny Mountain section, and the Ridge and Valley section, the hibernation period is more prolonged. Occasionally, during mild spells in midwinter they merge from their burrows and become active. Barbehenn tells me that he collected one jumping mouse in an old orchard with honeysuckle and poison-ivy ground cover near Rockville, Montgomery County, on 11 February 1960, in very mild weather.

During their active part of the year, meadow jumping mice wander freely and seldom make well-defined trails or runways. They con-

struct nests of grass and leaves under logs or occasionally in a clump of shrubs a few inches above the ground.

Krutzsch (1954, p. 428), citing various investigators, lists the following foods consumed by these mice: Insects, berries, seeds, nuts, fruits of various kinds, and roots. It has been noted that meadow jumping mice are highly insectivorous (Quimby, 1951, pp. 85-86).

According to Krutzsch (1954, p. 429), meadow jumping mice commence to breed shortly after they come out of hibernation, and the breeding season is prolonged until just before they reenter hibernation in the autumn. There are probably two litters produced each breeding season, and the number of young per litter varies from three to eight. Bailey (1923, p. 120) reported a specimen from Sandy Springs, Montgomery County, taken on 19 May 1906, that contained six large embryos. The gestation period is approximately 18 days.

Specimens examined.—*Allegheny County*: Dans Mountain, 1. *Charles County*: Marshall Hall, 1; Newport, 2. *Garrett County*: Cunningham Swamp, 4; Finzel, 1. *Montgomery County*: Cabin John Bridge, 2; Kensington, 1; Rockville, 2 miles W, 1; Sandy Springs, 2; Seneca 1/8 mile N, 1; Seneca, 3 miles W, 2. *Prince Georges County*: Branchville, 1; Laurel, 8; Patuxent Research Center, 2; Tuxedo, 1. *Worcester County*: Ocean City, 5 miles S (Assateague Island), 1. *District of Columbia*: 7.

Other records and reports.—*Baltimore County*: Patapsco State Park (Hampe, 1939, p. 7). *Montgomery County*: Forest Glen (one seen by G. S. Miller and reported by Bailey, 1896, p. 98). *Prince Georges County*: College Park (Krutzsch, 1954, p. 439).

Remarks.—According to Krutzsch (1954, p. 439), specimens from Maryland, Virginia, and North Carolina are more nearly average representatives of the subspecies *americanus* than are those from the region of the type locality.

WOODLAND JUMPING MOUSE

Napaeozapus insignis insignis (Miller)

Zapus insignis Miller, Amer. Nat., 25 : 742, August 1891.

Type locality.—Restigouch River, New Brunswick, Canada.

General distribution.—Eastern Canada, from Nova Scotia, New Brunswick, and Quebec south of St. Lawrence River, south into northeastern Ohio, northern West Virginia, and western Maryland.

Distribution in Maryland.—Allegheny Mountain section; may also occur in the Ridge and Valley section, but has not been reported from there as yet.

Distinguishing characteristics.—Teeth 1/1, 0/0, 0/0, 3/3, = 16; closely resembles the preceding species, but somewhat larger in size; coloration

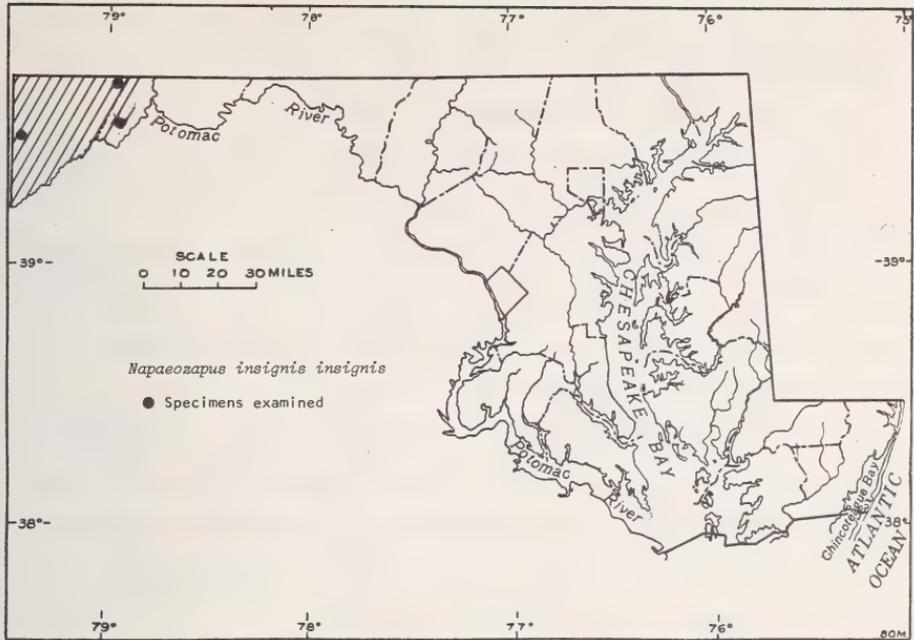


FIGURE 43.—Distribution of *Napaeozapus insignis insignis*.

similar to that of *Zapus*, but with a more brilliant orange on flanks tail grayish above, white below, with a distinct whitish tip; upper incisors grooved as in *Zapus*; only 3 molars present in maxillary, as opposed to 3 molar and 1 premolar in *Zapus*.

Measurements.—Measurements of six adults (Coll. U. Mich.) from 5 miles SE of Grantsville (alt. 2,500 ft.), Savage River State Forest, Garrett County, are as follows: Total length 223 (215–230); tail 134.7 (130–138); hind foot 30 (29–31); ear 16.2 (16–17); greatest length of skull 23.1 (22.2–23.7); zygomatic breadth 12.1 (11.8–12.3); interorbital breadth 4.5 (4.1–4.7); length of maxillary toothrow 3.6 (3.4–3.8).

Habitat and habits.—This species prefers the moist, cool forests where it is particularly abundant along the banks of mountain streams. One of the Maryland specimens was taken along Muddy Creek, near Swallow Falls, in a Rhododendron and hemlock forest which is typical woodland jumping mouse habitat. Handley and Patton (1947, p. 184) found that in Virginia they are most common at high altitudes among ferns, blackberry, and St.-Johns-wort in clearings surrounded by forest. The woodland jumping mouse is seldom found in open meadows, fields, or marshes where this is no heavy forest within close proximity.

This species makes no well-defined trails or runways, but utilizes the burrows of moles and larger shrews, or seeks shelter under rotting logs and fallen trees. Nests are usually placed several inches below

the ground and are made of leaves and dry grass. Sometimes the entrance to the nest is closed when the animal is in the burrow.

During the colder months of the year, woodland jumping mice hibernate, and their life processes are reduced to a minimum. In the autumn they eat heavily and accumulate large stores of fat on the body to carry them over the long period of hibernation. Their hibernation, deep and prolonged, is usually half of the year.

Hamilton (1941, pp. 260-261) lists the food of the woodland jumping mouse as insect larvae (particularly lepidopterous and dipterous forms), spiders, small soil worms, centipedes, various small invertebrates, small seeds, tiny nuts, small green leaves, blueberries, raspberries, and fragments of *Asplenium* fronds.

This species normally raises but one litter a year. The gestation period is between 20 and 23 days, and from two to six young, possibly eight, comprise a litter; the most frequent number appears to be five.

Specimens examined.—*Alleghany County*: Dans Mountain, 2. *Garrett County*: Finzel, 1; Grantsville, 5 miles SE (Savage River State Forest), 8 (Coll. U. Mich.); Muddy Greek Falls, 3 (Coll. U. Md.); Swallow Falls State Forest (along Muddy Creek), 1.

Remarks.—Although Preble (1899, p. 35) noted that the specimen he collected at Finzel showed no approach to *N. i. roanensis* (type locality: Roan Mountain, N.C.), it is my opinion that this specimen and one from Swallow Falls State Forest and eight from 5 miles SE of Grantsville show traits that are characteristic of *roanensis*. They are smaller in size and darker in coloration than typical *insignis*, and they appear to represent intergrades with *roanensis*. However, they are closer to *insignis* than *roanensis* in these characters and are herein assigned to the former subspecies.

Order CARNIVORA (flesh-eating mammals)

Family Canidae (dogs, foxes, etc.)

COYOTE

Canis latrans Say

Canis latrans Say, in Long, Account of an exped. . . . to the Rocky Mts. . . . , 1: 168, 1823).

Type locality.—Engineer Cantonment, about 12 miles southeast of the present town of Blair, Washington County, Nebr., on the west bank of the Missouri River.

General distribution.—Distributed primarily west of Mississippi River, from Alaska to Central America, with the center of population in the Great Plains of the United States. The species has recently been reported from a number of Eastern States, and apparently has been expanding its range eastward. Some of the eastern populations, however, may be derived from animals that escape from captivity, particularly those populations in Southern States.

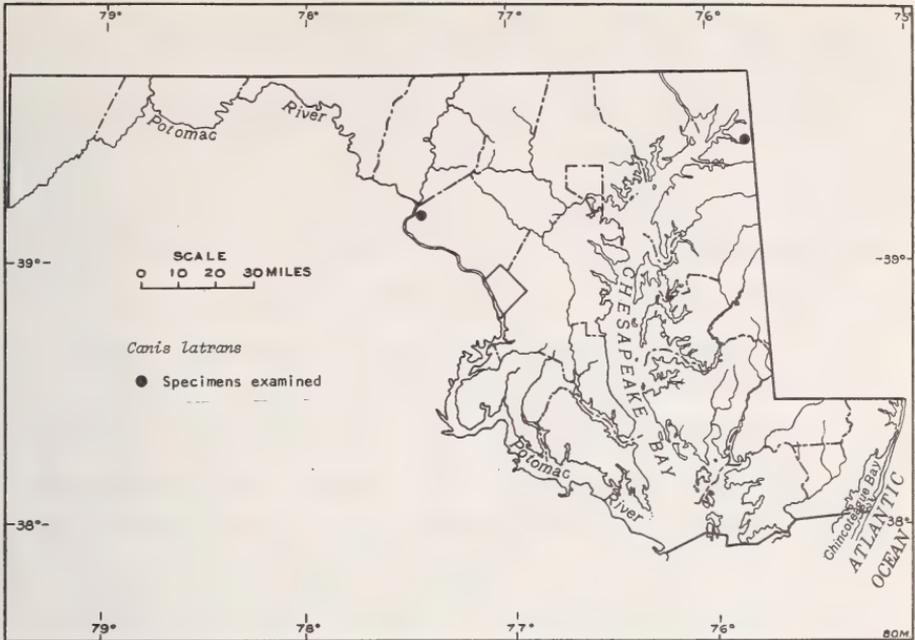


FIGURE 44.—Distribution of *Canis latrans*.

Distribution in Maryland.—May be expected anywhere in the State. See discussion in Remarks section.

Distinguishing characteristics.—Teeth 3/3, 1/1, 4/4, 2/3, = 42; closely resembles a small police dog, but with shorter legs, a bushier tail, and a more slender muzzle. Some feral dogs are so similar to coyotes that it is a difficult task for even an expert to distinguish them. The problem is further compounded because the coyote and dog may interbreed in the wild, although authentic reports of such crosses are scarce. There does not appear to be any certain way to distinguish coyote-dog hybrids from pure domestic dogs.

The coyote is grayish in coloration, and the dorsal hairs are tipped with black. There is a rusty or yellowish tint on the neck and along the sides, particularly on the flanks. The head is grizzled gray; the ears brownish. The feet are fulvous, and the throat and belly white. Since some domestic dogs may be similar to this in coloration, it is sometimes necessary to examine the skull to determine the species of the animal in question. The most important cranial difference between the two is that in the coyote the frontal region of the skull is always flattened, whereas in the dog it bulges to some degree. In some varieties of domestic dog this bulge is quite pronounced, in others it is less so, but it is generally more developed than in the coyote. The second most noticeable difference is found in the rostrum, which is slender and elongated

in the coyote and usually shorter and more blunt in the dog. In addition, the tips of the upper canines of the coyote fall below the level of the anterior mental foramina when the jaws are closed; in the dog they terminate above these foramina. The premolar teeth in the coyote are generally widely spaced; in the dog they are crowded. The ventral surface of the mandibular ramus is flattened in the coyote, whereas in the dog it is generally rounded. Various indexes have been developed to express numerically some of the above-mentioned cranial differences (see Howard, 1949, p. 171; Bee and Hall, 1951, pp. 73-77; Burt, 1946, pp. 61-62).

Certain specimens exhibit a confusing combination of dog and coyote characteristics. These animals may represent hybrids, but the characteristics of known hybrids have not been adequately documented. Until the problem of hybridization between the coyote and dog is thoroughly studied it seems advisable to refer any questionable specimens to the latter species. The domestic dog is one of the most variable animals with regard to its physical structure, whereas the coyote is a very uniform one (except for size). Because of this, it is possible for the domestic dog to exhibit some coyote traits without having any admixture of coyote blood, whereas it is far less likely that a coyote would exhibit dog traits without some dog intermixture.

In the field, the coyote at a distance may resemble a gray wolf (*Canis lupus*). The coyote, however, is much the smaller animal, has a more yellowish cast to the pelage, and carries its tail lower when running. The skull of the coyote is smaller than that of the gray wolf, and more lightly built; the teeth are much smaller, and the frontal region of the skull is flat, whereas in the gray wolf it is bulging as in the domestic dog.

Both the red fox and the gray fox are less doglike in general appearance than the coyote, and both are considerably smaller in size, and different in coloration.

Measurements.—Externally the coyote ranges in total length from 1,052 to 1,320 mm. with a tail varying from 300 to 394 mm. The hind foot averages between 177 and 220 mm. (Hall and Kelson, 1959, p. 843). Animals from southwestern localities are smaller than those from farther north, and males are larger than females.

A male from 5 miles northwest of Poolesville, Montgomery County, and a female from Cecil County, near the Delaware State line, west of Middlebury, Del., have the following cranial measurements: Condylbasal length 180.4, —; zygomatic breadth 99.8, 87.8; interorbital breadth 29.6, 31.5; length of maxillary toothrow 82.3, 78.7.

Habitat and habits.—The coyote prefers open or semiopen country. Young (Young and Jackson, 1951, p. 11) calls the coyote an "edge" animal, and believes that it has expanded its range as the forested

areas of the country vanished either through natural means such as forest fires or through manmade means such as logging etc. With the clearing of the land in the Northeastern United States, the coyote probably found habitat there to its liking, and has extended its range eastward.

The habits of the coyote are thoroughly discussed by Young and Jackson (pp. 47-105). The following is compiled primarily from their findings.

The home of the coyote is usually a den which it constructs on a bank or hillside, in wheat or corn fields, under houses, shacks, drainage pipes, or in hollow logs in thickets. Often the animal makes use of a fox or skunk den, enlarging it to suit its needs.

As a rule, coyotes do not mate for life, but some pairs may remain together for a number of years. There is evidence that the female may breed when she is 1 year of age. The breeding season is from February to March or April, being earlier apparently in northern than in southern latitudes (Hamlett, 1938). The gestation period is 60 to 63 days, and females have been known to deliver as many as 17 to 19 young, although 5 to 7 is the usual number.

Sperry (1941) examined the stomachs of 8,339 coyotes from western and midwestern localities and found that the principal food of the species is animal matter, of which more than 90% consists of mammals. In addition to carrion (25.1%), the chief mammals consumed are rabbits (33.2%), rodents (17.5%), domestic livestock (13.5%), big game mammals, principally deer (3.6%), and miscellaneous mammals such as skunks, badgers, weasels, shrews, moles, foxes, raccoons, cats, etc. (1%). Birds comprise some 2.9% of the coyote's diet, and other vertebrates 0.08%. Insects account for 1% of the diet, and vegetable matter, principally wild fruit and cultivated fruit, some 1.7%. These percentages vary according to seasonal availability.

Specimens examined.—*Cecil County*: Near Delaware line, west of Middletown, Delaware, 1. *Montgomery County*: Poolesville, 5 miles NW, 1.

Remarks.—The coyote has been reported from nearly all of the Eastern States. It is known that the species has been extending its range eastward. Probably the coyotes of our Northeastern States are a result of the natural expansion of the range of the species. On the other hand, coyotes have been introduced accidentally, or on purpose, into some of the Southeastern States, and present populations in those States may derive from these artificial introductions.

The first coyote discovered in Maryland was taken on 5 February 1921, on a farm 5 miles NW of Poolesville, Montgomery County. Jackson (1922, p. 187) in a discussion of this animal says:

The question naturally arises as to how a coyote reached this eastern locality. It is, of course, impossible to say definitely. The animal probably escaped from captivity. Or it may represent an extreme eastern extension of the geographic range of coyotes. There is no direct evidence for or against either of the suppositions. It is known that the range of the coyotes has gradually extended northward and eastward, but it would seem hardly probable that the species has, as yet, ingressed a region as far east as central Maryland.

The area in which this animal was taken was transversed by a major east-west arterial highway (U.S. Route 40) and it seems highly likely that the animal was brought into the area artificially. This view is supported by the fact that nearly 40 years elapsed before another coyote was discovered in Maryland. If the Montgomery County coyote really represented a southward or eastward extension of the range of the species, there probably would have been at least occasional reports of their presence in the State in later years. As it is, not until 21 April 1961 was another coyote discovered in Maryland. On this date, a coyote was shot in Cecil County near the Delaware border by employees of the Delaware Board of Game and Fish Commissioners. Here again, the area where the animal was shot is near a major east-west highway system and not very distant from the cities of Baltimore, Wilmington, and Philadelphia. It seems likely that the animal was brought east as a pet, and either was released or escaped from captivity. On the other hand, the increasing number of reports of coyotes from New England, New York, and other Northeastern States make it more probable now than it was 40 years ago that the species has reached Maryland in its natural range expansion. It is still, nevertheless, impossible to say definitely.

RED FOX

Vulpes vulpes fulva (Desmarest)

Canis fulvus Desmarest, Mammalogie . . . , pt. 1, p. 203, in Encyclopédie méthodique . . . 1820.

Type Locality.—Virginia.

General distribution.—Most of the Eastern United States, from southern Maine, southern Ontario and Wisconsin, south to Alabama, Georgia, and the Carolinas.

Distribution in Maryland.—Occurs in all sections of the State.

Distinguishing characteristics.—Dental formula as in *Canis*; similar in size and general characteristics to a small dog; nose sharply pointed; ears prominent and erect; tail long and bushy, fulvous, but strongly streaked with black, and always with a white tip; pelage long and soft; coloration rusty on face and occiput, usually mixed with whitish; upper parts colored bright yellowish red, or fulvous, darker on the median line, with the rump grizzled with whitish; cheeks, chin,

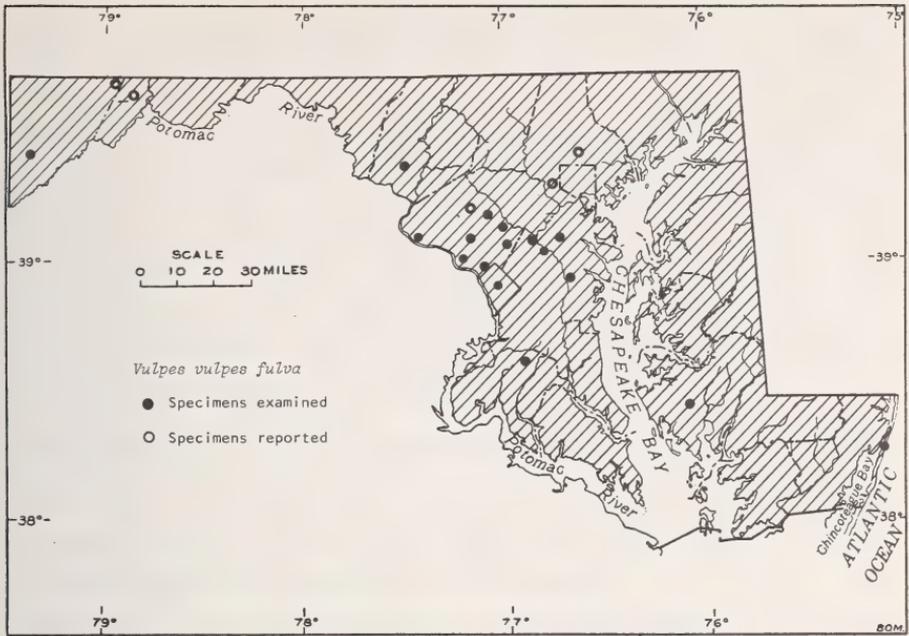


FIGURE 45.—Distribution of *Vulpes vulpes fulva*.

throat, and a band down the abdomen white; feet and outside of ears black.

Cranially, this fox differs from the gray fox (*Urocyon*) in that the temporal ridges enclose a narrow V on the top of the skull, whereas in the latter they are distinctly lyrate in shape; the upper incisors are lobed, in contrast to the unlobed condition in *Urocyon*.

Measurements.—Three adult males from Montgomery County have the following external measurements: Total length 1030, 1000, 995; tail 370, 372, 360; hind foot 170, 165, 160; ear 83, 86, 85. Cranial measurements of seven adults from Montgomery County are as follows: Basal length 139.7 (133.8–143.6); zygomatic breadth 72.0 (69.7–74.0); postorbital constriction 23.9 (22.0–28.8); alveolar length of upper maxillary tooththrow 61.8 (59.5–63.4).

Females average smaller than males in size.

Habitat and habits.—The red fox is cosmopolitan in its distribution, except that it is not generally found in dense forests and woods. It prefers rolling farmland, sparsely wooded areas, brushlands, and dense weed patches, usually in the vicinity of a stream or lake.

The species is now abundant in all sections of the State, although at one time it apparently was not found here. According to Mansueti (1950, pp. 27–28), the early American settlers hunted the gray fox (*Urocyon cinereoargenteus*). The Indians were unanimous in claiming that before the coming of the Europeans there were no red foxes

in the area. Sometime around 1650, red foxes were imported from England and released along the Eastern Shore of Maryland. These foxes apparently thrived and by the late 1670's had spread down the peninsula into Virginia. Today the species is widely distributed in Maryland, and is found even within the limits of metropolitan areas such as Baltimore and Washington, D.C. Whether the fox which now occurs throughout the State is the variety introduced by the English, or the native eastern North American form which has extended its range southward, will be discussed under the Remarks section.

The red fox is extremely abundant in some areas of the State. According to the League of Maryland Sportsmen (Rally Sheet 4(10), p. 6, December 1946) 79 were caught in a 5-week period at Mount Savage, Garrett County, in 1946. At the eastern end of the State on the outer barrier beach of Assateague Island, it is also abundant, and does some damage to nesting birds and their eggs. This species still roams in Rock Creek Park in the heart of Washington, D.C.

The food of the red fox varies from season to season. Llewellyn and Uhler, (1952, p. 198) found that in their Maryland sample, comprising mostly November, December, and January animals, 17 percent of the food was plant material consisting of fruits, berries, and other plant items. Persimmon, pokeberry, and wild grape were most often consumed, while in the fall beechnuts were heavily utilized. Apple, pear, and corn were eaten to a minor extent. The bulk of the red fox's food consists of animal foods, the most important part of which appears to be rabbit. Also consumed are rodents (meadow mice, muskrats, pine mice, gray and flying squirrels, house mice) and shrews. Birds and occasionally insects are eaten. In the spring and summer months the food consists of woodchucks, poultry, rabbits, small rodents, birds, snakes, turtles, eggs and varying amounts of vegetable matter particularly raspberries and blackberries. There is no question that red foxes prey to some extent on domestic livestock, particularly poultry when it is not properly housed. Sometimes red foxes may become quite bold. Vernon Bailey (unpublished report in files of U.S. Fish and Wildlife Service, 25 April 1936) tells of a pair raiding the henhouse of a farm in Brookville, Montgomery County; they were so bold that they often raided in broad daylight and took the hens before the eyes of their owners.

The red fox is monogamous and is believed to remain mated for life. The species is monestrous, with one season a year. Most matings take place in late January or February, and the gestation period is between 49 and 55 days. Litter size varies between one and eight, with four or five being the usual number.

The breeding or family den of the red fox is nearly always in a burrow, often that of a woodchuck, and is more often located in more

open land, such as a pasture, fence border, or cultivated field. Vernon Bailey (unpublished report, 1936) described one such den at Brookeville as follows:

The den had four openings, or doorways, 10, 15, and 20 feet apart, really the old doorways of a woodchuck den enlarged to fox size. Two opened out on each side of a big chestnut log, 3 or 4 feet in diameter. The burrows had been dug out by the foxes to about twice the diameter of the woodchuck burrows and enlarged to a comfortable fox nest room 20 feet back from the main entrance and 10 feet back from the other doorways. They ran 3 or 4 feet below the surface through hard clay full of rocks that necessitated many crooks and turns but ran uphill so the nest chamber was actually higher up than the actual doorway. All of the burrows centered at the nest, beyond which the original woodchuck burrow extended about 10 feet further but did not come to the surface.

There was no nest material in the nest chamber, but semidry earth made a comfortable bed for the young foxes with their dense woolly coats, and a uniform temperature that I should guess was around 55° F. gave them a healthy home in the den.

Both parents hunt for food to provide for the young. Bailey describes the food found in the den at Brookeville:

Much food had been brought into the den by the parent foxes. One white rooster had been all eaten but the wings and head and telltale feathers scattered around the doorway; one large house rat was lying near the doorway and two others were found in the nest chamber and parts of four others in the pantry, an excavation half full of food at one side of the upper entrance. It was about four feet below the surface and so cool that all of the meat was fresh though some of it several days old. From this were taken out part of a cottontail, half a crow, and a mouse.

Specimens examined.—*Anne Arundel County*: Fort George G. Meade, 1; Priest Bridge (near), 1. *Charles County*: Waldorf, 1. *Dorchester County*: Blackwater National Wildlife Refuge, 9. *Fredrick County*: Jefferson, 2. *Garrett County*: Oakland, 1. *Howard County*: no exact locality, 1. *Montgomery County*: Bethesda, 1; Brookeville, 1; Fairland, 1; Poolesville, 5 miles SW, 3; Potomac, 1; Rockville, 1; Sandy Spring, 1; no exact locality, 1. *Prince Georges County*: Laurel, 5; Patuxent Research Center, 4. *Worcester County*: Ocean City, 3 miles S (Assateague Island), 2. *District of Columbia*: 3.

Other records and reports.—*Allegany County*: Mount Savage (League of Maryland Sportsmen, Rally Sheet 4(10), p. 6, December 1946). *Baltimore County*: Loch Raven (Kolb, 1938); Patapsco State Park (Hampe, 1939, p. 6). *Garrett County*: Finzel (E. A. Preble in field report). *Montgomery County*: Laytonsville (rabid red fox reported in Washington Evening Star, 28 December 1956); Plummers Island (Goldman and Jackson, 1939, p. 132).

Remarks.—It is well established that the red fox was either scarce or did not occur in Maryland prior to the colonization of the State by Europeans. Churcher (1959, p. 514) states that "a red fox was native

to North American north of Lat. 40° N or 45° N, but was either scarce or absent from most of the unbroken mixed hardwood forests (to the south of this) where the gray fox was paramount."

The early Maryland colonists originally hunted the gray fox, but apparently at a very early date the European red fox was imported for hunting purposes and was released at various localities, one of which was the Eastern Shore. Since the red fox is now found throughout the whole of Maryland, as well as much of the Southeastern United States, the question arises whether these southern red foxes are the European variety or native North American red foxes which have extended their range southward.

Churcher (1959, pp. 513-520) has established that the European red fox and the North American red fox are subspecies of the same species *Vulpes vulpes*, the various subspecies intergrading in several major characters (shape of upper first molar, breadth of rostrum, development of sagittal crest) from western Europe, through Siberia, Alaska, Canada, to eastern North America. The two end products, the western European red fox and the eastern North American red fox are, however, quite different animals even if only subspecifically distinct. The European red fox is larger and has a more robust skull than its eastern American relative. It also has a shorter, broader rostrum, a relatively narrower interorbital region, and a well-developed sagittal crest which forms a distinct ridge along the top of the skull. In the native eastern American red fox the sagittal crest is occasionally developed but usually not into a conspicuous ridge. It narrowly diverges anteriorly into the temporal ridges which enclose a conspicuous V on the top of the skull. This conspicuous V formed by the temporal ridges is usually not as well developed, or is lacking, in the European form. The shape of the first upper molar also differs in the two subspecies. In the European variety this tooth is large and square in general outline, the buccal cingulum is rounded, the talon broad, and the mesial face convex. In the American form, the tooth gives the general appearance of being elongated laterally; the buccal face is deeply indented, the talon elongated, the mesial and distal faces concave, and there is a small protoconule.

All the Maryland red foxes (and those from farther south) that I have examined show the characters of the native eastern North American form, and there seems to be no indication of intermixture with European fox blood. In fact, Maryland specimens appear to be indistinguishable from those of Wisconsin, Michigan, southern Ontario, and New England, where I presume there was little or no importation of European stock by early colonists. It is possible that with the clearing of land in the Southeastern United States, the habitat became well suited to the native American red fox, which then invaded the area

from the north. The European red foxes, which may never really have been well established in the United States, were perhaps swamped by the influx of native American foxes and left no recognizable characteristics on the present fox population in Maryland or elsewhere in the Southeast.

GRAY FOX

Urocyon cinereoargenteus cinereoargenteus (Schreber)

Canis cinereo argenteus Schreber, Die Saugtheire . . ., Thiel 2, Heft 13, pl. 92, 1775.

Type locality.—Eastern North America.

General distribution.—Distributed from southern New York and Lower Peninsula of Michigan, south to South Carolina and Tennessee, west to eastern Illinois.

Distribution in Maryland.—Occurs in all sections of the State. It is more abundant, however, in the rolling hilly country of the Piedmont, Ridge and Valley, and Allegheny Mountain sections than in the low, flat, mashy country of the Eastern Shore section.

Distinguishing characteristics.—Dental formula as in *Canis*; coloration grizzled gray above with hairs banded with black and grayish white; inner sides of legs, sides of belly, neck, and band across chest reddish brown; belly and throat white; chin black; underfur soft and wooly, overlaid with short, coarse guard hairs; tail bushy, laterally compressed with a concealed mane of stiff black hairs on its upper side, near the base; legs short, feet equipped with well-curved claws that adapt the animal for climbing; skull with temporal ridges whose divergent branches enclose a lyrate area and never coalesce to form a distinct, sharp central sagittal crest.

This fox is somewhat smaller in size, has shorter legs, and is differently colored, than the red fox.

Measurements.—An adult male from Washington, D.C., has external measurements as follows: Total length 996; tail 356; hind foot 143; ear 71. The animal weighed 10½ lbs.

Six adults of both sexes from Laurel, Prince Georges County, have the following cranial measurements: Basal length 112.7 (110.8–114.0); zygomatic breadth 67.0 (63.0–70.8); interorbital breadth 24.9 (23.8–27.3); alveolar length of maxillary toothrow 51.6 (50.9–52.9).

There does not appear to be any appreciable size difference between the sexes.

Habitat and habits.—This animal is essentially a southern and western species that has apparently only recently invaded this northern portion of its range (Hamilton 1943, p. 176). It prefers timbered and rocky regions. Because of its relatively short legs, it has no great

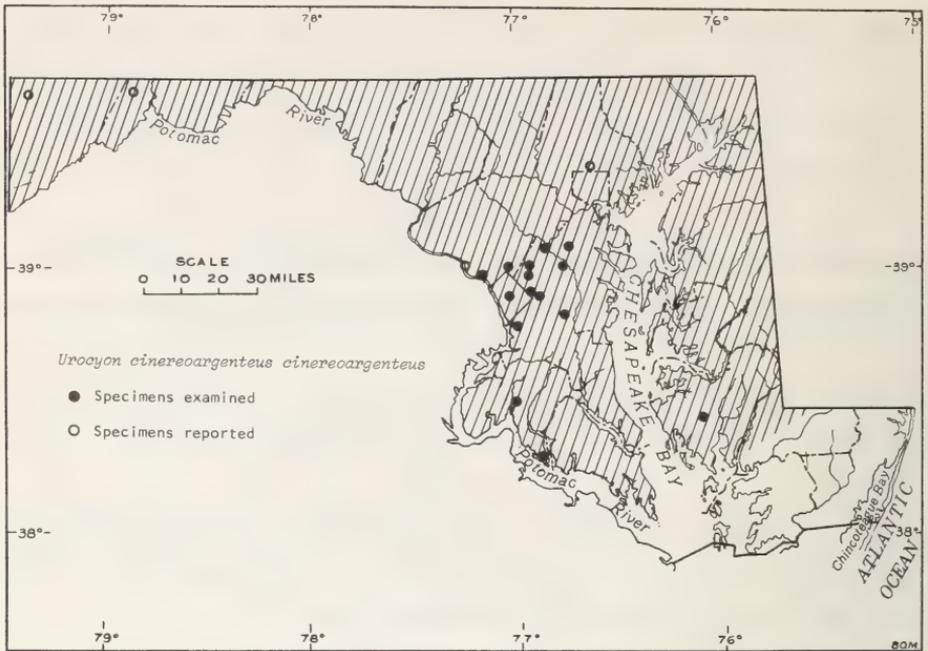


FIGURE 46.—Distribution of *Urocyon cinereoargenteus cinereoargenteus*.

speed and would perhaps have difficulty surviving in wide open areas. On the other hand, it is quite at home in the trees, being more arboreal than the red fox. For protection, it depends to some extent on rocky or brushy cover to which it can retreat, or forests where it can quickly climb a tree to escape a predator. Of 60 gray foxes trapped at the Patuxent Research Center, Prince Georges County, in the 1940's, the majority were taken in hedgerows and margins habitat, and most of the others in bottomland forests (Uhler and Llewellyn, 1952, p. 84).

This species selects a hollow tree or log for a den; occasionally it may use a burrow in the ground. It breeds but once a year, usually in February. Young are born from March to May and may number from two to seven, with the average being four. Both parents take part in caring for the young.

The food of the gray fox varies from season to season. Studies at the Patuxent Research Center (Llewellyn and Uhler, 1952, p. 199) indicate that in late fall and early winter approximately 30 percent of the gray fox's food is plant material, while about 70 percent is animal. Of the plant food consumed, persimmon was the most important item, while corn, pear, apple, and bechnut were also taken. Rodents were by far the most important animal food, but rabbits, birds, and insects were also consumed. Hamilton (1943, p. 177) lists rabbits as the most important food for the species. He also lists birds, small mammals,

particularly field mice, deer mice, wood rats, and shrews, snakes, turtles, and their eggs, lizards, insects, apples, beechnuts, corn, grapes, hickory nuts, persimmons, carrion, wild cherries, and grasses as additional food items.

The species is abundant in the Piedmont, Ridge and Valley, and Allegheny Mountain sections. Forty gray foxes were taken in only 5 weeks in 1946 at Mount Savage, Garrett County (League of Maryland Sportsmen, Rally Sheet 4(10), p. 6, December 1946). The species, however, is not abundant in the Eastern Shore section. In fact, the first gray fox ever taken on the Blackwater National Wildlife Refuge, Dorchester County, was obtained as late as 22 October 1943. Apparently much of the Eastern Shore section is too low, flat, and marshy for the animals' liking.

Specimens examined.—*Anne Arundel County*: Fort George G. Meade, 1. *Charles County*: La Plata, 1; Rock Point, 1. *Dorchester County*: Blackwater National Wildlife Refuge, 1 (baculum). *Montgomery County*: Plummers Island, 1; Silver Spring, 1. *Prince Georges County*: Beltsville, 1; Berwyn, 2; Landover, 1; Largo, 1; Laurel, 11; Marlboro, 1; Oxon Hill, 1; Patuxent Research Center, 11.

Other records and reports.—*Alleghany County*: Mount Savage (League of Maryland Sportsmen, Rally Sheet 4(10), p. 6, December 1946). *Montgomery County*: Cupids Bower (Bailey, 1923, p. 123.).

Family URSIDAE (bears)

BLACK BEAR

Ursus americanus Pallas

Ursus americanus Pallas, . . . Spicilegia zoologica, . . . fasc. 14: 5, 1780.

Type locality.—Eastern North America.

General distribution.—Wooded areas of North America, from Newfoundland to Alaska, and south into central Mexico.

Distribution in Maryland.—The black bear was once distributed throughout the State, but today is on the verge of extirpation and is found only in restricted areas in the Ridge and Valley and Allegheny Mountain sections.

Distinguishing characteristics.—Teeth 3/3, 1/1, 4/4, 2/3, = 42; largest wild mammal in Maryland; toes armed with strong claws; normal color both above and below black or very dark brown, except for cinnamon patch across muzzle and sometimes a white blotch on throat; pelage harsh and coarse. The black bear is so familiar as to scarcely need description.

Measurements.—"Total length, adult males, 1375 to 1780 mm. (54 to 70 in.); tail, 90 to 125 mm. (3.5 to 5 in.); hind foot, 215–280 mm.

(8.5 to 11 in.). Weight, adult males, 250 to 500 pounds, rarely 600 pounds or more, normally 300 to 400 pounds. Skull, adult males, length, 270 to 298 mm.; width, 158 to 185 mm. Total length, adult females, 1270 to 1475 mm. (50 to 58 in.); tail 80 to 115 mm. (3 to 4.5 in.); hind foot, 190 to 240 mm. (7.5 to 9.5 in.). Weight, adult females, 225 to 450 pounds. Skull, adult females, length 255 to 285 mm.; width, 148 to 172 mm." (Jackson, 1961, p. 313).

Habitat and habits.—The black bear prefers heavily wooded areas, and is now confined to the wildest and most inaccessible forests of the Allegheny Mountain section. Individuals may occasionally visit well-populated agricultural areas, but they usually do not remain in the neighborhood of humans for any length of time.

Except for females with cubs, the black bear is solitary in habits. It is nocturnal but usually does not wait until full darkness to venture forth; occasionally an individual may be seen abroad in the daytime. These bears remain dormant from about the end of November or early December until March or April, usually in a cavity dug under an overturned tree, most often at the roots. Sometimes other sites are chosen, such as a cave in rocks, a hollow tree, or dense thickets.

The female gives birth in January or February; the gestation period is about 225 days. One to five young may comprise a litter, but the usual number is two. Black bears normally breed only every other year.

The black bear is an omnivorous animal, consuming a wide variety of foods. It is especially fond of fruits and eats large quantities of blueberries, blackberries, strawberries, and raspberries. It also consumes quantities of mice, insects, and fish and occasionally will kill and devour sheep and pigs. In the autumn, when nuts are available, it feeds extensively on acorns and beechnuts. In addition, it will occasionally eat grass, roots, and fungi.

Remarks.—Mansueti (1950, pp. 14–16) has thoroughly investigated the former and present distribution of this species in Maryland. According to him, the black bear was at one time distributed throughout the State and was plentiful. Early settlers considered it the bane of their existence. Today the black bear still exists in restricted portions of the western part of the State, but in the past 2 or 3 decades it has been on the verge of extinction. A 1937 report by the U.S. Bureau of Biological Survey (Big-Game Inventory of the United States, 1937, Wildlife Research and Management Leaflet BS-122, January 1939) placed the total number of bears in Maryland at 150. The 1938 summary (Big-Game Inventory of the United States, 1938, U.S. Bureau of Biological Survey, Wildlife Leaflet BS-142, August 1939) placed the number at 50. By 1946 (Big-Game Inventory of the United States, 1946, U.S. Fish and Wildlife Service, Wildlife Leaflet

303, March 1948) the estimate was down to 25; in 1951 (Inventory of Big-Game Animals of the United States, 1950 and 1951, U.S. Fish and Wildlife Service, Wildlife Leaflet 342, October 1952) to 20; and by 1956 to 12.

Bears are still occasionally seen in Allegany and Garrett Counties. Théodore A. Bookhout, formerly with the University of Maryland's Natural Resources Institute, has informed me of several recent sightings. In the fall of 1963, one was seen near Murley's Branch, a few miles south of Flintstone, Allegany County; in October 1963, one was seen on Maryland Route 55, approximately 2 miles north of Corriganville, Allegany County; on January 3, 1964, bear tracks were seen on Wagner Road just north of Oldtown, Allegany County.

As Mansueti (1950, p. 16) notes, however, western Maryland is becoming more densely populated and the extensive forests are being laid waste, and the black bear will disappear mainly because it is unwanted. At most it will remain in only the most remote and inaccessible of Maryland wildlife sanctuaries.

Family PROCYONIDAE (raccoons, coatis, etc.)

RACCOON

Procyon lotor lotor (Linnaeus)

[*Ursus*] *lotor* Linnaeus, Syst. nat., ed. 10, 1: 48, 1758.

Procyon lotor maritimus Dozier, J. Mammal., 29(3): 286, August 1948. (Type locality: Blackwater National Wildlife Refuge, Dorchester County, Md.)

Type locality.—Pennsylvania (fixed by Thomas, Proc. Zool. Soc. London, p. 140, March 1911).

General distribution.—"Nova Scotia, southern New Brunswick, southern Quebec, and southern Ontario, south through the eastern United States to North Carolina from the Atlantic coast west to Lake Michigan, Indiana, southern Illinois, western Kentucky and probably eastern Tennessee." (Goldman, 1950, p. 33.)

Distribution in Maryland.—Common in all sections of the State, but particularly abundant in the Eastern Shore section.

Distinguishing characteristics.—Teeth 3/3, 1/1, 4/4, 2/2, = 40; size medium; form robust; fur long and coarse; coloration of upper parts grizzled gray, brownish, and blackish, there being considerable individual variation; sides paler than upper parts; under parts dull grayish brown, tinged with yellowish gray or white; black band, or mask, extends through eyes and across cheeks; remainder of face yellowish gray; tail alternately banded brownish gray or blackish and yellow, with five to seven dark rings, always terminating in a dark band.

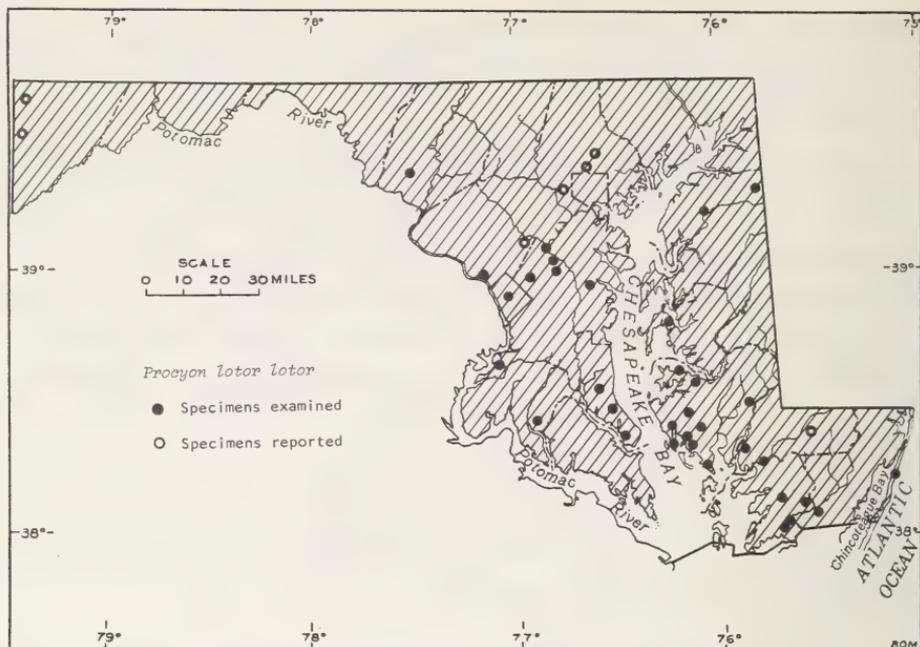


FIGURE 47.—Distribution of *Procyon lotor lotor*.

The raccoon is easily distinguished from all other Maryland mammals by the dark facial mask and the long-haired tail ringed with black and yellow.

Measurements.—External and cranial measurements of four adult females from the Blackwater National Wildlife Refuge, Dorchester County, are: Total length 749.5 (718–762); tail 236.7 (210–254); hind foot 108 (102–114); condylobasal length of skull 110.9 (107.1–114.2); zygomatic breadth 67.1 (62.7–69.7); postorbital breadth 23.3 (22.5–23.8); length of maxillary toothrow 41.3 (39.9–43.8); breadth of rostrum at incisors 23.7 (23.1–24.2). External measurements of three and cranial measurements of four adult males are: Total length 736, 736, 762; tail 229, 229, 254; hind foot 102, 102, 102; condylobasal length of skull 114.1 (110.9–117.9); zygomatic breadth 67.4 (64.9–69.9); postorbital breadth 22.5 (21.0–24.7); upper maxillary toothrow 26.1 (25.3–26.5).

Three adult males and three adult females from Laurel, Prince Georges County, measure cranially: Condylobasal length 109.6, 112.7, 111.7, 106.3, 104.4, 108.8; zygomatic breadth 67.4, 67.8, 74.9, 67.7, 68.4, 65.1; postpalatal breadth 24.2, 22.1, 23.5, 22.1, 22.4, 23.2; length of maxillary toothrow 40.9, 41.6, 41.1, 40.7, 39.0, 40.1; breadth of rostrum at incisors 25.6, 25.1, 26.1, 23.5, 22.5, 22.8.

Habitat and habits.—The raccoon is cosmopolitan in habitat preference, being found in woods, swamps, and marshes, including salt-

water marshes of the Atlantic barrier beaches. Uhler and Llewellyn (1952, p. 83) report that at the Patuxent Research Center, near Laurel, Prince Georges County, the outstanding habitat type was bottomland forest, followed by cultivated fields (mainly those with corn), hedge rows and wood margins, particularly if leading to cornfields. Raccoons were also abundant around marshy lake borders and in swamps.

The raccoon is a very adept climber. Although it usually makes its home in a hollow tree, it sometimes will utilize a fissure in a cliff, or a hole among rocks. Raccoons rapidly diminish in numbers when trees are cut over, and will either die off or leave the area after all the trees are gone.

The raccoon is nocturnal, and forages for its food after sunset. Its diet consists of fish, crayfish, frogs, and mussels, as well as poultry, mice, birds, eggs, reptiles, and insects. In season, it eats considerable amounts of vegetable matter such as nuts, fruits, berries, and corn.

In more northern climates the raccoon hibernates, but in Maryland it remains active the year round except in the coldest portions of the western part of the State. The species breeds in January and February, and some 63 days later females give birth to two to six young. The cubs are born blind and remain so for about 19 days; they suckle for 2 months, and remain in the family circle through the winter.

Remarks.—Maryland raccoons differ in no significant way from Pennsylvania and New York specimens. Dozier (1948a, p. 286) separated the raccoons inhabiting the marshes of the Delmarva Peninsula from those living in the surrounding woods as a distinct subspecies, *Procyon lotor maritimus*. I have examined the type of this race, as well as the series designated by Dozier as representing it, and am unable to separate it from raccoons inhabiting other parts of Maryland. All the diagnostic characters mentioned by Dozier (paler coloration; longer but more sparse guard hairs; much smaller size; shorter, more pointed and less prominently banded tail; relatively shorter caudal vertebrae; smaller and more distinctly curved baculum; and various cranial characters) are either within the limits of individual variation of *P. l. lotor*, or are so slightly marked that I have been unable to distinguish them. Consequently, I consider *Procyon lotor maritimus* Dozier to be a synonym of *Procyon lotor lotor* (Linnaeus).

Specimens examined.—*Anne Arundel County*: Rutland, 1. *Calvert County*: Prince Frederick, 1; St. Leonard (near), 1; Sollers, 9. *Charles County*: Marshall Hall, 1; Newport, 1. *Dorchester County*: Blackwater National Wildlife Refuge, 69; Cambridge, 1; Castlehaven Point, 3; Crapo, 1; Crocheron, 1; Golden Hill, 2; House Point, 11; Kirwan's Neck, 2; Meekins Neck, 1; Punch Island, 6; Robbins (near), 1; Shorters Wharf, 1; Vienna, 1; Worlds End Creek, 1. *Frederick*

County: Jefferson, 2. Kent County: Chestertown, 2; Millington (4 miles NE), 1. Montgomery County: Cabin John, 1. Prince Georges County: Bowie, 1; Branchville, 1; Laurel, 39; Patuxent Research Center, 4. Somerset County: Cokesbury, 4; Marumsco, 3; Rehoboth (near), 2; Westover, 2; Whitehaven (across Wicomico River from), 3. Talbot County: St. Michaels, 1. Wicomico County: Bivalve (near), 1; Whitehaven, 1. Worcester County: Assateague Island, 1; Pocomoke City (vicinity), 17. District of Columbia: 1.

Other records and reports.—Baltimore County: Bare Hills–Lake Roland area (Bures, 1948, p. 66); Loch Raven (Kolb, 1938); Patapsco State Park (Hampe, 1939, p. 5). Garrett County: Blooming Rose (Browing, 1928, p. 26); Cranesville Pine Swamp (Mansueti, 1958, p. 83). Montgomery County: Burtonsville (Herman et al., 1957, p. 113–114); Plummers Island (Goldman and Jackson, 1939, p. 132). Wicomico County: Salisbury, a few miles east (Kilham and Herman 1955, p. 499).

Family MUSTELIDAE (weasels, skunks, otters, etc.)

ERMINE

Mustela erminea cicognanii Bonaparte

Mustela cicognanii [sic] Bonaparte, Charlesworth's Mag. Nat. Hist., 2: 37, 1838.

Type locality.—Eastern United States.

General distribution.—Southeastern Ontario, southern Quebec, and Maine, south through extreme northeastern Ohio and Pennsylvania into Maryland.

Distribution in Maryland.—Probably very rare in the Allegheny Mountain, Ridge and Valley, and Piedmont sections, and absent from the Western Shore and Eastern Shore sections. The species is most numerous in the coniferous forests of the northern portion of its range, but even in the north it is uncommon in coastal regions and consequently it probably does not occur in Maryland's coastal plain. It has been reported from the State only once.

Distinguishing characteristics.—Teeth 3/3, 1/1, 3/3, 1/2, = 34; size medium; body long and slender; legs short; tail moderately short, averaging about 35 percent of head and body length, well haired and slightly bushy, tipped with black above and below; coloration of upper parts in summer dark brown extending to the outer parts of the legs and feet; color of underparts whitish, usually tinged with yellow; winter coloration white except for tip of tail which remains black.

This species resembles the long-tailed weasel (*Mustela frenata*) in general appearance and in coloration, but is considerably smaller, and shorter tailed. When using size as a criterion in separating the two species, it is necessary to take into account the sex of the individual.

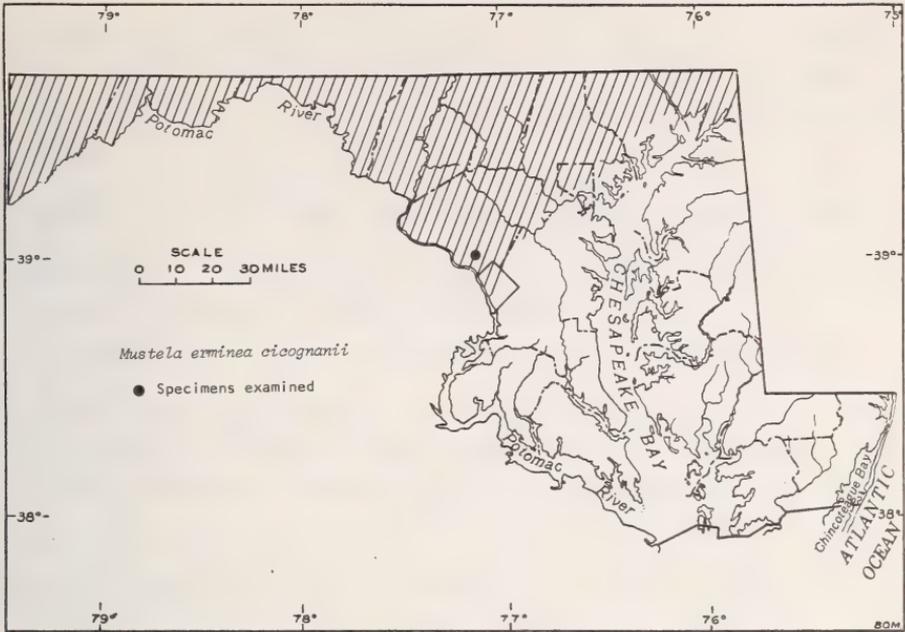


FIGURE 48.—Distribution of *Mustela erminea cicognanii*.

Male and female long-tailed weasels are larger than male and female ermines, but since the males in both species are larger than the females, a large male ermine may approach in size a small female long-tailed weasel.

Measurements.—Hall (1951, p. 119) gives the averages and extremes of external measurements of seven adult and subadult males from New York and Pennsylvania as follows: Total length 266 (240–295); length of tail 74 (66–80); length of hind foot 36 (33–39). He gives the external measurements of 12 adult and subadult females from Maine and the area south to central Pennsylvania as: Total length 243 (225–260); length of tail 63 (55–72); length of hind foot 29.8 (26–32).

Some cranial measurements given by Hall (1951, pp. 434–435) of nine adult and subadult males from New York and Pennsylvania are: Basilar length (of Hensel) 35.7 (33.8–37.6); zygomatic breadth 20.3 (19.0–20.6); interorbital breadth 8.6 (7.7–8.9); mastoidal breadth 18.2 (17.3–18.8). Four adult and subadult females from New York and Pennsylvania measure cranially: Basilar length (of Hensel) 32.4 (31.4–33.3); zygomatic breadth —, —, 17.5, 18.0; interorbital breadth 7.5 (7.2–7.8); mastoidal breadth 15.7 (average of 3, 15.3–16.0).

Vasquez (1956, p. 114), who collected the only Maryland record of this species, says that no external measurements are available for the specimen, but he does give the following cranial measurements for the female: Condylbasal length 38.1; basilar length (of Hensel) 34.3; mastoidal breadth 17.1; depth of skull at first molars 9.1.

Habitat and habits.—This animal is most abundant in the northern United States and Canada where it inhabits the deep spruce stands. In the southern part of its range it is often encountered in brushy fields and hedgegroves, and it is particularly fond of stone walls, where it can elude its enemies and catch the small mammals and birds which form its prey.

This weasel generally does not make its own home, but prefers to occupy the chambers of some other mammal, most often a chipmunk's cavity beneath a stump or pile of rocks. Its nest is composed of fur and feathers from the animals on which it feeds.

According to Hamilton (1943, p. 136) all the evidence suggests that these weasels mate in the early summer, and the fertilized eggs, after undergoing a short development remain quiescent for several months. Embryonic development continues in the late winter, and the four to nine young are born usually in mid-April. Hamilton states that the male weasel assists in bringing food to the young during their infancy and that there is much evidence that weasels remain paired throughout the year.

Hamilton (1933b, p. 333) reports fall and winter food of 191 ermine in New York State as composed of the following: Meadow mice 35.7 percent; undetermined mammals (principally mice) 16.3 percent; short-tailed shrews 15.1 percent; white-footed mice 11.4 percent; rabbits 9.0 percent; long-tailed shrews 4.9 percent; rats 4.4 percent; and chipmunks 3.6 percent. In addition, birds comprised some 2.1 percent, and reptiles and amphibians 1.2 percent of the fall and winter food of weasels (354 *Mustela erminea* and *Mustela frenata*).

Remarks.—This species has been recorded only once from Maryland. Vazquez (1956, pp. 113–114) reports that a cat killed an ermine on the heavily wooded grounds of the Honeywell School, 4 miles northwest of Bethesda, Montgomery County, on 27 May 1954. Prior to this, Maryland was considered far south of the normal range of the ermine, and it is possible that the animal escaped from captivity. Vazquez states that the coloration is peculiarly grayish, and that its cranial measurements are slightly larger than those of female *Mustela erminea cicognanii* and approach those of males of this race. The skin and skull of the specimen are in Vazquez' private collection and I have not examined them.

LONG-TAILED WEASEL

Mustela frenata noveboracensis (Emmons)

Putorius Noveboracensis Emmons, a report on the quadrupeds of Massachusetts, p. 45, 1840.

Type locality.—Williamstown, Berkshire County, Mass.

General distribution.—From Wisconsin east through Michigan, southwestern Ontario, southern Quebec, and southeastern Maine, south through the eastern United States to North Carolina, western South Carolina, northern Georgia, and Alabama, west to the Mississippi and St. Croix Rivers.

Distribution in Maryland.—Occurs in all sections of the State.

Distinguishing characteristics.—A large weasel, similar in coloration and general appearance to the ermine, but larger and with a longer tail. It is generally believed that except in the coldest portions of the Allegheny Mountain section, most Maryland long-tailed weasels remain in brown pelage the year round, and the majority of winter-killed specimens from Maryland that I have examined are in brown pelage. There is, however, one male from Gaithersburg, Montgomery County, and another from Patuxent, Prince Georges County, in the National collections that are entirely white except for the customary black tail tip.

Male long-tailed weasels are strikingly larger than females. So pronounced is this secondary sexual trait that some early writers

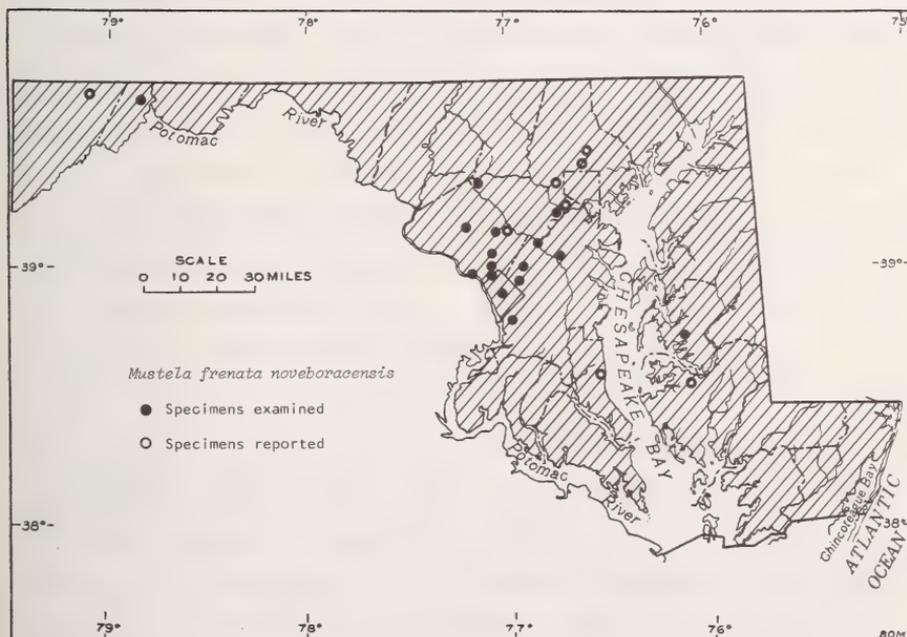


FIGURE 49.—Distribution of *Mustela frenata noveboracensis*.

thought the two sexes must represent distinct species. Since the female long-tailed weasel is so small, it is possible to mistake her for an ermine, and due allowance must be made for sex when separating these species on the basis of size.

Measurements.—External measurements of 12 adult males from various parts of Maryland are: Total length 382 (340–429); tail 131.6 (110–155); hind foot 48 (34–48). Seven females from various parts of the State have the following external measurements. Total length 286.6 (253–315); tail 93.1 (80–122); hind foot 34 (32–38).

Cranial measurements of 10 adult males from Laurel, Prince Georges County, are: Basilar length 42.7 (40.8–44.3); zygomatic breadth 25.6 (23.5–27.3); interorbital breadth 9.8 (9.0–10.8); mastoidal breadth 22.4 (21.4–24.0). Cranial measurements of three adult females from Laurel are: Basilar length 36.1, 36.4, 36.5; zygomatic breadth 21.5, 21.7, —; interorbital breadth 7.9, 9.1, 9.1; mastoidal breadth 18.9, 19.0, 18.2.

Habitat and habits.—This weasel prefers bushy field borders, brushland, open woodland, and woodland bordering cultivated fields and pastures. It is quite adaptable and willing to live in close proximity to man as long as suitable prey is available. Recently, I found one dead on a road in the middle of Kensington, Montgomery County, where the only suitable habitat for some distance was the bushy area bordering a railroad track that runs through the center of town. Uhler and Llewellyn (1952, p. 81) report that during a study made at the Patuxent Research Center in Prince Georges County, only four weasels were taken in three trapping seasons. Of these, two were taken along hedgerows, one in upland forest, and one along the Patuxent River. In the Bare Hills–Lake Roland area, Bures (1948, p. 66) thought these weasels were quite rare at first. Subsequent investigation revealed, however, that they were more common than he suspected, and that they range throughout the area except for the marsh and Serpentine. He says that they seem to use the railroad right-of-way as a natural highway regularly; their mortality rate was high there, since an average of four specimens a year were recorded killed by passing trains. In an area as small as that in which Bures was working, this is a high number of weasels.

This species generally does not make its own burrow, but uses an abandoned one of a chipmunk or mole. Sometimes it will utilize a hole among rocks or under a stump. The nest center is usually filled with grass and lined with fur and feathers from the weasel's prey.

Mating in this species occurs in July and August. The gestation period is very prolonged, averaging about 279 days, but as in the ermine, the embryo remains quiescent throughout most of this period and only begins to develop rapidly during the last 27 days. The young,

numbering between six and eight, are born from mid-April to mid-May. Hamilton (1933b, p. 328) states that the male stays with the female and assists in caring for the young. He says that he has several times seen a male of this species carrying food to a den of young ones.

Like the ermine, the long-tailed weasel is strictly carnivorous in diet. Hamilton (1933b, p. 333) lists the percentages of fall and winter food of this species in New York State as follows: Meadow mice 33.6; cottontail rabbits 17.3; white footed mice 11.3; rats 9.1; short-tailed shrews 5.9; squirrels 2.7; chipmunks 1.0; star-nosed moles 0.8; muskrat 0.8. In addition to this, a small percentage of birds and reptiles is consumed.

Specimens examined.—*Allegheny County*: Piney Mountain, 2 (Coll. U. Md.). *Anne Arundel County*: Patuxent (2 miles S), 1. *Howard County*: Hanover, 1; Long Corner, 1. *Montgomery County*: Bethesda, 1; Chevy Chase, 1; Foxhall Village (D.C.? not located in Maryland), 1; Gaithersburg, 1; Garrett Park, 1; Kensington, 1; Linden, 1; Olney, 1; Plummers Island, 3. *Prince Georges County*: Andrews Air Force Base (near), 1; Bladensburg, 1; Branchville, 1; Laurel, 17; Oxen Hill, 1. *Talbot County*: Easton, 1. *District of Columbia*: 8.

Other records and reports.—*Baltimore County*: Bare Hills—Lake Roland area (Bures, 1948, p. 66); Halethorpe (Hampe, 1943, p. 66); Loch Raven (Seibert, 1939, p. 21); Patapsco State Park (Hampe, 1938, p. 6). *Calvert County*: Plum Point (identified from photograph submitted by John F. Fales). *Dorchester County*: Cambridge (five specimens in collection of R. W. Jackson, examined by Hall, 1951, p. 228). *Garrett County*: Grantsville (E. A. Preble, in field notes, mentions seeing one, June 1899). *Montgomery County*: Sandy Spring (Bailey, 1923, p. 126).

(LEAST WEASEL)

Mustela nivalis allegheniensis (Rhoads)

Putorius allegheniensis Rhoads, Proc. Acad. Nat. Sci. Philadelphia, 52: 751, 25 March 1901.

Type locality.—Near Beallsville, Washington County, Pa.

General distribution.—From Wisconsin and northern Illinois eastward through northern Indiana, Michigan, and Ohio into southwestern New York and Pennsylvania, thence southward in the Appalachians to North Carolina.

Distribution in Maryland.—This species has not been recorded as yet from Maryland, but it has been taken in nearby Pennsylvania, West Virginia, and Virginia, and probably ranges through the Allegheny Mountain section of Maryland and possibly in the Ridge and Valley section as well.

Distinguishing characteristics.—A very small weasel, similar to both *M. frenata* and *M. erminea* in coloration and general form, but

considerably smaller than either. It may readily be distinguished from both these species by its very short tail and the complete lack of a black tail tip.

Measurements.—"Male: An adult or subadult from Fair Oaks, Pa., a subadult from Finleyville, Pa., and an adult from Huttonsville, W. Va., measure respectively as follows: Total length, 206, 194, 191 (average 197); length of tail, 37, 32, 28 (32); length of hind foot, 23 in each.

"Female: Two young from Leasuresville, Pa., and Middle Paxton Twp., Pa., measure respectively, as follows: total length, 188, 172; length of tail, 33, 30; length of hind foot, 20.5, 21." (Hall, 1951, p. 187-188.)

Some of the cranial measurements listed by Hall (1951, p. 440-441) of an adult male from Huttonsville, W. Va., and an adult female from Beallsville, Pa., are Basilar length (of Hensel) 28.5, 28.0, zygomatic breadth 16.7, 14.6; interorbital breadth 7.1, 6.2; mastoidal breadth 15.1, 13.5.

Habitat and habits.—This species inhabits both the deep forests and the fields and pastures within its range. It is a rare mammal however, and is seldom encountered.

Little is known of its habits. Hamilton (1943, p. 139) says that nests have been found beneath corn shocks, in shallow burrows bordering streams, and in similar places. The few nests that have been discovered were composed of grasses and mouse fur. Hamilton states that the breeding habits of this species apparently differ from those of its larger relatives. He says that young with unopened eyes have been discovered in midwinter, while nest young and lactating females have been found in Pennsylvania during October, January, and February. These litters numbered from three to six young. The female parent was always in attendance. From this he says that the young are probably born at various seasons and there is a likelihood of more than one litter a year.

Hall (1951, p. 177) says that food of the least weasel consists of harvest mice, deer mice, meadow mice, red-backed mice, and possibly insects.

MINK

Mustela vison mink Peale and Palisot de Beauvois

Mustela mink Peale and Palisot de Beauvois. A scientific and descriptive catalogue of Peal's museum, Philadelphia, p. 39, 1796.

Type locality.—Maryland.

General distribution.—Eastern United States from southeastern Maine, south to coastal North Carolina, and inland (excepting the higher elevations of the Appalachians) through Pennsylvania, Michigan, Georgia, and Alabama to Missouri.

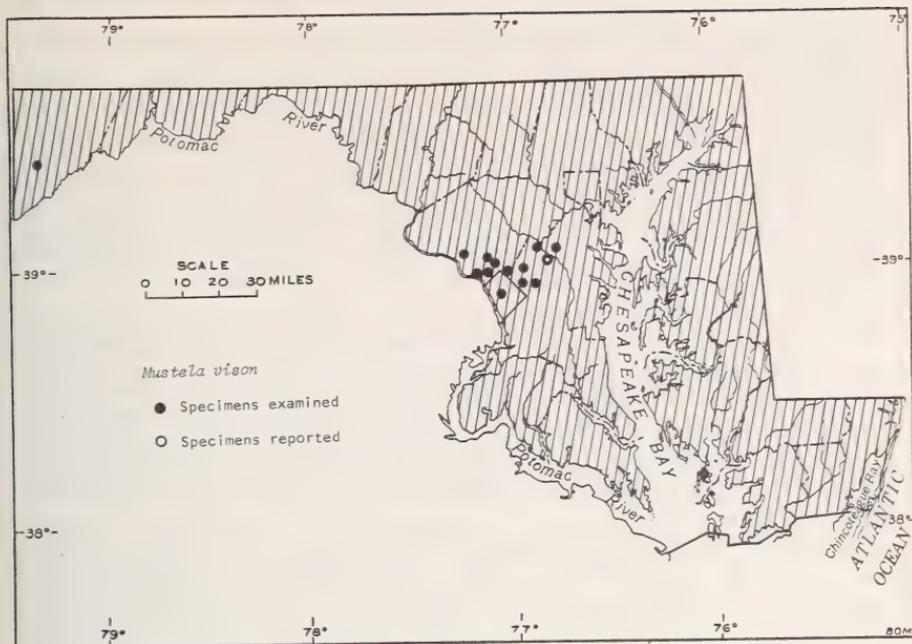


FIGURE 50.—Distribution of *Mustela vison*.

Distribution in Maryland.—The species is Statewide in distribution; the subspecies *mink* occurs throughout most of Maryland, but may be replaced by the race *vison* at higher elevations in the Allegheny Mountain section. This very dark northern race, *vison*, has been reported in the Appalachians to the south of Maryland (Kellogg, 1939, p. 262), but the only specimen available from the Allegheny Mountain section of Maryland is a zoo animal and its subspecific affinities are indeterminate.

Distinguishing characteristics.—A very large weasel, with a fairly long, bushy tail; coloration dark glossy brown over entire body, except for a whitish chin spot and an occasional white streak on the neck or white spot on the chest or belly; pelage thick and dense, adapted for an aquatic life.

The mink may distinguished from the long-tailed weasel by its larger size, and absence of a white belly. It is similar to an otter in coloration, but is smaller and does not have a broad-based tail.

Measurements.—Males considerably larger than females. A typical adult male and female from Montgomery County have the following external and cranial measurements: Total length 650, 547; tail 225, 193, hind foot 70, 54; basilar length 62.4, 56.0; zygomatic breadth 42.1, 36.3; interorbital breadth 12.9, 13.7; mastoidal breadth 34.4, 30.5.

Habitat and habits.—The mink always lives near water. It is found around lakes, in or near marshes, and along the banks of rivers or

streams. It prefers forested, log-strewn, and bushy areas. At the Patuxent Wildlife Research Center near Laurel, Prince Georges County, Uhler and Llewellyn (1952, p. 84) found them along lake margins, by a small stream, and along the Patuxent River. Bailey (1923, p. 125) reported that in the early 1920's they were fairly common along the banks of almost any stream in Washington, D.C., and that they followed Rock Creek well down into the city. Today, owing to stream pollution and other factors few, if any, mink occur along Rock Creek in Washington.

Mink make their home under large trees which line banks of streams along which they live. They also inhabit muskrat lodges or natural cavities along the banks of streams, rivers, lakes, or marshes. Males and females build separate nests, but females build more elaborate ones, lining them with grass, feathers, and fur to make a snug home for the young.

The breeding season for mink begins in January and extends through March; the gestation period is variable, from 39 to 76 days, depending on when mating has occurred; the later the mating, the shorter the gestation period. Three to six young are born in April or May, but as many as 10 have been reported.

Mink range over a wide area to procure their food, which consists of any reptiles, amphibians, small mammals, and birds obtainable. In areas where muskrat abound, such as the muskrat marshes of the Delmarva Peninsula, mink may feed extensively on them. Llewellyn and Uhler (1952, p. 199), in studies conducted at the Patuxent Research Center, report that it is usually difficult to get food-habits material from trapped mink since their digestion is so rapid. They state that frequently stomachs of the animals studied were empty, and only digested blood was found in the intestines. They were only able to obtain six stomachs and four scats suitable for tabulation. In none of these was there any plant food except for a few poison-ivy seeds which were found in a stomach that contained flicker remains. Presumably the bird had eaten these seeds before being captured by the mink. One mink sample in March and another in December contained rabbit hair only. Five other winter samples had 100 percent rodent remains consisting of one meadow mouse, three pine mice, and one "wood" mouse. In the two additional stomachs examined by Llewellyn and Uhler, one contained flicker remains and the other had a beetle fragment.

The mink sometimes does considerable damage to poultry. Bailey (1923, p. 125) says that he was told of a mink in the Washington area that visited a henhouse and killed 22 chickens in one night and returned the next night to kill 16 more. The following night, as the mink was returning to the henhouse again, it was caught by a dog.

Despite the great number being bred in captivity, wild-caught mink are still in some demand for their fur, and each year many are trapped throughout the country. Maryland does not rank high in wild mink production. In 1966, only 303 mink were reported trapped in the State (U.S. Fish and Wildlife Service, Fur Catch in the United States, 1966, Wildlife Leaflet 478). The high point in mink trapping in Maryland over the past decade was reached during the 1950-51 season when 4,370 animals were taken (U.S. Fish and Wildlife Service, Fur Catch in the United States, 1949-54, Wildlife Leaflet 367) for their pelage.

Specimens examined.—*Anne Arundel County*: Little Patuxent River, 1. *Dorchester County*: Bloodsworth Island, 1. *Garrett County*: Oakland (through National Zoological Park), 1. *Montgomery County*: Bethesda, 1; Cabin John, 2; Forest Glen, 2; Garrett Park, 1; Potomac, 1; Sligo Creek (near Takoma Park), 1; no exact locality, 2. *Prince Georges County*: Bladensburg, 1; Branchville, 2; College Park, 1; Lanham, 1; Laurel, 44; no exact locality, 1.

Other records and reports.—*Montgomery County*: Plummers Island (Goldman and Jackson, 1939: 132). *Prince Georges County*: College Station, 8 miles NE of Washington; Patuxent Research Center. (Uhler and Llewellyn, 1952, p. 84).

STRIPED SKUNK

Mephitis mephitis nigra (Peale and Palisot de Beauvois)

Viverra nigra Peale and Palisot de Beauvois, A scientific and descriptive catalogue of Peale's museum, Philadelphia, p. 37, 1796.

Type locality.—Maryland.

General distribution.—New England and southern Ontario south to Virginia, and west of the Allegheny Mountains from the lower peninsula of Michigan and southern Illinois south to central Mississippi, Alabama, and Georgia.

Distribution in Maryland.—Distributed throughout the State, but most abundant in the Allegheny Mountain, Ridge and Valley, and Piedmont sections; scarce or lacking in many areas of the Eastern Shore section. According to the Service Survey (U.S. Fish and Wildlife Service, vol. 3(4), p. 15, December 1943), with the breaking up of the former dense forest cover the striped skunk seems to be slowly making its way southward along the Delmarva Peninsula into Dorchester County from Talbot County.

Distinguishing characteristics.—Teeth 3/3, 1/1, 3/3, 1/2, = 34; size large; body heavy, particularly rearward; tail very thick and bushy; legs short; pelage dense and coarse; coloration black with a thin white stripe medially on the nose, and two white stripes running from head to tail. The amount of white on the striped skunk is subject

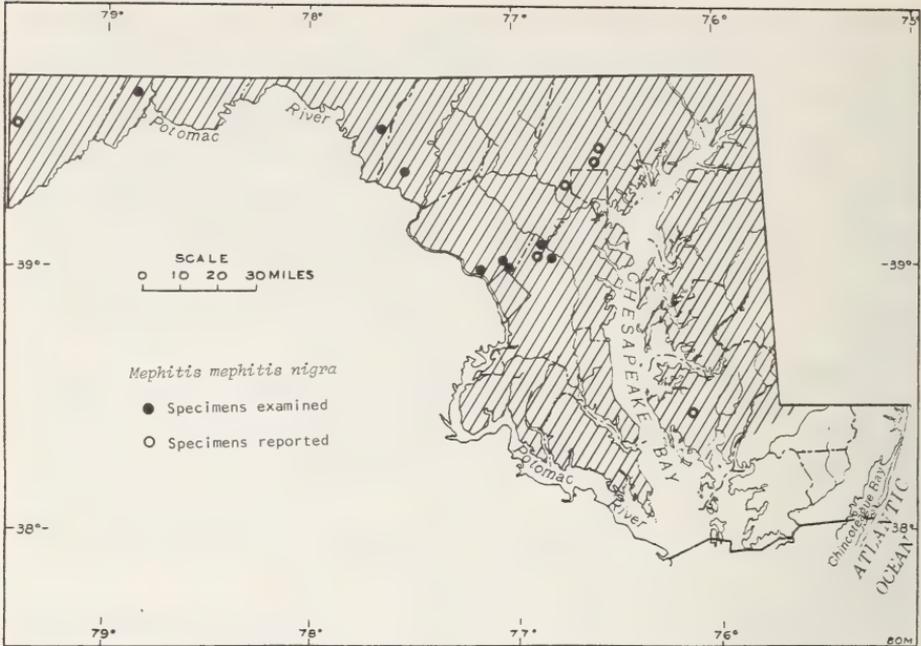


FIGURE 51.—Distribution of *Mephitis mephitis nigra*.

to considerable individual variation. Some animals are almost completely black, while others are predominately white on the back.

This species cannot be confused with any other Maryland mammal except possibly the spotted skunk (*Spilogale*), from which it differs in larger size and in having two rather than four white dorsal stripes. In *Mephitis* the nose patch is always a slender stripe, whereas in *Spilogale* it is a broad triangular patch.

Measurements.—Two adult males and two adult females from Cabin John, Montgomery County, have the following external and cranial measurements: Total length 597, 648, 568, 648; tail 228, 260, 235, 270; hind foot 64, 70, 57, 67; basilar length of skull 61.5, 60.5, 55.0, 60.0; zygomatic breadth 43.2, 46.7, 41.4, 41.9; least interorbital breadth 18.8, 19.6, 19.2, 18.1; maxillary toothrow 21.3, 20.7, 20.2, 20.5.

Habitat and habits.—This skunk is found in brushland, sparse woods weedy fields or pastures, under wood piles and rock piles, and around buildings. It is most common along brushy borders of streams and in rock piles and thickets at the base of cliffs.

The striped skunk makes its home in a burrow which it may dig in a brushy area or pasture, or it may occupy the burrow of some other animal such as a woodchuck. Occasionally the den may be in a cave or under a log or stump. Burrows average between 18 and 20 feet long and may reach to a depth of 3 to 4 feet below the surface of the ground.

The nest within the burrow is a somewhat wider area lined with dry leaves and grass.

The striped skunk is polygamous, and mating occurs from February until March, with the young being born in May or June. Only one litter is produced annually, and between two and 10 (usually six or seven) kits comprise a litter. The gestation period is 60 to 62 days.

Llewellyn and Uhler (1952, p. 200) studied the food habits of skunks at the Patuxent Wildlife Research Center, Prince Georges County. The results of their examination of 63 digestive tracts and 33 scats mostly taken in fall and winter are summarized as follows:

Plant material comprised some 10 percent of the food intake. The only plant item found regularly in the stomach was persimmon, which accounted for about 7 percent. Also occasionally found were beechnuts, acorns, corn, wheat, pokeberry, blackgum, smilax, and a few other fruits and berries; some of this plant material was apparently garbage. Animal matter comprised between 80 percent and 90 percent of the food intake; insects formed almost half of the total and were most prominent in the fall. About 20 percent of the insects consumed consisted of beetles, with scarabs such as June beetles (mostly larvae) and Japanese beetles (mostly adults) leading the list. Ground beetles were also found frequently. The next highest group (11 percent) was made up of grasshoppers and crickets. A large number (5 percent) of true bugs, chiefly stink bugs, were eaten. In later summer and fall, it was evident that in several instances the skunks had dug out yellow-jacket nests and eaten the occupants. Lamore (1953, p. 80) reports that he found a striped skunk dead on the highway near Beltsville, Prince Georges County, in August 1962. The animal's stomach was filled with yellow jackets.

Rodents, chiefly wood mice, meadow mice, and squirrels, comprised 15 percent of the diet; eight occurrences of rabbit totaled 5 percent. Llewellyn and Uhler (1952, p. 200) believe that the squirrels and rabbits were probably road kills, carrion, or hunting cripples, although remains of rabbits that could have been nestlings were found in two scats. Birds were found in 14 stomachs or scats and made up 7 percent of the volume. One box turtle, one king snake, and several undetermined snakes and salamanders were also found. Millipedes were found frequently in fall and winter and often made up entire meals. Spiders also appeared often, and centipedes occasionally, but their remains consisted mostly of legs, so that their volume constituted a small percentage of the total.

This skunk, like its spotted relative, possesses a powerful scent as a defense mechanism. The fluid which contains the scent can be ejected for a considerable distance, and if it should strike one's eye it will cause burning and smarting. Burning can be relieved by washing

the eye in lukewarm water, followed by flushing with boric acid. Turpentine is useful for removing skunk odor from clothing and from skin, and tomato juice is also effective.

Skunk fur is commercially valuable, and in the 1965-66 trapping season, 161 striped skunks were reported taken in Maryland by fur trappers (U.S. Fish and Wildlife Service, Fur Catch in the United States, 1966, Wildlife Leaflet 478).

Specimens examined.—*Allegany County*: Mount Savage, 1 (Coll. U. Md.). *Frederick County*: Jefferson, 1. *Montgomery County*: Cabin John, 4; Forest Glen, 1; Silver Spring, 1. *Prince Georges County*: Laurel, 6; Patuxent Research Center, 2. *Washington County*: Boonesboro, 1.

Other records and reports.—*Baltimore County*: Bare Hills-Lake Roland area (Bures, 1948, p. 66); Loch Raven (Kolb, 1938); Patapsco State Park (Hampe, 1939, p. 6). *Dorchester County*: Blackwater National Wildlife Refuge (Service Survey, U.S. Fish and Wildlife Service, 3(4), p. 15, December 1943). *Garrett County*: Cranesville Pine Swamp (Mansueti, 1958, p. 83). *Montgomery County*: Plummers Island (Goldman and Jackson, 1939, p. 132). *Prince Georges County*: Beltsville, near (Lamore, 1953, p. 80).

EASTERN SPOTTED SKUNK

Spilogale putorius putorius (Linnaeus)

[*Viverra*] *putorius* Linnaeus, Syst. nat., ed. 10, 1:44, 1758.

Type locality.—South Carolina.

General distribution.—"Southeastern United States from Alabama, Mississippi, and northern Florida northward through western and central Georgia and South Carolina and northward in the Appalachian Mountains to south-central Pennsylvania." (Van Gelder, 1959, p. 225).

Distribution in Maryland.—Ridge and Valley and Allegheny Mountain sections.

Distinguishing characteristics.—Teeth 3/3, 1/1, 3/3, 1/2, = 34; size small; coloration striking, the background being black, striped with four white dorsal stripes which run about to the middle of the back, the center ones being somewhat narrower than the outer; stripes breaking up into patches on the hind quarters, giving the skunk a spotted appearance; broad triangular white patch on nose and forehead; small white patch in front of ears; tail long and full, broadly tipped with white.

This skunk is readily distinguished from the striped skunk (*Mephitis mephitis*) by the patterning of its coloration. *Spilogale* has four white stripes on the body whereas *Mephitis* has two (these may be highly variable, however, in length and breadth). *Spilogale* has a

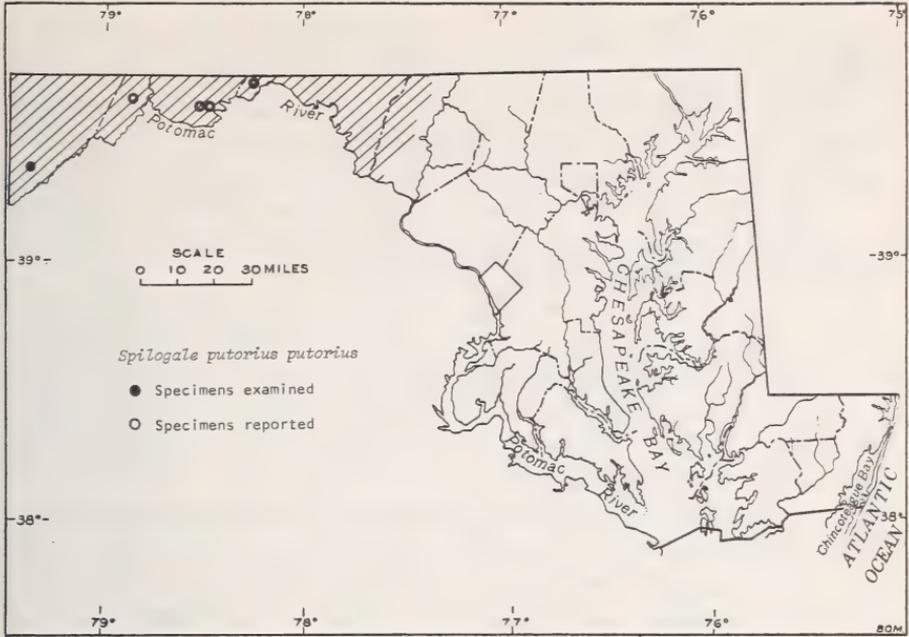


FIGURE 52.—Distribution of *Spilogale putorius putorius*.

broad triangular white nose patch, while *Mephitis* has only a thin white stripe medially on the nose. The spotted skunk is considerably the smaller species.

Measurements.—Van Gelder (1959, p. 255) gives external and some cranial measurements of this subspecies as follows: Males: Total length 506.6 (453–610); tail 180.9 (152–211); hind foot 47.8 (41–51); condylobasal length of skull 57.2 (53.6–61.9); zygomatic breadth 35.3 (32.5–37.8); interorbital breadth 15.5 (13.5–16.9); length of maxillary toothrow 18.4 (17.0–20.5). Females: Total length 450.7 (403–470); tail 171.9 (154–193); hind foot 44.0 (39–47); basilar length of skull 47.6 (45.0–50.0); zygomatic breadth 33.2 (31.8–34.8); interorbital breadth 15.0 (13.5–15.9); length of maxillary toothrow 17.7 (16.6–18.6).

A male from Piney Mountain, one-quarter mile north of U.S. Route 40 at Clarysville, Allegany County, has the following external and cranial measurements: Total length 425; tail 155; hind foot 45; ear 13; condylobasal length of skull 55.1; zygomatic breadth 34.1; interorbital breadth 14.8; length of maxillary toothrow 17.7.

Habitat and habits.—In the northern part of its range this species prefers to live in rock piles and crevices in cliffs. In more southern areas of the southeastern United States it often inhabits wasteland and cultivated fields and sometimes build its nest under farm buildings or lives in deserted woodchuck burrows. All of the areas in which

spotted skunks have been taken or observed in Maryland are similar. They are at or near the summits of mountains at altitudes above 1,600 feet. They are characterized by rocky outcrops which run parallel to the summits and which may be several hundred feet in length. The vegetation consists of second-growth oaks (*Quercus* spp.) and hickories (*Carya* spp.), with black locust (*Robinia pseudocacia*), Virginia pine (*Pinus virginiana*), and dense tangles of wild grape (*Vitis* spp.) occasionally present (Bookhout, 1964, p. 214).

Little is known of the breeding habits of the spotted skunk. Van Gelder (1959, p. 260-270) says that there is evidence that this subspecies has an extended breeding period, or that two litters a year might be produced since there are records of females nursing in both the spring and fall. There are between two and six young, with the usual number being four or five.

According to Hamilton (1943, p. 159) the food of this species during the winter months consists largely of rabbits, mice, and other small mammals; during the summer and fall it fattens on fruits, insects, and birds. Lizards, small snakes, and offal are not disdained, and the spotted skunk will steal eggs and kill chicks. It is fond of persimmons and various other fruits in season.

This skunk possesses a means of defense consisting of a characteristic evil-smelling fluid which is secreted by two anal glands. This fluid, or musk as it is sometimes called, can be ejected accurately up to several feet in the direction of attackers. It is more overpowering, blinding, and burning than that of *Mephitis*, and there are few animals that are not repulsed by it.

Specimens examined.—*Allegany County*: Piney Mountain, ¼ mile N of U.S. Route 40, at Clarysville, 1 (specimen taken 10 February 1964). *Garrett County*: Locklynn Heights, 1 (specimen taken in mid-January 1963).

Other records and reports.—Latham and Studholme (1947, p. 409) report a specimen from 4 miles west of Hancock, Washington County. James H. Beal, of Frostburg, tells me (in correspondence) that he collected a specimen on Town Hill (Mountain), Allegany County, near the beacon light in August 1962, and another near the same locality in 1959. The following records are from Bookhout (1964, p. 214): Green Ridge Mountain (elevation 1,400 ft.), Allegany County (one animal seen in December 1957); and Dan's Mountain (elevation 1,600 ft.), Allegany County (four specimens trapped since 1960).

Remarks.—The spotted skunk is essentially a southern species and has apparently extended its range into Maryland and Pennsylvania only within recent years. The first record of a spotted skunk in Pennsylvania was as recent as 40 years ago (Latham and Studholme, 1947,

p. 409) despite the fact that trappers, hunters, and collectors have been working in the Maryland and Pennsylvania mountains since Colonial times.

RIVER OTTER

Lutra canadensis lataxina F. Cuvier

Lutra lataxina F. Cuvier, in Dictionnaire des sciences naturelle . . .
27: 242, 1823.

Type locality.—South Carolina.

General distribution.—Coastal Plain and Piedmont of the eastern United States, from western Connecticut and southern New York, south to South Carolina.

Distribution in Maryland.—The species is statewide in distribution. The subspecies *lataxina* inhabits the Eastern Shore, Western Shore, and Piedmont sections, but may be replaced by *Lutra canadensis canadensis* in the Ridge and Valley and Allegheny Mountain sections where it is scarce or possibly absent (Bookhout, in correspondence). No specimens are available to establish the subspecific identity of the western Maryland otters (if they occur there), but since *L. c. canadensis* has been reported from the mountains of Virginia to the south (Handley and Patton, 1947, p. 133) and West Virginia to the west (Kellogg, 1937, p. 453), western Maryland specimens, if and when obtained, probably will prove referable to *L. c. canadensis*.

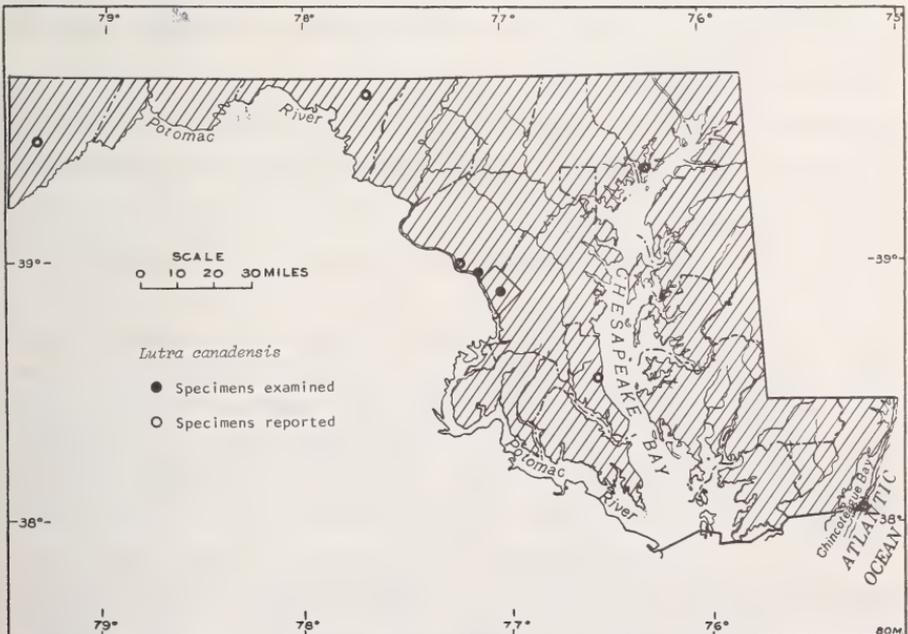


FIGURE 53.—Distribution of *Lutra canadensis*.

Distinguishing characteristics.—Teeth 3/3, 1/1, 4/3, 1/2, = 36; size large; body slender and elongated; head small, broad, and flattened; ears and eyes small and rounded; nose broad and flat; tail long, about a third of the total length of the animal, very heavy at the base and tapering toward the tip; legs very short, ending in large feet with webbed toes; pelage consisting of a dense underfur overlaid with silky guard hairs; coloration a rich deep brown, generally somewhat paler on the belly and often with a grayish mixture on the lips, chin, and throat. The subspecies *L. c. canadensis* is similar to the above but considerably darker in coloration.

The combination of large size, flat, broad head, thick, heavy tail, and webbed toes distinguish the otter from similar mammals in Maryland.

Measurements.—No external measurements are available for the Maryland and District of Columbia specimens in the National collections. Handley and Patton (1947, p. 134) give the range of external measurements in otters as follows: Total length 900–1,200; tail 300–400; hind foot 100–120.

A young male from Glen Echo, Montgomery County, and an unsexed (but apparently a male) old adult from Washington, D.C., have the following cranial measurements: Basilar length 95.8, 101.6; zygomatic breadth 65.3, —; postorbital breadth 19.1, 20.7; mastoidal breadth 62.9, 66.7; length of maxillary toothrow 35.2, 38.8. Two unsexed (but apparently female) adults from Washington, D.C., measure cranially: Basilar length 87.5, 90.6; zygomatic breadth 64.3, —; postorbital breadth 17.2, 19.2; mastoidal breadth 56.7, 59.9; length of maxillary toothrow 32.9, 34.2.

Habitat and habits.—The otter occurs along rivers, streams, and lakes, and it appears to be quite common in the marshes that border the Chesapeake Bay and the Atlantic Ocean. It occurs on Assateague Island, where Jacob Valentine, former manager of the Chincoteague National Wildlife Refuge, told me that as many as seven were living in 1958. Most of these, however, were in the Virginia portion of the island, on the Refuge.

Maryland's Eastern Shore supports a large population of otter. Audubon and Bachman (1851, p. 11) and Coues (1877, p. 211) reported them as common there in the 19th century. Brayton (1882, p. 58) says that the Eastern Shore of Maryland appears to have always been a favorite resort of the otter. Another area where this species is abundant is on the Proving Grounds near Edgewood Arsenal, Harford County.

Otters were at one time relatively common along the Potomac River and its tributaries in the vicinity of Washington, D.C., and have often been reported from the city proper. Bailey (1923, p. 125) records an otter at the north end of Rock Creek Park in 1920 and one taken at

Eastern Branch near Bennings in 1895. In nearby Maryland he reports that otter tracks were seen on Plummers Island in 1910 and 1922, and that one was observed swimming across the Potomac River near Seneca in April 1920. Otters still are not uncommon along the Potomac River both to the north and south of Washington. L. G. Henbest observed one swimming in the Potomac near Great Falls in late January and February 1964 and obtained a photograph of the animal when it climbed out onto a rock on the Maryland side of the river.

The otter may be active any time of the day or night, but tends to be more nocturnal than diurnal. Even though it may be common, it is seldom seen by the casual observer because it is shy and spends much of its time in water. These animals are powerful and graceful swimmers and dive with ease and agility. When swimming on the surface it holds its head high out of the water and both the forelegs and hind limbs are directed backward, progression being made primarily by twisting and moving the body and tail. The otter can reach a speed of 6 or 7 miles an hour on the surface, and nearly as great a speed when submerged.

The otter inhabits a well hidden den along the bank of the stream or river in which it lives. According to Liers (1951, p. 4) these animals seldom dig their own dens, but utilize abandoned beaver lodges or wood-chuck or muskrat burrows, enlarging them to suit their needs. Often these dens are simply short tunnels, but sometimes they may be extensive and complicated. The main entrance is always under water. In marshes, the otter may prepare a nest from dry marsh grasses.

Nothing has been published concerning the breeding habits of otters in Maryland. Liers (1951, p. 4) studied them in Minnesota under semiwild conditions and reports that otters breed there in winter and early spring. He found the gestation period to vary from 9 months 18 days to 12 months 15 days. Only one litter is produced a year, comprising generally two to four young. The male is allowed to rejoin the family group after the young have left the nest, and he assists the female in teaching them to swim and hunt for food.

The otter eats a variety of foods, but is primarily carnivorous, consuming crayfish, frogs, turtles, larvae of aquatic insects, angle-worms, and fish (Liers, 1951, p. 1). Jackson (1961, p. 388) says that the otter rarely eats muskrat, young beaver, or duck, and that the parts of land vertebrates occasionally found among its remains probably were eaten as carrion. On Assateague Island the otters appeared to be feeding largely on jumping mullet (*Mugil cephalus*).

Otter fur is currently commanding good prices on the market, being durable, soft, and dense. During the 1965-66 trapping season, 495 wild otters were trapped in Maryland for the fur market (U.S. Fish and

Wildlife Service, Fur Catch in the United States, 1966, Wildlife Leaflet 478).

Specimens examined.—*Montgomery County*: Glen Echo, 1. *District of Columbia*: 3.

Other records and reports.—*Calvert County*: Chesapeake Bay, near Stoakley (LeCompte, 1937: 15). *Garrett County*: Deep Creek Lake (Browning, 1928, p. 213). *Harford County*: Edgewood Arsenal area (personal observation). *Montgomery County*: Great Falls (identified from photograph taken by L. G. Henbest, February 1964). *Washington County*: near Leitersburg (Washington, D.C., Herald, 7 January 1909). *Worcester County*: Assateague Island (personal observation).

Family FELIDAE (cats)

BOBCAT

Lynx rufus rufus (Schreber)

Felis rufa Schreber, Die Säugthiere . . . , Thiel 3, Heft 95, pl. 109b, 1777.

Type locality.—New York.

General distribution.—In the eastern United States, this race formerly occurred from central New England south to northern Georgia, and west into the Dakotas, Iowa, Kansas, and Oklahoma. It is now absent or rare in the Coastal Plain in the southern portion of its range except in Virginia's Dismal Swamp.

Distribution in Maryland.—Formerly statewide in distribution, but now confined primarily to the Allegheny Mountain and Ridge and Valley sections. It has been entirely exterminated in the Eastern Shore section and is only rarely encountered in the Western Shore and Piedmont sections.

This species is uncommon enough in Maryland to produce local newspaper accounts when one is taken.

Distinguishing characteristics.—Teeth 3/3, 1/1, 2/2, 1/1, = 28; general appearance catlike, but considerably larger than a domestic cat, averaging about twice as much in size and weight; body short; ears prominent and with small conspicuous tufts on the tips; eyes large and with elliptical pupils; tail very short, less than a fourth of the total length of the animal; pelage fairly long and loose; coloration of upperparts grayish to brownish, darker along the midline, and spotted and blotched throughout; abdomen and inner sides of legs white, prominently marked with black spots; tail always tipped with black.

The only Maryland mammal with which the bobcat may be confused is the domestic cat, from which it is readily distinguished by its larger size and short black-tipped tail.

Measurements.—No external measurements are available for Maryland or District of Columbia specimens in the National collections.

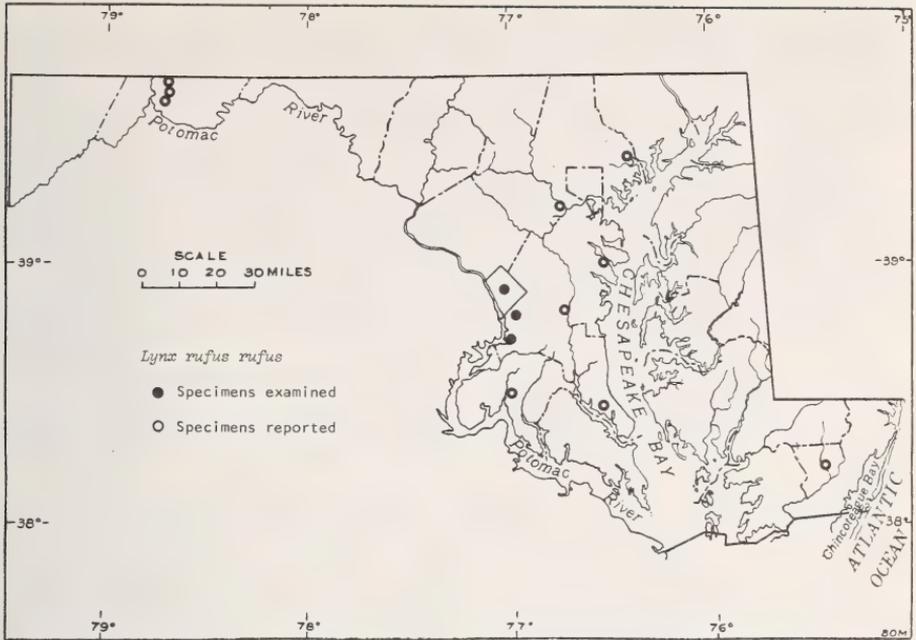


FIGURE 54.—Distribution of *Lynx rufus rufus*.

Kellogg (1937, p. 457) gives external measurements of 11 adult males from West Virginia as follows: Total length 870 (787–935); tail 146 (133–165); hind foot 171 (162–195). According to Jackson (1961, p. 402) the male bobcat averages about 10 percent longer than the female and weighs about 30 percent more.

A female from near Fort Washington, Prince Georges County, has the following cranial measurements: Greatest length 128.0; zygomatic breadth 83.7; interorbital breadth 23.2; maxillary toothrow 40.4.

Habitat and habits.—Bobcats prefer wild heavily wooded or brushy areas, particularly in rocky habitats and swamps. In Maryland the animal is still fairly numerous in the wilder areas of the Allegheny Mountain and Ridge and Valley sections, but is very scarce in the rest of the State. No specimens have been taken in the Eastern Shore section for many years, and presumably the animal is extirpated there. According to Mansueti (1950, p. 21) the species has been ruthlessly exterminated in Maryland as “vermin,” and is everywhere much scarcer than in the past.

Mansueti (1950, pp. 22–23) has gathered together a number of bobcat records in Maryland. He says that Meshach Browning is reported to have killed scores of bobcats in the early 19th century, and that they were an everyday occurrence in Garrett County then. Marye (1945) says that a generation ago bobcats were destructive to sheep near the Falls of the Patapasco River, and that in his time they were

occasionally killed in Baltimore County. He reports that in the 1920's he saw a large bobcat in Day's woods, between the Great and Little Falls of the Gunpowder River. He also cites some notes relative to the bobcat on the Eastern Shore and says that about 2 decades ago (also in the 1920's), a wild animal of the cat family was treed by dogs on the borders of the Nassawango Swamp, near Nassawango Bridge in Worcester County. The animal escaped and Marye doubts that any domestic cat could have done so under the circumstances imposed.

Mansueti (1950, p. 22) quotes an article from the Baltimore Evening Sun (18 February 1948) entitled "Bobcats Still Here," which says that Thomas Leary, hunter of Beans Cover, Allegany County, trapped a bobcat in 1948 on Evitts Mountain in Allegany County and the newspaper published a photograph of the animal, thus substantiating the capture.

Mansueti (1950, p. 23) says that John Hamlet, formerly with the U.S. Fish and Wildlife Service, told him that a few years ago (1945 or 1946) a bobcat was known to be roaming the Cypress Swamp region of Calvert County, and Watson Perrygo of the Division of Mammals, U.S. National Museum, tells me that bobcats are presently residing in wild areas on his property near Port Tobacco in Charles County.

Several interesting specimens of bobcats from Maryland and the District of Columbia are in the collections of the U.S. National Museum. One of these, a young female, was shot along with five others in a swamp near Oxon Hill, Prince Georges County, in 1941 when the swamp was being razed for a housing development. Another (an old female) was found dead in December 1958 on the curb of a downtown Washington Street, not far from Rock Creek Park. The animal was not examined for bullet wounds but probably was shot in the mountains west of Washington and then dumped from an auto onto the Washington Street, although it is remotely possible that it had wandered naturally into downtown Washington via Rock Creek Park. Bailey (1923, p. 121) lists several bobcat records from nearby Virginia.

The Maryland Conservationist (27(1), pp. 9, 28, Spring 1950) records the capture of a particularly large bobcat in Maryland. On Labor Day of 1949, Frank Wigfield killed the animal on Iron Mountain, about 5 miles east of Cumberland, Allegany County. It weighed 43 pounds and measured 53 inches from tip to tip.

The bobcat is shy and retiring, and primarily solitary in its habits. It is almost entirely nocturnal and is seldom abroad in daylight. Generally, it seeks shelter under shrubs or in rock crevices, but sometimes it dens in hollows trees, stumps, or logs. The den is lined with grasses, leaves, moss, and other vegetation, which are scraped and scratched into a nest.

Mating in this species occurs in February or March; the gestation period is about 50 days, and between one and four kittens are born, usually in April. At birth the young are blind; the eyes open after about 9 or 10 days. Although weaned when 60 to 70 days old, the young continue with the mother until autumn or sometimes late winter.

The food of the bobcat is entirely animal in nature, and consists to a large extent of rabbits as well as squirrels, mice, muskrats, and various kinds of birds. Bobcats often feed on deer; fawns are especially vulnerable prey, and no doubt deer carrion is often consumed. Domestic livestock, mainly calves and sheep but also occasionally poultry, are also eaten.

Mansueti (1950, p. 23) says that the bobcat is undoubtedly vanishing in Maryland, but its wary and secretive habits will insure its permanence in some of the more isolated portions of the State.

Specimens examined.—*Prince Georges County*: Fort Washington, near, 1; Oxon Hill, 1. *District of Columbia*: 1.

Other records and reports.—*Anne Arundel County*: Annapolis, 3 miles NW near Severn River (John C. Lingeback, in verbis). *Alleghany County*: Evitts Mountain (Mansueti, 1950: 22); Iron Mountain (Md. Conservationist, 27(1), pp. 9, 28, Spring 1950). *Baltimore County*: Day's Woods between the Great and Little Falls of the Gunpowder River (Mansueti, 1950, p. 22). *Calvert County*: Cypress Swamp along Battle Creek (Mansueti, 1950, p. 23). *Charles County*: near Port Tobacco (W. M. Perrygo, in verbis). *Howard County*: Falls of the Patapsco River (Mansueti, 1950, p. 22). *Prince Georges County*: Patuxent River, near Upper Marlboro (Bailey, 1923, p. 121). *Worcester County*: Nassawango Swamp, near Nassawango Bridge (Mansueti, 1950, p. 22).

Order ARTIODACTYLA (even-toed hoofed mammals)

Family CERVIDAE (deer)

SIKA DEER

Cervus nippon Temminck

Cervus nippon Temminck, Coup d'oeil sur la faune des îles de la Sonde et de l'empire du Japon, xxii, 1838.

Type locality.—Japan.

General distribution.—Native to Japan, eastern China, Korea, and Manchuria. Introduced into England, New Zealand, Denmark, France, Austria, Russia, and the United States.

Distribution in Maryland.—James Island, Taylors Island, and adjacent mainland in Dorchester County, and Assateague Island Worcester County.

Distinguishing characteristics.—Teeth 0/3, 1/1, 3/3, 3/3, = 34; size small; coloration brownish olive or reddish olive with the middorsal area somewhat darker and forming an indistinct dark line from the forehead to the rump; underparts somewhat lighter; dorsum, particularly posteriorly, faintly speckled with indistinct white blotches in both young and adults, the white blotches being more noticeable in summer than winter; prominent white rump patch with semierectile hairs; antlers in male narrow, seldom having over three points and standing erect over head.

This species is distinguishable from the white-tailed deer by a number of easily recognizable characters. It is considerably smaller, averaging a third less in weight; has speckled pelage in young and old of both sexes; has narrower antlers that stand erect above the head, rather than curving forward over head; and possesses a small canine tooth in both sides of upper jaw.

Measurements.—No external measurements are available for any of the Maryland specimens. The species ranges in shoulder height from 32 to 43 inches (Tate, 1947, pp. 341–342).

Cranial measurements of an adult male from James Island, Dorchester County, are: Greatest length 231; zygomatic breadth 97.1; interorbital breadth 69.3; maxillary toothrow 68.6. Cranial measurements for two adult females from James Island are as follows: Greatest length 220, 224, zygomatic breadth 91.3, 93.4; interorbital breadth 53.0, 60.0; maxillary toothrow 62.5, 65.9.

Habitat and habits.—In its natural range, this species prefers hilly regions with mixed large-leaved forests. It does best in areas which are not subject to heavy snowfall (Flerov, 1952, p. 128).

In Maryland, it has been introduced on Assateague Island, and on James Island, from which it has spread to neighboring Taylors Island and the adjacent Dorchester County mainland. According to Flyger (1960a), four or five sika deer were released on James Island about 1916 by Clemment Henry, who had kept them in an enclosure near Cambridge for an unknown period before releasing them on the island. They multiplied on James Island and spread to nearby Taylors Island, and eventually to the mainland. Flyger and Warren (1958) estimated that in the fall of 1957, 270 sika deer inhabited James Island. Regarding their introduction to Assateague Island, Flyger (1960a) says that Charles Law of Berlin, Md., stated that he purchased five sika deer (two males and three females) from a man in Cambridge in 1920. These deer were held in an enclosure near Berlin for several years, during which time three young were born and one of the original males died. Dr. Law sold these deer to a man who in turn released them on Assateague Island where they have prospered and grown into a herd

of over a thousand animals (Flyger, 1964, p. 213). Most of these, however, are located in the southern portion of the island in Virginia.

Sika deer can be hunted in Maryland during the regular deer hunting season, and nearly every year a few have been taken in Dorchester County. However, these deer are wilder and more timid than native white-tailed deer, and are more difficult to stalk. Because they are primarily nocturnal in habits many local people are even unaware of their existence in their neighborhood.

The sika deer has been introduced into various European countries, some of which are not pleased with the species since it is too secretive and wild to be a satisfactory game animal, and has a propensity for peeling bark from trees and competing with other species of deer for food (Flyger, 1959, p. 24). Whether it is a potential boon or threat to sportsmen in Maryland is still uncertain.

Little is known of the biology of this species in Maryland. In the Soviet Union where the animal has been widely introduced, Flerov (1952, pp. 128-129) reports that they are gregarious and that during certain periods their herds consist of many dozens of animals. Rutting begins in September and lasts for 1½ to 2 months. Rutting takes a very stormy course and is accompanied by roaring and terrific battles. After the rut, the males gather together in herds and remain apart from the females during the entire winter. Females with 2- or 3-year-old young also gather in separate groups just prior to winter. Calving occurs toward the end of May or June, generally one fawn, but occasionally twins, being produced.

These deer swim readily and sometimes will cross large bodies of salt water. Their food in Maryland is probably similar to that of the white-tailed deer, and it is feared that in areas where the sika deer becomes well established the native white-tailed species will not be able to compete for the available food supply.

Specimens examined.—Dorchester County: James Island, 8.

Remarks.—Presnall (1958, pp. 48-49) listed sika deer as occurring on Assateague Island, but incorrectly identified the deer from Dorchester County as hog deer (*Axis porcinus*). As pointed out by Flyger (1960a), not only are the Dorchester County animals *Cervus nippon*, but very probably they derive from the same stock as the Assateague Island populations.

In addition to Sika deer, Maryland supports small populations of introduced fallow deer (*Dama dama*). Presnall (1958, p. 48) says that a few animals remain from introductions in Worcester County (Mills Island in Chincoteague Bay) between 1920 and 1930, and in Talbot County between 1935 and 1945. Fallow deer are native to the Mediterranean region of southern Europe and western Asia, but have been widely introduced in northern Europe and the United States, where

colonies exist in Kentucky, Tennessee, Virginia, and elsewhere. This deer is about the size of a Maryland white-tailed deer, but with large palmate antlers which are directed upward. In summer pelage, the coloration is fawn, with numerous white spots; in winter, a uniform grayish (although melanism and albinism are not infrequent). Miller (1912, pp. 971-972) gives external measurements of a European adult male of this species as: Head and body length 1540; tail 190; hind foot (with hoof) 435; ear from crown 165.

WHITE-TAILED DEER

Odocoileus virginianus borealis Miller

Odocoileus americanus borealis Miller, Bull. New York State Mus. Nat. Hist., 8: 83, 21 November 1900.

Type locality.—Bucksport, Hancock County, Maine.

General distribution.—"Western Ontario, east across southern Quebec, New Brunswick, and Nova Scotia; and from near James Bay (Newport, Abitibi River), Gaspé Peninsula, and Anticosti Island south to southern Maryland, southern Pennsylvania, Ohio, Indiana, and Illinois. Southern boundaries fixed at Potomac and Ohio rivers and the western limits at the Mississippi and Red Rivers." (Kellogg, 1956, p. 40).

Distribution in Maryland.—At one time the white-tailed deer was nearly extirpated in Maryland. Today it is common in all sections of the State, and is found in the wilder areas of every county.

Distinguishing characteristics.—Size large, larger than sika deer; antlers heavy, and main beam directed forward, bearing the several tines behind; upper parts of body colored reddish brown in summer and grayish in winter, unspotted except in juveniles; underparts and underside of tail white; juvenile animals are reddish yellow and spotted with white.

Measurement.—Kellogg (1956, p. 40) gives external measurements of the largest male of this subspecies that he examined as: Total length 2400; tail 365; hind foot 538; height at shoulder 1041. Two adult males from Cumberland, Allegany County, have the following cranial measurements: Condylbasal length —, 261.8; width of orbit at frontojugal suture 129.7, 120.9; least interorbital breadth 74.2; length of maxillary toothrow 71.8, 72.5. Females average smaller than males in size.

Flyger (1958, p. 8) says that the average weight of 47 adult male deer from western Maryland was 127.5 pounds, and 17 from Worcester County averaged 125.4 pounds, whereas 6 from the Aberdeen Proving Grounds in Harford County averaged only 104.2 pounds. Wherever the deer population becomes so great that a scarcity of food results, the size and weight of the deer in that area become markedly reduced.

This was the case with the Aberdeen herd, where at the time of Flyger's study deer were over abundant.

Habitat and habits.—Deer are essentially animals of the "edges," preferring burned-over areas and second-growth timber. They are much less common in heavily forested sections because the dense foliage discourages the growth of low forage on which the deer feed. Since much of Maryland today consists of edge habitat, deer are probably even more abundant in the State than they were before the coming of the white man when most of the area was heavily wooded.

Even though much of Maryland was heavily forested in precolonial and colonial days, white-tailed deer were apparently numerous and supplied a good source of food for early settlers. According to Mansueti (1950, p. 13) there are countless references to the abundance of deer in early letters and accounts of conditions of the 17th, 18th, and 19th centuries.

Although deer originally occurred in every Maryland county, the species was almost exterminated from about 1900 until the early 1930's. This was due apparently to high hunting pressure and other factors. For example, Browning (1928) estimated that he killed between 1,800 and 2,000 deer during his hunting career in western Maryland, and that by 1839 the deer in Garrett and Allegany counties were beginning to become scarce. Other factors that were responsible for the decline in the deer herds in Maryland include wild dog packs and forest fires, both of which are known to have killed many individuals throughout the State.

The population increase in recent years has resulted from stocking and intelligent conservation, as well as from the increased "edge" habitat in many areas of the State. Today, the white-tailed deer occurs in all sections of Maryland, and in some places is overabundant. Such an area is the Aberdeen Proving Grounds in Hartford County, where according to Flyger (1958, p. 3) counting 100 or 200 deer in a single morning's observation is not at all unusual, and where a distinct browse line is evident in the woods. At the Proving Grounds, also, there have been several instances of mass die-off in recent years, an indication of overpopulation in a particular area. Flyger found that the deer herd in Cecil County, on the other hand, is still rapidly growing and the range there is more understocked than in any other part of the State.

The Maryland Conservationist (40(1), p. 15, Jan.-Feb., 1963) lists the total deer kill in various Maryland counties for the 1962 season as follows: Garrett 577, Allegany 699, Washington 344, Frederick 214, Carroll 114, Howard 12, Montgomery 2, Anne Arundel 5 Calvert 93, Prince Georges 12, Charles 208, St. Marys 33, Baltimore 95, Cecil

351, Harford 70, Kent 619, Queen Annes 124, Caroline 106, Talbot 180, Dorchester 696, Somerset 192, Wicomico 161, Worcester 377. In addition to the above, 418 deer were killed at Aberdeen Proving Grounds during the season. The Fish and Wildlife Service reports (Big Game Inventory for 1967, Wildlife Leaflet 481, September 1968) an estimated total of 75,000 deer in the State for 1967.

White-tailed deer are primarily nocturnal, but are often abroad during daylight hours. With regard to feeding habits of this species in Maryland and the availability of food within the State, Bitley (1963, pp. 8-9) says:

Deer require a varied diet and if you've ever watched them feed, they'll nibble here and there, take a twig of witch hazel, then red maple, some huckleberry and for dessert some greenbriar. . . . Whenever possible, they prefer browse, such as greenbriar, maple leaf viburnum, blueberry, sassafras, black oak, red maple and blackberry. After several winters of heavy browsing these species begin to disappear and the deer are forced to shift to less nutritious food.

During the winter a deer requires from 6 to 8 pounds of dry browse each day for body and heat maintenance. If the quality and quantity of food is insufficient they become victims of diseases (especially pneumonia) and parasites. Very few deer in this section of the United States ever actually starve to death; disease usually gets them first.

He says that surveys conducted in 1962 in western Maryland indicated heavy browsing pressure on the preferred foods. For instance, of the twigs within reach and available to deer, the following percentages had been browsed: Maple-leaved viburnum, 53.9; blackberry, 43.8; blueberry, 59.0; black birch, 38.8; black cherry, 14.3; dogwood 33.9; greenbriar, 77.6; hazelnut, 24.1; red maple, 25.9; black oak, 44.4; sassafras, 54.8. In the western three counties, an average of 29 percent of the annual growth was browsed each year. By contrast, on the Eastern Shore, only an average of 6.1 percent was taken. The statewide survey disclosed that a total of 58 species of woody plants had been browsed throughout Maryland.

The following life history notes on the white-tailed deer are extracted primarily from Severinghaus and Cheatum (1956, pp. 57-186).

It is generally agreed that social organization in this species is limited to the family group, which usually consists of an older doe with her fawns, sometimes including those of the previous year. Leadership of the group appears to rest with the old doe. The occasional antlered buck that may be seen with the family group is usually the yearling offspring of the old doe. In the Northern States, the breeding season begins in November and the young are born in May or June. Antlers begin to appear on the bucks in the summer. They grow from a pedicle of the frontal bone and are covered with a true skin (the velvet) during their growth. Antler growth is rapid,

usually full size being achieved within 4 months or less. During the period of antler growth, the buck is very careful of the sensitive appendages, but after full size is reached, the velvet is scraped away, and the polished antlers are used by the bucks in battles for mates. The necks of the bucks also swell considerably during the mating season. After the mating season the antlers are shed, usually in January or early February in Northern States, then the cycle continues.

Gestation period in this species varies from 189 and 222 days, with the average being about 201 days. The usual number of young, for older does, is two, occasionally three. A young doe, however, usually gives birth to only a single offspring. The fawns are spotted, and remain in thickets where they blend perfectly with the dappled shadows of the foliage. Both bucks and does generally achieve sexual maturity at 18 months of age, although well-nourished doe fawns, at least in northern areas, may breed at 6 to 8 months of age.

Specimens examined.—*Alleghany County*: Cumberland, 3.

Other records and reports.—White-tailed deer have been reported from every county in Maryland.

Remarks.—The subspecies of white-tailed deer that originally inhabited Maryland was *Odocoileus v. borealis*. By the turn of the present century, however, the species was nearly extinct in Maryland, as well as in most other eastern States. Widespread transplanting of deer from areas in which they were still abundant reestablished eastern herds. Deer from many areas, and representing a number of subspecies, were brought into Maryland, and consequently today it is impossible to assign the State's deer to any specific subspecies. According to Hosley (1956, p. 228): "One effect of the widespread transplanting of Lake States deer into the south and east and of other similar moves has been to mix up thoroughly the races existing in most of the deer range."

MARINE MAMMALS OF MARYLAND

The following list of marine mammals comprises only those that have stranded on Maryland beaches, or have been observed in waters off the Maryland coast and in Chesapeake Bay. The list does not include all the marine mammals that may occur in Maryland waters, and many additional species will eventually be discovered. Some of these unrecorded species have stranded on beaches to the north and south of Maryland and must also pass through Maryland waters. Only those, however, which have actually been reported from the State will be discussed in any detail.

Order PINNIPEDIA (pinnipeds)

Family PHOCIDAE (earless seals)

HARBOR SEAL

Phoca vitulina concolor De Kay

Phoca concolor De Kay, Zoology of New York . . . , Vol. 1, pt. I (Mammalia), p. 53, 1842.

Type locality.—Long Island Sound, near Sands Point, Nassau County, N.Y.

General distribution.—Along the Atlantic coast of North America from Ellesmere Island to South Carolina, but is rare in the northern and southern portion of this range.

Description.—A small seal that averages in total length about 4 or 5 feet and weighs 75 to 150 pounds. The pelage is coarse and varies from yellowish gray, spotted with dark brown to almost black, spotted with yellowish. The spotted pelage and small size are distinctive characters of this species.

Maryland records.—Harbor seals in Maryland waters are stragglers; they are not indigenous to the State. Mansueti (1950, pp. 28–29; 1955, p. 2) summarizes Maryland records as follows: One specimen taken in a seine in Chesapeake Bay near Elkton in August 1824; one animal feeding around Thomas Pouch Lighthouse, near Annapolis, in March 1894; one animal killed in Tangier Sound on 8 July 1898; one specimen sighted on 14 September 1898 on a beach above reach of heavy waves at Ocean City, Worcester County; several animals in Choptank River near Tilghman Island in the early part of February 1925; one specimen seen in Chesapeake Bay at Flag Pond in 1940; one animal sighted at Ocean City, Worcester County, in May 1955.

In addition, there is a fragmentary skin and partial skeleton of a harbor seal in the National collections; the specimen was found on the beach at Assateague Island, 3 miles south of Ocean City, Worcester County, on 12 May 1959.

HOODED SEAL

Cystophora cristata (Erxleben)

[*Phoca*] *cristata* Erxleben, Systema regni animalis . . . , 1:590, 1777.

Type locality.—Southern Greenland or Newfoundland.

General distribution.—North Atlantic coast from Greenland to Labrador. Newfoundland, Nova Scotia, and Gulf of St. Lawrence, south as an accidental to Florida.

Description.—A large seal, with males ranging up to 10 feet in total length and weighing up to 850 pounds. Females are smaller, averaging about 8 feet in length and weighing up to 400 pounds. Coloration slate-

gray to blackish dorsally, with sides paler and spotted with white. Males have a bladderlike protuberance on the nose which they can inflate in times of anger or danger.

Maryland records.—One recorded in 1865 as taken near Cambridge, Dorchester County, on an arm of the Chesapeake Bay, 18 miles from salt water (Cope, 1865, p. 273); one animal killed at Worton Point, near Chestertown, Kent County, about 1860 (Mansueti, 1950, p. 31).

It is possible that the seal from Tangier Sound previously listed as *Phoca vitulina concolor* may have been a hooded seal rather than a harbor seal. The Baltimore Sun of 9 July 1898, which reported the killing of the animal on 8 July 1898, said that it measured almost 6½ feet in length. If this measurement was accurate, the animal would fall within the size range of the hooded seal rather than the harbor seal.

Order CETACEA (cetaceans)

The order Cetacea is divisible into two distinct suborders distinguished primarily by the presence of teeth, or baleen in the mouth. Those that are toothed are classified as:

Suborder ODONTOCETI (toothed whales)

Toothed whales may have teeth in the lower jaws only, or in both upper and lower jaws. In some forms more than 100 teeth are present, while in others the teeth may be reduced to 2. Whales of this suborder never possess baleen.

Family ZIPHIIDAE (beaked whales)

GOOSE-BEAKED WHALE

Ziphius cavirostris G. Cuvier

Ziphius cavirostris G. Cuvier, Recherches sur les ossemens fossiles . . . , ed. 2, 5: 352, 1823.

Type locality.—Near Fos, Bouches-du-Rhone, France.

General distribution.—In the western North Atlantic, reported from Newport, Rhode Island, south to St. Simon Island, Ga.

Description.—A medium-sized whale, ranging up to 28 feet in length. The body is thickset and has a strongly marked median keel extending from the dorsal fin to the tail. The color pattern is extremely variable; the back is usually a purplish black and the underparts white. Males have a single tooth projecting an inch or more beyond the gum at the end of each lower jaw.

Maryland records.—On 5 September 1959, a whale of this species was sighted alive north of Fenwick Island, Del. It stranded that night at

Maryland Beach, Worcester County. This is the only Maryland record, although specimens have stranded at other localities to the north and south of the State.

Family PHYSETERIDAE (sperm whales)

SPERM WHALE

Physeter catodon Linnaeus

[*Physeter*] *catodon* Linnaeus, Syst. Nat., ed. 10, 1:76, 1758.

Type locality.—Kairston, Orkney Islands, Scotland (by restriction, Thomas, Proc. Zool. Soc. London, p. 157, 22 March 1911).

General distribution.—In western North Atlantic from Iceland and Davis Straits, south to Gulf of Mexico, West Indies, Lesser Antilles, and coast of Venezuela.

Description.—This species is the largest of the toothed whales, males sometimes reaching a length of 60 feet or more. Females are considerably smaller, generally under 40 feet in length. In coloration this whale is a uniform gray or dark bluish gray. The narrow lower jaw contains 20 to 30 heavy teeth. Usually no teeth are visible in the upper jaws. There is no dorsal fin.

Maryland records.—Only one sperm whale is known to have stranded on a Maryland beach. It came ashore at Green Run Inlet (now closed) just north of the Maryland-Virginia boundary on Assateague Island in December 1891. This specimen is preserved as a skeleton in the U.S. National Museum.

At times, sperm whales are numerous off Ocean City. They attract the attention of passing boats by their habit of raising their flukes clear of the water when sounding.

PIGMY SPERM WHALE

Kogia breviceps (Blainville)

Physeter breviceps Blainville, Ann. d'Anat. et de Physiol., 2: 337, 1833.

Type locality.—Region of Cape of Good Hope, Republic of South Africa.

General distribution.—In western North Atlantic recorded from Halifax Harbor, Nova Scotia, south to Jupiter Inlet, Florida. This is a pelagic species that is seldom found stranded on beaches.

Description.—A small edition of its larger relative the sperm whale, the pigmy sperm whale ranges in length from 9 to 13 feet. In coloration it is black above, white beneath. There are usually 14 or 15 small needlelike teeth in each lower jaw; no teeth visible in upper jaws. This species, unlike the large sperm whale, possesses a small dorsal fin.

Maryland records.—The pygmy sperm whale is known from Maryland by a live specimen that came ashore at Ocean City, Worcester County, in August 1959. Vacationers at the beach repeatedly tried to push the small whale back to sea. Eventually, during a high tide the animal worked its way into deeper water where it struggled away. The stranding of this whale is discussed in detail by Manville and Shanahan (1961, pp. 269–270).

Family DELPHINIDAE (porpoises and dolphins)

ATLANTIC DOLPHIN

Delphinus delphis Linnaeus

[*Delphinus*] *delphis* Linnaeus, Systema naturae, ed. 10, 1: 77, 1758.

Type locality.—European seas.

General distribution.—In western North Atlantic recorded from Iceland and Woods Hole, Massachusetts, south to Bahama Islands and Jamaica.

Description.—This is a small Cetacean, reaching a length of about 8 feet. The animal possesses a slender “beak” about 6 inches long, which is sharply marked off from the sloping forehead by a deep V-shaped groove. The mouth contains many sharp pointed teeth that interlock perfectly and are adapted for catching and holding the fish upon which the dolphin preys. In coloration, this species is blackish dorsally, including the dorsal surfaces of the flukes and pectoral appendages. The sides shade in coloration to a grayish green, mixed with elliptical bands of whitish on the flanks. The abdomen is white and there is a whitish band over the forehead with a narrow black band in the center that connects the black eye rings. Often there is a black band from the snout to the leading edge of the pectoral fin.

Maryland records.—No records of strandings of this species are available from Maryland, but Charles O. Handley, Jr., says (unpublished manuscript): “In September 1959, Mike Freeman of Washington, D.C., told me of having seen two kinds of porpoises in unusual abundance off Ocean City, Md., and running the Ocean City Inlet into Sinepuxent Bay. His descriptions indicated *Tursiops truncatus* and *Delphinus delphis*.”

This cetacean is probably one of the most abundant in Maryland waters, but it prefers deeper waters off shore, and hence is less likely to strand than several other less numerous species.

BOTTLE-NOSED PORPOISE

Tursiops truncatus (Montague)

Delphinus truncatus Montague, Mem. Wermerian Nat. Hist. Soc., 3: 75, 1821.

Type locality.—Totness, Devonshire, England.

General distribution.—In the western North Atlantic recorded from Massachusetts south to Florida.

Description.—Adults of this species reach a length of 11 or 12 feet, and may be recognized by the purplish lead-gray coloration of the upper parts, the short beak, seldom more than 3 inches long, and the lower jaw, which is slightly longer than the upper. There are 20 to 26 teeth on each side in both jaws of the mouth.

Maryland records.—True (1890, p. 197) says that he has been informed that this species ascends the Potomac River as far as Glymont, a fishing station on the Maryland shore about 18 miles below Washington, D.C.

On 27 and 28 July 1884, a porpoise, presumed to be of this species, was observed in the Potomac River above the Aqueduct Bridge in Washington, D.C. It was chased by boats and shot at repeatedly, but not captured. The species has been seen at various times near Alexandria (unsigned note in *The Pastime*, 3(2), p. 14, August 1884).

In the Chesapeake Bay, *Tursiops* has been reported as far up as Havre de Grace, Harford County (Maryland Tidewater News, 8, p. 40, 1952).

Specimens in the National collections are from the following Maryland localities: Point Lookout, St. Mary's County; Queenstown Creek, Queen Annes County; and Scientist's Cliffs, Calvert County.

In addition, bottle-nosed porpoises are often seen off Ocean City, Worcester County, and swimming in the Ocean City Inlet into Sinepuxent Bay. This is probably the most abundant marine mammal in Maryland waters.

Suborder MYSTICETI (baleen whales)

Whales of this suborder do not possess teeth. Instead, they are equipped with whalebone, or baleen, which hangs down in the mouth from either side of the upper jaws in long strips, with hairlike bristles on the inner edges. The apparatus thus formed serves as a strainer. In feeding, the baleen whales swim open-mouthed through swarms of plankton; then closing the mouth, they press the tongue against the baleen plates, squeezing out the water and leaving the plankton inside the mouth to be swallowed.

Family BALAENOPTERIDAE (fin-backed whales)

LITTLE PIKED WHALE

Balaenoptera acutorostrata Lacépède

Balaenoptera acutorostrata Lacépède, Histoire naturelle des Cétacée . . . , p. 37, 1804.

Type locality.—European seas.

General distribution.—Adults of this species apparently winter in tropical or warm temperate waters, and summer in cold temperate and boreal waters. Young animals, however, may frequent warm or temperate waters during the summer months. In the western North Atlantic, adults have been reported during the summer from Iceland and Greenland south to New Jersey and the Delaware River. There are records of this species in Florida waters during winter months. (see Schwartz, 1962, pp. 206-209).

Description.—The little piked whale resembles a small fin-backed whale in appearance, but is of somewhat stouter build. Adults reach a length of about 30 feet. There are approximately 50 ventral grooves in the throat region, and the baleen is entirely yellowish white in color. The body is blue-gray on the back and white on the abdomen.

Maryland records.—This species has been recorded from Maryland only once. On 12 July 1959, an immature female stranded at Dares Beach, Calvert County, in Chesapeake Bay. Schwartz (1962) discusses this specimen and its stranding in detail.

FIN-BACKED WHALE

Balaenoptera physalus (Linnaeus)

[*Balaena*] *physalus* Linnaeus, Systema naturae, ed. 10, 1: 75, 1758.

Type locality.—Spitzbergen Seas (See Thomas, Proc. Zool. Soc. London, 1911, pt. 1, p. 156, 22 March 1911).

General distribution.—In western North Atlantic, from Iceland and Greenland south to the Gulf of Mexico and Caribbean Sea.

Description.—This is a large baleen whale, the adults measuring between 50 and 65 feet in total length. The coloration is velvety black except for a small ash-colored area at the tip of the lower jaws, a cream-colored chin and throat and occasionally white or piebald underparts. The undersurface of the body in the region of the throat has numerous longitudinal grooves. The dorsal fin is high and triangular, usually with a concave posterior border. The baleen in this species exhibits asymmetry in coloration, the blades on the right side being white for more than a third of the distance from the tip of the snout and the remainder on that side, and all of the left side, being colored a dull blue-gray with streaks of white and yellow. This whale is known as the greyhound of the ocean because of its slender build and great speed in swimming.

Maryland records.—The type specimen of *Sibbaldius tectirostris* Cope (a species now regarded as a synonym of *Balaenoptera physalus*) washed ashore on the Maryland coast near Sinepuxent Inlet, Worcester County, in the winter 1868-69. The skull of this specimen is now in the U.S. National Museum collections.

There is a report in the Maryland Tidewater News (1953) that a whale 60 feet in length was stranded at Ocean City, Worcester County, in the spring of 1953 which probably was of this species.

Fin-backed whales are more numerous off the Maryland coast than these two stranding records would indicate.

BLUE WHALE

Balaenoptera musculus (Linnaeus)

[*Balaena*] *musculus* Linnaeus, Systema naturae, ed. 10, 1: 76, 1758.

Type locality.—Firth of Forth, Scotland (see Thomas, Proc. Zool. Soc. London, 1911, pt. 1, p. 156, 22 March 1911).

General distribution.—In the western North Atlantic, from Iceland and Greenland south to Panama.

Description.—This is the largest animal that ever lived, either on land or in water. Adults sometimes reach lengths in excess of 100 feet, the largest specimens usually being females. The color of this species is slate blue over the whole body with the exception of the tip and undersurface of the flippers, where pigmentation is absent. The blue coloration may be modified by a pale mottling that is sometimes diffused and sometimes concentrated in patches in different parts of the body. There are between 80 and 100 ventral throat grooves and the baleen in the mouth is jet black.

Maryland records.—This species is known from Maryland by a single specimen that grounded near Crisfield, Somerset County, in the summer of 1876. The skeleton of this juvenile individual, identified by G. S. Miller, Jr., is now in the museum of the Natural History Society of Maryland in Baltimore.

Remarks on Maryland Marine Mammals

The above list is composed only of species that have stranded or been observed off the Maryland coast. Many other species undoubtedly pass through Maryland waters and will someday be recorded for the State. Some, such as the short-finned blackfish (*Globicephala macrorhyncha*) and the Atlantic blackfish (*Globicephala melaena*), have stranded on beaches only a few miles south of the Maryland State line. The following is a list of species, presently unrecorded for the State, which probably occur at some time or other in Maryland waters:

Harp seal, *Phoca groenlandica* Erxleben.

Dense-beaked whale, *Mesoplodon densirostris* (Blainville).

Gulf Stream beaked whale, *Mesoplodon europaeus* (Gervais).

Northern beaked whale, *Mesoplodon mirus* True.

Striped porpoise, *Stenella coeruleoalba* (Meyen).

- Atlantic killer whale, *Grampus Orcinus* (Linnaeus).
 Atlantic blackfish, *Globicephala melaena* (Traill).
 Short-finned blackfish, *Globicephala macrorhyncha* Gray.
 Harbor porpoise, *Phocoena phocoena* (Linnaeus).
 Sei whale, *Balaenoptera borealis* Lesson.
 Hump-backed whale, *Megaptera novaeangliae* (Borowski).
 Right whale, *Eubalaena glacialis* (Borowski).

EXTIRPATED RECENT MAMMALS OF MARYLAND

Mansueti (1950) has discussed in detail the extirpated Recent mammals of the State. He lists six species that at one time occurred within Maryland but have vanished since the coming of the white man. As pointed out by Handley and Patton (1947, p. 78) :

Though it is regrettable that man has had a hand in the extinction of these creatures, he is not to be blamed too much, for the ascendency of one species and the extinction of another is a regular process of nature which has been repeated over and over again all down through the ages. Probably man did not have much or anything to do with the disappearance of wild horses, mammoths, mastodons, tapirs, wild pigs, ground sloths and camels which once roamed our lands, but they are gone nevertheless. As surely as a species of animal comes into being, it is destined to eventual extinction, whether by geologic catastrophies such as volcanic eruptions or earthquakes; or by great climatic changes involving vast spreading glaciers or desert wastes, or by the hand of man. Our geologists have given us proof of all this by the fossil record in the rocks.

The six species of extirpated Recent mammals of Maryland discussed by Mansueti (1950) are :

PORCUPINE

Erethizon dorsatum (Linnaeus)

This species apparently never was widely distributed in Maryland, nor was it ever abundant. Mansueti cites records from Allegany County; Blue Ridge Mountains; Frederick-Washington Counties; and Ellicott City, Howard County (all of these prior to 1881). Rhoads (1903, p. 115) cites porcupine records from Fulton and Somerset Counties, Pa., adjacent to Maryland on the north. The Cumberland (Maryland) Sunday Times for 9 August 1964 reported that recently a porcupine was shot on a farm at Rocky Gap, east of Cumberland. A photograph of this animal accompanied the news release. This may represent a valid state record, or the animal may have been brought to Maryland from elsewhere. This same article in the Cumberland Sunday News reports that in 1912 a boy in Frostburg brought some quills

to school from a porcupine he found dead on Mount Savage. It also says that during the fall of 1948 a hunter reported his dogs found a porcupine on Martins Mountain for they returned to him with their noses full of quills. He was not able, however, to locate the porcupine. The foregoing serves to show that there are records and reports of the porcupine in the western part of Maryland right up to the present day. The general consensus of opinion, however, regarding the status of this animal is that it is no longer a native inhabitant of the State.

GRAY WOLF

Canis lupus Linnaeus

The gray wolf originally inhabited the entire State of Maryland. Not only are there documents and publications to show that they were at one time statewide in distribution (see Mansueti, 1950, pp. 25-26), but the early settlers used the name "wolf" to designate many places throughout the State. The Gazetteer of Maryland (Maryland State Planning Comm., and Dept. of Geology, Mines and Water Resources, October 1941, p. 230) lists the following place names in Maryland that give a good idea of where early colonists found wolves: *Allegany County*: Wolf Gap, Wolf Rock; *Baltimore County*: Wolftrap Branch; *Caroline County*: Wolfpit Branch; *Carroll County*: Wolfpit Branch; *Frederick County*: Wolf Rock; *Garrett County*: Wolf Den Run, Wolf Gap, Wolf Swamp; *Somerset County*: Wolf Trap Creek. Mansueti (1950, p. 25) says that they even abounded on Assateague Island in Worcester County.

All evidence seems to indicate that the gray wolf was exterminated in Maryland at a very early date, except for those in more inaccessible parts of western mountains. Here the species probably persisted until late in the 19th century, and perhaps even to the early part of the present century.

MARTEN

Martes americana (Turton)

The marten was exterminated in Maryland as far back as 85 years ago. It apparently was not widespread in distribution, and never abundant. Heavy trapping pressure and destruction of suitable forest habitat appear to account for its demise. It was probably most abundant in the western part of the State, but there are reports from the District of Columbia and perhaps St. Marys County (see Mansueti, 1950, p. 23).

MOUNTAIN LION

Felis concolor Linnaeus

This species at one time occurred throughout the State, wherever there were white-tailed deer, which served as its principal food. The mountain lion was hunted with relentless energy by settlers and at very early date was exterminated from all but the wildest portions of the western part of the State. The date when the last mountain lion was killed in Maryland is not known, but it was probably sometime toward the end of the 19th century. In the 18th century, the species appears to have been abundant in the mountains of Maryland. Meshach Browning (1928) estimated that he killed more than 50 of them during his active period as a hunter in Garrett County from 1790 to 1836. There is no question that today, however, the species is extinct in Maryland despite the fact that from time to time there are reports of them in some of the more remote portions of the State. None of these recent reports of mountain lions in Maryland have ever been verified, and it seems that the species has been extirpated in the entire Eastern United States, with the exception of Florida where a few still persist in the swamps and hammocks in the Everglades.

WAPITI OR ELK

Cervus canadensis (Erxleben)

This species was at one time statewide in distribution. Mansueti (1950, pp. 11-12) lists a number of early references to it, not only from the mountains of the west, but also in the Tidewater. Its former occurrence within the State is attested to by the number of places that bear the name "elk." Thus, there is an Elklick Run in Anne Arundel County, Elklick Run in Garrett County, Elk Mills, Elk Neck, Elk River, and Elkton in Cecil County, Elk Mountain and Elkridge in Washington County, Elkridge in Harford County, Elkridge in Howard County, and Elkridge in Baltimore County. The last of Maryland's wapiti were apparently exterminated long before the middle of the 19th century. McAtee (1918, p. 52) places the date of their extirpation in Virginia as 1844.

BISON

Bison bison (Linnaeus)

According to Mansueti (1950, p. 10) the distribution of bison in Maryland and the District of Columbia must have been above the fall line. The bison thus was an inhabitant of the Piedmont, Ridge and Valley, and Allegheny Mountain sections of the State. When the first settlers arrived, however, the species was already becoming scarce, and

these settlers hastened its demise, exterminating the bison in Maryland by 1775. The Glades Star (publication of the Garrett County Historical Society) for 1943, says that around 1774 one of the Ashbys (early settlers in the Glades of Garrett County) and a neighbor were searching for the neighbor's cows one day in early winter. They followed the tracks of some animals in the light snow until they came to what is now the J. J. Ashby farm, when Ashby saw a bunch of woolly hair on a snag. Following the trail still farther to the hill southeast of the present town of Grellin, they spotted 4 bison. They shot the bulls and the cows escaped westward. These were the last seen in the Glades, and probably the last of Maryland's bison herd.

The former occurrence of the bison is still indicated by such place names as: Buffalo Road (Carroll and Frederick Counties); Buffalo Run, Little Buffalo Run, and Buffalo Marsh (Garrett County).

Mansueti (1950) lists 2 additional species (fisher, *Martes pennanti*; and Canada lynx, *Lynx canadensis*) that may have occurred in Maryland in the past but are not presently a part of the fauna of the State. There is no good evidence, however, that either of these species ever ranged as far south as Maryland.

REFERENCES

- ALLEN, D. L.
1950. The fabulous whistlepig. *Sports Afield*, 123: 28-29, 78-80. June.
- ARNER, D.
1949. Western Maryland beaver. *Maryland Conservationist*, 26: 23-24. Summer.
- AUDUBON, J. J., and J. BACHMAN.
1851. The viviparous quadrupeds of North America. Vol. 2: 334.
- BAILEY, J. W.
1946. The mammals of Virginia. Williams Printing Co., Richmond. 416 p. December.
- BAILEY, V.
1896. List of mammals of the District of Columbia. *Proc. Biol. Soc. Washington*, 10: 93-101. 28 May.
1923. Mammals of the District of Columbia. *Proc. Biol. Soc. Washington*, 36: 103-138. 1 May.
- BANGS, O.
1896. A review of the squirrels of eastern North America. *Proc. Biol. Soc. Washington*, 10: 145-167. 28 December.
- BARBOUR, R. W.
1951. The Mammals of Big Black Mountain, Harlan County, Kentucky. *Journal of Mammalogy*, 32: 100-110. February.
- BARKALOW, F. S., Jr.
1956. *Sciurus niger cinereus* Linne neotype designation. *Proc. Biol. Soc. Washington*, 69: 13-20. 21 May.

BEDNARIK, K. E.

1958. Nutria in the United States with management recommendations for Ohio. Ohio Department of Natural Resources, Division Wildlife, Game Management Publication 165: 1-22. 15 October.

BEE, J. W., and E. R. HALL.

1951. An instance of coyote-dog hybridization. Transactions Kansas Academy of Science, 54: 73-77.

BITELY, R. D.

1963. Maryland whitetails. Maryland Conservationist, 50: 8-10. September-October.

BOLE, B. P., Jr., and P. N. MOULTHROP.

1942. The Ohio Recent mammal collection in the Cleveland Museum of Natural History. Science Publications Cleveland Museum Natural History, 5: 83-181. 11 September.

BONWILL, A. H., and H. B. OWENS.

1939. The return of a native. Bulletin Natural History Society Maryland, 10: 35-45. December.

BOOKHOUT, T. A.

1964. The Allegheny spotted skunk in Maryland. Chesapeake Science, 5: 213-215. Winter.

BRAUN, E. LUCY.

1950. Deciduous forests of eastern North America. Blackiston Co., Philadelphia, 596 p.

BRAYTON, A. M.

1882. Report on the Mammalia of Ohio. Report Geological Survey Ohio, 4: 1-185.

BROWNING, MESHACH.

1928. Forty-four years of the life of a hunter. J. B. Lippincott Co., Philadelphia. 400 p.

BUBES, J. A.

1948. Mammals of a limited area in Maryland, an ecological study in the Bare Hills-Lake Roland area. Maryland Naturalist, 18: 58-72. Fall.

BURT, W. H.

1946. The mammals of Michigan. University of Michigan Press, Ann Arbor. 288 p.

CASLICK, JAMES W.

1956. Color phases of the roof rat, *Rattus rattus*. Journal of Mammalogy, 37: 255-257. May.

CHRISTIAN, J. J.

1956. The natural history of a summer aggregation of the big brown bat, *Eptesicus fuscus fuscus*. American Midland Naturalist, 55: 66-95. January.

CHURCHER, C. S.

1959. The specific status of the New World red fox. Journal of Mammalogy, 40: 513-520. 20 November.

COHEN, E.

1942. *Myotis keeni septentrionalis* (Trouessart) in Maryland. Journal of Mammalogy, 23: 96. February.

1944. A new homing record for the large brown bat. Maryland Naturalist, 14: 65-67. July.

CONAWAY, C. H.

1952. Life history of the water shrew (*Sorex palustris navigator*) American Midland Naturalist, 48: 219-248. July.

CONNER, P. F.

1959. The bog lemming *Synaptomys cooperi* in southern New Jersey. *Publ. Mus. Michigan State University, Biol. Series 1*: 161-248. 24 July.

COOPER, J. E.

1953. An abnormally colored mole from Maryland. *Maryland Naturalist*, 23: 78-79.

COPE, E. D.

1865. (Hooded seals in the Chesapeake Bay). *Proc. Biol. Academy of Science, Philadelphia*, 273.

COUES, E.

1877. *Fur bearing animals: A monograph of North American Mustelidae*. Department of the Interior, U.S. Geological Survey of the Territories Misc. Publ. 8. 348 p.

DAVIS, D. E., and W. T. FALES.

1949. The distribution of rats in Baltimore, Maryland. *American Journal of Hygiene, Baltimore*, 49: 247-254. May.

1950. The rat population of Baltimore, 1949. *American Journal of Hygiene, Baltimore*, 52: 143-146. September.

DAVIS, W. H.

1957. A new subspecies of the eastern pipistrelle from Florida. *Proc. Biol. Soc. Washington*, 70: 213-215. 31 December.

1959. Taxonomy of the eastern pipistrel. *Journal of Mammalogy*, 40: 521-531. November.

DAVIS, W. H., and R. E. MUMFORD.

1962. Ecological notes on the bat *Pipistrellus subflavus*. *American Midland Naturalist*, 68: 394-398. October.

DOZIER, H. L.

1948a. A new eastern marsh-inhabiting race of raccoon. *Journal of Mammalogy*, 29: 286-290. August.

1948b. Color mutations in the muskrat (*Ondatra z. macrodon*) and their inheritance. *Journal of Mammalogy*, 29: 393-405. November.

DOZIER, H. L., and H. E. HALL.

1944. Observations on the Bryant fox squirrel. *Maryland Conservationist*, 21: 1-12. Winter Issue.

DOZIER, H. L., M. H. MARKLEY, and L. M. LLEWELLYN.

1948. Muskrat investigations on the Blackwater National Wildlife Refuge, Maryland, 1941-1945. *Journal of Wildlife Management*, 12: 177-190. April.

FENNEMAN, N. M.

1938. *Physiography of eastern United States*. McGraw-Hill Book Co., New York and London. 714 p.

FLEROV, K. K.

1952. Musk deer and deer. *Fauna of the U.S.S.R. Mammals 1*: 1-257 (English translation, 1960, by National Science Foundation and Smithsonian Institution).

FLYGER, V. F.

1957. New record for red squirrel in Maryland. *Maryland Tidewater News*, March-April 1957, p. 1.

1958. The status of white-tailed deer in Maryland, 1956. *Resource Study Rept.*, Maryland Department of Research and Education, 13: 1-9. March.

1959. Maryland's new deer citizens. *Maryland Conservationist*, 36: 23-24. March.

- 1960a. Sika deer on islands in Maryland and Virginia. *Journal of Mammalogy*, 41 : 140. 20 February.
- 1960b. Movements and home range of the gray squirrel, *Sciurus carolinensis*, in two Maryland woodlots. *Ecology*, 41 : 365-369. April.
- FLYGER, V. F., and J. WARREN.
1958. Sika deer in Maryland. Additional big name animal or a possible pest. Proceedings 12th Annual Conference S. E. Association Game and Fish Commission, p. 209-211.
- FLYGER, VAGN, and N. W. DAVIS.
1964. Distribution of sika deer (*Cervus nippon*) in Maryland and Virginia in 1962. *Chesapeake Science*, 5 : 212-213. Winter.
- GARDNER, M. C.
- 1950a. A list of Maryland mammals. Part I. Marsupials and insectivores. *Proc. Biol. Soc. Washington*, 63 : 65-68. 25 May.
- 1950b. A list of Maryland mammals. Part II. Bats. *Proc. Biol. Soc. Washington*, 63 : 111-114. 29 December.
- GENTILE, J.
1949. A case of partial albinism in the short-tailed shrew. *Maryland Naturalist*, 19 : 11-12. Winter.
- GIDLEY, J. W., and C. L. GAZIN.
1933. New Mammalia in the Pleistocene fauna from Cumberland Cave. *Journal of Mammalogy*, 14 : 343-357. November.
- GOLDMAN, E. A.
1950. Raccoons of North and Middle America. *North American Fauna*, 60. 153 p.
- GOLDMAN, E. A., and H. H. T. JACKSON.
1939. Natural History of Plummers Island, Maryland. IX. Mammals. *Proc. Biol. Soc. Washington*, 52 : 131-134. 11 October.
- GRIZZELL, R. A., Jr.,
1949. Hibernating jumping mice in woodchuck dens. *Journal of Mammalogy*, 30 : 74-75. February.
- HALL, E. R.
1951. American weasels. University Kansas Publications, Museum Natural History, 4 : 1-466. 27 December.
- HALL, E. R., and K. R. KELSON.
1959. The mammals of North America. Ronald Press Co., New York. 2 vols., 1162 p. 31 March.
- HALL, J. S.
1962. A life history and taxonomic study of the Indiana bat, *Myotis sodalis*. Scientific Publications Reading Museum and Art Gallery, Reading, Pa., 12 : 1-68. 30 July.
- HAMILTON, W. J., Jr.
1930. The food of the Soricidae. *Journal of Mammalogy*, 11 : 26-39. February.
- 1933a. The insect food of the big brown bat. *Journal of Mammalogy*, 14 : 155-156. May.
- 1933b. The weasels of New York : Their natural history and economic status. *American Midland Naturalist*, 14 : 289-344. July.
1935. Habits of jumping mice. *American Midland Naturalist*, 16 : 187-200. March.
1937. The biology of microtine cycles. *Journal of Agricultural Research*, Washington, 54 : 779-790. 15 May.
1938. Life history notes on the northern pine mouse. *Journal of Mammalogy*, 19 : 163-170. 14 May.

1940. The biology of the smokey shrew (*Sorex fumeus fumeus*). *Zoologica* 25: 473-492. 31 December.
1941. The food of small forest mammals in eastern United States. *Journal of Mammalogy*, 22: 250-263. 14 August.
1943. The mammals of eastern United States. Comstock Publishing Co., Ithaca, N.Y. 432 p.
1950. The prairie deer mouse in New York and Pennsylvania. *Journal of Mammalogy*, 31: 100. 21 February.
- HAMLETT, G. W. D.
1938. The reproductive cycle of the coyote. U.S. Department Agriculture Tech. Bull. 616. 11 p. July.
- HAMPE, I. E.
1936. The occurrence and breeding of the Maryland shrew (*Sorex fontinalis*) in the Patapsco State Park. *Bulletin Natural History Society, Maryland*, 7: 17-18. December. (Mimeographed)
1939. Notes on the mammals of the Patapsco State Park. *Bulletin Natural History Society, Maryland*, 10: 4-7. September. (Mimeographed)
1943. Mammal note. *Bulletin Natural History Society Maryland*, 23: 66. April, May, June.
- HANDLEY, C. O., JR.
1956. The shrew *Sorex dispar* in Virginia. *Journal of Mammalogy*, 37: 435. August.
1959. A revision of American bats of the genera *Euderma* and *Plecotus*. *Proceedings U.S. National Museum*, 110: 95-246. 3 September.
- HANDLEY, C. O., JR., and C. P. PATTON.
1947. Wild mammals of Virginia. Commonwealth of Virginia Commission Game and Inland Fisheries, Richmond. 220 p.
- HARDY, J. D., JR.
1950. What is happening to the muskrat. *Maryland Conservationist*, 27: 8-9. 27. Fall.
- HARRIS, V. T.
1952. Muskrats on tidal marshes of Dorchester County. Chesapeake Biological Laboratory, Solomons, Md., Publication 91. 36 p.
1953. Ecological relationships of meadow voles and rice rats in tidal marshes. *Journal of Mammalogy*, 34: 479-487. November.
1956. The nutria as a wild fur mammal in Louisiana. *Trans. Twenty-first North American Wild. Conference*, p. 424-475.
- HARTMAN, C. G.
1952. *Possums*. University of Texas Press, Austin. 174 p.
- HERMAN, C. M., P. M. BAUMAN, and R. T. HABERMAN.
1957. The presence of *Eurytrema procyonis* Denton (Trematoda: Dicrocoeliidae) in some mammals from Maryland. *Journal Parasitology* 43: 113-114. February.
- HERMAN, C. M., and J. R. REILLY.
1955. Skin tumors on squirrels. *Journal of Wildlife Management*, 19: 402-403. July.
- HERMAN, C. M., and O. WARBACH.
1956. Incidence of Shope's rabbit fibroma in cottontails at the Patuxent Research Refuge. *Journal of Wildlife Management*, 20: 85-89. January.
- HINTON, M. A. C.
1931. Rats and mice as enemies of mankind. *British Museum (Natural History) Economic Series No. 8*. 70 p.

HOLLISTER, N.

1911. A systematic synopsis of the muskrats. *North American Fauna* 32. 47 p. 29 April.

HOOPER, E. T.

1942. The water shrew (*Sorex palustris*) of the southern Allegheny Mountains. *Occas. Papers Museum Zoology University of Michigan*, 463: 1-4. 15 September.

HOSLEY, N. W.

1956. Management of the white-tailed deer in its environment, pp. 187-259 in *The deer of North America*. Stackpole Co., Harrisburg, Pa., and Wildlife Management Institute, Washington, D.C.

HOWARD, W. E.

1949. A means to distinguish skulls of coyotes and domestic dogs. *Journal of Mammalogy*, 30: 169-171. May.

HOWELL, A. H.

1908. Notes on diurnal migrations of bats. *Proc. Biol. Soc. Washington*, 21: 35-38. 23 January.

1914. Revision of the American harvest mice. *North American Fauna* 36. 97 p. 14 June.

1925. Preliminary descriptions of five new chipmunks from North America. *Journal of Mammalogy*, 6: 51-54. February.

1929. Revision of the American Chipmunks (genera *Tamias* and *Eutamias*). *North American Fauna* 62. 157 p. 30 November.

1940. A new race of the harvest mouse (*Reithrodontomys*) from Virginia. *Journal of Mammalogy*, 21: 346. 14 August.

JACKSON, H. H. T.

1915. A review of the American moles. *North American Fauna* 38. 100 p. 30 September.

1922. A coyote in Maryland. *Journal of Mammalogy*, 3: 186-187. August.

1928. A taxonomic review of the American long-tailed shrews (genera *Sorex* and *Microsorex*). *North American Fauna* 51. 238 p. 24 July.

1961. *Mammals of Wisconsin*. University of Wisconsin Press, Madison.

JONES, J. K., Jr., and J. S. FINDLEY.

1954. Geographic distribution of the short-tailed shrew, *Blarina brevicauda*, in the Great Plains. *Transactions Kansas Academy of Science*, 57: 208-211. 2 August.

KELLOGG, R.

1937. Annotated list of West Virginia mammals. *Proceedings U.S. National Museum*, 84: 443-479. 7 October.

1939. Annotated list of Tennessee mammals. *Proceedings U.S. National Museum*, 86: 245-303. 14 February.

1956. What and where are the whitetails? p. 31-55 in *The deer of North America*. Stackpole Co., Harrisburg, Pa., and Wildlife Management Institute, Washington, D.C.

KILHAM, L.

1954. Cow-pasture nests of *Cryptotis parva parva*. *Journal of Mammalogy*, 35: 252. May.

KILHAM, L., and C. M. HERMAN.

1955. Severe infestation of blow flies in a raccoon. *Journal of Wildlife Management*, 19: 499. October.

KIRKWOOD, F. C.

1931. Swimming of the muskrat. *Journal of Mammalogy*, 12: 317-318. August.

KOLB, C. H.

1938. Mammals from the Loch Raven area. Bulletin Natural History Society, Maryland, 9: 1-5. September.

KREUTZSCH, P. H.

1954. North American jumping mice (genus *Zapus*). University Kansas Publication Museum Natural History, 7: 349-472. 21 April.

LAMORE, D.

1953. Common skunk has meal of yellow jackets. Maryland Naturalist, 23: 80.

LATHAM, R. M., and C. R. STUDHOLME.

1947. Spotted skunk in Pennsylvania. Journal of Mammalogy, 28: 409. 26 November.

LAYNE, J. N.

1955. Seminole bat, *Lasiurus seminolus*, in central New York. Journal of Mammalogy, 36: 453. August.

LECOMPTE, E. L.

1937. Otter caught in gill net. Maryland Conservationist, 14: 15. Summer Issue.

1942. Analysis of game kill statistics for season of 1941. Maryland Conservationist, 19: 4-5, 8.

LEWIS, J. B.

1940. Mammals of Amelia County, Virginia. Journal of Mammalogy, 21: 422-428. 14 November.

LIERS, E. E.

1951. Notes on the river otter (*Lutra canadensis*). Journal of Mammalogy, 32: 1-9. 15 February.

LLEWELLYN, L. M., and F. H. DALE.

1964. Notes on the ecology of the opossum in Maryland. Journal of Mammalogy, 45: 113-122. February.

LLEWELLYN, L. M., and C. O. HANDLEY.

1945. The cottontail rabbits of Virginia. Journal of Mammalogy, 26: 379-390. February.

LLEWELLYN, L. M., and F. M. UHLER.

1952. The foods of fur animals of the Patuxent Research Refuge, Maryland. American Midland Naturalist, 48: 193-203. July.

LONG, C. A.

1963. Mathematical formulas expressing faunal resemblance. Transactions Kansas Academy of Science, 66: 138-140.

MANSUETI, R.

1941. Trouessart's little brown bat around Baltimore. Bulletin Natural History Society Maryland, 11: 56-57. January-February.

1950. Extinct and vanishing mammals of Maryland and District of Columbia. Maryland Naturalist, 20: 1-48. Winter-Spring.

1952. Comments on the fox squirrels of Maryland. Maryland Naturalist, 22: 30-41.

1953. The varying hare, or snowshoe rabbit, in Maryland. Maryland Naturalist, 23: 71-75.

1955. Seal strays into Maryland waters. Maryland Tidewater News, 12: (3) 1. August.

1958. The Cranesville Pine Swamp. Atlantic Naturalist, 13: 72-84. April-June.

MANSUETI, R., and V. F. FLYGER.

1952. Longtailed shrew (*Sorex dispar*) in Maryland. Journal of Mammalogy, 33: 250. May.

MANVILLE, R. H., and R. P. SHANAHAN.

1961. *Kogia* stranded in Maryland. *Journal of Mammalogy*, 42: 269-270. May.

MARTIN, A. C., H. S. ZIM, and A. L. NELSON.

1951. American wildlife and plants. McGraw-Hill Book Co., New York. 500 p.

MARYE, W. B.

1945. Some extinct wild animals of Tidewater. *Maryland Tidewater. News*, 2: 1-3.

MAYNARD, C. J.

1889. Singular effects produced by the bite of a short-tailed shrew, *Blarina brevicauda*. *Contributions to Science*, 1: 57-59. July.

McATEE, W. L.

1918. A sketch of the natural history of the District of Columbia. *Bulletin Biological Society Washington*, 1: 3-142. May.

McKEEVER, S., et al.

1952. A survey of West Virginia mammals. Conservation Commission, West Virginia Pittman-Robertson Project 22-R. 126 p. 4 January. (Mimeographed)

MERRIAM, C. H.

1887. Do any Canadian bats migrate? Evidence in the affirmative. *Transactions Royal Society of Canada, Section 4*: 85-87.

1895. Revision of the shrews of the American genera *Blarina* and *Notiosorex*. *North American Fauna* 10. 125 p. 31 December.

MILLER, G. S., Jr.

1897. Revision of the North American bats of the family Vespertilionidae. *North American Fauna* 13. 140 p. 16 October.

1912. Catalogue of the mammals of western Europe. *British Museum (Natural History)*. 1019 p.

1924. List of North American Recent mammals, 1923. *Bulletin U.S. National Museum*, 128. 673 p.

MILLER, G. S., Jr., and R. KELLOGG.

1955. List of North American Recent mammals. *Bulletin U.S. National Museum* 205. 954 p. 3 March.

MITCHELL, A. L.

1934. Eastern extension of the range of *Peromyscus maniculatus bairdii*. *Journal of Mammalogy*, 15: 71. February.

MOULTHROP, P. N.

1938. The pairie white-footed mouse in New York State. *Journal of Mammalogy*, 19: 503. 14 November.

NELSON, E. W.

1909. The rabbits of North America. *North American Fauna* 29. 314 p. 31 August.

OSGOOD, W. H.

1909. Revision of the mice of the American genus *Peromyscus*. *North American Fauna* 28. 285 p. 17 April.

PATTON, C. P.

1939. Distribution notes on certain Virginia mammals. *Journal of Mammalogy*, 20: 75-77. February.

PEACOCK, D., and R. PEACOCK.

1962. *Peromyscus maniculatus bairdii* in Virginia. *Journal of Mammalogy*, 43: 98. February.

PEARSON, O. P.

1942. On the cause and nature of a poisonous action by the bite of a shrew (*Blarina brevicauda*). *Journal of Mammalogy*, 23: 159-166. May.

PEARSON, O. P., M. R. KOFORD, and A. K. PEARSON.

1952. Reproduction of the lump-nosed bat (*Corynorhynchus rafinesquei*) in California. *Journal of Mammalogy*, 33: 273-320. August.

POOLE, A. J., and VIOLA S. SCHANTZ.

1942. Catalog of the type specimens of mammals in the United States National Museum, including the Biological Surveys collection. *Bulletin U.S. National Museum* 178: 705 p. 9 April.

POOLE, E. L.

1932. *Lasiurus seminolus* in Pennsylvania. *Journal of Mammalogy*, 13: 162. May.

1937. Pennsylvania records of *Sorex cinereus fontinalis*. *Journal of Mammalogy*, 18: 96. 14 February.

1943. *Synaptomys cooperi stonei* from Eastern Shore of Maryland. *Journal of Mammalogy*, 24: 103. 20 February.

PREBLE, E. A.

1899. Revision of the jumping mice of the genus *Zapus*. *North American Fauna* 15: 42 p. 8 August.

PRESNAL, C. C.

1958. The present status of exotic mammals in the United States. *Journal of Wildlife Management*, 22: 45-50. January.

QUIMBY, D. C.

1951. The life history and ecology of the jumping mouse, *Zapus hudsonius*. *Ecological Monographs*, Durham, 21: 61-95. January.

RHOADS, S. N.

1903. The mammals of Pennsylvania and New Jersey. Privately published. Philadelphia. 266 p. After 11 April.

SCHWARTZ, F. J.

1962. Summer occurrence of an immature little piked whale, *Balaenoptera acutorostrata*, in Chesapeake Bay, Maryland. *Chesapeake Science* 3: 206-209. September.

SCHWARZ, E., and HENRIETTE K. SCHWARZ.

1943. The wild and commensal stocks of the house mouse, *Mus musculus* Linnaeus. *Journal of Mammalogy*, 24: 59-72. 20 February.

SEIBERT, HENRI

1939. Weasel. *Bulletin Natural History Society of Maryland*, 10(1): 21, September.

SEVERINGHAUS, C. W., and E. L. CHEATUM

1956. Life and times of the white-tailed deer, pp. 57-186 in *The deer of North America*. Stackpole Co., Harrisburg, Pa., and Wildlife Management Institute, Washington, D.C.

SHEFFER, D. E.

1957. Cottontail rabbit propagation in small breeding pens. *Journal of Wildlife Management*, 21: 90. January.

SHREVE, F., M. A. CHRYSLER, F. H. BLODGETT, and F. W. BESLEY.

1910. The plant life of Maryland. Maryland Weather Service. Baltimore, Johns Hopkins Press, 1910, v. 3. 533 p.

SILVER, JAMES

1928. Pilot black snake feeding on big brown bat. *Journal of Mammalogy*, 9: 149, May.

SMITH, F. R.

1938. Muskrat investigations in Dorchester County, Maryland, 1930-1934. U.S. Department of Agriculture Circular 474. 24 p. May.

SOLLBERGER, D. E.

1940. Notes on the life history of the small eastern flying squirrel. *Journal of Mammalogy*, 21: 282-293. 14 August.

1943. Notes on the breeding habits of the eastern flying squirrel (*Glaucomys volans volans*). *Journal of Mammalogy*, 24: 163-173. May.

SPERRY, C. C.

1941. Food habits of the coyote. U.S. Department of the Interior, Wildlife Research Bulletin 4. 70 p.

STEWART, R. E., and C. S. ROBBINS.

1958. Birds of Maryland and the District of Columbia. *North American Fauna* 62. 401 p.

STICKEL, LUCILLE F.

1946. The source of animals moving into a depopulated area. *Journal of Mammalogy*, 27: 301-307. 25 November.

1948. Observations on the effect of flood on animals. *Ecology* 29: 505-506. October.

STICKEL, W. H.

1951. Occurrence and identification of the prairie deer-mouse in central Maryland. *Proc. Biol. Soc. Washington*, 64: 25-32. 13 April.

TATE, G. H. H.

1947. *Mammals of eastern Asia*. Macmillan Co., New York. 366 p.

TROMBA, F. G.

1954. Some parasites of the hoary bat *Lasiurus cinereus* (Beauvois). *Journal of Mammalogy*, 35: 253-254. May.

TRUE, F. W.

1890. Observations on the life history of the bottlenose porpoise. *Proceedings U.S. National Museum*, 13: 197-203.

UHLER, F. M., and L. M. LLEWELLYN

1952. Fur productivity of submarginal farmland. *Journal of Wildlife Management*, 16: 79-86. January.

VAN GELDER, R. G.

1959. A taxonomic revision of the spotted skunks (genus *Spilogale*). *Bulletin American Museum Natural History*, 117: 229-392. 15 June.

VÁZQUEZ, A. W.

1956. A new southern record for *Mustela crminea cicognanii*. *Journal of Mammalogy*, 37: 113-114. February.

WETMORE, A.

1923. The wood rat in Maryland. *Journal of Mammalogy*, 4: 187-188. August.

WETZEL, R. M.

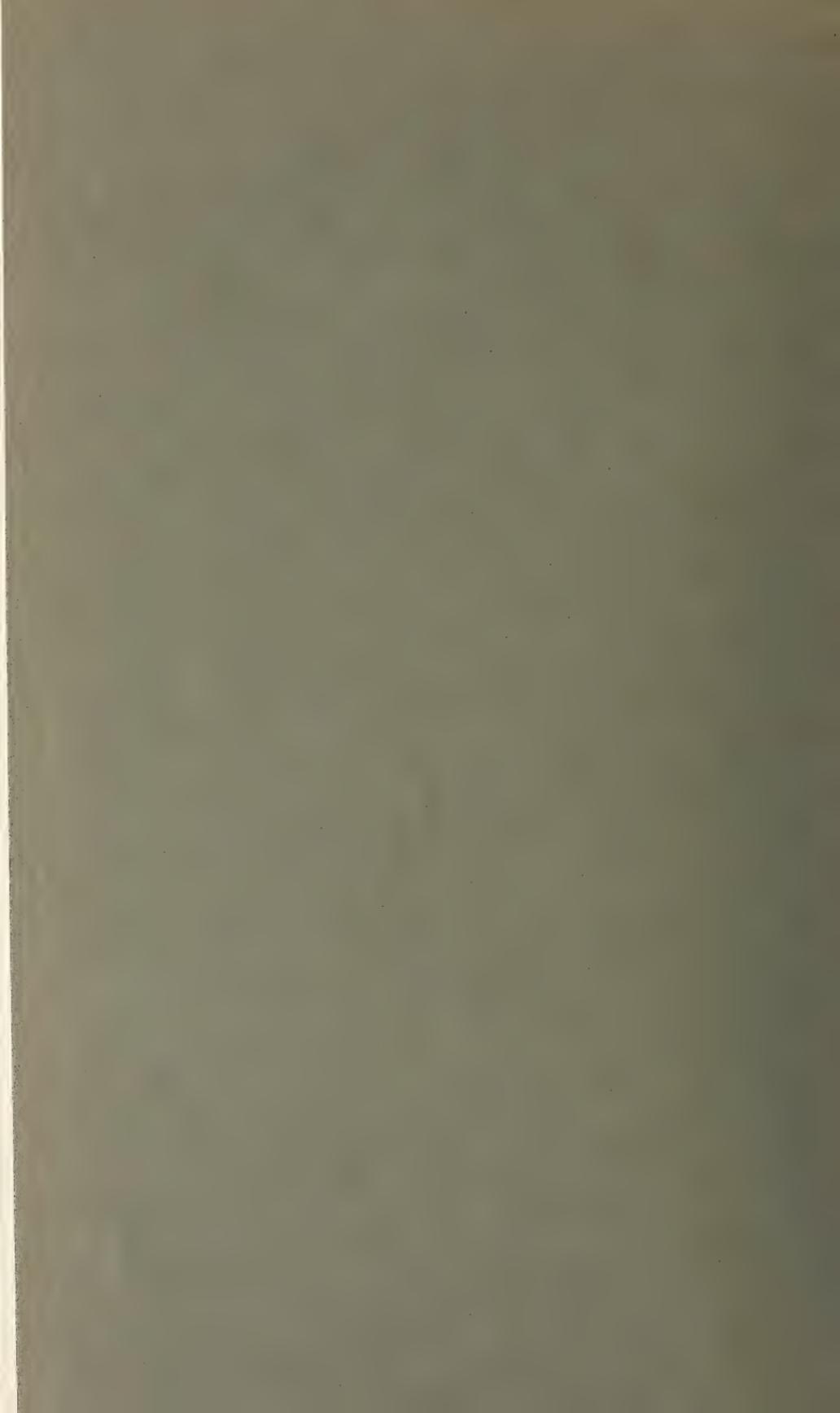
1955. Speciation and dispersal of the southern bog lemming, *Synaptomys cooperi* (Baird). *Journal of Mammalogy*, 36: 1-20. February.

YOUNG, S. P., and H. H. T. JACKSON.

1951. *The clever coyote*. Stackpole Co., Harrisburg, Pa., and Wildlife Management Institute, Washington, D.C. 411 p.

As the Nation's principal conservation agency, the Department of the Interior has basic responsibilities for water, fish, wildlife, mineral, land, park, and recreational resources. Indian and Territorial affairs are other major concerns of this department of natural resources.

The Department works to assure the wisest choice in managing all our resources so that each shall make its full contribution to a better United States now and in the future.



QL
151
N864
NH

NATURAL HISTORY
OF THE
KING RAIL



NUMBER 67

UNITED STATES
DEPARTMENT OF THE INTERIOR
BUREAU OF SPORT FISHERIES AND WILDLIFE



NORTH AMERICAN FAUNA

This publication series includes monographs and other reports of scientific investigations relating to birds, mammals, reptiles, and amphibians, for professional readers. It is a continuation by the Bureau of Sport Fisheries and Wildlife of the series begun in 1889 by the Division of Ornithology and Mammalogy (Department of Agriculture) and continued by succeeding bureaus—Biological Survey and Fish and Wildlife Service. The Bureau distributes these reports to official agencies, to libraries, and to researchers in fields related to the Bureau's work; additional copies may usually be purchased from the Division of Public Documents, U.S. Government Printing Office.

Reports in NORTH AMERICAN FAUNA since 1950 are as follows (an asterisk indicates that sale stock is exhausted):

- *60. Raccoons of North and Middle America, by Edward A. Goldman. 1950. 153 p.
- *61. Fauna of the Aleutian Islands and Alaska Peninsula, by Olaus J. Murie; Invertebrates and Fishes Collected in the Aleutians, 1936-38, by Victor B. Scheffer. 1959. 406 p.
- *62. Birds of Maryland and the District of Columbia, by Robert E. Stewart and Chandler S. Robbins. 1958. 401 p.
- *63. The Trumpeter Swan; Its history, habits, and population in the United States, by Winston E. Banko. 1960. 214 p.
- *64. Pelage and Surface Topography of the Northern Fur Seal, by Victor B. Scheffer. 1961. 206 p.
- 65. Seven New White-winged Doves From Mexico, Central America, and Southwestern United States, by George B. Saunders. 1968. 30 p.
- 66. Mammals of Maryland, by John L. Paradiso, 1969. 193 p.
- 67. Natural History of the King Rail, by Brooke Meanley. 1969. 108 p.

NATURAL HISTORY
OF THE
KING RAIL



King Rail near Jacksonville, Fla. (Photograph by Samuel A. Grimes)

**NATURAL HISTORY
OF THE
KING RAIL**

By Brooke Meanley, *Wildlife Biologist*

**Patuxent Wildlife Research Center
Division of Wildlife Research
BUREAU OF SPORT FISHERIES AND WILDLIFE**



NUMBER 67

UNITED STATES
DEPARTMENT OF THE INTERIOR
Walter J. Hickel, *Secretary*

Leslie L. Glasgow, *Assistant Secretary for
Fish and Wildlife, Parks, and Marine Resources*

FISH AND WILDLIFE SERVICE
Charles H. Meacham, *Commissioner*

BUREAU OF SPORT FISHERIES AND WILDLIFE
John S. Gottschalk, *Director*



North American Fauna, Number 67
Published by
Bureau of Sport Fisheries and Wildlife
May 1969

U.S. GOVERNMENT PRINTING OFFICE
WASHINGTON : 1969

Contents

	Page
INTRODUCTION.....	1
HISTORY AND SYSTEMATIC POSITION.....	4
History.....	4
Systematic position.....	6
Relationship to the Clapper Rail.....	6
DISTRIBUTION AND MIGRATION.....	10
Distribution.....	10
Migration.....	12
Local movements.....	14
ECOLOGICAL RELATIONS.....	16
Louisiana gulf coast marshes.....	16
The delta marsh.....	16
The subdelta marsh.....	17
The prairie marshes.....	18
Southern ricefields.....	20
Florida.....	25
South Carolina Low Country.....	27
Savannah National Wildlife Refuge.....	29
Upper Savannah River Valley.....	32
Chesapeake Bay Country.....	32
Tidewater Virginia.....	32
Virginia Eastern Shore.....	34
Maryland Eastern Shore.....	35
Inner Coastal Plain of Maryland.....	38
Delaware Bay, Del.....	39
Great Lakes region.....	41
North-central prairie marshes.....	42
Northern Great Plains.....	42
DESCRIPTION.....	43
Size.....	43
Adult plumage.....	43
Legs and feet.....	45
Bill.....	45
Tongue and lining of mouth.....	45
Eye.....	45
Notes on sexing and aging.....	45
Molting.....	46
BREEDING BIOLOGY.....	48
Homing.....	48
Territories.....	48
Defense of territories.....	49
Courtship behavior.....	50
Mating call and pair formation.....	50
Other calls.....	50
Display.....	51
Courtship feeding.....	53

	Page
Prenesting activity-----	53
Calling-----	53
Symbolic nest building-----	54
Copulation-----	54
Nesting period-----	54
Nest site and materials-----	57
Egg laying and clutch size-----	61
Clutch size-----	61
Description of eggs-----	61
Weight of eggs-----	62
Incubation-----	62
Hatching-----	64
Nesting success and survival-----	65
Breeding status of first-year birds-----	65
DEVELOPMENT AND BEHAVIOR OF CAPTIVE RAILS-----	66
Development of Young-----	66
First-day chick-----	66
One to thirty days-----	67
Thirty to sixty days-----	68
First winter plumage-----	72
Miscellaneous notes on behavior of young-----	72
Sleeping-----	72
Competition-----	73
Bathing-----	73
Winter behavior of captive rails-----	73
FOODS-----	75
Arkansas ricefields-----	77
Texas ricefields-----	79
Louisiana ricefields-----	79
Upper St. Johns River, Fla-----	79
Currituck Sound, N.C-----	79
Patuxent River, Md-----	80
Beaver Dam, Wis-----	80
Chicago, Ill-----	80
FEEDING BEHAVIOR-----	81
Pellet casting-----	81
Feeding young-----	82
Regional observations-----	83
Arkansas ricefields-----	83
Delaware Bay marshes-----	83
Savannah National Wildlife Refuge-----	84
Some unusual observations-----	85
MORTALITY FACTORS-----	86
Manmade objects-----	86
Predation-----	86
Hurricanes-----	88
THE KING RAIL AS A GAME BIRD-----	90
Methods of hunting-----	90
Patuxent River, Md-----	91
Eagle Lake area, Tex-----	93
Other areas-----	93
SUMMARY-----	95
LITERATURE CITED-----	98

APPENDIX 1—METHODS OF CAPTURING FOR BANDING.....	103
Types of capturing devices.....	103
Long-handled dip or clap net.....	103
All-purpose or cloverleaf trap.....	103
Tending traps.....	105
Age for banding King Rail chicks.....	106
Need for banding data.....	106
APPENDIX 2.—LOCAL NAMES.....	107

ILLUSTRATIONS

Frontispiece, King Rail near Jacksonville, Fla.....	ii
FIGURE	
1. A King Rail walking.....	3
2. Mated King Rail and Clapper Rail collected in Delaware....	8
3. Approximate breeding range and principal distribution of the King Rail in North America.....	10
4. Louisiana coastal marshes.....	17
5. Prairie marsh, Grand Chenier, La.....	18
6. Southern bulrush, fall panicum, and alligatorweed in the Prairie Marsh type.....	21
7. King Rail wading through ricefield.....	22
8. Arkansas Grand Prairie near Stuttgart.....	23
9. Nest of King Rail in wet rice stubble.....	24
10. Habitat of King Rail, Indian River County, Fla.....	26
11. King Rail habitat on Seminole Indian Reservation, Glades County, Fla.....	27
12. Floodgate and ricefield canal near Savannah, Ga.....	28
13. South Carolina Low Country: ricefield nesting habitat along Savannah River, Jasper County.....	30
14. Alligatorweed in canal at Savannah National Wildlife Refuge..	31
15. Big cordgrass habitat, Nanticoke River marsh, Md.....	33
16. Winter abode of King Rail, Rappahannock River near Tappa- hannock, Va.....	34
17. Switchgrass habitat of King Rail, Elliott Island, Md.....	36
18. Nest and eggs of King Rail in Nanticoke River marsh, Vienna, Md.....	37
19. Nest and 9 eggs of King Rail in brackish marsh, Long Marsh Island, Eastern Bay (of Chesapeake Bay), Md.....	38
20. Taylor's Gut at low tide, Kent County, Del.....	39
21. Displays of the King Rail.....	52
22. Canopy on King Rail nest in roadside ditch, Arkansas Grand Prairie.....	58
23. King Rail nest in roadside ditch near Stuttgart, Ark.....	58
24. King Rail incubating in nest of cattails in roadside ditch, Arkansas Grand Prairie.....	59
25. King Rail incubating in open nest along roadside ditch, Mamou, La.....	59
26. Distraction display of King Rail near nest.....	64
27. Downy young King Rail, 31 days old, with juvenal plumage beginning to develop.....	69
28. Ventral view of 31-day-old King Rail showing development of white juvenal plumage in sternal and abdominal regions and crural tract.....	70

	Page
29. Fifty-day-old King Rail with juvenal plumage nearly complete.....	71
30. Captive King and Clapper Rails at Patuxent Wildlife Research Center, Laurel, Md.....	74
31. Foods of the King Rail in a brackish bay marsh, Kent County, Del.....	77
32. Regurgitated King Rail pellets from Dorchester County, Md...	82
33. Method of hunting railbirds in Patuxent River wildrice marshes, Maryland.....	91
34. Railbird boats tied up after the hunting season.....	92
35. Method of hunting railbirds in southern ricefields.....	94
36. All-purpose or cloverleaf trap and drift fence in shrub swamp at Patuxent Wildlife Research Center.....	104
37. All-purpose or cloverleaf trap.....	104

Photographs are by the author unless otherwise credited.

Introduction

The King Rail (*Ballus elegans* Audubon), largest of North American rails, is indeed an elegant bird, as its Latin name implies. Its striking appearance (fig. 1), secretive nature, and association with a variety of wetland habitats make it a favorite of bird students and rail hunters. The King Rail is found in most of the eastern half of North America, from the Atlantic coast to the Great Plains and from the Gulf of Mexico to southern Canada. It is most abundant in the fresh and brackish tidal marshes of the Atlantic and Gulf Coastal Plain, the domestic ricefields of Arkansas, Louisiana, and Texas, and the marshes of southern Florida. It is fairly common in parts of the Midwest Prairie and Great Lakes region.

I began my studies of this interesting bird in 1950 in the Arkansas ricefields, and have continued them until 1967, both in the field and in the laboratory.

Many of the field observations, particularly those of courtship behavior, were made from an automobile which served as an admirable mobile blind. Such a blind was used to follow courting rails along roadside ditches in Arkansas and Louisiana, making it possible to study the detailed nuptial courtship behavior of 20 different pairs and the prenuptial behavior of four. Under these conditions it was possible also to distinguish the sexes by their behavior rather than by their size differences, which are sometimes difficult to ascertain in the field.

The highly vocal nature of the King Rail and its characteristic calls, varying with different conditions, enhance the value of field observations and made the call-count census a practical technique.

Studies of growth and development of the young were made with captive birds, which are quite tractable if obtained early in life from nests or hatched from eggs in incubators.

Studies of breeding biology were made mostly on the Arkansas Grand Prairie in the vicinity of Stuttgart from 1950 through 1955. Subsequent studies on life history and ecology were made at Mamou, Evangeline Parish, La.; Broadway Meadows near Woodland Beach, Kent County, Del.; the Pee Dee River at Georgetown, S.C.; the Savannah National Wildlife Refuge, Jasper County, S.C.; and the Patuxent Wildlife Research Center, Laurel, Md.

I have supplemented my own observations with a review of the published studies of others and have attempted to bring all information on the King Rail together into a monographic treatment.

My discussions in this paper include the history of the discovery of the King Rail as a distinct species by Audubon in 1834 and its systematic position in relation to the Clapper Rail, as taken mostly from the literature. The discussions of other topics are largely from my own observations, but supplemented with literature reports. The principal topics include distribution and migration; ecological relations; physical characteristics; breeding biology; development and behavior of captive rails; foods and feeding; mortality factors; and the King Rail's position as a game bird. Appendixes include methods of capturing and banding and a list of local names. Aquatic plant names used in the text are from Hotchkiss (1950) unless otherwise indicated.

I am indebted to many persons for assistance with this project. Anna Gilkeson Meanley, my wife, assisted with the fieldwork over a 7-year period in Arkansas and Louisiana. E. R. Kalmbach, former Director of the Denver Wildlife Research Center, made the sketches of courtship displays and offered encouragement and many suggestions during the early phases of the study in Arkansas. Other colleagues from the Bureau of Sport Fisheries and Wildlife who were most helpful in various phases of the work include Nancy C. Coon, John W. Aldrich, Van T. Harris, Lucille F. Stickel, Paul A. Stewart, Robert E. Stewart, Charles C. Sperry, Neil Hotchkiss, Francis M. Uhler, Frederick C. Schmid, Glen Smart, Johnson A. Neff, Robert G. Heath, Luther C. Goldman, and David K. Wetherbee. Anthony J. Florio of the Delaware Game and Fish Commission was helpful in Delaware studies. I am grateful to Samuel A. Grimes of Jacksonville, Fla., for his photograph of a King Rail used as the frontispiece.



FIGURE 1.—A King Rail walking. One foot is placed in front of the other, producing a single line of tracks.

History and Systematic Position

HISTORY

John James Audubon published the first description of the King Rail as a distinct species. The Great Red-breasted Rail or Fresh-water Marsh Hen, as he called it, was introduced with the publication of his painting in *Birds of America* (Audubon, 1834, plate 203). A year later a description of this new rail appeared in his *Ornithological Biography* (Audubon, 1835, p. 27-32).

Alexander Wilson, Audubon's predecessor, encountered this same species but thought it was the adult form of the Clapper Rail (*Rallus longirostris*), "following the current opinion of gunners that it was a very old example of that species" (Stone 1908, p. 110). Elaborating on this point, Audubon (1835, p. 27) stated:

No doubt exists in my mind that Wilson considered this beautiful bird merely the adult *Rallus crepitans* [*Rallus longirostris crepitans*], the manners of which he described, as studied at Great Egg Harbour, New Jersey, while he gave in his works the figure and colouring of the present species. My friend, Thomas Nuttall, has done the same, without, I apprehend, having seen the two together. Always unwilling to find fault in so ardent a student of nature as Wilson, I felt almost mortified when, after having in the company of my worthy and learned friend, the Reverend John Bachman, carefully examined the habits of both species, which in form and general appearance, are closely allied, I discovered the error which he had in this instance committed. Independently of the great difference as to size between the two species, there are circumstances connected with their habits which mark them as distinct. The *Rallus elegans* is altogether a fresh-water bird, while *R. crepitans* never removes from the salt-water marshes . . .

J. d'Arcy Northwood (1956, p. 224), commenting on Audubon's discovery, said:

The king rail was one of Audubon's scoops. Here was a large rail, not particularly rare, that lived unknown and undescribed under the noses of the experts in Philadelphia. Audubon realized that it was distinct from the clapper rail of the salt marshes, with which it had been confused, and named it the Great Red-breasted Rail or Fresh-Water Marsh Hen.

The type locality given in the American Ornithologists' Union *Check-list of North American Birds* (1957, p. 152) is Kentucky, South Carolina, Louisiana, and north to Camden, N.J., and Philadelphia = Charleston, S.C.

Although Audubon collected and observed the King Rail in several localities prior to his field studies in company with Bachman in the

Charleston, S.C., region, it is apparent from his original description (Audubon, 1835) that he finally decided that it was indeed a new species on the basis of their work in that region. It would seem that the species distinctness may even have been brought to his attention by Bachman, who in a letter to Audubon sent from Charleston, S.C., and dated December 27, 1832, posed this question:

May not the Northern Marsh Hen, be the Bird which we here call the Fresh Water M. Hen & our Ash coloured one that keeps to the Marsh be peculiar to the South? I should like to have this matter ascertained.

In a letter from Charleston dated March 27, 1833, Bachman, again referring to the Marsh Hen, said (Deane, 1929, p. 180, 184), "My opinion first expressed [in the letter of December 27, 1832] is every day strengthened."

Audubon (1835, p. 27-28) reported that he caught a female at Henderson, Ky., on May 29, 1810, and also collected a female near Camden, N.J., in July 1832.

Stanley C. Arthur (1937, p. 503), a biographer of Audubon, believed that Audubon's painting of the Fresh-water Marsh Hen was made at New Orleans in 1821 when he spent the winter, spring, and fall there. Audubon obtained birds from the city market and from two hunters engaged to collect for him, and painted over 100 birds from this area (including work in the St. Francisville area in West Feliciana Parish). An entry in Audubon's journal, dated December 20, 1821 (Corning 1929, p. 224), says that he "Rec^d a nondescript rail." And an entry made the next day says, "Drew a streaked Rail." This may have been a King Rail, but if it was, apparently it was not recognized as a new species at that time.

An interesting letter from Rodolphe M. deSchauensee, Curator of Birds at the Academy of Natural Sciences in Philadelphia, dated February 7, 1962, sheds some light on the possibility of an existing type specimen or cotype:

I have gone into the question of the type specimen of the King Rail mentioned in your letter of February 1 with what I think are interesting results.

Some years ago Fletcher and Phillips B. Street gave to the Academy a collection of birds which had belonged to Edward Harris who was a friend of Audubon. On looking through our collection I found in this lot an immature specimen of the King Rail. In vol. 3 (p. 28) of Audubon's Ornithological Biographies he says "I killed one female in New Jersey, a few miles from Camden, in July, 1832 in company with my friends Edward Harris and Mr. Ogden . . ."

In the *Elephant Folio* (vol. 3) pl. 203 engraved in 1834 two birds are shown, an adult and an immature. The bird in Harris's collection agrees very well both in color and measurements with the bird depicted as the immature specimen. As the bird was collected in 1832 the plate engraved in 1834 and Audubon's original description published in 1835, there is every reason to suppose that this is the bird shown on the plate.

In view of all the above I feel that it is justifiable to regard this specimen as a cotype. Audubon described an adult male, a female and an immature. If

these three birds all existed today they would of course all be cotypes. In the plate the female is not figured, only the adult male and young.

If this specimen were to be accepted as a cotype, the type locality would have to include Camden, N.J. However, in his original description of *R. elegans*, Audubon (1835) said that most of his observations of this species were in South Carolina.

SYSTEMATIC POSITION

The King Rail belongs to the order Gruiformes, which in North America includes the cranes, limpkins, rails, gallinules, and coots. Birds of this group mostly inhabit wetland environments, particularly marshes.

The suborder Grues includes the families Gruidae (cranes) and Aramidae (limpkins). Rails, gallinules, and coots belong to the suborder Ralli, which contains a single family, Rallidae. In North America this family comprises seven genera and nine species.

The three North American species of the genus *Rallus*, *R. elegans* (the King Rail), *R. longirostris* (the Clapper Rail), and *R. limicola* (the Virginia Rail), have laterally compressed bodies which facilitate passage through dense marsh vegetation; rather long, slender, and slightly curved bills which are as long as or longer than the tarsi, and longer than the heads; large, strong legs; long, slender, unwebbed toes; short, rounded wings (with vestigial claws); short, tip-up, pointed tails less than half as long as the wings; flanks conspicuously barred with white; olive or grayish dorsal regions which are striped with black or dusky markings; and buffy or rufescent breasts. *R. elegans* is larger than *R. limicola*, which it resembles in color, and is more rufescent than races of *R. longirostris* but is about the same size as that species.

Two races of the King Rail are generally recognized: *Rallus elegans elegans* of North America, and *Rallus elegans ramsdeni*, the Cuban form. Apparently a third form, *Rallus elegans tenuirostris*, occurs in the fresh-water marshes of the Valley of Mexico. There is a difference of opinion concerning the systematic position of *tenuirostris*, some authors assigning it to *Rallus elegans* and others to *Rallus longirostris*. The recent work of Warner and Dickerman (1959) seems to indicate that the plumage and inland distribution of this form are more like that of *Rallus elegans*.

RELATIONSHIP TO THE CLAPPER RAIL

Some ornithologists believe that King and Clapper Rails are merely races of the same species. Structurally and behaviorally they are similar. The plumages of several Clapper races closely resemble that of the King Rail. Their breeding ranges overlap in numerous coastal brackish marshes, in at least one of which there is absolute evidence of interbreeding resulting in the production of viable eggs.

Oberholser (1937, p. 314-315), in discussing the relationship of these two species, stated that—

it remains yet to determine the status of the king rail, *Rallus elegans*, of the Eastern United States, and its single subspecies, *Rallus elegans ramsdeni*, of Cuba. This is an unusually difficult matter to decide, and one concerning which there may well be difference of opinion. The chief external characters separating the king rails from the clapper rails consist in the much more reddish bend of the wing, and in the rich rufescent-olive tinge of the upper parts of the former birds, this involving both the centers and margins of the feathers. There is little or no trenchant difference in behavior, voice, nest building, or other habits between these two species. Neither one of the external characters of plumage above mentioned, nor any difference in size or proportions, is entirely trenchant when all the races of *Rallus longirostris* are included.

The occurrence of King and Clapper Rails in the same breeding grounds has been observed by several ornithologists. Robert E. Stewart (personal communication) observed a King and a Clapper Rail together with brood at Chincoteague Island on the coast of Virginia in June 1951. He has also on numerous occasions observed King and Clapper Rails together in the tidal marsh along Ape Hole Creek, a tributary of Pocomoke Sound, Somerset County, Md. H. M. Stevenson reported seeing a Clapper Rail walking directly in front of a King Rail at Alabama Point, Ala., June 6, 1965 (Stewart, J. R., 1965, p. 553). In April 1956, I collected a King Rail and a Clapper Rail from the same pond at Grand Chenier, Cameron Parish, La. In this area, the narrow chenier (stranded rim of the sea or old shoreline) serves somewhat as a barrier between the fresh and salt marsh, and these two species merely have to walk a hundred yards or so to be together. It is difficult to separate the two species in the field in the gulf coast marshes, although the breast of the resident Clapper race, *R. l. saturatus*, is duller brown in contrast to the more rufescent breast color of the King Rail.

On the South Atlantic coast, Ivan R. Tomkins (1958, p. 11) encountered a similar situation near Savannah, Ga. He wrote:

This brackish area, a place of transition from fresh to salt, has some peculiar situations in respect to bird habitats. In the middle of Elba Island I have seen both King and Clapper Rails on territory so close together that both birds were in view at the same time.

In the New York City region, John Bull (1964, p. 169) reported 11 specimens and 19 sight records of King Rails in coastal salt marshes and a January record of two King Rails feeding with a Clapper Rail on a mud flat at Lawrence.

On May 18, 1960, John S. Webb and I observed a King Rail and a Clapper Rail together in a brackish tidal marsh along the Delaware Bay near Fleming's Landing, Kent County, Del. The mated pair (fig. 2) were observed on their nesting territory on numerous occasions thereafter and were collected on June 11. The nest was also located on that date, and the five eggs were removed and placed in an incubator. Despite the fact that optimal incubation conditions were main-



FIGURE 2.—Mated King Rail (subadult female) left, and Clapper Rail (adult male) right, collected at Taylor's Gut, Kent County, Del., June 11, 1960. Eggs of pair were fertile. (Photograph by Frederick C. Schmid.)

tained (64 percent relative humidity and 37.8° C. forced draft) (Wetherbee, 1959) the embryos died between the 17th and 19th days of incubation. The embryos appeared to be normal, and the deaths were believed to have been accidental rather than indicative of genetic incompatibility.

Subsequent observations revealed that King and Clapper Rails frequently were found together in the extensive brackish bay marshes in the Taylor's Gut area known as Broadway Meadows and located between Fleming's Landing and Woodland Beach, Del. (Meanley and Wetherbee, 1962, pp. 453-457; Meanley, 1965, pp. 3-7).

During the breeding seasons of 1960-64, a series of specimens was collected in the Broadway Meadows marsh for plumage analysis. Specimens were obtained at three stations: (a) the upper reaches of the brackish marsh at Fleming's Landing, where King Rails only were observed; (b) the outer brackish marsh at Woodland Beach on Delaware Bay, where Clapper Rails only were observed; and (c) the intermediate area between these two stations at Taylor's Gut, where both Kings and Clappers occurred. Specimens from the intermediate area showed a wide variation from typical King plumage to typical Clapper plumage (table 1).

In addition to the localities mentioned, there are undoubtedly many other such areas in the brackish marshes of the Atlantic and Gulf Coastal Plain where mixed King Rail and Clapper Rail populations occur. In fact, almost any Coastal Plain river that has extensive brackish marshes and a sizable fiddler crab population is a potential King-Clapper mixing ground.

TABLE 1.—Specimens randomly collected from Taylor's Gut, Del., an area of mixed King and Clapper Rail populations

Species and age	Sex	Collection date
King Rail:		
Adult.....	Male.....	May 13, 1961
Do.....	Female.....	Apr. 15, 1963
Do.....	do.....	Aug. 23, 1963
Do.....	do.....	May 29, 1964
Do.....	do.....	July 30, 1964
Subadult.....	do.....	¹ June 11, 1960
Do.....	do.....	June 30, 1960
Juvenile.....	do.....	July 14, 1964
Clapper Rail:		
Adult.....	Male.....	¹ June 11, 1960
Do.....	do.....	June 25, 1960
Do.....	do.....	June 29, 1964
Do.....	Female.....	May 13, 1961
Do.....	do.....	Aug. 30, 1963
Hybrid(?):		
Adult.....	Male.....	Aug. 23, 1963
Do.....	do.....	Do.
Do.....	Female.....	Aug. 30, 1963

¹ Paired and active nest found.

Distribution and Migration

DISTRIBUTION

Unlike the Clapper Rail, which in the eastern United States is mainly restricted to a rather narrow band of salt marshes along the Atlantic and gulf coasts, the King Rail is found throughout the eastern half of North America. In general, its breeding range extends from the Gulf of Mexico to southern Canada and from the Atlantic coast to about the 100th meridian in the Great Plains (fig. 3).

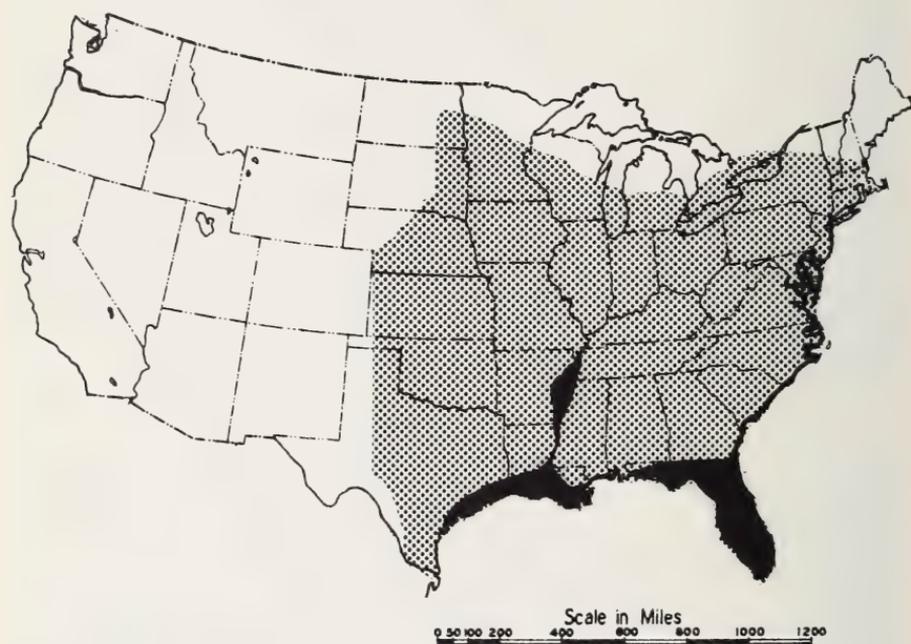


FIGURE 3.—Approximate breeding range and principal distribution of the King Rail in North America (black shaded area along Gulf and Atlantic Coasts and in Lower Mississippi Valley and peninsular Florida indicates main wintering range).

The boundaries of the breeding range as given in the American Ornithologists' Union Check-list (1957, p. 152) and supplemented by additional records, mostly from the distribution files of the Section of Migratory Non-Game Bird Studies, Migratory Bird Populations Station, Laurel, Md., and from *Audubon Field Notes*, are as follows: The northern boundary extends from southeastern North Dakota

(western Dickey County), central Minnesota (Otter Tail and Hennepin Counties), southern Wisconsin (Jamesville, Madison, Racine), central Michigan (Saginaw Bay), southern Ontario (St. Clair Flats to Toronto), and New York (Buffalo, Branchport, Ithaca, Long Island), to Massachusetts. The western boundary extends from southeastern North Dakota, eastern Nebraska, western Kansas (Cheyenne and Meade Counties), and central Oklahoma, to southern Texas (Corpus Christi). Collections of specimens at Brownsville, Tex., on September 27, 1911, and April 2 (year not given) (Griscom and Crosby, 1925, p. 527) suggest the possibility of breeding in that area. The eastern boundary extends from Massachusetts southward along the Atlantic coast to the southern Everglades. The southern boundary includes the gulf coast region, in places virtually to the edge of the gulf itself.

Records of occurrence near or beyond the limits of the normal breeding range are as follows: St. John's, Newfoundland (October 20, 1935); Wellington, Prince Edward Island, Canada (March 28, 1917); Ottawa, Ontario (May 7, 1896); Crane Lake, Ontario (July 31, 1931); Port Perry, Ontario (April 21, 1923); Bucksport, Maine (November 22, 1909); Fargo, N. Dak. (October 15, 1925); Key West, Fla. (November 2, 1895); Dry Tortugas, Fla. (May 1961) (W. B. Robertson, personal communication); and Tlacotalpan, Veracruz, Mexico (January 18, 1901).

The King Rail's principal wintering range coincides with that part of the breeding range where the species is most abundant, in the tide-water country from the Delaware Valley to southeastern Georgia, and southward through interior Florida into the Everglades, westward through the gulf coast marshes and the rice belts of Louisiana and Texas, and north into the Arkansas rice belt.

The King Rail is a regular winter resident along the Atlantic coast as far north as New York City and in the Mississippi Valley to southeastern Missouri. Southernmost winter records in the United States are from the Lower Rio Grande Valley, in the vicinity of Brownsville, Tex. (December 28, 1911, and January 10, 1923) (Griscom and Crosby, 1925, p. 527).

Some of the numerous winter records (mainly from the distribution files of the Section of Migratory Non-Game Bird Studies, Migratory Bird Populations Station, Laurel, Md.) north of the principal winter range are as follows: LaSalle, Ontario (December 15, 1930); Lorne Park, Toronto, Ontario (December 26, 1960); Falmouth, Maine (December 17, 1899); Cambridge, Mass. (December 30, 1896); Cape Cod, Mass. (December 30, 1951); Hillsdale, Mich. (December 11, 1896); Detroit, Mich. (February 6, 1907); Port Huron, Mich. (December 6, 1902); Vicksburg, Mich. (February 6, 1909); Prudensville, Mich. (December 7, 1938); Monroe County,

Mich. (December 30, 1934, and February 8, 1934); Bayside, Long Island, N.Y. (December 24, 1924); Miami and Meade Counties, Kans. (late December); and Montauk Point, Long Island, N.Y. (December 27, 1951).

In the New York City region, Bull (1964, p. 169) reported 15 winter specimens, 5 in December, 7 in January, 1 in February, and 2 the first week in March. Eleven of the fifteen were taken in salt marshes, and there were 19 sight records in salt marshes, nearly all in December and January.

On the basis of extensive field observations by several ornithologists, including Robert E. Stewart, Milton B. Trautman, D. J. Nicholson, T. D. Burleigh, Oliver H. Hewitt, and myself, and as a result of an intensive literature review, the most important areas of concentration probably have been determined.

The King Rail occurs in greatest numbers in the vast coastal marsh and ricefield area of southern Louisiana. Other areas supporting high populations include the coastal marsh-rice belt of Texas; the Arkansas rice belt; the fresh and brackish tidal marshes of the Carolinas and Georgia; the Everglades, the Kissimmee Prairie, and the St. Johns River marshes of Florida; and the tidal marshes of the Delaware Valley and Chesapeake Bay. The Lake Erie marshes of northern Ohio and the St. Clair Flats opposite Detroit, Mich., are two important concentration areas in the North Central States.

MIGRATION

Throughout most of its range the King Rail is migratory. Evidence of movements between wintering and breeding grounds is based on recoveries of banded birds, and birds heard calling overhead at night, striking beacons, and appearing in odd places such as city streets during periods of migration.

The Atlantic Coastal Plain, particularly its outer section, and the Mississippi Valley are important flyways of the King Rail. The occurrence of King Rails near the Atlantic coast during migration is due to movements to and from breeding grounds in that area. King Rails commonly breed at many places less than 50 miles from the coast. Several known localities include Butler Island near Darien, Ga.; Savannah National Wildlife Refuge, Jasper County, S.C.; Georgetown, S.C.; Currituck Sound, N.C.; Norfolk, Va.; the coastal sea islands and Delaware Bay marshes.

A King Rail collected by I. N. Gabrielson in the Atlantic coast salt marshes at Wachapreague, Va., August 25, and several taken by hunters in September at Chincoteague, Va., indicate the probable route of migration of at least some northeast Atlantic coast breeding birds.

During 7 years' residence in the lower Mississippi Valley, I heard migrating King Rails regularly every spring at Alexandria, La., and

Stuttgart, Ark. On the night of March 11, 1956, single King Rails were heard calling as they migrated northward over the city of Alexandria at 8:30, 9:30, and 11 p.m. They appear to be less vociferous while migrating in the fall. The most commonly uttered call of migrating King Rails is a *chur-r-r-r-r* (the *r* like the German "R"). Another call occasionally given is *chac-chac-chac*.

Probably most fall migration takes place after molting, which is completed about the first of September. In Delaware, I have collected flightless birds in the last week in August that would still have been flightless through the first week in September. However, some rails collected in late August had nearly or completely renewed their flight feathers.

The fall departure schedule for three species of rails at the Patuxent Wildlife Research Center, Laurel, Md., was determined by a trapping and banding program extending from midsummer to early winter. King Rails were the first to leave the area (the last by late September); they were followed by Soras (the last by early November), and lastly by Virginias (the last of December).

David C. Hulse (personal communication) wrote that a definite influx of King Rails is noticed annually at Decatur, northern Alabama, in late September: "Local birds are still here and at this time must be augmented by migrants. Departure is gradual and by late October rails become gradually scarce."

King Rails breeding at the southern limit of their range in the gulf coast region are probably permanent residents or may perform short coastwise migrations.

Winter records for the Middle Atlantic and North Central States suggest the possibility of permanent residency by some individuals. In the Chesapeake Bay region of Maryland there are two records of King Rails banded in August and recovered in the same marsh the following January. Also, a 6-week-old chick banded July 12, 1968, at the Patuxent Wildlife Research Center, Laurel, Md., was recovered December 12, 1968, at the same place.

As of January 1966 there have been only two recoveries of King Rails that migrated an appreciable distance from the point of banding. Only one of these was a direct recovery (bird recovered within 12 months of banding date). A 2-week-old chick was banded at Stuttgart, Arkansas County, Ark., on June 2, 1952, and recovered at Cut Off, Lafourche Parish, La., December 1, 1952, having traveled a distance of about 350 miles. The other recovery concerned a King Rail banded at Lassie, Wharton County, Tex., June 9, 1949, and recovered at Brookville, Montgomery County, Ohio, 1,000 miles away, on May 2, 1951. A King Rail banded at Ruthven, Palo Alto County, Iowa, August 25, 1951, and recovered at Lake View, Sac County, Iowa,

September 10, 1951, had traveled some 60 miles and was probably migrating.

Spring arrival and fall departure dates are given in table 2. Some of these dates are questionable; those for the interior northern part of the range may be more reliable than those along the Atlantic coast where so many King Rails winter.

LOCAL MOVEMENTS

Information on local movements was obtained at two marshy impoundments at Patuxent Wildlife Research Center, Laurel, Md., during the summers of 1965 and 1966. In 1965, four pairs of King Rails nested in an impoundment known as Knowles Unit 2; in 1966, no King Rails nested there because of deep water. Knowles 2 has an area of 20 acres, of which about 10 acres are shrub swamp or marsh or a mixture of the two. Knowles Unit 1, the other impoundment, is larger, but contained only about 6 acres of marsh and shrub swamp at the time. One pair of King Rails nested there in 1965 and 1966.

TABLE 2.—*Spring arrival and fall departure dates for migrating King Rails*

Location	Arrival	Departure	Source
Mississippi Flyway:			
Stuttgart, Ark.....	Feb. 15 to Mar. 30.....	Mid-October to mid-November.	Meanley, unpublished.
Missouri.....	Mar. 21 to 31.....	Late October.....	Widmann, 1907, p. 59.
Buckeye Lake, Ohio.....	Apr. 11 to 20.....	Late September.....	Trautman, 1940, p. 229.
Chicago, Ill.....	Mid-April.....	Late October.....	Ford, 1956, p. 33.
Knox County, Ind.....	Apr. 15 to 30.....		Section of Migratory Nongame Bird Studies, Migratory Bird Populations Station, unpublished.
Kansas.....	Apr. 18 (median date).....		Johnston, 1964, p. 611.
Vicksburg, Mich.....	Apr. 19.....	Oct. 10 (latest).....	Rapp, 1931, p. 7.
Southern Michigan.....	Apr. 21 to May 10.....	Late August through September.	Wood, 1951, p. 146-147.
Southern Minnesota.....	Late April.....	Late September.....	Roberts, 1936, p. 440.
Clay County, Iowa.....	May 1 to 7.....	Early September.....	Tanner and Hendrickson, 1956, p. 54.
Decatur, Ala.....		Late October.....	Hulse, personal communication.
Atlantic Flyway:			
Raleigh, N. C.....	Late March.....		Brimley, 1917, p. 299.
Western Pennsylvania.....	Mid to late April.....		Todd, 1940, p. 183-184.
New York, N. Y.....	Late April.....		Cruikshank, 1942, p. 156.
Connecticut River Valley.....		September, early October.	Bagg and Eliot, 1937, p. 178-180. Sage and Bishop, 1913, p. 48.
Massachusetts and Connecticut.....			Meanley, unpublished.
Broadway Meadows.....		September.....	Meanley, unpublished.
Kent County, Del.....			
Laurel, Md.....		September.....	Meanley, unpublished.

One of a pair of nesting King Rails trapped and banded on June 12, 1965, in Knowles 2, was first recaptured on August 2, approximately 200 yards from where it was banded. This bird was recaptured a second time on August 7, approximately 350 yards from the second site and 500 yards from the original site.

The young of the 1965 nest in Knowles 1 were hatched on July 2 and 3. Earlier, one of the adults was banded and color-marked while incubating. Both adults and the brood remained within 100 feet of the nest most of the time until at least July 24, a period of 3 weeks.

On July 8, 1966, the same color-marked adult, its mate, and their brood of eight 2-week-old chicks were trapped in Knowles 1, 50 feet from where the color-marked adult had nested the previous year. The unbanded adult and the chicks were banded when trapped.

On July 16, two of the eight chicks were captured and the rest of the family was observed on an island in Knowles 2, 0.4 mile from the site of their original capture in Knowles 1 on July 8. To reach the island in Knowles 2, the 3-week-old flightless chicks had not only walked nearly half a mile but had swum across 50 feet of open water that had a depth of 3 feet.

Ecological Relations

The King Rail probably occurs in a wider variety of habitats than any other rail. The species ranges from coastal salt and brackish marshes to shrub swamps and occasionally is found even in upland fields near marshes where it forages for grasshoppers and grain, and where it sometimes nests.

The distribution of the King Rail's habitat coincides rather closely with that of the muskrat (*Ondatra zibethicus*). Muskrats create optimum habitat for rails by opening up marshes and producing networks of pathways leading to plunge holes. When the tide goes out, water is trapped in the holes, and rails use them as drinking places. Muskrat trails are also favorite places for crayfish burrows. The crayfish are a prime food of the rails and are usually carried to the tops of muskrat houses for eating.

Because of the geographic as well as the local variation in habitats of the King Rail, the ecological relations will be discussed on a regional basis.

This chapter will cover both my own observations on the ecology of the King Rail in Louisiana, Arkansas, South Carolina, Delaware, and Maryland, and those of other authors in different States or areas.

LOUISIANA GULF COAST MARSHES

The King Rail and the Louisiana Clapper Rail, a brownish form virtually indistinguishable from the King Rail in the field, occur together in some sections of the Louisiana coastal marsh. This vast marsh area of more than 4 million acres is divided into three major divisions, each of which is a distinct habitat type and will be discussed separately: the delta marsh, subdelta marsh, and prairie marsh (St. Amant 1959, p. 97-101) (fig. 4).

The delta marsh

The delta marsh, near the mouth of the Mississippi River, comprises only 7 percent of the total coastal marsh area of Louisiana. Important plant species of the delta marsh are cattails (*Typha spp.*), roseau cane or reed (*Phragmites communis*), common three-square (*Scirpus americanus*), dog-tooth grass (*Panicum repens*), giant cutgrass (*Zizaniopsis miliacea*), saltmarsh cordgrass (*Spartina alterniflora*), delta duck potato (*Sagittaria platyphylla*), alligatorweed (*Alternanthera philoxeroides*), and water hyacinth (*Eichhornia crassipes*).

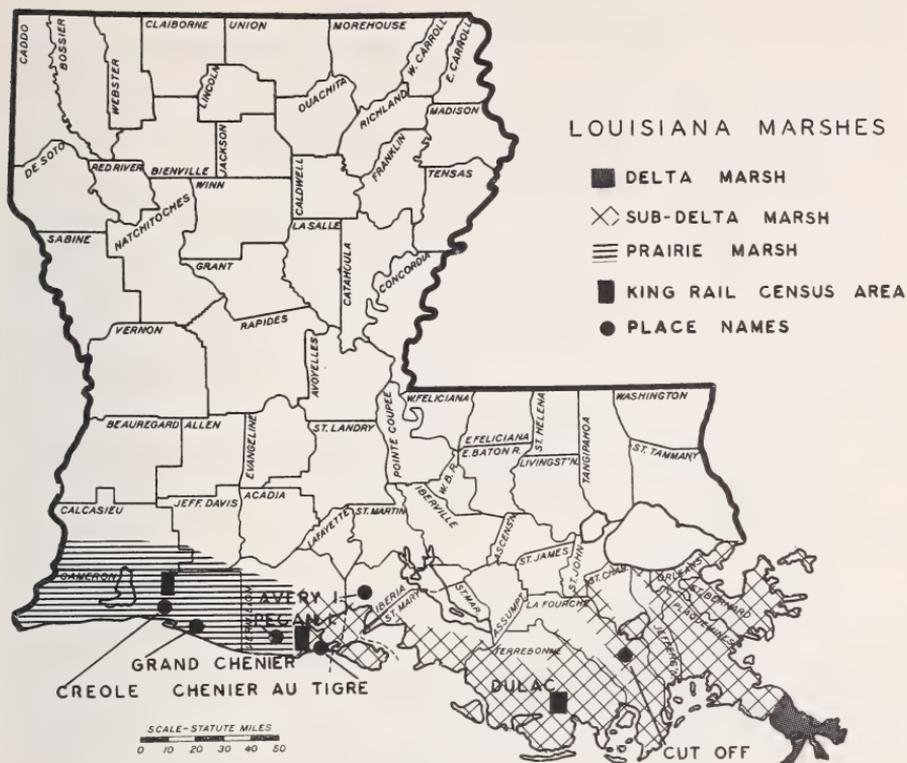


FIGURE 4.—Louisiana gulf coast marshes.

Oberholser (1938, p. 109, 201) reported the collection of a King and six Clapper Rails in the delta marsh at the mouth of the Mississippi River, indicating their presence in this habitat type.

The subdelta marsh

The subdelta marsh, comprising 74 percent of the Louisiana coastal marsh, extends westward from the Mississippi River Delta to Cow Island and Chenier au Tigre in Vermilion Parish. Both its fresh-water and brackish marshes are of two types, floating or with a firm floor of clay. The predominant plant species in both types is "paille fine" or maidencane (*Panicum hemitomon*). Associated with it are cattail, southern bulrush (*Scirpus californicus*), sawgrass (*Cladium jamaicense*), wapato (*Sagittaria latifolia*), alligatorweed, and water hyacinth. In brackish areas either saltmeadow cordgrass (*Spartina patens*) or Olney's three-square (*Scirpus olneyi*) is dominant; the latter is dominant if there is management (burning) for muskrat production. Salt marshes in this area are dominated by needlerush (*Juncus roemarianus*), saltmeadow cordgrass, and saltmarsh cordgrass.

Both banding returns and collections of birds substantiate the occurrence of King Rails in the subdelta marsh. A King Rail banded at Stuttgart, Ark., in June 1952, was recovered at Cut Off, Lafourche

Parish, in the subdelta marsh, in December 1952. Cut Off is approximately 25 miles south of New Orleans. King Rails were collected at Chenier au Tigre, January 1, 3, and 5, 1934, by A. M. Bailey (Oberholser 1938, p. 199); at the same location on March 31 and April 1, 1947, by I. N. Gabrielson; and at Avery Island, May 7, 11, 13, and 15, 1930, by E. G. Wright (Oberholser, 1938, p. 199).

I made a census, based on calls, in Terrebonne Parish, 1.2 miles south of Dulac, on January 3, 1963, to determine the abundance of King Rails in the area (table 3). The birds were heard calling from what appeared to be an abandoned silted-in canal where shallow ponds were interspersed with dense patches of vegetation dominated by clump grass (*Spartina spartinae*). In a 1-mile strip, 50 feet wide, 19 King Rails were counted. Short-billed Marsh Wrens (*Cistothorus platensis*), Soras, Virginia Rails, and Common Gallinules (*Gallinula chloropus*) were also common in this same census strip.

The prairie marshes

The prairie marshes in the southwestern part of the Louisiana gulf coast (Vermilion and Cameron Parishes) comprise 19 percent of the total area. Near the gulf coast much of the prairie marsh is bisected by ridges known as cheniers (stranded rims of the sea or old shoreline) that parallel the coast (fig. 5). Cheniers extend in straight lines for many miles and in most places are wide enough only for a



FIGURE 5.—Prairie marsh, Grand Chenier, La., March 1956. Mixed King and Clapper Rail populations sometimes occur in the same marsh type in this area. Both species were collected from the same half-acre pool near here, April 1956.

road bordered on each side by a line of live oaks. In some places there are a few houses. In some sections, cheniers separate fresh and brackish marshes.

TABLE 3.—Abundance of King Rails in certain areas, as indicated by censusing

Location	Number of King Rails	Date	Cover type
Black and Pedee Rivers, Georgetown County, S.C.	25 in 100 acres ^{1 2}	Apr. 10-12, 1961	Giant cutgrass, cattail, big cordgrass, arrow- arum.
Savannah River, Jasper County, S.C.	14 in 13 acres ^{1 3}	Apr. 20, 1961	Softstem bulrush.
10 miles south Fellsmere, Indian River County, Fla.	30 in 100 acres ³	May 8, 1964	Maidencane.
Savannah National Wildlife Refuge, Jasper County, S.C.	46 along 7-mile route ⁴ .	Apr. 12, 1960	Giant cutgrass, cattail, sawgrass.
Dulac, Terrebonne Parish, La.	19 along 1-mile route ⁴ .	Jan. 3, 1963	Clump grass, or needle cordgrass.
4 miles north Creole, Cameron Parish, La.	24 along 1-mile route ⁴ .	Jan. 5, 1963	Fall panicum.
3 miles north Pecan Island, Vermilion Parish, La.	20 along 1-mile route ⁴ .	Jan. 4, 1963	Fall panicum.
Stuttgart, Arkansas County, Ark.	22 along 6-mile route ⁴ .	Apr. 1955	Rice stubble, broom- sedge, cattail, sofrush.

¹ Males only.

² Two-stage sampling.

³ Strip census.

⁴ Roadside count.

In this area salt marshes near the coast are dominated by a salt-grass-saltmeadow cordgrass-saltmarsh cordgrass association. Landward from this association, brackish marshes extend north to the Creole and Grand Chenier ridges. Principal plants of the brackish marsh are saltmeadow cordgrass, Olney's three-square, and saltmarsh bulrush (*Scirpus robustus*). In the transition areas between brackish and fresh water, such plants as giant cutgrass, bull tongue, pickerelweed (*Pontederia cordata*), and wild millet (*Echinochloa crusgalli*) grow. The fresh-water marshes lie mainly north of the Grand Chenier and Creole ridges. In the higher parts of those marshes the following plants are found: bull grass (*Paspalum boscianum*), lake grass (*Paspalum distichum*), dotted smartweed (*Polygonum punctatum*), squarestem spikerush (*Eleocharis quadrangulata*), and delta duck potato. Sawgrass is the climax type in the lower parts of the fresh-water marsh.

In the vicinity of the cheniers, King and Clapper Rails occur close to one another or together. Referring to this situation, Lowery (1955, p. 227) made the following statement:

The King and Clapper Rails are extremely similar in appearance and are, for the most part, simply ecological representatives of each other. The former generally inhabits fresh-water marshes and is widespread in the interior of the United States; the latter is always found on or near the seacoast in brackish- or salt-water marshes. . . . There are brackish marshes in which both breed side by side without intermingling; . . .

I find it difficult to believe that the two species do not interbreed in the prairie marshes. Several King-Clapper pairs (and their nests and

eggs) have been collected recently in Delaware brackish marshes, indicating that they do sometimes interbreed when they occur together (Meanley and Wetherbee, 1962, p. 453-457).

Near the village of Grand Chenier, I collected both Kings and Louisiana Clapper Rails from the same small pond on the south side of the chenier. The dominant vegetation in the immediate area was clumpgrass. On the south side of this narrow chenier, in the brackish marshes, the gulf coast form of the Clapper Rail is the dominant species, but the marsh on the landward side is the King Rail's domain. Rivers, such as the Mermentau, and canals crossing the chenier extend the brackish water landward, and occasionally storm tides also affect large areas of the marsh, extending salt water into the fresh-water zone and changing the habitat. This area may well be described as a mixing ground of plants and animals. A common avian associate of the rails breeding in the clumpgrass and saltgrass marsh was the Mottled Duck (*Anas fulvigula*).

I also encountered four King Rail broods, still in downy black plumage, and three single adults 4 miles north of Grand Chenier on July 23, 1955. At this station the marsh was composed of a mixture of southern bulrush, cattail, a *Sagittaria*, probably *lancifolia*, and water-hyacinth.

A census of King Rails, based on calls, was made in a marsh bordering the Pecan Island road, 2 miles south of the old Intracoastal Canal, Vermilion Parish, on January 4, 1963. Twenty birds were counted in 20 minutes along a 1-mile strip approximately 200 yards wide, at 6 p.m. (table 3). The dominant vegetation in the census area was fall panicum (*Panicum dichotomiflorum*). A similar census was made 5 miles south of the Intracoastal Canal on the east side of the road to Creole, Cameron Parish, on January 5, 1963. Between 5:30 p.m. and 6 p.m. 24 birds were counted along a 1-mile strip approximately 200 yards wide (table 3). The dominant vegetation types in the area were southern bulrush and fall panicum (fig. 6). Soras were also abundant in the same habitat.

SOUTHERN RICEFIELDS

The gradual shift in the domestic rice (*Oryza sativa*) growing industry from the South Atlantic coast to the South Central States of Louisiana, Texas, Arkansas, and Mississippi after the Civil War opened up a new marsh habitat for King Rails and other water birds. Much of the land where rice is grown today was once a vast natural tall-grass prairie in which the Greater Prairie Chicken (*Tympanuchus cupido*) was abundant. Harmon, Thomas, and Glasgow (1960, p. 153) reported that approximately 3 million acres in this area were devoted to rice growing by 1958, and that this acreage wintered 4 million ducks and geese. Many aquatic plants grow in ricefields, and



FIGURE 6.—Southern bulrush (*Scirpus californicus*), fall panicum (*Panicum dichotomiflorum*), and alligatorweed (*Alternanthera philoxeroides*) in prairie marsh type near Creole, Cameron Parish, La., January 5, 1965. Between 5:30 and 6 p.m., January 5, 1963, 24 King Rails were counted along a 1-mile transect through this marsh.

virtually all produce seeds utilized by a variety of water birds. Rice-fields furnish an optimum all-purpose habitat for King Rails for nearly 6 months during the summer half of the year, and a source of food for them in winter (fig. 7).

On the gulf coast prairie of Louisiana and Texas, rice planting begins in March. Some early varieties are harvested by late July, but most fields are harvested from early August to early October. The planting season in Arkansas is about 2 weeks later, and harvest is from late August to early November. The fields are irrigated by wells or by canal systems fed from reservoirs or bayous. Water remains on the fields for 3 or 4 months and is maintained at a constant level of from 6 to 10 inches.

On the Arkansas Grand Prairie I found the nesting density of King Rails in one ricefield to be at least one nest per 15 acres, a figure based on the location of five nests in a 75-acre field in July. These nests were located by a team of men walking abreast and systematically covering the field to remove a pest plant, the coffeebean (*Sesbania exaltata*). The height of the nesting season was several months past, and these nests probably represented a renesting effort or a second



FIGURE 7.—King Rail wading through ricefield toward nest on dike, Stuttgart, Ark., July 13, 1952.

nesting after an earlier first successful nesting. It is not to be construed that this is an average nesting density for Grand Prairie ricefields.

Since much of the rail nesting in rice country is completed before the rice is high enough to provide nesting cover, a better idea of nesting density could be obtained from nest counts or mating call counts in the spring when most of the rails are found in roadside ditches and canals and occasionally in rice stubble. As an example, in April 1955 I located 22 occupied nesting territories along 6 miles of continuous roadside ditch beginning 2 miles north of Stuttgart, Ark. (table 3 and fig. 8).

In Evangeline and Jefferson Davis Parishes in Louisiana I found many nests in roadside ditches where the dominant vegetation was paille fine (maiden cane) and soft rush (*Juncus effusus*). In Arkansas Grand Prairie ditches in 1952 and 1953, nests were found mainly in stands of soft rush, cattail, common spikerush (*Eleocharis palustris*), and lake sedge (*Carex hyalinolepis* and *C. lacustris*), a plant which grows to a height of 3 feet or more and forms very dense stands that persist intact through the winter. Lake sedge was available for nesting cover earlier than any plant in the roadside ditches. Ten years



FIGURE 8.—Arkansas Grand Prairie near Stuttgart, Ark., May 1952. Rails nest in roadside ditches in April and May. Vegetation in ditches is mostly soft rush (*Juncus effusus*) and two sedges (*Carex stipata* and *C. hyalinolepis*). In June, rails move into ricefields (left of ditch) for late nesting or renesting as rice begins to form nesting cover.

later (1962), in those same ditches, awl-fruited sedge (*Carex stipata*) was the dominant plant, and four of six nests located during May of that year were constructed of this plant.

Old rice stubble is sometimes used for nesting. On the southwestern Louisiana rice prairie where farming is less diversified than on the Arkansas Grand Prairie, many farmers let the stubble fields lie out through the winter and spring for cattle grazing. In one such wet stubble field at Mamou, Evangeline Parish, I located two rice-straw nests on May 5, 1957 (fig. 9).

During the summer, when the rice is growing and the fields appear as a vast green marshland, virtually all King Rails in the rice belt frequent the fields. Some are renesting, and others are wandering about with their broods in search of crayfish, minnows, and aquatic insects which abound here.

Nesting associates of the King Rail in Louisiana ricefields are the Fulvous Tree Duck (*Dendrocygna bicolor*), the Purple Gallinule (*Porphyryla martinica*), the Least Bittern (*Ixobrychus exilis*), and along the southern border of the rice belt the Mottled Duck. The most common bird in the area is the Red-winged Blackbird (*Agelaius phoeniceus*). In the northern part of the principal Louisiana rice belt, at Mamou, Evangeline Parish, I found the Long-billed Marsh Wren (*Telmatodytes palustris*) nesting in rice.



FIGURE 9.—Nest of King Rail in wet rice stubble, Mamou, La., May 5, 1957. Photographed as found.

In 1955 a rice farmer at Mamou located six Fulvous Tree Duck nests in a 400-acre block of rice, and in the same locality I found 22 active Purple Gallinule nests in a 10-acre section of a 25-acre ricefield. In the Arkansas ricefields the Purple Gallinule is an uncommon breeding bird. There are no breeding records for the Fulvous Tree Duck in Arkansas ricefields, but there are several early fall occurrence records. The Short-billed Marsh Wren has been found nesting in Arkansas ricefields in August and September.

King Rails are more secretive in winter than at other seasons and often are present in good numbers in some localities although seldom or never seen. For 5 years in the Arkansas rice belt, I was in the field daily without ever seeing one in the dead of winter. Yet they were present, as a mink trapper brought me several each January.

On the Arkansas Grand Prairie, I have often come across trails forming tunnels which often continue for many feet beneath the matted vegetation of a ditch bank. These trails appear to have been made by some mammal, yet many tell-tale signs, particularly the characteristic regurgitated pellets and roundish droppings about the size of a silver dollar, are proof that King Rails use them. Regardless of whether these trails are made by rails, mink (*Mustela vison*), rabbits (*Sylvilagus floridanus*), or rats (unidentified), trapping indicates that they are used by all four species. King Rails also spend the winter in small marshy tracts along the bayous that dissect the Grand Prairie.

At Stuttgart, Ark., a King Rail used a long water pipe about 1½ feet in diameter and running from a pumphouse to a small reservoir

as its winter retreat. From late November to mid-December, I stopped by almost daily to see its fresh tracks leading from the pipe to the mudflat of the reservoir.

A rather surprising wintering habitat is the cutover longleaf pine (*Pinus palustris*) land of central Louisiana. Bobwhite and Woodcock hunters flush King Rails from little damp spots or seepage areas in the bluestem (*Andropogon tener* and *A. divergens*) range. Crayfish, a prime food of the rail, also are found there.

FLORIDA

A. H. Howell (1932, p. 202), in commenting on the status of the King Rail in Florida during the early 1930's, said it was probably most numerous in the Everglades and big marshes of the upper St. Johns River. D. J. Nicholson of Orlando (personal communication, 1962), who has made an intensive study of Florida birds since 1900, told me the King Rail is still a common to abundant breeding bird in many parts of central and southern Florida, although extensive drainage projects in the area have destroyed thousands of acres of marsh habitat. In addition to the two areas mentioned by Howell, Nicholson included the open wetlands of the Kissimmee Prairie as an important King Rail area. He added that the King Rail is common in the St. Johns River marshes in Seminole, Orange, Volusia, Brevard, and Indian River Counties; and is found in good numbers nesting on Merritt Island, Brevard County, "both in the salt marshes near Wayne's Clapper Rail, as well as in numerous fresh water ponds on that island."

S. A. Grimes (personal communication) reports that, in northern Florida, the King Rail occurs in most of the fresh-water marshes of Duvall County. Two of the several nests he found were in open cypress bayheads.

A. D. Cruickshank (personal communication), in writing from Brevard County, said that the King Rail is decidedly more common there in winter than during the breeding season, with peak numbers usually coming in late December and January. Apparently the local population is augmented by migratory populations from north of Florida. Evidence of local abundance in this area is based on the annual Audubon Society Christmas bird count conducted within a 15-mile radius of Cocoa, Fla. (Cruickshank et al., 1953-66). The numbers of King Rails reported has ranged between 11 and 93 over the past 14 years and averaged 40 per year. Cruickshank reports that the best localities are (a) fresh-water marshes around Lake Poinsett, a large lake in the St. Johns River, and (b) fresh-water marshes on Merritt Island.

During the period May 4-8, 1964, I examined some marshes in Indian River, Osceola, and Glades Counties. Approximately 10 miles south of Fellsmere, Indian River County, at the junction of State

Highways 60 and 512, I found King Rails common where maiden-cane and pickerelweed formed a high percentage of the vegetation of the wetter marshes (fig. 10). Apple snails (*Pomacea paludosa*), the,



FIGURE 10.—Habitat of King Rail, 10 miles south of Fellsmere, Indian River County, Fla., April 1967. Marsh vegetation in foreground is mostly maiden-cane (*Panicum hemitomon*) and pickerelweed (*Pontederia cordata*), in background sawgrass (*Cladium jamaicense*). White waterlily (*Nymphaea odorata*) in pond left of center. Forest community is pond cypress (*Taxodium ascendens*). The density of King Rails in this area was estimated at 30 birds per hundred acres.

major food of the Limpkin (*Aramus guarauna*), and the eggs of these snails, were scattered abundantly throughout the wetter marshes, but were absent from the drier ones. Houses of the round-tailed muskrat (*Neofiber alleni*) were abundant in both wetter and drier marshes. Limpkins and rails use the tops of these houses as their "dinner tables." King Rails were most commonly in the drier marshes. I estimated a density of approximately 30 birds per hundred acres in a tract on the east side of Highway 512 (table 3).

On the Brighton Seminole Indian Reservation, Glades County, I heard and saw King Rails in marshes composed largely of pickerelweed, bull tongue (*Sagittaria lancifolia*), and dotted smartweed (fig. 11). While on a trip through the reservation in January 1958, I saw two very dark-plumaged King Rails in a small pickerelweed marsh.



FIGURE 11.—King Rail habitat on Seminole Indian Reservation, Glades County, Fla., May 5, 1964. Predominant plants in marsh are bull tongue (*Sagittaria lancifolia*), pickerelweed (*Pontederia cordata*), and dotted smartweed (*Polygonum punctatum*).

SOUTH CAROLINA LOW COUNTRY

King Rails are common to abundant in many fresh-water and brackish tidal-river marshes of the South Carolina Low Country. These marshes are along the famous rice rivers of colonial times: the Ashpoo, Black, Combahee, Edisto, Pee Dee, Santee, Savannah, Waccamaw, Wando, and others. It was in such marshes that domestic rice was grown until about 1915. Remnants of the old ricefield dikes and canals built by slaves are still evident in the marshes (fig. 12).

The dominant vegetation type of most sections of the marshes today is giant cutgrass. Because of the blanched appearance of the giant cutgrass in winter, these marshes were referred to by the early explorer-naturalists as the "white marsh." Giant cutgrass provides excellent escape and nesting cover for rails but apparently is of no food value to them, although Purple Gallinules, Red-winged Blackbirds, and Bobolinks (*Dolichonyx oryzivorus*) feed on its flowers and seeds.

A survey of the marshland in the Low Country from the lower Cape Fear River at Wilmington, N.C., to the Altamaha River at Darien, Ga., seems to indicate that the King Rail is largely associated with the "white marsh" zone of these coastal rivers. It should be emphasized, however, that many secondary plant communities occur within this zone with varying King Rail population densities depending upon local ecological conditions.



FIGURE 12.—Floodgate and ricefield canal near Savannah, Ga., April 1960. The land is irrigated as the tide rises from the Savannah River. King Rails nest in giant cutgrass (*Zizaniopsis miliacea*) seen along right-hand edge of canal. The high population density in this area is probably due to good nesting cover and the abundance of the red-jointed fiddler crab (*Uca minax*), a favorite food of the rail.

In the Low Country, March and April appear to be the best months for censusing, as King Rails are more vociferous at this time than during any other period of the year. A narrow strip of marshland bordering a river is the most suitable place for censusing.

The marshland on the west side of the Pee Dee River and one of its tributaries, the Black River, for a distance of 8 miles north of Georgetown, S.C., totalling 3,000 acres, was selected as a sampling area. The sampling design was suggested by Dr. Don W. Hayne of the Institute of Statistics, North Carolina State College, Raleigh, N.C.

Georgetown is approximately 8 miles inland from the coast on Winyah Bay at the confluence of the Pee Dee and Waccamaw Rivers. The Black River flows into the Pee Dee about 2½ miles north of Georgetown. The mean tidal range at Georgetown is 3½ feet. At Georgetown the river is slightly brackish, and big cordgrass (*Spartina cynosuroides*) is an important plant component of the marsh, especially along old ricefield canals. Six 10-acre plots were composed mainly of the following plants: big cordgrass, 35 percent; Olney's three-square, 20 percent; cattail, 14 percent; giant cutgrass, 13 percent; arrow-arum (*Peltandra virginica*), 11 percent; softstem bulrush, 5 percent; and river bulrush (*Scirpus fluviatilis*), 2 percent.

Vegetation analyses were made also of three 10-acre plots 8 miles north of Georgetown on the Black River. On the Black River,

giant cutgrass formed 52 percent of the marsh vegetation, arrow-arum 36 percent, and cattail 12 percent.

For the actual census, the entire marsh area, as shown on U.S. Geological Survey maps, was blocked off into 64 primary sampling units, each a 630-foot-wide transect extending from the edge of the river to the land. Each transect was divided into 10-acre plots, the number in a transect depending upon the width of the marsh at that location along the river.

Ten of the 64 transects were randomly selected as primary sampling units, and one 10-acre plot from each was chosen for censusing. At least 1 hour between 5 and 8 a.m. or 5 and 7 p.m. during the period April 10 through 12, 1961, was spent in each plot counting calls.

The number of male King Rails in a transect was estimated by multiplying the number of 10-acre plots in that transect by the number of birds heard in the census plot. The estimated total of 755 males in the 3,000-acre marsh was derived by multiplying the average number of birds per sample transect by the total number of transects. The density estimate of 25.2 male birds per 100 acres was calculated by dividing the total population by 30 (the number of 100-acre units in the 3,000-acre marsh). Since some of the calling King Rails were undoubtedly already mated, and most of the others would be eventually, the average number of breeding rails per 100 acres could be inferred to be 25 pairs (table 3).

Sampling indicated that the density of the King Rail population was higher at Georgetown in the Pee Dee River marshes than several miles up river along its tributary, the Black River. One 10-acre plot at Georgetown had six calling rails, and four other plots had four each. None of the Black River plots had more than two rails. The higher density at Georgetown could be attributed to the higher proportion of red-jointed fiddler crabs (*Uca minax*).

Savannah National Wildlife Refuge

The Savannah National Wildlife Refuge in South Carolina and Georgia, near Savannah, is about 25 miles upriver from the ocean on what was formerly a rice plantation (fig. 13) and is divided by the Savannah River. The larger acreage is on the South Carolina side. Its marsh is the fresh tidal type, with a tide which rises about 1 foot.

Giant cutgrass is the dominant vegetation of much of the marsh on the refuge. The old growth of cutgrass forms a nearly pure stand, and has an average height of about 5 feet, but will average higher when the new growth matures. Arrow-arum, dotted smartweed, and swamp smartweed (*Polygonum hydropiperoides*) are scattered about the marsh, particularly along the edges and on high spots. There are numerous small holes made by the red-jointed fiddler crab, an important food of the King Rail, along the tidal creeks and edges of the marsh. While making a survey of King Rail populations in April



FIGURE 13.—South Carolina Low Country: ricefield nesting habitat in Jasper County along the Savannah River, fall 1958.

1960, I estimated a density of one pair per acre in the cutgrass marsh bordering the river. A year later I also heard many King, Virginia, and Sora Rails calling at night in the same marsh.

Much of the refuge canal system and some of the ponds are choked with alligatorweed, a plant that forms extensive mats upon which rails, gallinules, coots, herons, and several species of ducks do much of their foraging for aquatic insects (fig. 14). Small patches of giant



FIGURE 14.—Alligatorweed (*Alternanthera philoxeroides*) in canal at Savannah National Wildlife Refuge, Jasper County, S.C., April 1960. This plant forms spongy, extensive mats upon which rails, gallinules, coots, herons, and ducks forage for aquatic insects, fish, amphibians, and crustaceans. Such mats have an obvious value to birds that utilize its growth form to facilitate their quest for food. Note alligator on far side of canal. Alligators feed on many forms of animal life including various water-birds such as rails.

cutgrass in which Purple Gallinules nest are sparsely distributed along the canals. I located many King Rail pairs with feeding territories along sections of the canals. Some of these territories were not more than 20 feet square, indicating the high food productivity of these aquatic mats. All of the King Rails that I observed feeding in the choked-up canals, however, nested on the other side of the dike in a deep-water impounded marsh containing a mixture of giant cutgrass, sawgrass, cattail, royal fern (*Osmunda regalis*), buttonbush (*Cephalanthus occidentalis*), and myrtle (*Myrica cerifera*).

I made a roadside count of calling males on April 12, 1960, along a 7-mile route beginning at the north entrance to the refuge on U.S.

Highway 17, continuing along the east dike, through the string of island hammocks, and ending at the Savannah River just inside the south entrance on U.S. Highway 17. On this census, made between 6 and 7 p.m., 46 males were tallied (table 3).

On April 20, 1961, I estimated the breeding King Rail population in a nearly pure softstem bulrush (*Scirpus validus*) marsh along U.S. Highway 17A, about 2 miles north of Savannah, Ga. The bulrush averaged about 5 feet in height, and the marsh had a firm bottom covered with 1 to 2 inches of water. A 13-acre section was marked off into transects, and King Rail territories were then spot-mapped on the basis of three calls from any one area. This mating-call count indicated a breeding population of 14 males in the 13-acre tract (table 3).

Upper Savannah River Valley

King Rails also nest further upriver in the Savannah River Valley section of the Upper Coastal Plain in South Carolina. Norris (1963, p. 2, 19) described the typical nesting habitat as a "Carolina bay"—an oval-shaped water-filled depression with rank growths of maiden-cane and other aquatic plants.

CHESAPEAKE BAY COUNTRY

Tidewater Virginia

Tidewater Virginia is the section of the Middle Atlantic Coastal Plain that extends from the fall line (the line separating the Piedmont Plateau from the Coastal Plain) to the Chesapeake Bay. It is dissected by numerous rivers, the largest of which are the Potomac, the Rappahannock, the York, and the James.

The King Rail is common throughout the year in much of Tidewater Virginia and usually occurs in greatest numbers in marshes where big cordgrass is dominant. Big cordgrass is one of the best cover plants for King Rails in Tidewater because of its height and occurrence in fairly dense stands, and because it retains its life form throughout most of the year (fig. 15). In the early 1960's, I found King Rails common in the big cordgrass marshes at Norfolk, West Point, and Tappahannock.

Other marsh types, especially Olney's three-square, wild rice (*Zizania aquatica*), and cattail, are important for the King Rail, but there is less acreage of these types, and wild rice does not provide cover in the winter. During the winters of 1958 and 1961, I encountered several muskrat trappers who were inadvertently catching King Rails in the extensive Rappahannock River brackish marsh flats across the river from Tappahannock. These flats are dominated by Olney's three-square (fig. 16). Several King Rails were removed from muskrat



FIGURE 15.—Big cordgrass (*Spartina cynosuroides*) (tall plant) and arrow-arum (*Peltandra virginica*) (broad-leaved plant next to water) along tidal creek, Nanticoke River marsh, Wicomico County, Md., August 1967. Big cordgrass usually grows along the margins of tidal guts in brackish bay marshes, but may form extensive, nearly pure stands in brackish tidal-river marshes. It is one of the most important cover types for King Rails in the Chesapeake Bay region. (Photograph by Luther Goldman.)



FIGURE 16.—Winter abode of King Rail. Rappahannock River near Tappahannock, Va., January 1961. Vegetation is mainly Olney's three-square (*Scirpus olneyi*) and saltmarsh cordgrass (*Spartina alterniflora*).

traps as I watched a trapper run his line. In these and other tidemarsh habitats, tidal action along the creeks and over adjacent marshlands keeps the water open throughout much of the winter.

At Hog Island, Surry County, in the James River opposite historic Jamestown, C. C. Steirly found both King and Clapper Rails breeding. Steirly (1959, p. 47-48) made the following comments about the rail habitat on the island:

Apparently there is a salinity gradient between the east side of the refuge and the west side of Cobham Bay. Hog Point might be the dividing line. There seems to be a slight difference in the tidal vegetation between the two sides of the refuge although the cord grass marsh seems to be the dominant feature along the east or down river side. The King Rail is most often seen on the west side; however, there is as yet no proof that it does not breed on the east side. In one of the particular haunts of the King Rail, pickerel weed (*Pontederia cordata*) and bulrush (*Scirpus robustus*) occur in some abundance where there is less tidal fluctuation.

Virginia Eastern Shore

The Eastern Shore peninsula of Virginia lies between Chesapeake Bay and the Atlantic Ocean. While King Rails would be expected to occur on the bay side of the peninsula, their presence on the offshore barrier islands on the ocean side would seem rather surprising; nevertheless, on these salty coastal islands King Rails are found in

land-locked fresh-water marshes. Montagna and Wimsatt (1942, p. 434-436) collected a female on Rogue Island 11 miles off the coast between Hog and Cobb Islands. The specimen had a fully developed swollen brood patch, and its oviduct contained an egg with shell.

There are several records from Chincoteague Island. Robert E. Stewart encountered paired adult King and Clapper Rails with a brood in a salt meadow cordgrass marsh on this coastal island. The Chincoteague salt marshes are one of the important Clapper Rail hunting grounds along the Atlantic Coast, and King Rails occasionally turn up in hunters' bags.

One of the best King Rail areas on the bay side of the eastern shore peninsula is Bullbegger Creek, a tributary of the Pocomoke River. Big cordgrass is the dominant plant in this creek marsh.

At Knott's Island, at the head of Currituck Sound, partly in Virginia and partly in North Carolina, A. J. Duvall (1937, p. 462) and party collected a female King Rail and five chicks along a roadway in a salt marsh on June 1, 1936.

Maryland Eastern Shore

In Maryland the King Rail is mainly associated with tidal marshes of the Chesapeake Bay system, and is found in greatest numbers in the extensive brackish tidal-river marshes of the Eastern Shore, especially in the vast area of fresh and brackish bay marshes of Dorchester County (see R. E. Stewart, 1962, for a description of Maryland Chesapeake Bay marsh communities). In this area, the following plants are usually present as pure stands or are found in some combination in areas where King Rails occur: big cordgrass, broad-leaf and narrow-leaf cattail (*Typha latifolia* and *T. angustifolia*), Olney's three-square, switchgrass (*Panicum virgatum*), softrush, and rosemallow (*Hibiscus moscheutos*).

The importance of big cordgrass in the Maryland section of the Chesapeake Bay is comparable to that in Tidewater Virginia.

In the brackish tidal-river marsh community of the Choptank River at Dover Bridge between Talbot and Caroline Counties, a muskrat trapper caught 50 King Rails in a single season (January 1 to March 15). Most of the birds were caught where big cordgrass was dominant but usually mixed with Olney's three-square and switchgrass. Because of the sparseness of winter marsh cover, King Rails often seek means of escape and places for hiding different from those used during the rest of the year. A muskrat trapper on the Choptank River in Maryland reports that whenever he surprises a rail along a tidal gut in the marsh it almost invariably darts into a muskrat hole along an embankment.

Robert E. Stewart has observed both King and Clapper Rails in the same big cordgrass marsh along Ape Hole Creek in Somerset County.

Both species are common there, probably because of the abundance of such prime rail foods as blue crabs (*Callinectes sapidus*), mud crabs (*Sesarma reticulatum*), red-jointed fiddler crabs, periwinkle snails (*Littorina irrorata*), and salt-marsh snails (*Malampus lineatus*).

In a brackish bay marsh community at Elliott Island, Dorchester County, on May 28, 1959, I heard King Rails calling between 11 p.m. and midnight. Most were calling from the narrow band of big cordgrass that characteristically borders the sides of Pokata Creek. Soras, Virginias, and Black Rails (*Laterallus jamaicensis*) were heard at the same time and in the same general area, but mostly in a salt-meadow marsh type community.

In a fresh bay marsh community north of Savannah Lake, Elliott Island, King Rails occur where the switchgrass marsh extends inland for a mile or so forming an understory beneath a loblolly pine (*Pinus taeda*) forest (fig. 17). It seems rather strange to flush a King Rail



FIGURE 17.—Habitat of King Rail in loblolly pine (*Pinus taeda*) and switchgrass (*Panicum virgatum*) association, Elliott Island, Dorchester County, Md., August 1967. (Photograph by Luther Goldman.)

from beneath a stand of loblolly pine. The Short-billed Marsh Wren was found nesting and wintering in this same pine-switchgrass association. Switchgrass, which attains a height of 5 feet, retains its life form throughout the year, thus affording excellent cover, especially in winter when several other marsh plants have deteriorated.

On June 10, 1965, I made a King Rail survey of a section of the Nanticoke River marshes, Wicomico County, across the river from the town of Vienna. This was a typical muskrat marsh in which Olney's three-square was dominant, with rosemallow scattered throughout. Four King Rail nests, located at the bases of rosemallow plants, were found in a 20-acre section of the marsh. The life form of this plant, with its cradle-like base and broad leaves forming a protective cover above, makes it well suited for nest cover (fig. 18).



FIGURE 18.—Nest and eggs of King Rail in Nanticoke River marsh, Vienna, Wicomico County, Md., June 10, 1965. Nest found in section of marsh dominated by Olney's three-square (*Scirpus olneyi*) interspersed with rose mallow (*Hibiscus moscheutos*). Four nests found in this marsh were all in rose mallow. Because of the life form of this plant, the rail does not have to build a canopy over its nest as it does when using other plants.

In May 1959, while censusing Red-winged Blackbirds on a number of small islands in Chesapeake Bay, I was surprised to find King Rails on almost all of them. The islands provide a brackish environment. On Long Marsh Island, May 26, 1959, I observed a nest constructed mostly of saltmeadow cordgrass and containing nine eggs (fig. 19).



FIGURE 19.—Nest and nine eggs of King Rail in brackish marsh, Long Marsh Island, Eastern Bay (of Chesapeake Bay), Queen Annes County, Md., May 26, 1959. Nest constructed of saltmeadow cordgrass (*Spartina patens*) and Olney's three-square (*Scirpus olneyi*).

Small patches of saltmeadow cordgrass were scattered throughout the dense growth of hightide-bush (*Iva frutescens*) on the island. The King Rail nest was only 15 feet from a Black Duck (*Anas rubripes*) nest. On another Chesapeake Bay island (Miller's Island) a King Rail nest was found in a pure stand of saltmarsh cordgrass.

Inner Coastal Plain of Maryland

Four pairs of King Rails nested in 10 acres of shrub swamp-marsh mixture at the Patuxent Wildlife Research Center, near Laurel, Md.,

during May and June 1965. Softrush, tussock sedge (*Carex stricta*), and arrowhead (*Sagittaria* sp.) were the common emergent herbaceous plants. Woody marsh plants included swamp viburnum (*Viburnum nudum*), arrow-wood (*V. dentatum*), buttonbush, alder (*Alnus serrulata*), winterberry (*Ilex verticillata*), red maple (*Acer rubrum*), and willow (*Salix nigra*). In late summer Woodcock (*Philohela minor*) were common in this same area.

DELAWARE BAY, DEL.

King and Clapper Rails inhabit the extensive brackish bay marshes known as Broadway Meadows between Fleming's Landing and Woodland Beach, Kent County, Del. Two King-Clapper pairs and their nests were found in June 1960 at Taylor's Gut approximately halfway between Fleming's Landing and Woodland Beach (fig. 20).



FIGURE 20.—Taylor's Gut at low tide, Kent County, Del., September 30, 1963. Vegetation in this breeding habitat of mixed King and Clapper Rail populations is mainly saltmarsh cordgrass (*Spartina alterniflora*), big cordgrass (*Spartina cynosuroides*), saltmarsh bulrush (*Scirpus robustus*), and hightide-bush (*Iva frutescens*). (Photograph by Frederick C. Schmid.)

The section of marsh at Taylor's Gut where mixed populations occur is more typical of Clapper Rail than of King Rail habitat. The domi-

nant vegetation types are saltmarsh cordgrass and saltmarsh bulrush (table 4). Hightide-bush borders the tidal guts.

TABLE 4.—*Plant composition at three stations in Broadway Meadows, Del., in 1960*

[In percent, based on estimates for five 10-foot-square quadrats at each station; tr. = trace]

	Fleming's Landing (King Rails only)	Taylor's Gut (Intermediate area; King and Clapper Rails)	Woodland Beach Causeway (Clapper Rails only)
Saltmeadow cordgrass.....	50	tr.	tr.
Saltmarsh cordgrass.....	15	50	70
Saltmarsh bulrush.....		30	20
Big cordgrass.....	5	10	10
Olney's three-square.....	25		
Hightide-bush.....	5	10	
Saltgrass.....	tr.	tr.	
Groundsel-bush.....	tr.		

Two miles inland at Fleming's Landing only King Rails were observed. The vegetation at Fleming's Landing is composed mostly of saltmeadow cordgrass and saltgrass (*Distichlis spicata*). Occasional patches of Olney's three-square, big cordgrass, and saltmarsh cordgrass were distributed through the saltmeadow marsh, and as in the intermediate area at Taylor's Gut, hightide-bush bordered some of the tidal guts.

Two miles further toward Delaware Bay along the Woodland Beach Causeway, Clapper Rails were abundant, but King Rails were not observed. Saltmarsh cordgrass and saltmarsh bulrush were the dominant plants at this station. Hightide-bush was not present.

It is interesting to note that in the Taylor's Gut area salinity readings are intermediate between those at the other stations (table 5).

TABLE 5.—*Salinity determinations at three stations in Broadway Meadows, Del. in 1960*

[In parts per million. Water samples were analyzed in the chemistry laboratory, Patuxent Wildlife Research Center, Laurel, Md.; sea strength is 32,000 to 35,000 p.p.m.]

	Fleming's Landing	Taylor's Gut	Woodland Beach Causeway
Low tide.....	4,380	7,190	7,600
High tide.....	3,700	5,670	7,480

The red-jointed fiddler crab was abundant at Taylor's Gut during the period 1959 through 1963, and formed the main food of the rails. There was a marked diminution in the fiddler crab population in 1964, and a corresponding decrease in the rail population.

Other breeding birds at Taylor's Gut in order of relative abundance are the Long-billed Marsh Wren, Red-winged Blackbird, Song Sparrow (*Melospiza melodia*), Seaside Sparrow (*Ammospiza maritima*),

Swamp Sparrow (*Melospiza georgiana*), Black Duck, and Least Bittern. The muskrat, raccoon (*Procyon lotor*), and rice rat (*Oryzomys palustris*) are common mammals in the area.

GREAT LAKES REGION

In Lake County, Ill., Beecher (1942, p. 13-14) found the *Carex lacustris* consocieties or lake sedge-marsh wren community to be the optimum breeding habitat of the King Rail. Three nests were located in 5.39 acres (Beecher, 1942, p. 29). Beecher characterizes this marsh type as follows:

Although the *Typha* consocieties is so distinctive in its characteristics, there is considerable overflow of the species presumably finding their optimum within its bounds into the lake sedge which usually adjoins it in shallower water. *Carex lacustris* tends to exist as a closed community; it is more completely dominant in its own zone and its boundaries more sharply marked out than those of any other plant in the hydrosere. To state that it has the same lifeform as *Typha* means nothing, since, though much coarser than the grass-like sedges which follow it, the stalk offers little support. Nests of bittern, gallinule and blackbird are decidedly less frequent than in cattails, those of the redwing being constructed on a stool, generally. But the King and Sora Rails and the Prairie Marsh Wren are much more abundant in this sedge than in cattails, suggesting that it has qualities of its own. Primarily, it offers the tussock or stool type of substrate so attractive to rails, and anyone viewing this community for the first time would appreciate its fitness for the wrens. The growth is denser, less erect and, doubtless, easier to work.

The King Rail also formerly occurred commonly in the extensive cattail marshes of the southwestern shore of Lake Erie. On May 30, 1931, Milton Trautman (personal communication) recorded 18 King Rails in 1 hour in these marshes. Trautman further stated that in the Sandusky Bay region, on many June and July evenings during the years between 1925 and 1934, he saw from one to eight broods on roads adjacent to marshes. At Buckeye Lake in east-central Ohio, Trautman (1940, p. 229-230) reported more than 50 pairs nesting annually between 1922 and 1930. Trautman told me that by 1959 only two or three pairs nested there. Surveys in 1961 by Trautman and others to determine the status of the King Rail in Ohio revealed that it was disappearing at an alarming rate.

In Ontario, Baillie (1940, p. 109) reported five breeding localities (based on the presence of nests or broods) along the southern edge of Ontario from Lake St. Clair to Toronto: St. Anne's Island, Lake St. Clair, Lambton County, May 1882 (nest of 13 eggs); eastern end of the north shore of Lake Erie, at Point Abino, Welland County, May 30, 1894 (nest of 10 eggs); north shore of Lake Erie, at Long Point, Norfolk County, summer of 1921 and 1926 (young); western end of the north shore of Lake Ontario at Toronto, August 22, 1938 (young); and at Hamilton, August 6, 1939 (young).

NORTH-CENTRAL PRAIRIE MARSHES

Tanner and Hendrickson (1956, p. 54-56) studied the King Rail in the marshes of Dewey's Pasture Public Shooting Ground, Clay County, Iowa, from April 1951 to April 1953. Their description of the habitat in this area is as follows:

* The 402-acre research area included 28 marshes lying in the hollows between gently sloping prairie knolls. These marshes ranged in depth from several inches to 4 feet and in area from 0.2 acres to 18.0 acres. Of the total 96.4 acres of marsh, 81.4 acres supported emergent vegetation habitable by rails. The remaining 15.0 acres consisted of open water. The predominant species of emergent vegetation in the shallowest water along the shores were blue-joint grass [*Calamagrostis canadensis*], prairie cordgrass [*Spartina pectinata*], tussock sedge and fox sedge [*Carex vulpinoidea*]. In waters of intermediate depth the most abundant species of emergent plants were river grass [*Fluminea festucacea*], lake sedge, sweet flag [*Acorus calamus*] and water smartweed [*Polygonum coccineum*]. In deeper waters the predominant species were broad-leaved cattail, narrow-leaved cat-tail, river bulrush [*Scirpus fluviatilis*], hard-stemmed bulrush [*Scirpus acutus*], pale great bulrush [*Scirpus heterochaetus*] and large bur-reed [*Sparganium eurycarpum*]. The plant names follow Hayden (1943), Four of the six nests were found in areas of marsh in which lake sedge was the predominant vegetation, while the others were found in pure stands of river bulrush and were attached to plants of that species. Of the four nests located in the lake sedge cover-type, only one was actually attached to plants of that species. The others were supported by tussocks of blue-joint grass or cordgrass, or clumps of hard-stemmed bulrush, which occurred here and there among the lake sedge.

The estimated number of breeding adults in the 81.4 acres of marsh was 12. In the same area there was an estimated adult breeding population of 54 Virginia Rails and 52 Soras.

NORTHERN GREAT PLAINS

The King Rail rarely breeds in the northern Great Plains, but R. E. Stewart (personal communication) located a breeding pair in a prairie pothole in the Missouri Coteau of western Dickey County, N. Dak., in June 1961. This pothole was a fresh-water type and was composed chiefly of whitetop grass (*Fluminea festucacea*) and slough sedge (*Carex atherodes*), with an outer border of river bulrush. Several pairs of Virginia Rails and Soras were also observed in this same pothole. Stewart also recorded single King Rails on June 5 and 24, 1963, about 12 miles west of Buchanan, Stutsman County, N. Dak., where common cattail and common spikerush were the dominant plants.

Description

SIZE

The male King Rail is generally larger and heavier than the female. Males in my study weighed about 100 grams more than females. Six of nine adult males weighed over 400 grams each, and the average of all nine was 415.4 grams, whereas the average of nine females was 306.0 grams. These weights do not differ greatly from those of Clapper Rails (table 6).

Measurements of body length and wing length also reflect the difference in size of the sexes. These are compared in table 7 along with measurements of the Clapper Rail, which is somewhat smaller in these dimensions.

ADULT PLUMAGE

There are no apparent differences between the plumages of the male and the female King Rail. Ridgway and Friedmann (1941, p. 83) described the plumage as follows:

Forehead, crown, occiput, and nape deep, rich mummy brown, the feathers of the forehead and crown with shiny black shafts; scapulars, interscapulars, upper and lower back, rump, upper tail coverts, and rectrices deep fuscous to fuscous-black, the feathers broadly edged with tawny-olive to buckthorn brown, the edges becoming broader on the more posterior parts, often occupying (between the two margins) more than half the width of the feather on the long scapulars and the feathers of the rump and the upper tail coverts, narrow on the anterior interscapulars; upper wing coverts deep hazel to bright russet, some of the outer median and greater coverts with narrow whitish tips and a concealed narrow subterminal whitish band; remiges sepia, the outer web of the outermost primary often slightly paler—Saccardo's umber; a light strip from the base of the maxilla over and behind the eye light pinkish cinnamon; rest of lores, circumocular area, cheeks and auriculars grayish mummy brown; lower cheeks and sides of throat cinnamon; chin and middle of upper throat white; lower throat, breast, and upper abdomen cinnamon becoming paler in the mid-ventral part of the upper abdomen, the feathers faintly tipped with white on the upper abdomen, without pale tips on the breast feathers; middle of abdomen light buff; thighs similar but transversely barred with deep drab to hair brown; flanks sepia barred with white, the feathers tipped with white and crossed by two or three white bars each; vent similar to flanks; under tail coverts white, not buffy, and with sepia areas reduced making the white bars wider; the outer webs of the lateral ones wholly white; axillars and under wing coverts deep rich sepia tipped and crossed by narrow bars of white; . . .

Ridgway and Friedmann described the dark and light phase adult plumages of the King Rail, and suggested that the light phase rarely

occurs. My recent investigations indicate that the so-called light phase plumage is probably the result of hybridization or intergradation in areas of mixed King and Clapper Rail populations, or it may be due simply to individual variation.

In my collection I have a series of 16 King and Clapper Rail specimens taken from a 1-square-mile area of brackish marsh in Delaware (table 1). In this series there are Kings and Clappers with typical plumages and also gradations from one type to the other. Some of the specimens appear to be light phase King Rails. Ridgeway and Friedmann (1941) made no mention of locality, habitat, or the possibility of mixed populations where so-called light-phased birds were collected.

TABLE 6.—Weights of King and Clapper Rails

[In grams. All specimens were adults. Bottom line shows mean weights.]

King Rail (<i>R. e. elegans</i>) ¹		King Rail (<i>R. e. tenuirostris</i>) ²		Clapper Rail (<i>R. l. crepitans</i>) ³		Clapper Rail (<i>R. l.</i>) ⁴	
Males	Females	Males	Females	Males	Females	Males	Females
339.9	253.0	271	220	332.2		300	275
366.0	272.0	306	255	335.0		325	275
367.9	305.0	317	268			300	275
421.0	313.3	331				325	275
427.0	319.0					300	275
436.0	320.0					350	275
438.3	322.0					300	250
453.0	323.0					300	
490.0	325.0					325	
						350	
						350	
						350	
						350	
						325	
415.5	305.9	306.3	247.7	333.6		320.8	271.4

¹ From Arkansas, Delaware, and Louisiana (author's data).

² All from Mexico (Warner and Dickerman, 1959, p. 50).

³ Both from Delaware (author's data).

⁴ All from South Carolina, each to nearest 25 grams; race (*R. l. crepitans* or *R. l. waynei*) not specified (Blandin, 1963, p. 33).

TABLE 7.—Measurements of King and Clapper Rails

[From Ridgeway and Friedmann, 1941. All specimens were adults. All measurements are given in mm. Wing measurements are for the chord, from bend of wing to tip of longest primary]

	King Rail (<i>R. e. elegans</i>)				Clapper Rail (<i>R. l. crepitans</i>)			
	Males ¹		Females ²		Males ³		Females ⁴	
	Range	Average	Range	Average	Range	Average	Range	Average
Wing.....	159.0-177.0	163.4	147.0-162.0	154.3	142.5-159.5	151.1	135.5-160.0	146.8
Tail.....	56.0- 72.5	65.9	60.0- 70.0	64.4	55.0- 69.0	64.6	55.0- 69.5	61.9
Exposed culmen.....	58.0- 65.5	62.5	50.0- 63.0	61.9	55.0- 69.5	63.3	53.5- 67.0	59.6
Tarsus.....	52.0- 64.0	58.4	49.5- 58.0	54.0	48.0- 56.0	51.7	41.0- 56.0	48.1
Middle toe without claw.....	50.5- 60.5	55.1	46.0- 56.0	50.8	45.5- 53.5	48.8	40.0- 52.0	45.9

¹ 18 specimens from Illinois, Missouri, District of Columbia, Virginia, Alabama, Louisiana, South Carolina, and Florida.

² 14 specimens from Illinois, District of Columbia, Maryland, Virginia, Louisiana, and Florida.

³ 21 specimens from Massachusetts, New York, New Jersey, Virginia, and North Carolina.

⁴ 17 specimens from New Jersey, Virginia, and North Carolina.

NOTE.—An incubating female (adult?) King Rail collected at Stuttgart, Ark., May 1962, had a left wing measurement (chord) of only 141.0 mm.; a paired female (adult?) collected at Taylor's Gut, Kent County, Del., Apr. 15, 1963, had a left wing measurement (chord) of 145.0 mm.

The most unusual plumage that I have seen was that of a very dark brown, almost blackish bird near Lake Okeechobee, Fla., January 1958. William B. Robertson (personal communication) told me of seeing several birds with similar dark plumage in the Everglades, and Luther C. Goldman collected such a specimen near Cape Sable, Fla. Dr. Harry C. Oberholser examined the specimen and remarked that it had a most unusual plumage. Apparently he did not make a critical study of it, and it has since been lost.

LEGS AND FEET

Legs and feet are pale brownish gray. An adult male collected at Welch, La., January 12, 1963, and two adult males collected in August 1963, in Delaware, had a pinkish-brown color on the inside and outside heel areas and immediately above. This heel color is apparently typical of birds in their second year or older.

BILL

In most adult birds the bill is orange-yellow from the base to at least the nares in the upper mandible, and usually slightly beyond in the lower mandible. The outer part of the bill is brownish. However, one marked wild bird known to be at least 2 years old had a lightish-brown bill more typical of immatures. A captive immature did not attain the color at the base of the bill until it was 10 months old. The color was then yellowish rather than orange-yellow. Young wild birds 2 to 3 months of age had lightish brown bills. The upper mandibles of these birds were darker.

TONGUE AND LINING OF MOUTH

Tongues and mouth linings of birds 1 year or older, examined immediately after collection, were a bright orange-red. Young birds in juvenal plumage, collected during the summer, had yellow tongues and mouth linings.

EYE

Irides of adult King Rails are reddish-orange while pupils are grayish-black. Eyes of newly hatched chicks are grayish-brown, and 1- and 2-month-old birds have dull-brown irides.

NOTES ON SEXING AND AGING

In a 50-bird sample from Louisiana, examined 3 months after collection in late fall, I was able to sex 47 of 50 birds by weight, and age 36 of 45 by color of the bill and heel. As an aging criterion, the color of the bill is used most accurately with live or freshly killed birds, because with time it fades. Wing measurements can also be used as an aid in sexing birds, since the average for males is nearly 10 milli-

meters greater than that for females. From late summer to at least early winter, the presence of a bursa in young birds will distinguish them from adults.

MOLTING

Adult King Rails have a complete molt and are flightless for nearly a month. Young of the year undergo a partial molt which does not include the tail and flight feathers.

In the Middle Atlantic States the molting season for King Rails extends from the beginning of the breeding season in late May until the beginning of fall migration in early October.

In this study, breeding birds found in molt during May and June were replacing only body feathers. Molt of the remiges and rectrices was not observed until the first week in July. I have not been able to ascertain the relation between the partial molt during the breeding season and the complete molt in the summer. Birds that are renewing their body feathers while nesting in May and June may be undergoing prenuptial molts or early postnuptial molts during which the wing and tail feathers are not dropped.

Bent (1926, p. 262) stated that adult King Rails undergo a partial molt of the contour plumage during early spring. Eight specimens collected in the Middle Atlantic States in March and April showed no signs of molt. An adult female King Rail in the U.S. National Museum, taken at Alligator Bluff, Kissimmee River, Fla., April 9, 1901, was molting body feathers when collected. This could well have been a breeding bird because in Florida this species begins nesting in late winter. In my records the earliest recorded dates of molting by King Rails are May 28, 1960, and May 29, 1964, when an adult or subadult male and female, respectively, were found in breeding condition at Woodland Beach, Del. The male had pinfeathers on the underside of the neck, the sternal region, and the crural tract. Feather renewal on the female appeared to be about three-fourths complete and was proceeding simultaneously in most areas of the body. Three King Rails in breeding condition examined at Laurel, Md., June 12 and 18 and July 3, 1965, also were molting body feathers.

Molting rails in breeding condition have previously been reported. Watson (1962, p. 350) collected molting Spotted Rails (*Pardirallus maculatus*) in breeding condition in Cuba; Warner and Dickerman (1959, p. 50), working near Mexico City, reported two female King Rails (*Rallus elegans tenuirostris*) molting in May during the nesting season.

My earliest example of a King Rail molting its wing and tail feathers was at Laurel, Md., July 7, 1965. This bird was flightless. Two other birds trapped at Laurel, one on July 14, 1967, the other on July 24, 1967, also were flightless. A female collected near Woodland Beach,

Del., July 30, 1964, had nearly completed molting. Its new remiges and rectrices were about half grown, and there was evidence of a late stage of feather replacement in all tracts except the head and upper neck regions.

A captive subadult female began molting wing and tail feathers by the latter half of July. Two of three adults collected in Delaware on August 23, 1963, had nearly completed their molts of wing and tail feathers; the third had no wing or tail feathers.

On August 3, 1967, I took two birds from the Nanticoke River marsh, Vienna, Md., that had not yet begun to molt.

The molting period for the Clapper Rail in the Middle Atlantic States is apparently the same as that for the King Rail. A pair of molting Clapper Rails in breeding condition was collected at Woodland Beach, June 29, 1964. Only the body feathers were being molted.

Robert E. Stewart (1952, p. 57) trapped and banded many Clapper Rails at Chincoteague, Va., and made the following notes on their molt:

During the trapping period [July 16–August 31] most of the adults were undergoing their post-nuptial molt . . . The individual molting period lasts about one month. The first adult observed in full molt was trapped on July 21. During the period August 24 to August 31 (period just before hunting season) a total of 11 adults were trapped. Of these only 5 had completed their molt and were capable of flight, while 4 were in heavy molt, and were completely flightless. Surprisingly enough the other two adults had not even started to molt and were in very worn plumage.

In a group of young captive King Rails, the postjuvenile molt was underway when they were 50 days old. Molting of the body feathers began before the young could fly, when the flight feathers were about one-half to three-fourths unsheathed. Another group of young King Rails, raised in captivity after being hatched on June 7, completed their postjuvenile molt by the end of the first week of September.

Breeding Biology

Studies of the breeding biology of the King Rail were made mostly on the Grand Prairie in Arkansas and Prairie Counties, Ark., during the period 1951-55.

In late winter when rails return to the prairie from more southern latitudes or simply become conspicuous in areas where they have been present all winter, the most suitable habitat for the establishment of nesting territories is the narrow strip of marsh found in roadside ditches. At this season there is little suitable cover elsewhere. Old rice stubbles are sometimes used for nesting, but many of these are dried up or whipped down by winter winds and rains or are plowed under in the early spring.

HOMING

Some males or females return to the same territory in consecutive years. An incubating bird of undetermined sex banded on a nest at Stuttgart, Ark., May 6, 1952, was recaptured the following year on May 1, on a nest 30 feet from the previous year's nest site. An incubating bird of undetermined sex was banded on its nest at the Patuxent Wildlife Research Center, Laurel, Md., July 3, 1965, and recaptured in a trap with a mate and brood of eight young on July 8, 1966, 50 feet from the 1965 banding site.

TERRITORIES

Territories occupied by King Rails in roadside ditches consist of small strips of fresh-water marsh. The dominant plants in most of these small marsh strips (in order of relative abundance and consequently of relative importance as nesting cover for King Rails in 1952) were soft-rush, awl-fruited sedge, bottlebrush sedge (*Carex comosa*), lake sedge, common spikerush, beakrush (*Rhynchospora* sp.), an undetermined Graminae, broad-leaved cattail, and smartweed (*Polygonum* sp.).

The schedule of arrival of males in the area and the stage of courtship determine size and choice of territory. It is conceivable that the earlier arrivals manage to claim larger and more suitable territories than those which arrive later when competition is keener. However, territorial boundaries are rather fluid during the earlier part of the courtship period. As additional males move into an area of suitable

roadside ditch habitat, the large courtship-feeding territories of the first contingent tend to shrink.

Initial occupation of territories is indicated by the mating call. During the last week in February and the first week in March 1955, one male King Rail gave the mating call at various points along 975 linear feet of roadside ditch. By the second week in March its mating call was heard from about 500 feet of roadside ditch; its territory then was about half its original size. The diminishing of the territory was caused by: (a) Pressure from another courting male, (b) burning of cover along part of the ditch bank within the original calling territory, and (c) relatively modest territorial requirements for nesting, particularly if there is plenty of water and ample aquatic animal life for food in the area about the nest.

Approximate sizes of nesting territories were determined by measuring the distances between three active nests in the same ditch; from the center nest it was 298 feet to the nest on one side and 166 feet to the nest on the other side. The ditch was about 30 feet wide at all three points.

Defense of territories

King Rails defend their territories both inter- and intra-specifically. When another King Rail invades a territory, the possessor often prepares to charge by coming to a "freeze," assuming a partial crouch, drawing in its neck, and slowly ruffling its feathers. It then chases the intruder on foot and on the wing.

As additional King Rails move into suitable nesting habitat, there is much fighting, particularly near boundaries of the more desirable territories. I observed a typical skirmish in a narrow ditch bordering a secondary road on April 21, 1955. At this unstable territorial boundary, two males attacked each other with bill and claws, sparring like fighting cocks for about 20 seconds. Then the battle suddenly ended, and the birds moved in opposite directions.

On April 22, 1955, in a rice stubble which appeared to be a common feeding ground for the occupants of the adjacent section of roadside ditch, two males (each already paired) "squared off" in a bitter encounter lasting 3 minutes. There was much chasing both on foot and on the wing and clashing "fighting cock style." W. E. D. Scott (Bent, 1926, p. 287-288) reported similar fighting by Clapper Rails (*Rallus longirostris scotti*) during the courtship period:

"During the mating season the male birds are very pugnacious and resent any intrusions from others of the species. At such time I have seen them have pitched battles, and finally, one giving in and taking to flight, the victor would pursue the vanquished on the wing for several hundred feet . . .

Sora Rails, migrating through the Arkansas rice country in spring, frequent roadside ditches occupied by King Rails on established nest-

ing territories. One King Rail made four passes in running flight at a Sora in order to evict it from his territory. Virginia Rails received the same treatment from King Rails.

A call, presumably agonistic, heard when two male King Rails were in the same territory, could be described as *kik-kik-kur-r-r-r-r*.

COURTSHIP BEHAVIOR

Mating call and pair formation

With the first warm days of late February, the mating calls of King Rails are heard for the first time in the roadside ditches adjacent to rice stubbles or other fields. Rails feed in the shallow water of the ditch and use the broomsedge (*Andropogon* spp.) on ditchbanks or outside levees of old ricefields as places of retreat or hiding. Moreover, the rails use little lanes or pathways, such as those made by cottontails (*Sylvilagus* sp.), for traveling in concealment along the ditchbanks. In late February the only vegetation that offers much concealment to calling King Rails is the perennial ditchbank sedge which is also the winter abode of the Short-billed Marsh Wren on the Grand Prairie; consequently, much of the early season calling emanates from behind or among clumps of this grass. However, where there happens to be an old growth of cattails in the ditch, rails may call from this cover.

The male King Rail calls its mate from a concealed, partly concealed, or completely exposed position. The purpose of this call is first to attract a mate and later, after pair formation, to rally her.

The mating call is one of the least difficult calls to describe. It is most commonly given as a harsh *kik-kik-kik-kik-kik*-, but occasionally varies from a series of *kiks* to a series of *kuks* or *bups*. This variation may be a matter of interpretation, possibly depending upon the observer's distance from a calling bird. The pitch of the call is steady, but the tempo increases from time to time. One bird was heard and seen to give this call continuously for 18 minutes. In the Arkansas ricefields this call was heard at almost any time during daylight, but less frequently at night. At Elliott Island, Md., in the Chesapeake Bay country, I often heard the mating call after 10 p.m. D. J. Nicholson (personal communication) heard dozens of these rails calling all through the night on the Kissimmee Prairie, Fla., in January and February 1962.

I have never heard a female give the mating call.

Other calls

The most characteristic call of the King Rail, the primary advertising call, is the one that is heard throughout the breeding season. It may be written as *jupe-jupe-jupe-jupe-jupe*- or *cheup-cheup-cheup-cheup-cheup*- or sometimes as *gelp-gelp-gelp-gelp-gelp*-. The first several notes in a series are louder than succeeding ones, and the tempo

increases rapidly toward the end of the call when the notes run together. One rail gave 25 distinct *jupes* in a single series, not including those in the rapid ending which could not be counted. This call carries a greater distance than the mating call and is sometimes answered by a number of other King Rails. It is sometimes used when a bird is startled and occasionally serves as an "all is well" call when a pair of separated birds are reunited. In addition, I have often observed an incubating bird using this call when it wishes to be relieved at the nest. The primary advertising call of the King Rail is slower and more deliberate than that of the Clapper, which is usually more of a rapid *chac-chac-chac-chac*.

A call uttered during prenuptial courtship by both the male and the female, but more frequently after pairing, is a soft and rapid *tuk-tuk-tuk-tuk-tuk*-. This sound reminds me somewhat of the clapping together of the mandibles of the Barred Owl (*Strix varia*), and is seldom audible to the human ear beyond 20 or 30 feet. The King Rail uses the "tuk" call as a rallying call or gives it to indicate its position to its mate.

Display

The display of the male during prenuptial courtship is relatively simple and consists mostly in walking about with tail uplifted and white undertail coverts extended (fig. 21-1). In this position the white undertail coverts can be seen from a considerable distance. While flashing its white undertail coverts, the rail usually flicks its tail up and down slightly. Females that I observed during the period of prenuptial courtship made no attempt to display.

There were other forms of posturing during the period of courtship and mating, but apparently the cocked tail and well-exposed white undertail coverts, accompanied by the mating call, are the principal means of attracting a mate.

On two occasions I observed what appeared to be another form of display, the "pursuit display." The circumstances and the behavior of the male were essentially the same both times. In each case the male apparently had not succeeded in attracting a mate to his territory. On March 1, 1955, at 8:30 a.m., I saw a small and very rufescent King Rail, later established to be a female, moving along a rice levee bordering a roadside ditch and approaching a calling male. The female continued along the water's edge at a slow but steady gait and passed beyond the male that was standing in the ditch. As soon as she was ahead of him, the male followed her at a fast walk with head and neck outstretched, bill open (but emitting no sound audible at 40 feet), tail cocked, and white undertail coverts extended (fig. 21-2).

Following pair formation much of the posturing and calling that characterized the period of prenuptial courtship continues, at least

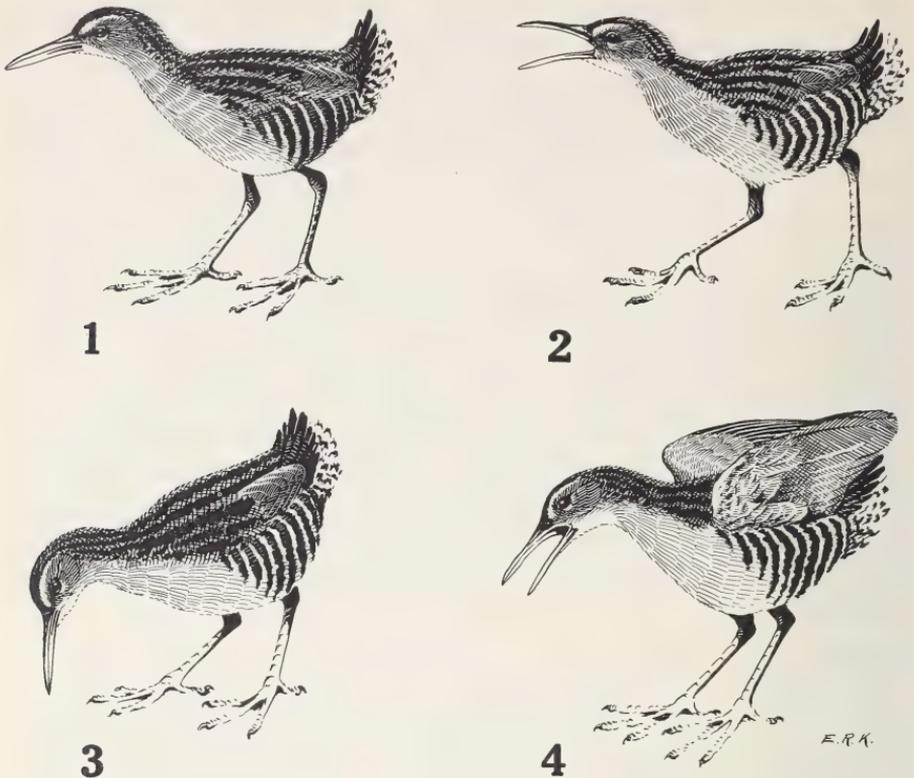


FIGURE 21.—Displays of the King Rail: (1) In the Advertising Display the tail is cocked and the white undertail coverts extended. (2) The Pursuit Display is given when the male pursues the female during prenuptial courtship; the male walks fast or runs with tail slightly cocked, white undertail coverts extended, and bill wide open. (3) The Invitational Display is assumed by the mated male when the female approaches; the bill points downward and slowly swings from side to side, and the tail is displayed. (4) A variation of the Invitational Display consists in wings arched, head turned to one side, bill open, and tail displayed.

in the earlier phases of nuptial courtship. While pair formation is in progress, but infrequently during the nuptial courtship period, the female utters a *purr* or *churr* sound, like the *purr* of a cat, especially after the male has given the mating call.

The male uses the mating call (*kik-kik-*) infrequently and with less vigor when rallying a newly won mate which often strays when foraging. I observed a good example of the use of this call shortly after pairing on the evening of March 2, 1955. During an 18-minute period beginning at 5:30 p.m., a paired male, while standing partially concealed on a ricefield border levee, uttered the complete mating call seven times. Six of the seven times his mate ran to him from a distance of 100 feet or less where she had been feeding. When the female came up beside him, the male spread his white undertail coverts and bent his head and neck so that his bill was perpendicular to and

nearly touching the ground (fig. 21-3). From this position, he often turned his bent head with bill open toward the female. At one of these meetings the male appeared to be about to mount the female and begin to rise up with his bill still wide open, but the female evidently was not ready for copulation and walked away.

I observed the same posture many other times, but the birds were usually standing in water. On these occasions the bill usually touched or slightly dipped into the water. Males assumed the pose after pairing, when the feeding female that had been at some distance away came within 3 or 4 feet of her mate. On one occasion a male under such circumstances arched his partly opened wings (fig. 21-4).

Courtship feeding

Courtship feeding, a type of symbolic display that aids in maintaining the pair bond, was observed during the courtship, egg laying, and incubation periods of the King Rail. In the Arkansas ricefields, the crayfish was the only food that I ever saw presented to a female. In Delaware Bay marshes, the fiddler crab was used for this purpose. The male usually brings the food item to the female, but sometimes he may stand where he catches the crustacean, holding it in his bill, until the female approaches and takes possession.

A mated pair of rails that I observed for a number of days on their Delaware breeding territory would descend at low tide from the marsh to a pool in the bed of a tidal creek. The female would usually stand in the pool while the male hunted food for her. He would frequently run up the winding creek bed for 25 yards or so, catch a fiddler crab, and run back to present it to the female. Why he often traveled such distances when there were plenty of fiddlers nearby is not known.

During a 2-hour period of observation in an Arkansas ricefield, I saw the male of a pair catch seven crayfish, five of which he presented to his mate.

PRENESTING ACTIVITY

Calling

As the nesting season approached, the mating call and undertail covert flashing by the male all but ceased, and the addition of a number of calls, mostly soft or subdued, increased the repertoire of the mated pair. Paired rails used such calls as rallying devices when separated or as reassuring answers to one another's calls when together.

A call frequently given by both birds, particularly as nesting approached, was a very soft *poyeek-poyeek-poyeek-poyeek-poyeek-*, or *wyeek-wyeek-wyeek-wyeek-wyeek-*, which seemed to act as an inquiry of the whereabouts of the mate.

Several males gave one of the more unusual calls, a deep booming sound requiring an effort which caused the body to appear to expand

slightly and sounding something like *óom-óom-óom-óom-óom*-. The purpose of his "booming" call is not known. It is not very loud, and the females were not nearby when it was uttered, unless they were well concealed.

Symbolic nest building

Symbolic nest building was observed at Stuttgart, Ark. In this case a male King Rail was observed carrying nesting material into a hole in a ricefield dike through which water was draining into a roadside ditch. The dike was about 2½ feet in height, and the hole was large enough for the bird to pass easily from one side to the other. The light stream of water did not prevent an accumulation of nesting material. However, the nest was not completed. Two days later (April 2) the true nest was started about 10 yards from the hole in the dike.

Copulation

Copulation usually takes place near the nest site, before and during egg laying. Although no nests with eggs were found on the Arkansas Grand Prairie before March 25, rails were observed copulating as early as March 3, in 2 different years. Perhaps these birds nested earlier than March 25.

On one nesting territory, the male came within 20 feet of the nest (containing one egg), called, and was answered by the female who left the nest and came to the male for copulation. The *jupe-jupe-jupe-jupe-jupe*- call often precedes copulation during this period. Copulation is performed with the female assuming a crouch and the male mounting with legs and feet placed on the female's back.

NESTING PERIOD

The nesting period varies with latitude, being longer and starting earlier in the southern part of the range. The nesting period in Florida extends from late January, at least, until the middle of July, and in Louisiana from early March to September. It is quite conceivable, therefore, that in such States as Florida and Louisiana the breeding season covers 7 to 8 months. Unlike the Bobwhite (*Colinus virginianus*), Redwinged Blackbird, and several other species which do not nest much earlier in the gulf coast region than in the northern States, the King Rail takes advantage of the long warm period, and nests over a longer period of time. The long period of nesting in the South should result in a greater total production of young, because of the much greater opportunity for renesting and second broods. The nesting season in the Middle Atlantic States is about 4 months; adults with downy young have been observed in early August in Delaware.

With the long warm period prevailing in the Deep South, time for raising more than one successful brood would seem to be ample. A breeding pair is busy with nesting activity for about 2 months (approximately 10 days for laying, 21–22 days for incubation, and 24–30 days with brood). As yet there is no evidence that the King Rail is double-brooded; however, no attempt has been made to determine this. The closely related Clapper Rail in South Carolina is double-brooded (Blandin, 1963, p. 66–67), and it is probable that some King Rails in the Deep South also have more than one successful brood during a season.

A nest found in a cypress pond in southern St. Johns County, Fla., in February 1933 contained 11 eggs in an advanced stage of incubation (Hallman, 1934, p. 18). Allowing a 21- or 22-day incubation period plus 11 days for laying, it is conceivable that this nest was started in January. D. J. Nicholson found a dead King Rail at Orlando, Fla., on February 16, 1925, with a hard-shelled egg ready for deposit (Howell, 1932, p. 203). A single downy young King Rail was seen on March 10, 1950, 2 miles west of 40-mile Bend, Dade County, Fla., by J. C. Moore and D. B. Beard (U.S. National Park Service files). W. B. Robertson, Jr. (personal communication), found several young King Rails at Royal Palm Hammock, in the Florida Everglades, on March 5, 1952. These last two examples indicate February nesting.

Adults with six young approximately 2 weeks old were recorded in Lee County, Fla., July 30, 1966, indicating that the nesting season in Florida extends into July (Frederick H. Lesser, personal communication).

At Oakland Plantation, a few miles north of Charleston, S.C., a brood of 10 young were seen by Francis Porcher on March 22, 1913 (Sprunt and Chamberlain 1949, p. 193). In this case nesting started in early or mid-February. I found young 1 to 4 days old (egg tooth present) and a nest of nine eggs in Jasper County, S.C., near Savannah, Ga., on April 16, 1961, and young at Georgetown, S.C., on April 25, 1961.

At Grand Chenier, Cameron Parish, on the southwestern coast of Louisiana on April 8, 1956, I observed a pair of King Rails feeding 2-week-old young. Back-dating about 38 days to cover the age of the young and the incubation period, laying began about March 3.

Fifty miles north in the Louisiana rice country, nesting probably gets underway a little later than on the coast. A nest of seven eggs was found at Mamou, March 30, 1957. A late nest containing eight eggs was found at Mamou, August 6, 1955.

On the Arkansas Grand Prairie, the important nesting months are April, May, and June (table 8). The earliest indication of nest build-

ing is in late March (March 25). During March 1952, nearly all King Rails seen were in pairs.

In Maryland, most clutches are laid between May 15 and June 30. A brood of chicks and their parents were seen by P. J. Van Huizen near the Blackwater River, Dorchester County, on May 21, 1965, giving evidence that some King Rails begin nesting in April.

In Central Ohio, Milton B. Trautman and R. Bales located 42 nests, 34 of which were found in May and 8 in June (M. B. Trautman, personal communication). Seven of the June nests were found during the first half of the month, and 26 of the May nests were found during the last half of that month. From this, the main nesting period seems to extend from May 15 to May 31.

TABLE 8.—Nesting dates, clutch size, and habitat of King Rail nests at Stuttgart, Ark.

Nest number	Date found	Number of eggs ¹	Complete clutch size ²	Number hatched	Location	Dominant vegetation
1	Apr. 1, 1952	1	11	8	Ditch	<i>Typha latifolia</i> .
2	Apr. 10, 1952	b	2d		Canal	<i>Juncus</i> sp.
3	Apr. 15, 1952	4	12	12	Ditch	<i>Typha latifolia</i> .
4	Apr. 16, 1952	11	11	9	do.	Grass?
5	Apr. 21, 1952	10	10	9	do.	<i>Juncus effusus</i> .
6	do.	14	14	14	do.	<i>Carex hyalinolepis</i> .
7	Apr. 24, 1952	4	4d		do.	<i>Carex hyalinolepis</i> .
8	Apr. 25, 1955	6			do.	<i>Eleocharis</i> sp.
9	Apr. 26, 1955	13			do.	Sedge.
10	do.	2			do.	<i>Juncus effusus</i> .
11	do.	new			do.	<i>Juncus effusus</i> .
12	May 1, 1952	1	1d		do.	Sedge?
13	do.	11	11	11	do.	<i>Typha latifolia</i> .
14	May 2, 1952	new	d		do.	<i>Juncus effusus</i> .
15	do.	11	11	10	do.	Sedge?
16	May 5, 1962	10		8	do.	<i>Carex stipata</i> .
17	May 6, 1952	5	11	9	do.	<i>Juncus effusus</i> .
18	May 9, 1950	4	5d		Ricefield	<i>Oryza sativa</i> .
19	do.	6	11		Ditch	<i>Juncus effusus</i> .
20	May 10, 1948	12	12		Oat field	<i>Avena</i> (var.).
21	May 10, 1952	9	9	9	Ditch	<i>Juncus effusus</i> .
22	do.	11	11	10	Canal bank	<i>Bromus secalinus</i> .
23	May 11, 1952	12	12	10	Ditch	<i>Juncus effusus</i> .
24	May 12, 1962	12		(?)	do.	<i>Carex stipata</i> .
25	May 13, 1952	10	10	0	do.	<i>Juncus effusus</i> .
26	May 13, 1962	11			do.	<i>Eleocharis palustris</i> .
27	May 15, 1962	10		(?)	do.	<i>Carex stipata</i> .
28	May 26, 1952	2	2d		Canal bank	Grass?
29	May 26, 1954	10		10	Ditch	<i>Eleocharis</i> sp.
30	May 28, 1952	4	8	8	do.	<i>Juncus effusus</i> .
31	June 3, 1954	3		(?)	do.	Grass? and sedge?
32	June 4, 1952	eb			Weedy field	<i>Avena</i> (var.).
33	June 9, 1952	10	10	10	Canal bank	<i>Oryza sativa</i> .
34	June 13, 1952	7			Ricefield	<i>Paspalum distichum</i> .
35	do.	eb			Pond edge	<i>Paspalum distichum</i> .
36	do.	9			do.	<i>Oryza sativa</i> .
37	June 19, 1952	eb	0		Ricefield	<i>Oryza sativa</i> .
38	June 25, 1952	10	10		do.	<i>Oryza sativa</i> .
39	July 15, 1950	(?)			do.	<i>Oryza sativa</i> .
40	do.	(?)			do.	<i>Oryza sativa</i> .
41	do.	(?)			do.	<i>Oryza sativa</i> .
42	do.	(?)			do.	<i>Oryza sativa</i> .
43	do.	(?)			do.	<i>Oryza sativa</i> .
44	July 18, 1951	7	9		do.	<i>Oryza sativa</i> .
45	Aug. 1, 1950	6	8d		do.	<i>Oryza sativa</i> .
46	Aug. 9, 1951	5	5d		do.	<i>Oryza sativa</i> .
47	Aug. 9, 1963	5	5	0	do.	<i>Oryza sativa</i> .
48	Aug. 10, 1951	6	6d		do.	<i>Oryza sativa</i> .
49	Aug. 29, 1951	9			Ditch	<i>Echinochloa</i> sp.

¹ b = building; eb = eggs broken.

² d = deserted.

³ Nest and eggs found; clutch size not recorded.

Tanner and Hendrickson (1956, p. 54) reported that in Clay County, Iowa, nesting begins soon after the arrival of the birds during the first week of May.

In 1951 the nesting season extended for a period of 42 days from May 13, the date that the first egg was laid, until June 23, the date that the last egg hatched.

NEST SITE AND MATERIALS

The usual nest site is in the shallow-water part of a marsh. The water depth was 4 to 18 inches at Clay County, Iowa (Tanner and Hendrickson 1956, p. 55), 2 feet at Buckeye Lake, Ohio (Trautman 1940, p. 229), and 6 to 8 inches in Arkansas ricefields. In South Carolina, Wayne (1910, p. 35) found nests in buttonbushes 8 to 18 inches over water.

In a giant cutgrass marsh near Savannah, Ga., each of five nests located was within 20 feet of the edge of the marsh, although the vegetation density and other characteristics appeared uniform over extensive areas.

Occasionally a nest is placed on a dry-land site such as an oat or wheatfield, or on a grassy embankment. In 1952, on Long Island, N.Y., Roy Latham (1954, p. 3-9) found a nest on the ground in a potato field, 150 yards from the edge of a salt marsh where Clapper Rails were nesting.

The nest site appears to be chosen by the male. On two occasions, I have seen a male initiate nest-building.

Most King Rail nests are placed in fairly uniform stands of vegetation and are well concealed, but the shape of the nest canopy (whether cone-shaped or round) sometimes disrupts the uniform pattern of the vegetation and reveals the location of the nest to the human eye (figs. 22 and 23).

The life form of some plant in the territory, such as a tussock of grass or the stool of a rice plant, often determines the exact nest site. A nest may be placed in a clump of grass or a sedge tussock, or between several clumps, parts of which are used in fashioning the canopy and sides of the nest. The bases of most Arkansas nests were made of wet decaying plants, and the platforms or cups were of dead dry grasses, sedges, or rushes. These materials are obtained near the nest site. The base of one nest found in Arkansas was made entirely of mud and was $2\frac{1}{4}$ inches in depth.

Nest materials used in some Iowa nests consisted of one or two species of plants (Tanner and Hendrickson 1956, p. 55). Most nests in Arkansas ricefields were made of rice plants; a few were made from "weed" plants in the fields, such as wild millet. The completed nest is a round, elevated platform with a saucer-shaped depression (figs. 23, 24, and 25). It usually has a round or cone-shaped canopy and a ramp, and is nearly twice as large as that of the Virginia Rail or Sora.



FIGURE 22.—Canopy of King Rail nest in roadside ditch, Arkansas Grand Prairie. In a uniform stand of vegetation the canopy is often quite conspicuous. Canopy composed of spikerush (*Eleocharis palustris*) and smartweed (*Polygonum* sp.).



FIGURE 23.—King Rail nest in roadside ditch near Stuttgart, Ark., May 30, 1952. Nest constructed of soft rush (*Juncus effusus*).



FIGURE 24.—King Rail incubating in nest constructed of cattails (*Typha latifolia*) in roadside ditch, Arkansas Grand Prairie, April 1952.



FIGURE 25.—King Rail incubating in open nest along roadside ditch, Mamou, La., April 1957.

Dimensions of 11 eastern Arkansas nests were: average height from ground to canopy, 43.0 cm.; average height from ground to rim, 16.5 cm.; average exterior diameter, 28.0 cm.; and inside depth, 1.5 cm. (Meanley, 1953, p. 265).

The height of the nest above water usually depends upon the depth of the water. Eggs in most nests in Arkansas Grand Prairie ricefields were less than a foot above the water level. In tidal marshes along the lower Savannah River, S.C., the eggs in two nests were about 2 feet above the low tide mark and about 1 foot above the high water mark. Nests in dry locations, such as oatfields, canal banks, or dry ditches, are usually elevated very little, and the eggs may rest within an inch or two of, or actually on, the ground. Nests placed above 2 or 3 inches of water may be elevated as much as a foot during a heavy rain or when a dry ricefield is being flooded.

After a heavy rain on the Arkansas Grand Prairie, an incubating rail was observed working rapidly to build up its cattail nest above the rising water in a roadside ditch. By reaching out with its bill all around the nest and picking up materials (mostly cattail leaf fragments), which it tucked beneath the eggs, and by using most of the canopy for the same purpose, the bird managed to keep the eggs about 2 inches above the rising water. The ditch was nearly dry before the rain, and the eggs were then 5 inches from the ground. At peak depth, the water was 21 inches deep. On another occasion, a nest with eggs 2½ inches from the ground was located in a ricefield that had been temporarily drained. The next day, the field was flooded to a depth of 5 inches, and the eggs were raised to 7 inches from the ground. As the water continued to rise, the incubating bird persisted in elevating the eggs by tucking rice leaves from the canopy under them.

On one occasion I came upon a bird constructing a nest on a canal bank, and watched the process only a minute or so before its mate came to continue the work. The bird that was relieved left to feed in a nearby ditch. I watched the newcomer for about 3 minutes, and then collected it. Upon dissection it proved to be the male.

Apparently the male takes the more active part in nest building. Males on three occasions were observed gathering nest material within 20 feet of the nest site. A captive male purred like a domestic cat constantly as it carried nesting material to the nest site. The nest is shaped as the bird (all observations were of males) sits in a clump of grass or between clumps and semirotates its body. It later piles up dead vegetation, and shapes the cup. The canopy is formed by bending over the tops of stalks of adjacent plants. One Arkansas nest was observed under construction at 8 a.m. and 6:30 p.m. of the same day, another one at 12:15 p.m. and 5:15 p.m.

The nest is not always completed before the first egg is laid. While driving along a paved road 5 miles south of Stuttgart, Ark., at 5:30

p.m. one day in May, I heard two rails uttering their characteristic *jupe-jupe-jupe-jupe-jupe* call. One of the birds was standing in a nearby ditch, and after about 3 minutes of watching, I saw the grass move on the bank near the rail in view. As the same grass continued to move, it was evident to me that the mate was building a nest. Actually the bird was pulling in grass to form the sides and canopy for a nest. After watching it for a few minutes I departed. The next morning I found that construction was in the initial stage, but two eggs had been laid on the bare ground and were surrounded by just a few dead plant fragments.

A Purple Gallinule, another species of Rallidae, was reported by Grimes (1944, p. 63) to have a nest platform 6 inches thick when the first egg was laid. As the eggs began to hatch, the nest was built up until it was 13 inches thick.

Similar nest building activity by Clapper Rails at Frogmore, S.C., was reported by Hoxie (1887, p. 181) :

The first time I found the nest it contained only one egg, and did not seem wide enough to hold more than one more. . . . As each new egg was laid they added fresh material to the outside, until the nest was at least amply sufficient to contain the full set of eight.

Several brood nests, usually without canopies, are constructed near the egg nest.

EGG LAYING AND CLUTCH SIZE

Eggs were deposited daily at five Arkansas nests. In one Arkansas nest, the eggs were laid between 7 p.m. and 7 a.m. In one South Carolina nest, Wayne (1910, p. 36) noted that each egg was deposited after 11 a.m.

Parasitism or "dumping" was recorded by B. H. Swales (1896, p. 142) in St. Clair County, Mich. On June 9, a King Rail was flushed from a nest containing 17 eggs; nine were apparently laid by the King Rail, seven by a Virginia Rail, and one by a Sora.

Clutch size

Clutches of 10, 11, or 12 King Rail eggs are most frequently found (table 9). A smaller clutch may represent a replacement clutch, depending upon when it occurs. On the Arkansas Grand Prairie, the earliest clutch of eight eggs was found on May 28, approximately 2 months after the beginning of the laying season. In Maryland, in July, I observed three complete clutches of six eggs each.

Description of eggs

Bent (1926, p. 261) gives the following description of the eggs:

They are ovate in shape and the shell is smooth and slightly glossy. The ground color averages lighter than in eggs of the clapper rails, but not so light as in

those of the California species; it is pale buff, varying from "cream buff" to "pale olive buff." They are sparingly and irregularly spotted, mostly in small spots, with various shades of "vinaceous drab," "army brown" and "vinaceous brown" and sometimes with a few spots of brighter browns. The measurements of 56 eggs averaged 41 by 30 millimeters, the eggs showing the four extremes measure 44 by 32, 38.5 by 28 millimeters.

I measured 20 eggs at Stuttgart, Ark. two from each of 10 nests. The average measurement was 40.8 by 30.4 millimeters, with extremes of 42.0 by 32.0 and 39.5 by 29.5.

Table 9.—*Clutch sizes in King Rail nests at three locations*

Clutches with—	Number of clutches found		
	Stuttgart, Ark. ¹	Northern and central Ohio ²	Delaware Valley ³
8 eggs.....		3	1
9 eggs.....	1	1	3
10 eggs.....	3	9	3
11 eggs.....	7	11	2
12 eggs.....	3	9	4
13 eggs.....	1	3	
14 eggs.....	1	1	1
Total.....	16	37	14
Mean number of eggs.....	11.2	10.9	10.6

¹ Meanley, unpublished.

² Trautman, 1940, p. 229; R. Bales, ms.

³ Stone, 1937, p. 332; R. F. Miller, correspondence.

Weight of eggs

At Stuttgart, Ark., three eggs weighing 18.9, 20.3, and 18.8 grams were marked on the day they were laid and were weighed on every seventh day until hatching (table 10). The average weight loss was 0.47 gram during the first week, 0.83 gram during the second week, and 1.0 gram during the third week. The average total loss from laying to hatching was 2.30 grams.

INCUBATION

The incubation period is about 21 or 22 days. Roberts (1936, p. 440) stated that A. M. Bailey found the incubation period to be about 21 days. In Clay County, Iowa, Tanner and Hendrickson (1956, p. 55) found it to be approximately 21 days. Incubation periods of four Arkansas clutches were 21 days, 22 days, 22 or 23 days, and approximately 23 days.

One Arkansas nest was under daily observation from the time the first egg was laid on April 1 until the last egg hatched on May 4. Eleven eggs were in the completed clutch, and incubation started with the laying of the 10th egg on April 10. At another nest in Arkansas incubation began on April 22 or 23, and the eggs hatched on May 13 and 14. A nest at Mamou, La., contained 9 eggs on June 9 and 10 hatching eggs on June 30.

Both sexes incubate. To prove this, one night between 9 and 10 p.m., I placed white paint in a small can at the end of a long stick and poured it on the backs of incubating birds at two nests. On subsequent visits to the nests, unmarked birds were often seen incubating.

TABLE 10.—*Weight loss in three King Rail eggs during incubation*

[In grams]

	Weight on—			
	Day 1	Day 7	Day 14	Day 21
Egg 1.....	18.9	18.7	17.8	16.7
Egg 2.....	20.3	19.5	18.8	17.9
Egg 3.....	18.8	18.4	17.5	(1)
Mean.....	19.33	18.86	18.03	17.3

¹ Clutch destroyed.

Later that season an exchange of sexes was observed at a nest during the incubation period. At 5:18 p.m. an incubating bird called from the nest, whereupon its mate immediately came from the cattails across the road to a point about 20 yards from the nest, and began walking toward the nest until it was within 5 feet. The incubating bird then left the nest and was replaced by its mate, which remained on the nest for 17 minutes, when an exchange again took place.

In another instance, when one member of an Arkansas pair nesting near a road was killed by an automobile, its mate continued to incubate the eggs. An incubating bird caught on a nest at 5:45 p.m. May 16, was a male.

Incubating birds seldom flush until an intruder is within 10 feet or less of the nest. As the hatching date approaches, they become more tenacious. On several occasions I was able to band incubating birds, but not without considerable resistance from them. On one occasion when I approached a nest at hatching time, the bird flew from the nest and struck me in the chest. On other occasions birds have struck at my legs or have run to my feet where they remained with wings outstretched. Frequently they feigned injury by spreading the wings, fluttering through the vegetation (fig. 26), and uttering a distress call which might be written as a guttural *rack-k-k-*, *rack-k-k-*, *rack-k-k-*, sometimes varying to sound like *chur-ur-ur-ur* (the roll on the *ur* is like the German "R"). Other scolding notes given by a rail flushed from its nest are a resonant *gip-gip-gip-* and *kik-kik-kik-*.

In contrast to this type of behavior, the Clapper Rail is usually gone before the intruder gets near the nest. At Chincoteague, Va., I have examined some 200 Clapper Rail nests, and only on some half dozen occasions has an incubating bird remained while approached to within 10 feet. This appears to be a striking behavioral difference between these two closely related species.



FIGURE 26.—Distraction display of King Rail near nest. This display is characterized by feigning injury and emitting distress call.

HATCHING

Eggs in four Iowa nests hatched within a 24- to 48-hour period, and were pipped from 24 to 48 hours before hatching (Tanner and Hendrickson, 1956, p. 55).

Hatching was observed at Stuttgart, Ark., May 26–29, 1954. When located at 12 noon on the 26th, the nest contained 10 eggs, only one of which showed signs of hatching and had two small pip holes. By 4:30 p.m. the following day (May 27), 9 of the 10 eggs were pipped. At 1 p.m. May 28, 3 eggs had hatched; by 5:30 p.m. that evening, 5 eggs had hatched; and by 10 a.m. May 29, all eggs had hatched. At 4 p.m. May 29, the entire brood and both parents were at the nest; but at 9:30 p.m. the entire family had deserted the nest and was probably spending the night in a nearby brood nest.

At one Arkansas nest the parent birds alternately participated in brooding newly hatched young and hatching eggs. Toward the end of the hatching period the nonbrooding parent was usually observed within 25 feet of the nest, accompanied by several of the chicks.

As eggs hatch the shells are disposed of in several ways. One brooding bird at an Arkansas nest ate most of an egg shell about 5 minutes after the egg had hatched. Shell fragments were found in the stomachs of several adult birds collected during the breeding season. Some shells

remain in the nest, disintegrate, and eventually filter down into the base of the nest. Shell fragments are found in virtually all nests that have hatched young.

A pair may remain with their brood for more than a month after hatching. I have collected three-fourths grown young rails that were still traveling with an adult pair in August. In one instance a pair, one of which was marked, and their 3-day-old young still spent most of the day within 20 yards of their nest, and 19 days later were seen only 10 yards from the nest! Once I came upon a brood of young King Rails approximately 3 weeks old traveling with three adult birds.

The call given by an adult with young chicks when all is well is a soft continuous *woof-woof-woof-* (corresponding to the *cluck-cluck-cluck-* of a barnyard hen). An alarmed parent with brood emits a sharp *gip-gip-gip-*, which causes the young to scatter to a hiding place.

NESTING SUCCESS AND SURVIVAL

In Clay County, Iowa, Tanner and Hendrickson (1956, p. 55) found that four of six observed nests hatched one or more eggs each. Of 60 eggs in the six nests, 39 hatched.

Of 16 Arkansas nests I observed, 12 hatched one or more eggs each. The average number of eggs hatched in each of these 12 nests was 9.9. Of a total of 147 eggs in all 16 nests, 119 hatched.

An index of survival based on the number of young over 2 weeks of age is difficult to obtain because complete broods are not always seen. In Arkansas, I observed 10 broods with what I believe were full complements. In each observation, the parent birds were unaware of my presence as the family was crossing a road, feeding in a newly sown ricefield, or moving about in some other comparatively open spot. The number of young per brood ranged from two to nine and averaged five. If my estimate of an average hatching success of 9.9 is correct, then survival rate until 2 weeks of age was about 50 percent.

BREEDING STATUS OF FIRST-YEAR BIRDS

Although I know of no example of juvenile or immature birds being marked and recaptured in breeding condition or in the act of nesting, I collected a nesting bird in what appeared to be first-year plumage in the Delaware Bay marshes. Only the lower throat and upper breast regions of this bird were cinnamon, a whitish area covered most of the lower breast and axillary regions, and the side of its head was considerably paler than average for mature birds. The greater coverts were heavily barred with whitish subterminal bars. The specimen, a female, was extremely small. Measurements were as follows (with adult female average in parentheses): Wing 147.0 mm. (154.3); exposed culmen 54.0 mm. (61.9); tarsus 50.0 mm. (54.0).

Development and Behavior of Captive Rails

DEVELOPMENT OF YOUNG

First-day chick

The newly hatched King Rail is very weak and wet. Contrary to the statements of Audubon (1835, p. 28) and Howell (1932, p. 203), it is unable to run about and follow its parents as soon as it is hatched. Sometimes it emerges from the shell on its back and lies kicking and struggling for some minutes before righting itself. A nest mate may grab its toes or beak and so stimulate further activity. Most of the chicks I have observed were more than an hour old before they were able to go over the side of the nest and return. Chicks 15–20 minutes old had considerable difficulty when we placed them in weeds and water outside their nest, and they could not get back into the nest under their own power.

As the down dries out, the young bird moves more actively about the nest, the undeveloped wings assisting in this effort. As the rail chick begins to gain strength, it sits on its tarsi and assumes a begging display, with wings extended for balance.

The period of fluffing-out often takes half an hour or longer. It took 4½ hours for one of the chicks I observed. The fluffing-out process may be necessary to produce buoyancy needed to enter the water safely, as Gullion (1954, p. 389) suggests for the Coot (*Fulica americana*).

Chicks took food from their parents' beaks the first day, but I did not see them picking up food from the ground until the second day.

The day-old chick has at least two calls: a loud begging call, *chee-up*; and a soft lower-pitched call of contentment, *wee* and *wee-up*.

The day-old chick is covered with black down that has a faint greenish sheen or cast except in areas where it is most dense. The down is very dense on the abdomen and sparse on the crown. The bill has a pied pattern; the basal half of the bill is grayish black, the narial region is white, the distal portion is flesh-colored, and the egg tooth, retained at the tip for 4–6 days after hatching is white. The legs and feet are brownish gray although, at a quick glance, they appear to be black. Eyes are grayish brown. A vestigial claw is present on each wing.

The young bird loses weight throughout the first day of life. One female chick weighed 16.3 grams at hatching, 16.0 grams at 1 hour, 15.7 grams at 2 hours, and 13.2 grams at 24 hours (table 11).

One to thirty days

During the first month of life the major change in the appearance of the King Rail chick is one of size and conformation (fig. 27). A young captive male weighed 16.7 grams when he was 1½ days old, and 96.3 grams when he was a month old. His measurements at 1½ and 30 days, respectively, were: exposed culmen, 11.0 and 28.0 mm.; tarsus, 20.0 and 42.0 mm.; middle toe with claw, 22.0 and 50.0 mm. (table 11.).

The thick natal down is present during most of the first month, but during the fourth week there is evidence of development of the juvenal plumage.

TABLE 11.—*Growth of four King Rails*

Age	Weight (grams)	Length of—		
		Exposed culmen (mm.)	Middle toe with claw (mm.)	Tarsus (mm.)
Bird A:				
Hatched.....	16.3			
1 hour.....	16.0			
2 hours.....	15.7			
1 day.....	13.2	11.0	20.0	20.0
8 days.....	14.0	12.5	26.0	21.5
21 days.....	40.0	19.5	36.0	29.0
60 days.....	202.0	40.0	57.0	53.0
90 days.....	265.0	49.0	57.0	53.0
Bird B:				
1 day.....	15.6			
7 days.....	18.9			
17 days.....	37.0	20.0		
21 days.....	50.7			
30 days.....	75.4	25.0	42.5	38.5
45 days.....	177.9	40.0	49.0	52.0
Bird C:				
1½ days.....	16.7	11.0	22.0	20.0
7-8 days.....	25.7			
17-18 days.....	46.5	21.0	36.0	32.0
21 days.....	63.8			
30 days.....	96.3	28.0	50.0	52.0
45 days.....	219.8	40.0	61.0	56.0
60 days.....	327.0	48.0	61.0	58.0
Bird D:				
1½ days.....	15.6			
7-8 days.....	19.7			
17-18 days.....	32.0			
21 days.....	47.7			
30 days.....	70.8	25.0	43.0	36.5
45 days.....	176.0			
60 days.....	258.6			

¹ Wet.

Toward the end of the first month the young rail begins walking more deliberately and assumes the gait of the adult bird. When it is seeking food, it tips its tail in typical adult fashion. Tail tipping was observed in one 2-week-old chick.

Month-old King Rails have at least four calls: (1) *seep-seep-seep-* (repeated) indicates general satisfaction and, particularly, acknowledges the presence of others and notifies them of its presence: (2) *tah-ee! tah-ee!* (repeated), very high pitched and progressively lower in volume as sleep approaches, indicates relaxed comfort and sleepiness: (3) *soo, tsoo (tsōo)* indicates lonely dissatisfaction: (4) *keelp-keelp-keelp-*, a series of five or six hoarse notes in rapid sequence, expresses protest.

Thirty to sixty days

During the second month the juvenal body plumage replaces the natal down. The first juvenal feathers may be obscured by down until the young rail is nearly a month old, but by the seventh or eighth week the development of nearly all of the body feathers is complete. The plumages of four captive King Rail chicks developed at about the same rate through the first 6 weeks, but the rate varied considerably thereafter.

The first evidence of change from the natal down plumage is the appearance of white auricular tufts and pale juvenal feathers on the underparts and flanks (figs. 27 and 28). Feather development in these areas during the fourth week is as follows:

(1) The sternal region of the ventral tract: The pinfeathers are pale buffy brown, and are tipped with natal down that is being pushed out.

(2) The crural tract: Pinfeathers are whitish with black down at the tips.

(3) The femoral tract: Feathers are approximately the same color as those of the ventral tract.

By the latter part of the fifth week the juvenal plumage of most young rails is developing in all body areas, but feathering of the crown and back of the neck may begin slightly later in some individuals. The abdominal region, axillary region, chin, and upper throat are whitish and contrast rather sharply with the dusky upperparts, particularly the lower back and rump. The dark brown feathers of the upper back and humeral tract are well advanced, feathers of the cervical region (lower throat) are approaching a cinnamon color, and the thighs and flanks are faintly barred. The upper and undertail coverts are making their appearance, and the anal circlet is surrounded by short white feathers.

Quills began to appear the latter part of the fifth week on the wings and tails of two of four captive birds. The primary and secondary coverts developed more rapidly than did the primaries and secondaries. The linings of the wings developed last.

By the sixth week the side of the head is whitish and faintly washed with gray. A white superciliary stripe is beginning to ap-



FIGURE 27.—Downy young King Rail, 31 days old, with juvenal plumage beginning to develop. White auriculars (of ear region) and white feathers of crural tract are visible; tip of bill and nares are white.



FIGURE 28.—Ventral view of 31-day-old King Rail showing development of white juvenile plumage in sternal and abdominal region and crural tract.



FIGURE 29.—Fifty-day-old King Rail with juvenal plumage nearly complete. Tail and wings are undeveloped. This individual is slightly behind the average for its age.

pear. The legs and bill approach flesh color, and the distal half of the bill is darker than the proximal half. The eyes have brown irides and black pupils.

By the seventh or eighth week the juvenal body plumage is almost completed, and the young King Rail has a more brownish and less dusky appearance (fig. 29). The cinnamon coloring of the lower throat and breast approaches that of the adult. The juvenal featherings of the crown and nape are complete, and the flight feathers and tail are well advanced on most birds.

There may be considerable variation in weight and size of young rails during the second month of development. At two months a captive male and two captive females weighed 327.0, 258.6, and 202.0 grams respectively.

The juvenal plumage is nearly complete by the age of 60 days. Remiges have developed enough so that some juveniles can make short flights after the ninth week.

Ridgway and Friedmann (1941, p. 84) have presented a detailed account of the juvenal plumage, as follows:

Above similar to adult, dark phase, but the dark centers of the feathers of the back, etc., less fuscous, more dull black, the edges grayer and less well developed on the interscapulars and not at all developed on the lower back and rump which are uniformly blackish, the long scapulars being the only feathers with well-developed tawny-olive margins; lesser and some of the outer greater

upper wing coverts tipped with white and crossed by another narrow white band about 7 mm. anterior to the tip; sides of head as in pale phase adult, but the light ochraceous-buff areas cross-banded with narrow dusky lines (actually the tips of the feathers); lower throat pale, light ochraceous-buff narrowly barred with grayish hair brown to deep drab; anterior part of breast more heavily washed with pale ochraceous-buff; rest of breast and entire abdomen white, crossed by broad, closely spaced, but somewhat broken bands of grayish hair brown, the middle of the abdomen and lower breast unbarred; sides and flanks dusky grayish olive-brown barred with white or buffy white; thighs and vent like sides of breast but somewhat darker; under tail coverts and under wing coverts as in adult.

Call notes of young rails remain essentially the same during the second month of life as they were during the first month, but the voice becomes a little hoarser and deeper. During the second month the young rail frequently exercises by jumping up and down, flapping its wings at the same time.

The begging display may still be observed occasionally during the ninth and tenth weeks, but it soon disappears.

A considerable change in calls occurs during the ninth and tenth weeks. Some of them now approximate the calls of the adults. The call most like that of an adult bird is a raucous crying squawk or cat-like "meow." This call is made when a bird is separated from the family group or is excited. The typical *jupe-jupe-jupe*-call of the adult was not heard until the fifth month.

First winter plumage

For most individuals the first winter plumage is similar to that of the adult. Some individuals, however, have whitish juvenal-like plumage of the underparts and less distinct markings about the face. Most rails in juvenal and first-winter plumage have some white barring on the wing coverts. This is also true of some adults.

MISCELLANEOUS NOTES ON BEHAVIOR OF YOUNG

Sleeping

From the time captive birds hatched until they were approximately a month and a half old, the three to six occupying the same cage slept together. Thereafter, as they assumed a somewhat different sleeping posture, they usually slept separately, but sometimes still slept as a group in the same part of the cage.

During the first 2 weeks after hatching, a warm quart-sized bottle of water was placed in the box with the downy young. When sleepy the chicks would huddle around the bottle, but not always in contact with one another. However, if the bottle was removed, the chicks huddled together when sleeping.

When just a few days old, chicks sleep in a prostrate position. They simply flop down on their bellies, usually with one side of their heads

(cheeks) against the ground. Shortly thereafter, and until they reach the age of 1½ to 2 months, they assume a sitting posture for sleeping. Older young sleep more in the manner of adults, standing on one or both legs, with the head turned around and the bill tucked beneath the feathers of the back, or with the neck drawn in and the bill pointed down to the ground.

Competition

Virtually no peck order was exhibited by captive King Rail chicks during the first 2 weeks of life, when they fed together amicably in one area. Thereafter, they competed for food, and after obtaining a morsel from the common feeding site, would run away and ingest it or run around the cage for several minutes before swallowing it.

Because of size variation of individuals older than 2 weeks of age, there was an obvious peck order, but with little antagonism. A smaller or more agile chick often would not hesitate to steal a morsel from a larger competitor.

Bathing

When bathing, the King Rail assumes a partial squatting position. By an up and down movement of the legs, the body moves in one cadence, then the wings in another, and finally the head, dipping water and flipping it over the back, in still another. The body feathers are extended (somewhat ruffled), the closed wings are loose and moving, and the head is immersed while cocked sideways, presumably for more surface area, and hence functions better as a paddle in flipping water over the body. Water also reaches the plumage through the up and down action of the body and the movements of the wings. The bathing operation usually takes 1 or 2 minutes. A captive bird evicts another from the bathtub by pecking at its feet rather than at some other part of its body.

WINTER BEHAVIOR OF CAPTIVE RAILS

During extended freezes or when there is a snow cover, water for drinking is obtained by ingesting snow or small chunks of ice. Captive King Rails were observed ingesting snow and ice during periods of heavy snowfall and during freezeups in a cage on Bluegill Pond at the Patuxent Wildlife Research Center, Laurel, Md. One bird was observed as it ingested a chunk of ice 3 inches in length and ½ inch in width.

Captive King and Clapper Rails at Bluegill Pond preferred to rest on the ice rather than in a more protected section of the cage provided with a windbreak and a bedding of straw (fig. 30). During alternating periods of freezing and thawing, spherical chunks of ice, up to the size of a baseball, stuck to the tails of the Clapper Rails, and smaller particles stuck to their breasts. Strangely, particles of ice virtually never adhered to any part of the plumage of the King Rails.



FIGURE 30.—Captive King and Clapper Rails at Patuxent Wildlife Research Center, Laurel, Md., January 1960.

Foods

Crustaceans and aquatic insects are the preferred foods of the King Rail in most areas. Fish, frogs, grasshoppers, crickets, and seeds of aquatic plants also have a high palatability rating with this species. During the winter, particularly when the birds are hard pressed, considerable quantities of grain or some other vegetable matter may be consumed. In the southeastern Arkansas rice country, domestic rice formed 30 percent by volume of the King Rail's winter food. A stomach collected in December at Beaver Dam, Wis., was full of wheat. In South Carolina, Audubon (1835, p. 29) examined a gizzard crammed full of oats and collected King Rails in corn fields in autumn near Charleston.

Some unusual foods found in gizzards include cherry (*Prunus* sp.) seeds, skunk (*Mephitis* sp.) hair, feathers and vertebrae of a female Red-winged Blackbird, King Rail eggshell fragments, a small water snake (*Natrix* sp.), a mouse (*Peromyscus* sp.), a shrew (*Sorex* sp.), fall army worms (*Laphygma frugiperda*), blackgum (*Nyssa sylvatica*) seeds, acorns (*Quercus* sp.), and pine (*Pinus* sp.) seeds. A bird collected near Fleming's Landing, Del., on September 30, 1961, had its gizzard crammed with seeds of both waxmyrtle (*Myrica cerifera*) and bayberry (*M. carolinensis*).

The King Rail is more diversified in its choice of foods than its salt-water relative, the Clapper Rail, as might be expected because of its wider range and more variable ecology, which may find it feeding on the edge of a salt marsh along the coast or in an oat field a thousand miles inland.

Its adaptability to subsistence on a wide variety of foods in addition to its usual diet of crustaceans and aquatic insects enables the King Rail to winter much further north than is generally realized. A King Rail observed by I. W. Knight at Lorne Park, Ontario, on December 26, 1960, remained in that locality until at least mid-January. It was seen along an open stream where it was observed feeding on a frog and the berries of "deadly" nightshade (Solanaceae) (Woodford and Burton, 1961, p. 326).

In some parts of its breeding range, particularly in brackish tidal-river marshes of the Middle and South Atlantic coast, the King Rail sometimes subsists largely on a 1-item diet, the red-jointed fiddler crab.

From 1959 to 1961, several hundred observations were made during the nesting season of King Rails feeding in brackish marshes along the Delaware Bay between Fleming's Landing and Woodland Beach, Del., where the red-jointed fiddler crab occurs in great abundance. This little crab formed the main diet of the rail; the only other item of any importance was a clam (*Macoma balthica*) (fig. 31). Stomach examinations confirmed field observations.

TABLE 12.—Principal foods of 118 King Rails from Arkansas ricefields

[Volume=percent of total volume of stomach contents. Occurrence=percent of stomachs in which found]

Food item	Collected in—								Annual volume, 118 stomachs
	Winter (Dec.-Feb.) 33 stomachs		Spring (Mar.-May) 48 stomachs		Summer (June-Aug.) 16 stomachs		Fall (Sept.-Nov.) 21 stomachs		
	Vol- ume	Occur- ence	Vol- ume	Occur- ence	Vol- ume	Occur- ence	Vol- ume	Occur- ence	
ANIMAL:									
Invertebrate:									
Crayfish.....	7	18	61	81	22	25	3	5	23
Aquatic beetles.....	20	76	7	21	19	31	10	48	14
Land beetles.....	1	13	8	56	11	87	4	38	6
Grasshoppers.....	5	24	3	8	6	63	14	57	7
Aquatic bugs.....	5	24	-1	15	10	44	6	29	6
Other insects.....	(1)	21	2	17	8	75	5	38	4
Spiders.....	(1)	3	(1)	2	(1)	13	1	10	(1)
Snails.....	3	12	2	8	(1)	6	(1)	10	1
Vertebrate:									
Fish.....	7	30	1	21	8	19	26	43	11
Frogs.....	5	21	4	15	5	50	4	24	5
Miscellaneous.....	5	7	6	8					3
Total.....	58		95		90		74		79
PLANT:									
Rice.....	30	52	4	19	10	31	21	29	16
Ricefield weed seeds.....	(1)	36	(1)	4	(1)	56	2	38	1
Woody plant seeds.....			1	2			3	10	1
Tubers.....	12	21							3
Total.....	42		5		10		26		21

¹ Trace.

There is considerable variation in food items taken by different individuals in the same habitat and at the same time. Two birds collected from a tidal marsh on the Choptank River in Maryland in February 1961 present an interesting contrast. Bird A fed entirely on fish, while bird B ate a wide and rather unusual assortment of foods including the seeds of arrow-aryum, hackberry (*Celtis occidentalis*), halberd-leaved tearthumb (*Polygonum arifolium*), dogwood (*Cornus florida*), and grape (*Vitis* sp.). Bird B had also eaten crayfish and a snail (Gastropoda). The seeds of arrow-aryum contain calcium oxalate crystals and apparently are rejected by virtually all water birds except the Wood Duck (*Aix sponsa*). This was the only time I encountered them during my studies of rail foods.

Only in the Arkansas ricefields has a fairly complete seasonal survey of King Rail foods been made (Meanley, 1956, p. 252-258).



FIGURE 31.—Foods of the King Rail in brackish bay marsh, Broadway Meadows, Kent County, Del.: (1) Mud crab (*Sesarma reticulatum*); (2) red-jointed fiddler crab (*Uca minax*); (3) clam (*Macoma balthica*). (Photograph by Frederick C. Schmid.)

Small series of stomachs have been collected from a few other localities. Most of these were examined by John C. Jones of the U.S. Fish and Wildlife Service.

ARKANSAS RICEFIELDS

In the Grand Prairie rice-producing area near Stuttgart, Ark., 118 stomachs were collected between 1950 and 1955 by Karl Kitler and myself (table 12).

Animal life comprised 79 percent of the King Rail's annual diet. It constituted 90 percent or more in spring and summer, dropped to 74 percent in the fall (the largest number of stomachs were collected in November and may have made the figure lower than if there had been better representation of the early part of this season), and was still lower (58 percent) in winter.

The shift in feeding grounds from roadside ditches in the spring to ricefields in summer and early fall, and finally back to natural drainage ditches and small cattail marshes in winter, may account for

some of the seasonal variations in diet. However, seasonal fluctuation in the abundance of aquatic animal life is apparently the basic explanation.

The crayfish was the principal food of the King Rail in the rice area, constituting 23 percent (by volume) of the annual diet; it formed 61 percent in spring; 22 percent in summer; 3 percent in fall; and 7 percent in winter. Since crayfish were available the year round, it appears that consumption of this crustacean was influenced as much by the availability of other favored foods as by the abundance of crayfish. Possible seasonal variations in the size, agility, and/or palatability of the crayfish according to age may have been factors bearing upon the extent of seasonal use by the King Rail.

Another staple food available at all seasons was fish, which composed 26 percent (by volume) of the diet in the fall when many fish had become impounded in the shallow borrow pits of drained ricefields and were easy prey for the foraging birds.

Aquatic insects were important foods, especially certain beetles and waterbugs which were available the year round. Predaceous diving beetles (Dytiscidae) furnished 19 percent of the winter diet.

Land beetles, chiefly ground beetles (Carabidae), scarabs (Scarabaeidae), and snout beetles (Curculionidae) made up 6 percent of the rail's annual food, while grasshoppers (Orthoptera) constituted 7 percent.

A wide variety of other insects were taken in small quantities. During the summer and fall they formed 8 percent and 5 percent, respectively, of the food. Among these insects were dragonfly (Odonata) nymphs, back-swimmers (Notonectidae), horsefly (Tabanidae) larvae, fall army worms, rice water weevils (*Lissorhoptrus simplex*), and rice stinkbugs (*Solubea pugnax*).

Frogs accounted for about 5 percent of the annual diet.

The King Rail apparently is more of a vegetarian than its salt marsh counterpart, the Clapper Rail. John Oney (1954, p. 23), in studying fall foods of the Clapper Rail along the Georgia coast, found that plant materials constituted only trace items of the Clapper Rail's diet at that season. Martin, Zim, and Nelson (1951, p. 82) found the volume of plant food in the Clapper Rail's diet to be 11 percent in winter, 1 percent in spring, 0 percent in summer, and 3 percent in fall. In the Arkansas area, vegetable matter in the diet of the King Rail made up the following volumetric percentages during the 4 seasons: 42 percent in winter, 5 percent in spring, 10 percent in summer, and 26 percent in fall.

Cultivated rice seed was taken in larger quantities than any other plant food, forming 16 percent of the annual diet. Increased consumption of rice seed during fall and winter was due in part to the abundance of waste grain left in the stubble. Kalmbach (1937, p. 60),

in his study of the food of blackbirds in Louisiana, suggested that the hard siliceous hulls of rice seed may be used in the gizzard for grinding.

Ricefield weeds, abundant in all rail habitats, furnished some food through the year. Seeds of jungle-rice (*Echinochloa colonum*), wild millet, bullgrass, rice-cutgrass, beakrush, and smartweed (*Polygonum* spp.) were found as traces in many stomachs in each season except fall when they composed 2 percent of the contents.

The following seeds of woody plants were found in several stomachs: blackberry (*Rubus* sp.), snowball (*Styrax americana*), blackgum, and oak. Tubers of marsh plants, probably sedge (Cyperaceae), were found in several stomachs, and one rail had eaten tubers of an arrowhead.

TEXAS RICEFIELDS

Twelve stomachs were collected in ricefields at Eagle Lake, Colorado County, Tex., during September 1938 by Valgene W. Lehmann.

Three items formed the bulk (63 percent) of the food and occurred in at least half of the stomachs. The most important, the coneheaded grasshopper (*Neoconocephalus* sp.), occurred in nine stomachs and formed 30 percent by volume; dragonflies (Odonata) formed 20 percent by volume; and crayfish formed 13 percent by volume. An assortment of insects accounted for most of the remainder. Rice seed was the only plant food taken and comprised only 5 percent of the total food consumed.

LOUISIANA RICEFIELDS

Nine stomachs were collected in ricefields in the gulf coast region of Cameron and Vermilion Parishes in the summer of 1925 by E. R. Kalmbach and in 1955 and 1965 by myself.

Crayfish were in seven of nine stomachs and were the major item in six. Crickets (*Gryllus* sp.) were found in four stomachs and were the most important items in three of those. Weevils were the only other important food.

UPPER ST. JOHNS RIVER, FLA.

Six stomachs were collected in marshes in the Persimmon Hammock area during the spring of 1905 by W. W. Worthington.

Crayfish were the major items in five of the six stomachs. Short-horned grasshoppers (Acrididae) occurred in all of the stomachs, but were important percentagewise in only one. Aquatic and land beetles formed the balance of the food.

CURRITUCK SOUND, N.C.

Seventeen stomachs were collected, mostly in October, November, and December, 1909 and 1910, at Church's Island by J. B. White and W. L. McAtee.

Animal life formed 88 percent of the food with seeds of aquatic plants forming most of the balance. Important animal foods were sunfish (Centrarchidae) and perch (Percidae), grasshoppers and locusts, and aquatic insects (mostly Belostomatidae, Hydrophilidae, and Haliplidae).

PATUXENT RIVER, MD.

Six stomachs were collected in fresh tidal-river marshes along the Patuxent River in southern Maryland in early fall between 1923 and 1958, by O. J. Tremis, C. H. M. Barrett, and unknown rail bird hunters.

An interesting assortment of materials was found in this small series, including killifish (*Fundulus heteroclitus*), crayfish, dragonfly nymphs, snails (*Amnicola* sp.), grasshoppers, and crickets; leaves of a bulrush (*Scirpus* sp.) and rice-cutgrass; seeds of dotted smartweed, halberd-leaved tearthumb, arrow-leaved tearthumb (*Polygonum sagittatum*), burreed (*Sparganium eurycarpum*), water parsnip (*Sium suave*), silky dogwood (*Cornus amomum*), and wild cherry.

BEAVER DAM, WIS.

Eleven stomachs were collected in various marsh types during summer and fall, 1889–1908, by W. D. Snyder and C. F. Zimmerman.

Crayfish constituted over 90 percent by volume of the food in 6 stomachs and occurred in 9 of 11. Snails, soldier flies (*Odontomyia* sp.), dragonfly larvae, a mollusk (*Stagnicola palustris*), grasshoppers, and a fish (Etheostominae) were major items in the other four stomachs.

CHICAGO, ILL.

Five stomachs were collected during spring (April–May), 1912–17, by G. Eifrig and K. W. Kahmann. Crayfish were the major items (50 percent plus by volume) in four of the stomachs, and dragonfly nymphs were the major items (55 percent by volume) in the fifth. Stalks of a bulrush (*Scirpus* sp.) were important (40 percent by volume) in one stomach, and horsefly larvae were common (42 percent by volume) in another.

Two stomachs were collected during the summers (July) of 1878 and 1915 by S. A. Forbes and K. W. Kahmann. Frogs (*Rana* sp.) were the most important food (54 percent by volume) in one, and larvae of soldier flies (94 percent by volume) in the other.

Crayfish were a major item (45 percent plus by volume) in each of the three stomachs collected in the fall (September–October), one in 1913 and two in 1915 by K. W. Kahmann. Frogs (*Rana* sp.) were important (51 percent by volume) in one stomach.

Feeding Behavior

King Rails usually feed in areas concealed by plant cover or in comparatively open areas where they blend well with their surroundings and are only a few steps from cover. Sometimes, however, they are very conspicuous, as when feeding at low tide on mud flats or in open roadside ditches. Dawson (1903, p. 443) observed such feeding activity in Ohio:

In a region where they were in little fear of molestation, I have seen them deploy upon an extensive mud flat in broad daylight and go prodding about in company with migrant sandpipers, for the worms which riddle the ooze with their burrows.

In tidewater areas, feeding probably occurs most frequently at low tide. Whenever I visit the brackish marshes of the Delaware Bay at ebb tide, I see King and Clapper Rails feeding in the tidal creek beds.

I suspect that King Rails do very little feeding at night, although they are sometimes active during this period, as they are occasionally heard calling, particularly during the courtship period. King Rails that I kept in captivity in Louisiana and Maryland were relatively inactive at night. In fact, some of them would habitually return to a favorite spot in the cage each evening at dusk, sit down, and remain quiet for long periods.

Generally King Rails forage in water so shallow that only the bill, or part of it, disappears beneath the surface while food is sought. However, on March 25, 1954, on the Arkansas Grand Prairie, I observed a pair of rails feeding in a roadside ditch where the water varied from 6 to 12 inches in depth. Both of these birds immersed their entire heads and necks in water, and several times their entire bodies disappeared beneath the surface. In fact, they occasionally fed by "tipping up" like dabbling ducks.

Since King Rails are accustomed to procuring their food from the water, if perchance they obtain a food item from land and are near an aquatic environment they usually carry the morsel to the water and immerse it before ingestion.

PELLET CASTING

Both the King Rail and the Clapper Rail, whose major food is crustaceans, reject most of the exoskeletal fragments of these animals through the regurgitation of pellets (fig. 32).

King Rail pellets examined in Arkansas and Maryland were composed of crayfish and aquatic insect fragments. Nearly every pellet

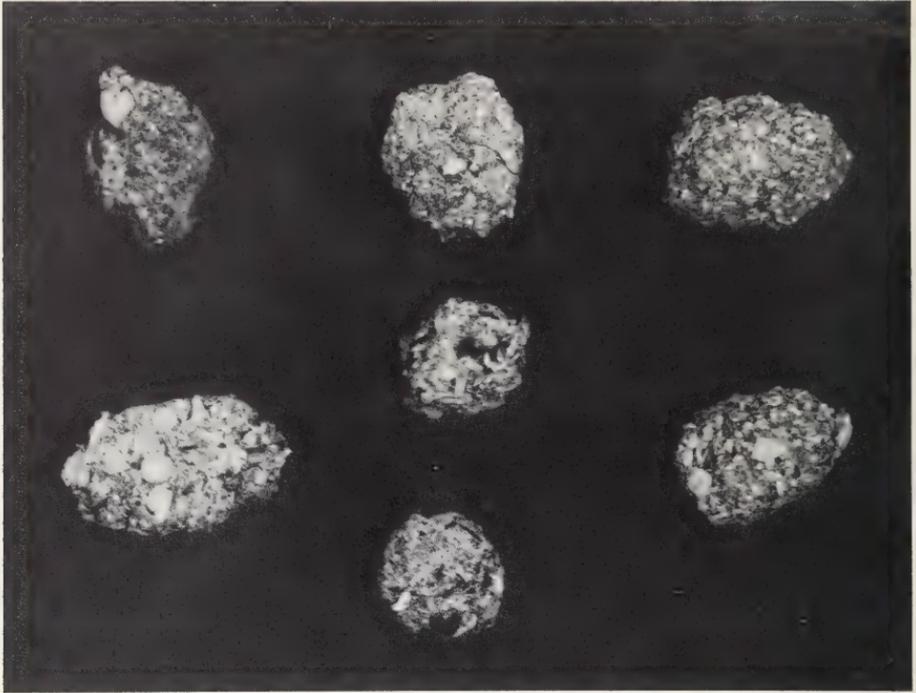


FIGURE 32.—Regurgitated King Rail pellets from Dorchester County, Md. Note the round gastroliths of the crayfish (*Cambarus* sp.) in top and bottom pellets at left. Pellets averaged 2 cm. in length by 1.5 cm. in width. (Photograph by Frederick C. Schmid.)

examined contained the hard cylindrical convex-shaped gastroliths of crayfish.

In brackish marshes near Woodland Beach, Del., where King and Clapper Rails occur together, pellets contained exoskeletal fragments of the red-jointed fiddler crab and a clam (*Macoma balthica*). As many as 14 pellets were found on a single muskrat house.

FEEDING YOUNG

I have observed King Rails feeding their chicks within 2 hours after hatching. Gross and Van Tyne (1929, p. 439) reported the same for the Purple Gallinule, another member of the family Rallidae.

When the very small young are abroad, they follow one or both parents about as food is caught for them. Larger food items such as crayfish and large grasshoppers are dismembered and fed to the young in pieces.

Sometimes, however, the young remain in a concealed place and wait for the parent to bring them food. At Grand Chenier, La., April 8, 1956, I observed a pair of adult rails for over an hour as they kept up a steady pace to and from a small pond catching fish and carrying them to young hidden behind tussocks of grass 30 or so feet distant.

Similar feeding was observed in a Louisiana ricefield where adults brought crayfish to young that remained in the same spot.

As the young grow older, they not only accept food from their parents but also begin to forage for themselves. An interesting example of this dual feeding activity was observed near Woodland Beach, Del., on July 29 and 30, 1959. An adult King Rail and three young approximately 5 to 6 weeks of age were observed feeding on clams at low tide in the bed of a creek. The adult bird dug in the mud for the clams, usually inserting its entire head beneath the surface. It would eat four or five clams and then carry one to the young. The clams were swallowed whole. Sometimes one of the young, standing next to its parent, would watch the digging operation and then start digging for itself. The parent and its young were seen digging for clams in the same place on both days. A raccoon also came to this spot and dug many clams.

REGIONAL OBSERVATIONS

Arkansas ricefields

During March, April, and May 1952 it was not unusual to see 15 or 20 King Rails in the evening feeding along ditches bordering certain highways leading out of Stuttgart, Ark. The variety of rail food available in these roadside ditches includes crayfish, tadpoles, frogs, aquatic insects, small fish, and snails. Toward the end of May the rails move out of the ditches and into ricefields, where they are found until harvest. During the winter they are found about the network of ricefield canals and natural drainage, often moving from place to place along runways beneath matted vegetation.

The King Rail feeds almost exclusively in ricefields during the summer. About the only time it emerges from this cultivated marsh type is to move from one ricefield to another. When a field of nearly mature grain is drained preparatory to harvesting, the rails move over to a field of younger rice which is often contiguous to the dry field. Some ricefields have a few low wet spots which prove attractive to rails, even up to harvest time; but the last feeding place in nearly all drying ricefields is along the "borrow" or ditch bordering the levees.

This typical bird of the rice country performs a service to the rice grower by consuming large numbers of crayfish that bore holes in the ricefield levees. A single large crustacean is usually torn apart and eaten in the course of several minutes; in one case the dismembering operation was timed at 7 minutes. Small crayfish are ingested whole.

Delaware Bay marshes

In the brackish tidal marshes between Fleming's Landing and Woodland Beach, Del., I have found King and Clapper Rails feeding

in the same tidal gut. An important food of the rails here is the red-jointed fiddler crab, which is found further upstream than other species of fiddler crabs, but not far above the brackish zone and, as far as I know, not beyond tidewater in this area.

In some areas, fiddlers' holes or dens are concentrated mostly along or just beneath the top of the embankment of a tidal gut, and at high tide are inundated. Rails seem to feed mostly at low tide. When stalking fiddlers, rails are very slow and deliberate. When within striking distance, a rail makes a quick thrust or stab at the crab. When a fiddler is caught, it is often taken to some favorite feeding spot, such as a muskrat house or pile of drift debris, for dismembering. The large claw of the male crab is disengaged in the following manner, as described by Oney (1954, p. 24-25) for the Clapper Rail:

The bird grasps the crab with its bill between the claw and the body. Then holding the crab, it vigorously shakes its head. The claw goes one way and the crab another. The bird then runs over and picks up the body and swallows it. The female crab does not get the same treatment because both of their claws are nearly equal size.

Some fiddlers, too large to swallow, are hacked to pieces and then eaten bit by bit.

Savannah National Wildlife Refuge

In early April 1960, I made observations of feeding King Rails along an alligatorweed-choked canal on the Savannah National Wildlife Refuge. Alligatorweed forms extensive mats upon which rails, gallinules, coots, herons, and several species of ducks do much of their foraging for aquatic insects, fish, tadpoles, frogs, and crustaceans. While this vegetation type has no apparent value in a waterfowl management program, it is of obvious value to birds that utilize its growth form to facilitate food gathering. Some King Rail feeding territories along the alligatorweed-choked canal were no more than 20 feet square, indicating the high rail-food productivity of these aquatic mats.

The most frequently observed pair of rails defended their feeding territory vigorously. Although they nested on the other side of the dike some 40 yards distant in a sawgrass marsh, they consistently returned to the same section of the canal for feeding.

The base of operations in the pair's feeding territory was a pile of debris, possibly an old alligator nest, at the edge of a small clump of giant cutgrass. From here the rails radiated out to feed on the mat of alligatorweed. Whenever a crayfish or some other large morsel was obtained, it was brought back to the pile of debris for "servicing" and eating. Old earthen dikes still much in evidence throughout the abandoned ricefield marshes of the Carolina Low Country are also used for this purpose.

Along the low banks of the canals, and sometimes partially submerged in the alligatorweed, numerous alligators, some 5 to 6 feet in length, sun themselves on warm spring days (fig. 14). They lie motionless for several hours at a time, and if they move there is simply a splash and complete submergence. It would seem that, to a waterbird wading around in the canal, an alligator sunning along the water's edge would look like another one of the many logs lying half submerged in the alligatorweed. But this is not the case. Rails, gallinules, and other birds feeding in the canal recognize the alligator as an enemy and usually give it a wide berth. Sometimes, however, they feed to within 2 feet of an alligator before circling the animal or retreating.

SOME UNUSUAL OBSERVATIONS

A very unusual feeding performance was recorded by Earle McPeak (Trautman, 1940, p. 230) at Buckeye Lake, Ohio. On June 11, 1929, an adult King Rail was observed to uncover, break, and eat five eggs of a painted turtle (*Chrysemys picta*), which on the preceding day McPeak had watched the turtle lay in a hole and cover with earth.

Another unusual field observation concerned the capture and devouring of a Semipalmated Sandpiper (*Ereunetes pusillus*) by a King Rail. E. D. Greaves (Chamberlain, 1960, p. 443) reported this incident, which took place at Pea Island, N.C., May 22, 1960:

The rail darted out of the grass, picked the sandpiper from a feeding flock and after stabbing it repeatedly, pulled it apart and devoured it.

In June 1960, at low tide in Taylor's Gut, Kent County, Del., I saw a King Rail pursue and peck at a 3-foot-long water snake (*Natrix* sp.) for a distance of some 50 feet. Finally, the snake stopped and remained motionless for about 2 minutes as the rail continued to peck at it. Eventually each took off in a different direction. Possibly the rail was chasing the snake out of its nesting territory rather than pursuing it for food.

At Grand Chenier, La., March 1956, I observed a rail catch a crab in an open spot in the marsh. As the rail headed for cover to feed on the morsel, it was harassed so much by a Boat-tailed Grackle (*Cassidix mexicanus*) that it surrendered the crab to the blackbird.

Nauman (1927, p. 218) reported the following unusual feeding activity which took place at his home in Iowa during a snow storm. On April 16, 1921, when there were 8 inches of snow on the ground, a King Rail was observed walking around on the porch picking up bread crumbs. Until the snow melted, it returned to the porch on numerous occasions to feed on crumbs.

At the Patuxent Wildlife Research Center, a captive 10-month-old female King Rail attempted to eat a mouse and choked to death.

Mortality Factors

The most important factors in mortality of King Rails are (1) striking (or being struck by) manmade objects and (2) predation. In recent years, pesticides may also have become an important factor. From time to time, hurricane-caused floods decimate coastal marsh populations.

MANMADE OBJECTS

Since King Rails are nocturnal migrants, they strike various illuminated objects such as television towers, ceilometers, tall buildings, and lighthouses. On their breeding grounds in the southern rice belt, I have found dead King Rails under telephone lines and impaled on barbed wire fences.

The automobile is an increasing hazard because of the network of roads in the intensively cultivated rice country and the marshland of the South Central States. Over a 3-month period (March 1–June 1, 1952), I found 24 dead adult King Rails along a 10-mile stretch of paved road leading north from Stuttgart, Ark.

During floods in the gulf coast marsh country of Louisiana, King Rails and other water birds are literally flushed out of the marshes to the nearest high ground, which is often a well-traveled highway. During one period of high water in the marsh bordering the highway between the Intracoastal Canal and Creole, La., I saw 30 King Rails (mostly adults with broods) walking back and forth across the road in the face of heavy traffic. Many were being killed, particularly the young.

Wherever muskrats are trapped, King, Virginia, and Sora Rails become casualties since they use the runways where the traps are placed. Whenever I have encountered muskrat trappers in the course of my travels from New Jersey to Louisiana, I either have seen King Rails removed from traps or have been told of the many that are caught incidental to muskrat trapping. One trapper encountered in Maryland caught 50 King Rails during the course of a single trapping season (2½ months).

PREDATION

Judging from the many examples of predation in the literature, the King Rail appears to have a wide variety of natural enemies. Fur bearers are probably the most important, chiefly the raccoon, because of its fondness for eggs, and its abundance in most marsh habitats.

At a Lonoke, Ark., fish hatchery two rail nests found along the edge of a pond had been broken up by raccoons as evidenced by numerous tracks leading from the nest to a point in the open where the eggs had been taken and destroyed.

The mink may also be an important predator of this rail. The Rev. John Bachman, pioneer naturalist from Charleston, S.C., was quoted by Audubon (1835, p. 29-30) regarding the fate of the King Rail as follows:

Its feathers are frequently found lying on the banks of rice-fields, ponds and lagoons, in places where the tracks of the minx plainly disclose the plunderer.

Similarly, on the Arkansas Grand Prairie, a mink trapper told me of finding typical mink signs at freshly killed King Rails. In Currituck County, N.C., Kenneth Wilson (1954, p. 199-307) found six species of birds taken by mink, including the King Rail. Wilson also cited one case in which an otter (*Lutra canadensis*) ate one of these large rails.

Predation by a bobcat (*Lynx rufus*) was noted by Bachman and cited in Audubon (1835, p. 29-30) as follows:

. . . while placed on a stand for deer, I saw a wildcat creeping through a marsh that was near to me, evidently following by stealthy steps something that he was desirous of making his prey. Presently he made a sudden pounce into a bunch of grass, when I immediately heard the piercing cries of the Marsh-Hen, and shortly after came passing by me the successful murderer with the bird in his mouth.

Tanner and Hendrickson (1956, p. 56) found a dead King Rail at the den of a red fox (*Vulpes fulva*) in Iowa:

During May and June 1951, the den of a red fox on the research area was visited almost daily and the remains of prey brought to the den by the parent fox examined. The only rail seen at the den was an adult King Rail found May 12. Since this bird had not been present May 11, and obviously had been dead several days, it seemed likely that it had been found dead by the foxes and brought to the den as carrion. The carcass had not been mutilated.

Bachman (in Audubon, 1835, p. 29) also found remains of a King Rail in the stomach of a large moccasin (probably *Agkistrodon piscivorus*). Another ornithologist of the Charleston area, Arthur T. Wayne, also cited an example of cottonmouth predation on the King Rail (1910, p. 36):

In the month of April, 1900, I was observing a nest of this species in a button-wood bush, which was in a pond of water, and, about every other day, I waded into the pond to see how many eggs were there. About the 8th of May, I judged that the full complement of eggs would be completed, and upon visiting the nest in the afternoon, which was very cloudy, I saw what I supposed to be the bird incubating. But upon close inspection I was very much surprised to find that what I took for the bird was a huge Moccasin (*Ancistrodon piscivorus*), which I promptly shot. This snake had eaten all the eggs and perhaps caught the bird as the feathers were scattered around the nest.

John W. Aldrich (personal communication) collected a fox snake (*Elaphe vulpina*) that had several King Rail eggs in its digestive tract, in Little Cedar Point Marsh on Lake Erie in Ohio.

Alligators (*Alligator mississippiensis*) are known to take King Rails. Kellogg (1929, p. 32) found remains of King Rails in 4 of 15 stomachs of alligators taken in Cameron Parish, La., in 1926.

Coulter (1957, p. 18) examined the gastrointestinal tracts of 157 common snapping turtles (*Chelydra serpentina*) from Maine marshes and found bird remains in about one of every four.

Forty-two specimens contained evidence of a minimum of 52 birds including 25 ducks, 11 grebes, 3 rails and 13 unidentified birds.

No mention is made of the rail species taken. Birds the size of a King Rail could easily be taken by a large snapper. As an example, one 31-pound turtle consumed five birds including one Ring-necked duck (*Aythya collaris*), one Common Golden-eye (*Bucephala clangula*), and three Pied-billed Grebes (*Podilymbus podiceps*).

Hawks and owls take their toll of rails, gallinules, and coots. This is to be expected since virtually all birds of prey hunt in marshes as well as in uplands. Errington and Breckenridge (1936, p. 835) found the remains of a King Rail in a Marsh Hawk (*Circus cyaneus*) collected in August 1934 in the North Central States prairie region. Errington (1932, p. 182) also found remains of a King Rail in a Great Horned Owl (*Bubo virginianus*) pellet collected in April 1930 in southern Wisconsin.

The Fish Crow (*Corvus ossifragus*), well known as a plunderer of Clapper Rail eggs, is also known to take eggs of other rails. Frank C. Kirkwood and John Sommer found broken King Rail, Virginia Rail, and Least Bittern egg shells beneath an active Fish Crow nest at Gum Swamp Island, Blackwater Marsh, Dorchester County, Md., on June 16, 1929 (from Kirkwood's field notes, 1929).

HURRICANES

An interesting account of King and Clapper Rail behavior during a hurricane in the Louisiana prairie marsh country was given by Robert J. Newman (1957, p. 409), from information based on eye witness accounts of H. W. Belknap, graduate student from Louisiana State University, and J. H. Sutherlin, Manager of Sabine National Wildlife Refuge. Hurricane Audrey was Louisiana's worst coastal storm of the present century and struck with its greatest force along the southwest Louisiana coast on the morning of June 27, 1957. Newman's report was as follows:

Rafts of marsh debris, ranging in size from 10×10 to 20×100 feet, went floating by (HWB, JHS). On them huddled a strange company of water moccasins, nutria, rails, and gallinules—sometimes as many as 20 birds to a raft. Occasionally as the great rollers surged forward, the mats of vegetation would buckle

and disintegrate. Then, according to Sutherlin, the Purple Gallinules would drown, but the supposedly less aquatic Clapper or King Rails would swim adeptly away through the rough water and flying spindrift.

The rain-drenched lawn at Sabine headquarters became a sanctuary within a sanctuary. The wildlife congregated there included water snakes, a marsh deer, a skunk, armadillos, and 200 to 250 King or Clapper Rails.

The King Rail as a Game Bird

Although a prized game bird, this large rail is seldom hunted because of the difficulty of maneuvering in its habitat, and the unlikelihood of finding concentrated numbers. Hence there are few localities where the King Rail can be considered an important game bird. In the gulf coast domestic rice producing areas of Texas and Louisiana, where King Rails are most numerous, they are probably shot in greater numbers than anywhere else; however, here considerably less than 1 percent of the local population is shot. In the Middle Atlantic States, the largest numbers are taken by hunters shooting Sora in the wild-rice marshes of the Delaware Valley and Chesapeake Bay. However, in this area, some hunters will gun the wildrice marshes all season without seeing a King. Elsewhere in its range, the King Rail is shot only incidentally. Quail hunters in the South frequently encounter them and take a few.

Probably the best known hunting grounds in the Delaware Valley are in the wildrice marshes of Salem and Cumberland Counties, N.J. The tidal marshes of the Maurice and Cohansey Rivers in Cumberland County are famous rail hunting areas. The Patuxent River marshes near Upper Marlboro are the most important areas in the Maryland part of Chesapeake Bay; while in Virginia Tidewater, King Rails are hunted mostly along the lower James River in the upper reaches of some of its tributaries such as the Chickahominy; and along the Pamunkey and Mattaponi, famous Sora shooting rivers which downstream form the York. One of the most popular spots for King Rail shooting in Texas ricefields is the Eagle Lake area in Colorado County.

A few King Rails are killed by Clapper Rail hunters in coastal salt marshes. Hunters Tom Reed and Gordon Clark killed 3 Kings and 50 Clappers in 2 days of gunning at Chincoteague, Va., during September 1961.

In the open piney woods of Central Louisiana it seems odd to see a King Rail during the winter in some wet spot in the bluestem range. I know of several hunters in that locale who take one or two in each quail and woodcock season.

METHODS OF HUNTING

Contrary to popular opinion, the King Rail is not always an easy mark for the hunter despite its alleged weak flight. Characteristics

of its habitat and other circumstances govern the manner in which it flies, and I have seen several fly at a fast clip for 300 yards.

The Marsh Hen, as this bird is sometimes called, tends to be secretive, but at times it is found in completely open situations near cover. It is not readily flushed, usually escapes by running, and flies only as a last resort. Flight begins with the legs dangling, but as the bird levels off, it flies in a straight line close to the ground with its legs extended straight back beyond the tail and its neck stretched forward.

Methods of hunting King Rails in the wildrice marshes of Chesapeake Bay and the Delaware Valley are quite different from those in the domestic ricefields of Louisiana and Texas. In the Chesapeake Bay and Delaware River tidal marshes, rails are hunted mostly from long, narrow, flat-bottom boats that are poled through the flooded wildrice beds by a "pusher" (figs. 33 and 34). When tides reach peak level, the rails flush as the boat approaches them.

Patuxent River, Md.

On the Patuxent River in the Southern Maryland tobacco country, rail hunting has been a sport enjoyed by the tobacco growing aristocracy since Colonial times. Perc Blogg (1944, p. 67-68), famous Maryland sportsman of the "good old days," presents an account of the hunting of Soras and King Rails on the Patuxent in his delightful



FIGURE 33.—Method of hunting railbirds in Patuxent River wildrice marshes in Maryland. Boat is poled through marshes at flood tide (September 1958).



FIGURE 34.—After the hunting season: railbird boats tied up at dock in December. Low tide on old wildrice marsh on the Patuxent River in Maryland.

little book *There Are No Dull Dark Days*. He begins his essay with a poem about the Marsh Hen:

Give me a gun and some old Marsh
Where the pusher's voice calls mark right!
As the king rail springs from the ditch beyond
Then as suddenly drops out of sight.

"Dah he! Mark left!" What a thrill as the excited "pusher" calls the first bird on a beautiful September morn. This is the moment for which the gunnerman has waited many a month.

We are on the Patuxent. Everything has clicked; the wind is southeast and gentle, the day warm but not hot. . . . high tide at 7:30 a.m. As far as the eye can see on both sides of the river, artistic stalks of wild "oats" stand. Over on the higher marshes, a solid mass of brilliant yellow blossoms, called *butterweed* by the natives, greets the eye.

Rails, being in good requisition for the table, have been extensively hunted, particularly on the marshes of the Delaware and Chesapeake bays. Most sought after of the rails is the little sora or Carolina rail. The Virginia and king rail often add variety to the bag, however.

It is next to impossible to make these birds take wing when they are able to run. Because of this, rail are hunted only when the tide is so high that the flooded marshes afford no shelter and make it impossible for them to run. While the pusher poles a small skiff over the flooded marsh, the hunter stands in the bow, gun in hand. Every now and then a bird will jump, sometimes almost from under the boat, flying away with apparent feebleness, just over the tops of the foliage. As it flies, its legs dangle awkwardly. This ruse, however, is merely to prepare it for the sudden drop which often leaves the surprised hunter drawing a bead

on empty space. Oftimes the gunner doesn't even see the rail announced by *Mark right, Mark left*, or simply "*Dah he goes.*"

On the Patuxent marshes in the 1940's, I would flush about 2 Virginia and 1 King to each 100 Sora.

Eagle Lake area, Tex.

The method of hunting King Rails in the Texas ricefields was described by Dev Klapp (1961, p. 14) :

On the Gulf Coast the rail is found in the great ricefields where it seeks its food. The close-knit rice stalks afford the bird ideal cover, and any attempt to hunt such terrain in an orthodox manner is next to useless. The hidden rail would merely sneak away as the hunter approached and never be seen.

So Texans waste no time slopping around through ankle-deep gumbo mud chasing a bird that refuses to flush. They patiently wait until rice harvest time, then, by the hundreds they take to the fields.

Beginning about October 1, reapers appear in the fields to gather the grain. The machines take positions at the outer perimeter of the fields and, as the sun rises above the horizon, go into action. Snorting and rocking, they circle the fields time and again, gradually working toward the center. Running side by side, usually in pairs, they cut a swath some 30 feet wide.

The hunters wait until all but a 30-foot swath of rice is cut, then hurriedly take stands to each side of the uncut grain. In this narrow strip, they know, all the rail in the field are crowded. Reluctant to fly, the birds have crept through the standing grain, just ahead of the oncoming machines, until forced into this bit of cover.

As the reapers get about half-way through this swath the birds begin to panic. That's when the fun starts. A hunter suddenly shouts, "There's one!" as the first rail rises from cover, almost straight up. Before the bird has set its course it is brought down.

The combine (fig. 35) has replaced the reaper in most areas, but the method of hunting is still the same.

Other areas

Milton B. Trautman (personal communication) reported that between 1907 and 1918 King Rails were hunted in the marshes of Indian Lake, Logan County, Ohio, and that bags of half a dozen birds a day were not uncommon. M. G. Vaiden, an ornithologist from Rosedale, Miss., told me that while Bobwhite hunting in the delta, January 30, 1945, he shot five King Rails and three Bobwhites; and on January 27, 1946, he shot four King Rails. The Rails were flushed from boggy spots in growths of ragweed (*Ambrosia* sp.).

In the days of the market gunner, rails were shot in much greater numbers than at present, and were sold in the markets of most of the large cities along the eastern seaboard. To the epicures, the King Rail of the fresh-water marsh was far superior to the Clapper Rail of the salt marsh. Charles S. Westcott ("Homo") writing in *Forest and Stream* magazine in the 1880's, said (Stone, 1937, p. 332) :

Many of the latter, however, carefully plucked were palmed off for King Rails on those less expert in identifying them.



FIGURE 35.—Method of hunting railbirds in southern ricefields. As rice is harvested the hunter walks beside the reel of the combine which flushes the birds. (Arkansas Grand Prairie, September 1953.)

Summary

Audubon described the King Rail. Alexander Wilson and, for a while at least, Audubon considered it to be some form, perhaps an adult, of the Clapper Rail. Audubon and Bachman, staunch friends, spent a lot of time together in the Charleston area, where Bachman was able to show Audubon that the large rufescent rail was associated almost entirely with the fresh-water marshes and ricefields, while the "ash-coloured" rail was a denizen of the salt marshes. By so doing, Bachman apparently convinced Audubon that the two were distinct species.

The King Rail is essentially an inhabitant of fresh and brackish marshes, while the Clapper Rail is more an inhabitant of salt marshes. In some transition areas, however, particularly in the lower reaches of brackish river marshes, both species occur and sometimes interbreed. Viable eggs resulting from a mixed mating are known to occur, and some specimens taken in areas of interbreeding appear to be hybrids. Further study is necessary to understand more precisely the relationship between King and Clapper Rails.

Rallus elegans elegans is restricted mostly to the humid section of North America, east of the 100th Meridian. The Cuban form, *R. e. ramsdeni*, is restricted to Cuba and the Isle of Pines. A third form, *R. e. tenuirostris* (sometimes considered to be a race of *Rallus longirostris*), is restricted to the fresh-water marshes of the Valley of Mexico. In the United States the King Rail is found in greatest numbers in the South Atlantic and Gulf Coastal Plain provinces, especially in coastal fresh and brackish marshes and in ricefields.

While it has been shown that the King Rail is migratory, so few birds have been banded that little is known about the time, distance, and routes of migration. Apparently the major routes are along the Atlantic Coastal Plain and through the Mississippi Valley. Most birds probably arrive on the breeding grounds in the north during April and May and depart in August and September. Although most King Rails migrate to the South Atlantic and Gulf Coastal Plains in the fall, a few individuals may be found wintering almost anywhere within the geographic range of the species. Since there are numerous records of birds wintering in the middle and northern latitudes, it is not known whether birds seen in the spring are recent arrivals from the south or birds that have wintered in the area. Rails are very secretive in winter, becoming quite vociferous with the onset of the breeding season; thus spring arrival dates may be based on sighting or hearing of birds that have been present in the area for some time prior

to the recorded date. During the summer King Rails may restrict their activities to a relatively small area for as long as 3 months, during which time the adults are nesting and molting, and the young, flightless for about 2 months after birth, are growing.

The 4,000,000-acre Louisiana coastal marsh is the largest block of breeding habitat in the range of the King Rail. The southern rice-fields are a good example of an optimum breeding habitat. The breeding density of a King Rail population in a South Carolina river marsh was 25 males per 100 acres; in an inland Florida marsh the density was 30 males per 100 acres. King and Clapper Rails were found breeding in the same brackish marshes in Louisiana, Maryland, and Delaware.

King Rail sexes appear to be alike in plumage. The male averages larger than the female. Immature birds apparently can be externally distinguished from adults during the first autumn by the color of the soft parts. Most rails in juvenal and first-winter (immature) plumage have some white barring on the wing coverts. This is also true of some adults. The light-phase adult plumage described by Ridgway and Friedmann (1941) is probably typical of hybrids. The small sample of weights and measurements given in this report indicates that the King Rail averages slightly larger than the Clapper Rail.

Molt is not well understood. Apparently all individuals molt after the nesting season, but some also molt during it.

King Rails are known to return to the same section of the same marsh for several consecutive years to breed. Territories are established and maintained by aggressive behavior, primarily that of the male. The mating call, given by the male, presumably serves the same purpose as the song of a passerine bird on its territory, namely to attract a mate and to repel other birds of the same sex (but also, in the case of the King Rail, to maintain contact after pairing).

The display of the male during prenuptial courtship consists mostly in walking about with tail uplifted and white undertail coverts extended. After pairing, other forms of display and a repertoire of subdued calls are used to maintain the pair bond.

Copulation takes place near the nest site, before and during egg laying.

The nesting season of the King Rail is one of the longest among birds in the South. In Florida, there is evidence of nesting from January to July; and in Louisiana, from March to September. In the middle and northern latitudes the nesting season is usually about 3 to 4 months long.

Since the Clapper Rail in South Carolina is known to be double-brooded, it is possible that the King Rail in the southern part of its range may also have more than one successful brood; however, this has not yet been established.

Clutch size is large, averaging 10 or 11 eggs. There appears to be no geographic variation in clutch size.

Nesting success appears to be high in most areas. In one Arkansas sample, success was 75 percent; and in one Iowa sample it was 67 percent. Such success is probably due in some measure to the incubating birds' pugnacity toward would-be offenders. Survival of young until 2 weeks of age was about 50 percent in the Arkansas rice belt.

Downy young of the King Rail are black. A change from the downy plumage begins at about 1 month. Juvenal plumage is obtained in about 60 days, and wings are developed enough for short flights after the ninth week.

Usually chicks are more than 1 hour old before they can go over the nest and return. During the first month six different calls were recorded.

The King Rail occurs in a wider range of habitats and feeds on a greater variety of foods than most other North American rallids. Aquatic animals, particularly crustaceans, are its main food. Plant food items are taken more under emergency conditions. When the King Rail occurs in the same environment as the Clapper Rail, it may subsist mostly on a 1-item diet like that species.

In most areas King Rails feed mainly in shallow water where the depth is usually 2 or 3 inches. In Delaware Bay marshes, King Rails fed almost entirely on mud flats, exposed at low tide, and on the Arkansas Grand Prairie, in summer, they fed almost exclusively in ricefields.

In some areas King Rails were observed to have feeding territories to which they returned regularly at times other than the breeding season.

Most food items are ingested whole, but larger crustaceans often are dismembered before eating.

Mortality of King Rails apparently is due mainly to birds coming in contact with manmade objects, and to natural predation, especially the destruction of eggs by raccoons. Studies to determine the effects of pesticides on this rail have not been made; however, its favorite food, aquatic animal life, is highly susceptible to these chemical agents. In at least one intensive agricultural area, the Arkansas rice belt, where ecological conditions have not changed during the last 20 years, the King Rail has shown a marked decline.

The King Rail is one North American game bird that certainly is not overhunted. This is so primarily because the population is generally scattered and its habitat is usually difficult for hunters to work through. The only time that I found them concentrated and fairly easy to shoot was during the harvest in the Louisiana ricefields. A few are shot incidentally in the course of hunting Sora in the Middle Atlantic States, and Bobwhite in the deep South in damp piney woods.

Literature Cited

AMERICAN ORNITHOLOGISTS' UNION.

1957. Check-list of North American birds. 5th ed. Baltimore. 691 p.

ARTHUR, STANLEY CLISBY.

1931. The birds of Louisiana. State of Louisiana, Department of Conservation, Bulletin 20. New Orleans. 598 p.

1937. Audubon, an intimate life of the American woodsman. Harmanson, New Orleans. 517 p.

AUDUBON, JOHN JAMES.

1834. Birds of America, vol. III. Robert Havell, Jr., London. 435 p.

1935. Ornithological biography, vol. 3. Adam and Charles Black. Edinburgh. 631 p.

BAGG, AARON CLARK, and SAMUEL ATKINS ELIOT, Jr.

1937. Birds of the Connecticut Valley in Massachusetts. The Hampshire Bookshop, Northampton, Mass. 813 p.

BAILLIE, JAMES L., Jr.

1940. King Rail breeding in Southern Ontario. *Auk*, vol. 57, No. 1, p. 109-110.

BEECHER, WILLIAM J.

1942. Nesting birds and the vegetation substrate. Chicago Ornithological Society. 69 p.

BENT, ARTHUR CLEVELAND.

1926. Life histories of North American marsh birds. Smithsonian Institution, U.S. National Museum Bulletin 135. 490 p.

BLANDIN, WARREN W.

1963. Renesting and multiple brooding studies of marked clapper rails. *In* Proceedings of the Seventeenth Annual Conference, Southeastern Association of Game and Fish Commissioners, Hot Springs, Ark., p. 60-68.

BLOGG, PERCY THAYER.

1944. There are no dull dark days, H. G. Roebuck & Son, Baltimore. 92 p.

BRIMLEY, C. S.

1887. Notes from Raleigh, N.C. *Ornithologist and Oologist*, vol. 12, No. 12, p. 201.

1917. Thirty-two years of bird migration at Raleigh, North Carolina. *Auk*, vol. 34, No. 3, p. 296-308.

BULL, JOHN.

1964. Birds of New York area, Harper & Row, New York. 540 p.

CHAMBERLAIN, B. RHETT.

1960. Nesting season—Southern Atlantic Coast region. *Audubon Field Notes*, vol. 14, No. 5, p. 441-444.

CORNING, HOWARD.

1929. Journals of John James Audubon during his trip to New Orleans in 1820-1821. Club of Odd Volumes, Harvard Press, Boston. 234 p.

COULTER, MALCOLM W.

1957. Predation by snapping turtles upon aquatic birds in Maine marshes. *Journal of Wildlife Management*, vol. 21, No. 1, p. 17-21.

CRUICKSHANK, ALLAN D.

1942. Birds around New York City. American Museum of Natural History, Handbook Series No. 13. 489 p.

——— (compiler).

1953-1966. (14 yearly counts 1952-1965). Christmas bird count (Cocoa, Florida). Audubon Field Notes, vols. 7-20, Nos. 2. Page numbers variable.

DAWSON, WILLIAM LEON.

1903. Birds of Ohio. Wheaton Publishing Company, Columbus. 671 p.

DEANE, RUTHVEN.

1929. Some letters of Bachman to Audubon. Auk, vol. 46, No. 2, p. 177-185.

DUVALL, ALLEN J.

1937. Birds observed on the coast of Virginia and North Carolina. Auk, vol. 54, No. 4, p. 461-463.

ERRINGTON, PAUL L.

1932. Food habits of southern Wisconsin raptors; Part I, Owls. Condor, vol. 34, No. 4, p. 176-186.

——— and W. J. BRECKENRIDGE.

1936. Food habits of marsh hawks in the Glaciated Prairie Region of North-Central United States. American Midland Naturalist, vol. 17, No. 5, p. 831-848.

FORBUSH, EDWARD HOWE.

1925. Birds of Massachusetts and other New England states, vol. 1. Massachusetts State Board of Agriculture. 481 p.

FORD, EDWARD R.

1956. Birds of the Chicago Region. Chicago Academy of Science, Special Publication No. 12. 117 p.

GILLESPIE, JOHN D.

1956. Bird names of the Mikasuki Seminoles. Florida Naturalist, vol. 29, No. 4, p. 119-125.

GRIMES, S. A.

1944. Birds of Duval County. Florida Naturalist, vol. 17, No. 4, p. 57-68.

GRISCOM, LUDLOW, and MAUNSELL S. CROSBY.

1925. Birds of the Brownsville region, southern Texas. Auk, vol. 42, No. 4, p. 519-532.

GROSS, ALFRED O., and JOSSELYN VAN TYNE.

1929. The purple gallinule (*Ionornis martinicus*) of Barro Colorado Island, Canal Zone. Auk, vol. 46, No. 4, p. 431-446.

GULLION, GORDON W.

1954. The reproductive cycle of American coots in California. Auk, vol. 71, No. 4, p. 366-412.

HALLMAN, R. C.

1934. Notes from St. Johns County. Florida Naturalist, vol. 7, No. 2, p. 17-18.

HARMON, BOBBY G., CARL H. THOMAS, and LESLIE GLASGOW.

1960. Waterfowl foods in Louisiana ricefields. Transactions of the 25th North American Wildlife and Natural Resources Conference, Wildlife Management Institute, Washington, D.C., p. 153-161.

HAYDEN, ADA.

1943. A botanical survey in the Iowa lake region of Clay and Palo Alto Counties. Iowa State College Journal of Science, vol. 17, No. 3, p. 277-416.

HOTCHKISS, NEIL.

1950. Checklist of marsh and aquatic plants of the United States. U.S. Fish and Wildlife Service, Wildlife Leaflet 210. 34 p.

HOWELL, ARTHUR H.

1932. Florida bird life. Florida Department of Game and Fresh Water Fish. Coward-McCann, New York. 579 p.

HOXIE, WALTER.

1887. Observations on nest building. *Ornithologist and Oologist*, vol. 12, No. 11, p. 181-182.

JOHNSTON, RICHARD F.

1964. The breeding birds of Kansas. University of Kansas, Publication of the Museum of Natural History, vol. 12, No. 14, p. 575-655.

KALMBACH, E. R.

1937. Blackbirds of the Gulf Coast in relation to the rice crop. Unpub. MS in files of U.S. Fish and Wildlife Service, Denver. 76 p.

KELLOGG, REMINGTON.

1929. The habits and economic importance of alligators. U.S. Department of Agriculture, Technical Bulletin 147. 36 p.

KIRKWOOD, F. C.

1895. A list of the birds of Maryland. *Transactions of the Maryland Academy of Sciences*, Baltimore, p. 241-381.

KLAPP, DEV.

1961. Ricefield rail. *Texas Game and Fish*, vol. 19, No. 10 (October), p. 14-15.

LATHAM, ROY.

1954. Nature notes from Orient (L.I.). *Long Island Naturalist*, vol. 3, p. 3-9.

LOW, SETH H.

1935. Methods of trapping shore birds. *Bird-Banding*, vol. 6, No. 1, p. 16-22.

LOWERY, GEORGE H., Jr.

1955. Louisiana birds. Louisiana Wildlife and Fish Commission. Louisiana State University Press, Baton Rouge. 556 p.

MARTIN, ALEXANDER C., HERBERT S. ZIM, and ARNOLD L. NELSON.

1951. *American wildlife and plants*. McGraw-Hill, New York. 500 p.

MEANLEY, BROOKE.

1953. Nesting of the king rail in the Arkansas ricefields. *Auk*, vol. 70, No. 3, p. 262-269.

1956. Food habits of the king rail in the Arkansas ricefields. *Auk*, vol. 73, No. 2, p. 252-258.

1965. King and clapper rails of Broadway Meadows. *Delaware Conservationist*, vol. 9, No. 1, p. 3-7.

——— and DAVID KENNETH WETHERBEE.

1962. Ecological notes on mixed populations of king rails and clapper rails in Delaware Bay marshes. *Auk*, vol. 79, No. 3, p. 453-457.

MONTAGNA, WILLIAM, and WILLIAM A. WIMSATT.

1942. Bird records from Virginia. *Auk*, vol. 59, No. 3, p. 434-436.

NAUMAN, E. D.

1927. Notes on the Rails. *Wilson Bulletin*, vol. 39, No. 4, p. 217-219.

NEWMAN, R. J.

1957. Nesting season—Central Southern region. *Audubon Field Notes*, vol. 11, No. 5, p. 409-413.

NORRIS, ROBERT A.

1963. Birds of the AEC Savannah River Plant Area. Contribution of the Charleston Museum XIV, Charleston, S.C. 78 p.

NORTHWOOD, J. D'ARCY.

1956. Audubon's firsts. *Atlantic Naturalist*, vol. 11, No. 5, p. 222-229.

OSBERHOLSER, HARRY C.

1937. A revision of the clapper rails (*Rallus longirostris* Boddaert). *Proceedings of the U.S. National Museum*, vol. 84, No. 3018, p. 313-354.

1938. Bird life of Louisiana. State of Louisiana, Department of Conservation, Bulletin 28. 834 p.

ONEY, JOHN.

1954. Final report: clapper rail survey and investigation study. Georgia Game and Fish Commission, Atlanta. 50 p.

RAPP, F. W.

1931. Bird list of Vicksburgh, Michigan. Privately printed. 35 p.

RIDGWAY, ROBERT, and HERBERT FRIEDMANN.

1941. Birds of North and Middle America, part 9. Smithsonian Institution, U.S. National Museum Bulletin 50. 84 p.

ROBERTS, THOMAS S.

1936. The birds of Minnesota, vol. 1. University of Minnesota Press, Minneapolis. 821 p.

SAGE, JOHN HALL, and LOUIS BENNETT BISHOP.

1913. The birds of Connecticut. Connecticut Geological and Natural History Survey, Bulletin 20. 370 p.

SPRUNT, ALEXANDER, JR., and E. BURNHAM CHAMBERLAIN.

1949. South Carolina bird life. University of South Carolina Press, Columbia. 585 p.

ST. AMANT, LYLE S.

1959. Louisiana wildlife inventory and management plan. Louisiana Wildlife and Fisheries Commission, New Orleans. 329 p.

STEIRLY, C. C.

1959. Breeding clapper rail in James River cord grass marshes. Raven, vol. 30, Nos. 5 and 6, p. 47-48.

STEWART, JAMES R., JR.

1965. Nesting season—Central Southern region. Audubon Field Notes, vol. 19, No. 5, p. 552-554.

STEWART, ROBERT E.

1952. Clapper rail studies. In Aldrich, John W., et al., Investigations of woodcock, snipe, and rails in 1951. U.S. Fish and Wildlife Service, Special Scientific Report—Wildlife 14, p. 56-58.

1954. Migratory movements of the northern clapper rail. Bird-Banding vol. 25, No. 1, p. 1-5.

1962. Waterfowl populations in the Upper Chesapeake Region. U.S. Fish and Wildlife Service, Special Scientific Report—Wildlife 65. 208 p.

STONE, WITMER

1908. The birds of New Jersey, in Annual Report of the New Jersey State Museum (for 1909). John L. Murphy Publishing Company, Trenton. 432 p.

1937. Bird studies at old Cape May, vol. 1. Delaware Valley Ornithological Club, Philadelphia. 520 p.

SWALES, B. H.

1896. A "Full Set of Rails." Nidologist, vol. 3, No. 12, p. 142.

TANNER, WARD D., JR., and GEORGE O. HENDRICKSON.

1956. Ecology of the king rail in Clay County, Iowa. Iowa Bird Life, vol. 26, No. 3, p. 54-56.

TODD, W. E. CLYDE.

1940. Birds of western Pennsylvania. University of Pittsburgh Press, Pittsburgh, Pa. 710 p.

TOMKINS, IVAN R.

1958. The birdlife of the Savannah River Delta. Georgia Ornithological Society, Occasional Publication 4. 68 p.

TRAUTMAN, MILTON B.

1940. The birds of Buckeye Lake, Ohio. University of Michigan, Museum of Zoology Miscellaneous Publication 44. 466 p.

WARNER, DWAIN W., and ROBERT W. DICKERMAN.

1959. The status of *Rallus elegans tenuirostris* in Mexico. Condor, vol. 61, No. 1, p. 49-51.

WATSON, GEORGE E.

1962. Notes on the spotted rail. Wilson Bulletin, vol. 74, No. 4, p. 349-356.

WAYNE, ARTHUR TREZEVANT.

1910. Birds of South Carolina. Contribution from the Charleston Museum I, Charleston, S.C. 254 p.

WETHERBEE, DAVID KENNETH.

1959. Artificial incubation of wild birds' eggs and developmental condition of neonates. Ph. D. Thesis, University of Connecticut (Library of Congress Card No. Mic 59-3872). 153 p.

WIDMANN, OTTO.

1907. A preliminary catalog of the birds of Missouri. Transactions Academy of St. Louis, St. Louis. 288 p.

WILSON, KENNETH A.

1954. The role of mink and otter as muskrat predators in northeastern North Carolina. Journal of Wildlife Management, vol. 18, No. 2, p. 199-207.

WOOD, NORMAN A.

1951. Birds of Michigan. University of Michigan Museum of Zoology, Miscellaneous Publication 75. 559 p.

WOODFORD, JAMES, and DONALD E. BURTON.

1961. Winter season and winter bird population study—Ontario-western New York region. Audubon Field Notes, vol. 15, No. 3, p. 326.

Appendix 1—Methods of Capturing for Banding

Most of the King Rails captured for banding have been taken in traps or with long-handled dip or clap nets. A few downy young have been caught by hand. Some King Rails are inadvertently caught in the course of trapping ducks.

TYPES OF CAPTURING DEVICES

Long-handled dip or clap net

This device is very effective in capturing King Rails on nests. Traps equipped with drift fences and placed in breeding territories will also capture rails during the nesting season as the birds wander about their territories. However, in such situations, where only one or two birds are involved, long-handled nets are more efficient because of the time required to install traps. Most incubating King Rails can be approached closely enough to be caught on a first attempt. The long-handled net I use has a bamboo handle $7\frac{1}{2}$ feet in length, a hoop 2 feet in diameter, and a net 3 feet in depth.

Nest traps are effective in catching incubating King Rails, but are time-consuming to construct and are probably no more effective than long-handled nets. Blandin (1936, p. 62–63) described a nest trap for the Clapper Rail, a species that flushes more readily from the nest than does the King Rail.

All-purpose or cloverleaf trap

As nearly as I can ascertain, this is the type of trap most often used for capturing King and Clapper Rails (figs. 36 and 37). Seth H. Low (1935, p. 16–20) originally designed this trap for catching shore birds for banding. He used long leads or drift fences placed at right angles to the trap and running up to the trap entrance. Robert E. Stewart (1954, p. 1) caught nearly 1,000 Clapper Rails with this type of trap at Chincoteague, Va., and designed a very effective gathering cage that prevents rails from getting back into the trap (fig. 37). The effectiveness of Stewart's design is due to a ramp that begins at the opening at ground level and runs toward the top and rear of the cage. When a rail reaches the top of the ramp it drops down into a small chamber where it is well contained and easily retrieved.

The all-purpose trap used by Stewart and other Patuxent Wildlife Research Center biologists is about $6\frac{1}{2}$ feet in length. Each of the two

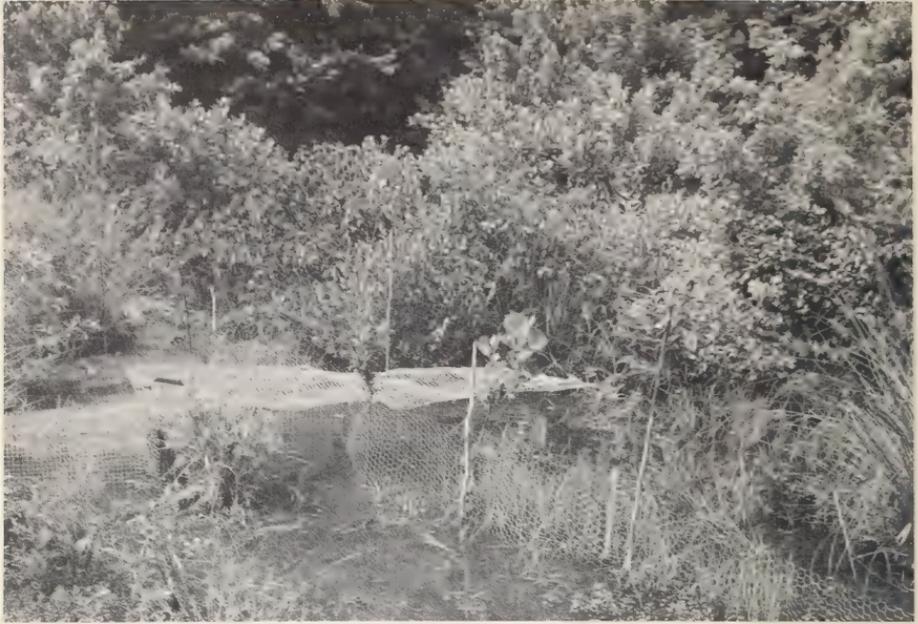


FIGURE 36.—All-purpose or cloverleaf trap and drift fence in shrub swamp at Patuxent Wildlife Research Center, Laurel, Md.

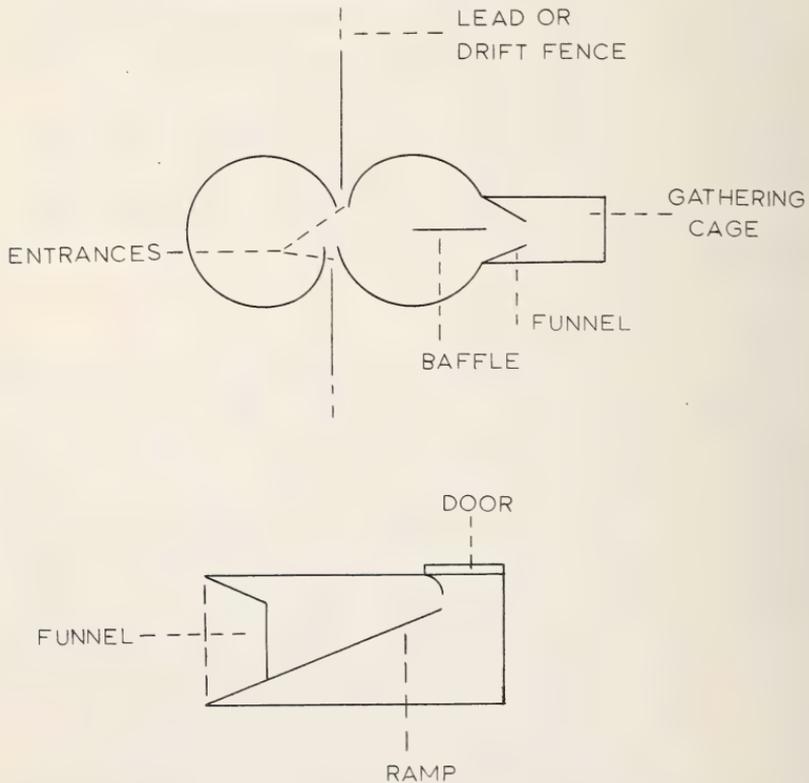


FIGURE 37.—All-purpose or cloverleaf trap.

cells is about 3 feet by 3 feet; flattened out, each cell section is approximately 9 feet in length by 1½ feet in width. The top is 7 feet by 4 feet.

The trap is best made of hardware cloth or welded wire. A less expensive and also less durable trap can be made of 1-inch poultry mesh (chicken wire). A trap made of poultry mesh should have a hardware cloth gathering cage.

The lead wire or drift fence should be a minimum of 1 foot in height. Two feet is better. One-inch poultry mesh is an ideal size for the drift fence. Downy young of banding age can probably get through a 2-inch mesh.

The length of the lead or drift fence depends upon the trapping situation. In marshy impoundments at the Patuxent Wildlife Research Center near Laurel, Md., I used some half-dozen different trapping designs at various times.

The trap is placed in that part of a marsh known to be inhabited by rails. Their presence is determined by hearing a bird call regularly from the same area during the course of several consecutive days, by locating a nest, or by hearing the cries of young that have been separated from their parents. The general area should be checked for tracks, droppings, and fragments of crayfish or other rail foods, and when tracks along a well-worn runway or path are found, the strategy then is to block it off with the drift fence.

Rails often feed along the edge of a marsh on a mud flat bordering open water. In such a situation, the drift fence should extend a foot or so out into open water and landward 10 or 15 feet (or more) to the trap. At low tide, in cordgrass marshes in Delaware, King and Clapper Rails feed along the exposed muddy bottoms of narrow creeks. In such a situation, a drift fence leading to a trap on either bank can be placed across the creek. Thus the rail's passage is cut off, and it tends to follow the fence toward the trap and often goes into it.

In a 10-acre shrub swamp-marsh mixture at the Patuxent Wildlife Research Center, the most select area for rails was in a 1-acre cattail patch. By placing four all-purpose traps about 30 feet apart in a row and connecting them with drift fences, I was able to block off an extensive area and succeeded in catching many rails (King, Virginia, and Sora). Numerous Common Snipe (*Capella gallinago*), Red-winged Blackbirds, Rusty Blackbirds (*Euphagus carolinus*), Swamp Sparrows and Song Sparrows were also captured. A few Wood Ducks, Woodcocks, American Bitterns (*Botaurus lentiginosus*), and Green Herons (*Butorides virescens*) were taken as well. The trap placed at the pond end of the cattail patch caught more rails than did the three in the interior of the patch.

TENDING TRAPS

The number of times a day that traps should be tended depends somewhat upon the size of the population in the area of interest and

the frequency of catch. In high population areas, such as some Clapper Rail marshes, traps should be checked four or five times a day. In areas of low population, two or three times a day is adequate, as too frequent disturbance will frighten rails from trapping sites.

In areas of high predation by raccoons, opossums (*Didelphis virginiana*), minks, and domestic rats, it is well to leave traps open at night. When operating on a 24-hour basis it is important to check the trap at dusk or shortly thereafter. Rails left in traps at night in areas of high predator populations will almost without exception be destroyed. This is especially so because paths made by the operator seem to become natural highways for mammals.

Between dusk and dawn I virtually never caught rails (King, Virginia, or Sora) in traps at the Patuxent Wildlife Research Center. Most species of North American Rallidae are not as active at night as during the day. Some rails are vociferous at night especially during the breeding season; however, at that time they call mainly from territories.

When I first started trapping rails, I expected to encounter trouble with muskrats getting into traps. They do get into traps occasionally, but burrow out quickly, and I have never had to remove a single animal.

AGE FOR BANDING KING RAIL CHICKS

Downy young can be banded at 2 weeks of age, a few individuals as early as 10 days. The band size is number 5.

NEED FOR BANDING DATA

In view of the paucity of information on movements and population dynamics of rails, a large number of these birds should be banded. To accomplish this, it is necessary to know which methods are best for capturing rails, where to place traps, and in what geographic areas.

The all-purpose or cloverleaf trap with drift fences is the best known device for capturing rails for banding.

The best areas for trapping are usually determined by noting calls, reading "sign" (tracks, droppings, piece of discarded crayfish), and locating nests.

Localities in which I have found high populations are as follows: In Louisiana marshes near the intersection of the Intracoastal Waterway and the road to Pecan Island; just below the intersection of the Waterway along the road to Creole, and in a silted-in canal near Dulac; in marshes across the river (north) from Savannah, Ga.; and in marshes on the Savannah National Wildlife Refuge near Savannah.

Appendix 2—Local Names

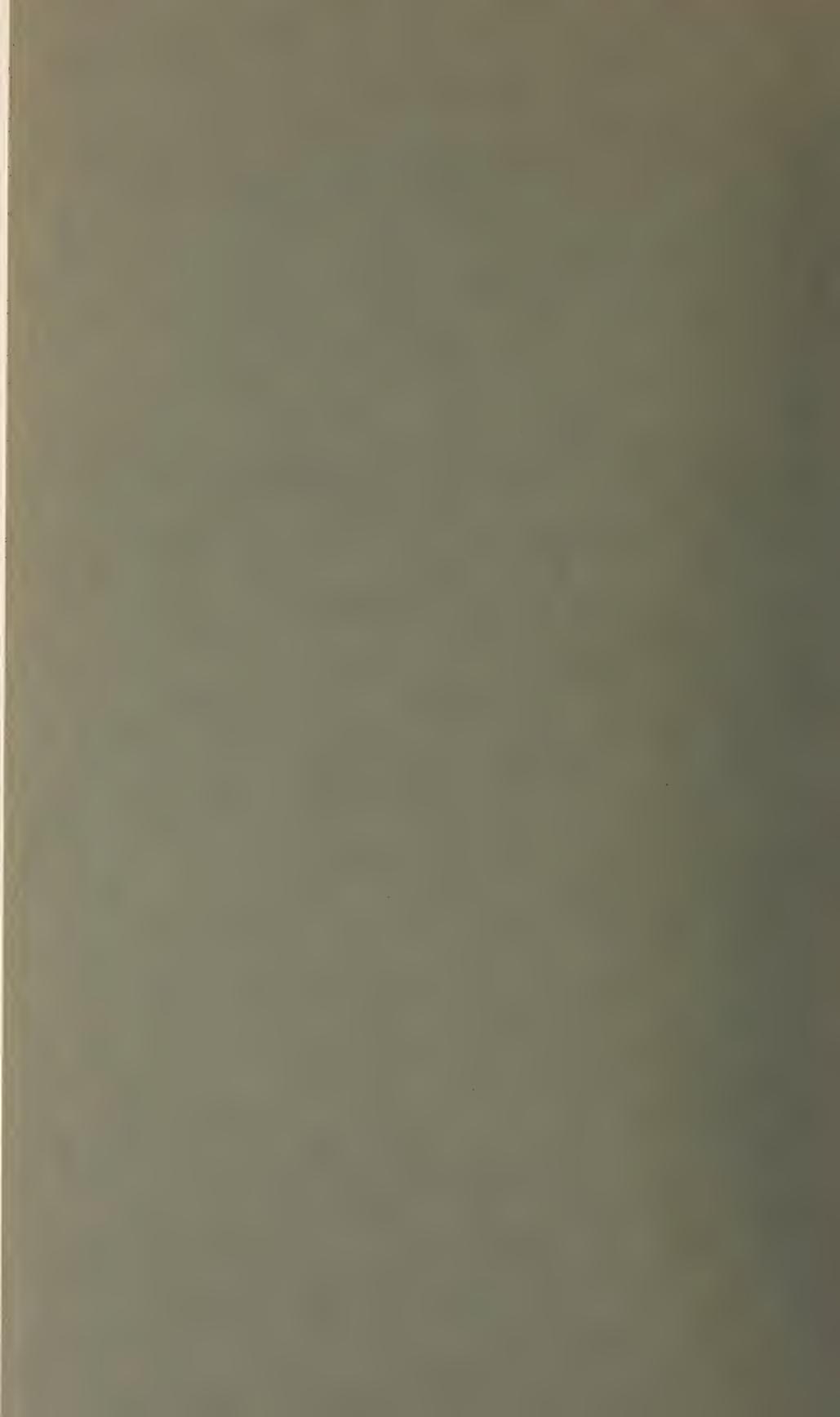
The King Rail is probably better known in life to marsh hunters and trappers than to most ornithologists, and to these hunters and trappers it has its own special name depending upon locality. I picked up many of these names while working in the marshes and ricefields of the South.

Great Red-breasted Rail	-----	Audubon (1835, vol 3, p. 27).
Fresh-Water Marsh Hen	---	Audubon (1835, vol. 3, p. 27).
Rale de Prairie	-----	Creole hunters of Louisiana according to Audubon (Arthur, 1931, p. 235).
English Rail	-----	Hunters on Arkansas Grand Prairie, Ark. (author).
Slash Guinea	-----	Hunters on Arkansas Grand Prairie, Ark. (author).
Sage Hen	-----	Southeastern Arkansas (Chicot County) rice farmers (author); also muskrat trapper, Rappahannock River, Va. (author).
Rice Guinea	-----	Northeast Arkansas rice belt around Weiner and Hickory Ridge (author).
Rice Chicken	-----	Northeast Arkansas rice belt around Weiner and Hickory Ridge (author).
King Sora	-----	Potomac River, Va. (Kirkwood, 1895, p. 278); Powhatan River, Va. (author).
King Ortlan	-----	Patuxent River, Md. (author).
King Water Rail	-----	Muskrat trapper, Choptank River, Md. (author).
Marsh Pullet	-----	Allen's Fresh, Wicomico River, Md. (author).
Mud Hen	-----	New England (Forbush, 1925, vol. 1, p. 352).
Injun Hen	-----	Raleigh, N.C., area (Brimley, 1887 p. 201).

- Okankiskoki (ruddy raven)- Big Cypress Seminole Indians
(Mikasukis), Florida (Gilles-
pie, 1956, p. 123).
- Oklani kahki (ruddy raven)- Cow Creek Seminole Indians
(Muskogee), Florida (Gilles-
pie, 1956, p. 123).
- Marsh Hen----- Many localities.
- Stage Driver----- Lake Erie marshes, Ohio (author).

As the Nation's principal conservation agency, the Department of the Interior has basic responsibilities for water, fish, wildlife, mineral, land, park, and recreational resources. Indian and Territorial affairs are other major concerns of America's "Department of Natural Resources."

The Department works to assure the wisest choice in managing all our resources so each will make its full contribution to a better United States—now and in the future.



QL
151
N864
NH

THE SEA OTTER

IN THE

EASTERN PACIFIC OCEAN



NUMBER 68



UNITED STATES
DEPARTMENT OF THE INTERIOR
BUREAU OF SPORT FISHERIES AND WILDLIFE

355-847 - INTERIOR - Reg. No. 1711

NORTH AMERICAN FAUNA

This publication series includes monographs and other reports of scientific investigations relating to birds, mammals, reptiles, and amphibians, for professional readers. It is a continuation by the Bureau of Sport Fisheries and Wildlife of the series begun in 1889 by the Division of Ornithology and Mammalogy (Department of Agriculture) and continued by succeeding bureaus—Biological Survey and Fish and Wildlife Service. The Bureau distributes these reports to official agencies, to libraries, and to researchers in fields related to the Bureau's work; additional copies may usually be purchased from the Division of Public Documents, U.S. Government Printing Office.

Reports in NORTH AMERICAN FAUNA since 1950 are as follows (an asterisk indicates that sale stock is exhausted):

- *60. Raccoons of North and Middle America, by Edward A. Goldman. 1950. 153 p.
- *61. Fauna of the Aleutian Islands and Alaska Peninsula, by Olaus J. Murie; Invertebrates and Fishes Collected in the Aleutians, 1936-38, by Victor B. Scheffer. 1959. 406 p.
- *62. Birds of Maryland and the District of Columbia, by Robert E. Stewart and Chandler S. Robbins. 1958. 401 p.
- *63. The Trumpeter Swan; Its history, habits, and population in the United States, by Winston E. Banko. 1960. 214 p.
- *64. Pelage and Surface Topography of the Northern Fur Seal, by Victor B. Scheffer. 1961. 206 p.
- 65. Seven New White-winged Doves From Mexico, Central America, and Southwestern United States, by George B. Saunders. 1968. 30 p.
- 66. Mammals of Maryland, by John L. Paradiso. 1969. 193 p.
- 67. Natural History of the King Rail, by Brooke Meanley. 1969. 108 p.
- 68. The Sea Otter in the Eastern Pacific Ocean, by Karl W. Kenyon. 1969.

THE SEA OTTER
IN THE
EASTERN PACIFIC OCEAN

By **Karl W. Kenyon**, *Wildlife Biologist*

Division of Wildlife Research
BUREAU OF SPORT FISHERIES AND WILDLIFE



NUMBER 68

UNITED STATES
DEPARTMENT OF THE INTERIOR

Walter J. Hickel, *Secretary*

Leslie L. Glasgow, *Assistant Secretary for
Fish and Wildlife, Parks, and Marine Resources*

FISH AND WILDLIFE SERVICE

Charles H. Meacham, *Commissioner*

BUREAU OF SPORT FISHERIES AND WILDLIFE

John S. Gottschalk, *Director*



North American Fauna, Number 68

Published by

Bureau of Sport Fisheries and Wildlife

August 1969

U.S. GOVERNMENT PRINTING OFFICE

WASHINGTON : 1969

PREFACE

This report is the result of studies conducted from 1955 to 1967 by the Division of Wildlife Research of the Bureau of Sport Fisheries and Wildlife. In addition to field data gathered primarily in the Aleutian Islands, many unpublished reports, letters, and memorandums in U.S. Fish and Wildlife Service files were used. As a biologist working on studies of the Pribilof Islands population of northern fur seals from 1947 to 1955, I developed an interest in the sea otters of the Aleutian Islands. I was therefore pleased to be assigned as project leader of sea otter studies.

Many people contributed help in the field and laboratory. The following undertook special studies and have kindly permitted me to include their results. Dr. D. G. Chapman (statistical studies of phases of population dynamics); Dr. F. H. Fay (parasitism); Miss Neva Karrick (nutritional values of foods); Dr. J. K. Ling (skin structure); Dr. R. L. Rausch (parasitism); Dr. E. C. Roosen-Runge (reproduction in the male); Dr. R. P. Scapino (jaw muscles and joints); Dr. V. B. Scheffer (pelage and dentition); and Dr. D. B. Scott (dental attrition).

J. E. Burdick collected specimens and analyzed stomach contents. It would be impossible to list all those who assisted in other ways, but the following have been notably helpful: J. J. Alles, G. Baines, A. W. F. Banfield, V. D. Berns, A. Bezezekoff, F. Bezezekoff, K. L. Binkley, E. L. Boeker, R. A. Boolootian, J. W. Brooks, C. A. Brosseau, D. V. Brown, J. J. Burns, J. G. Carlisle, C. E. Carlson, C. H. Conaway, I. McT. Cowan, K. W. Cox, L. W. Croxton, S. V. Dorofeev (deceased), Y. E. Dawson (deceased), M. A. Edwards, C. H. Fiscus, R. M. Gilmore, I. Golodoff, C. J. Guignet, E. Gunther, W. J. Hamilton, Jr., G. D. Hanna, S. J. Harbo, A. C. Hartt, L. G. Hertlein, C. L. Hubbs, A. Jensen, A. M. Johnson, E. J. Johnson, M. L. Johnson, R. D. Jones, Jr., M. C. Keyes, J. G. King, C. M. Kirkpatrick, D. R. Klein, E. G. Klinkhart, H. R. Krear, W. S. Laughlin, D. L. Leedy, C. J. Lensink, P. T. Macy, E. G. Magee, L. Margolis, V. F. Martin, P. A. McLaughlin, E. D. Mitchell, H. W. Mossman, K. A. Neiland, U. C. Nelson, I. M. Newell, T. P. O'Brien (deceased), R. T. Orr, R. L. Peterson, R. G. Prasil, J. Radovich, J. Rankin, C. A. Repenning, F. Richardson, A. Y. Roppel, L. V. Sagen, E. Sczuck, A. H. Seymour, A. A. Sinha, A. G. Smith, T. A. Smith,

D. L. Spencer, R. Thomas, J. S. Vania, F. Vincenzi, A. D. Welander, N. J. Wilimovsky, L. Williams, V. L. Yadon, C. E. Yunker, and M. Zhan.

The cooperation of Game Biologists of the Alaska Department of Fish and Game was of particular value. Reproductive tracts, stomachs, other specimens, and information contributed by them furnished much of the material upon which this report is based.

The Woodland Park Zoo, Seattle, and the Point Defiance Aquarium, Tacoma, generously furnished facilities and care for captive otters and routinely recorded certain observations on behavior, molt, and food consumption.

The help of Mrs. Ethel I. Todd, not only in typing the manuscript but in assisting in many other phases of its preparation, was indispensable.

All or a substantial part of the manuscript was read and editorial assistance was given by P. A. DuMont, C. Larson, R. H. Manville, D. W. Rice, V. B. Scheffer, K. Schneider, D. W. Slater, and F. Wilke.

Weights and linear measurements of animals were taken in either the metric or the English systems. The original measurement is shown first, followed by the conversion in parentheses.

Nautical charts show distances in nautical miles (1 nautical mile equals 1.15 statute or land mile). In the present report, "miles" means nautical miles unless otherwise specified. Depths are usually given in fathoms (1 fathom equals 6 feet) because of their use on nautical charts. Depths are given in meters when depth bears no particular relation to nautical charts. Maps are adaptations from U. S. Coast and Geodetic Survey charts.

Trade names referred to in this publication do not imply endorsement of commercial products.

Much work on the biology of the sea otter remains to be done. Many of the studies included in this report are preliminary approaches to subjects that will require years of future study.

CONTENTS

	Page
Preface	iii
Introduction	1
Systematics	4
Physical characteristics	6
Identification of the river otter and the sea otter	9
Body measurements	19
Pelage and skin	31
Feeding mechanisms	42
Age determination	52
The senses	55
Habitat requirements	57
General behavior	59
Daily cycle of activity	59
Locomotion	60
Sleeping	71
Grooming	74
Voice	76
Handedness	80
Tool-using	82
Defense and escape	86
Maternal and filial behavior	87
Relation to other animals	102
Food and feeding behavior	105
Food gathering	106
What food is eaten	110
Where food is eaten	112
Stomach analyses	113
Fecal analyses	123
Food quantities required	126
Relative values of sea otter foods	127
Depletion of food resources	128
Unusual food items	131
Conclusions	131
Distribution and numbers	133
Original	133
Modern	137
Summary	198
Home range	200
Territoriality	204
Reproduction	206
Sex ratio	206
Segregation of sexes	208
Breeding behavior	214
Reproduction in the female	224
Reproduction in the male	247

	Page
Limiting factors	249
Natural mortality	250
Predation	278
Environmental pollution	281
Poaching	281
Summary	282
In captivity	284
Capture	284
Environmental needs of captives	287
Food and feeding of captives	293
Daily cycle of activity	303
Causes of death in captivity	309
Drug use	311
Transportation of captives	315
Transplant attempts	319
Management	323
References	326
Appendix 1—Field studies of sea otters, 1954-66	337
Appendix 2—Tabular summary of sea otters studied from 1955 through 1965	341

ILLUSTRATIONS

FIGURE

1. Pelage appearance shortly after a sea otter emerged from the water and shook himself	7
2. Front feet of the sea otter	8
3. The external ear of the sea otter resembles the ear of an otariid seal	9
4. Dorsal and ventral views of a newly born female sea otter	10
5. Adult male river otter	12
6. A small adult female sea otter	13
7. Eight sea otters asleep in a kelp bed at Amchitka Island	14
8. Plantar surface of the left hind foot of an adult male sea otter	15
9. The skeleton of an adult female sea otter to show the general location and shape of the bones	16
10. The baculum of an adult male sea otter	17
11. Adult male sea otter	17
12. Adult female sea otter eating the head of a large codfish	18
13. At birth the claws are white and curved	21
14. Hair from the mid-back of adult male sea otter	32
15. Plastic impression of pelage sheared near skin surface from midback of adult male sea otter	33
16. Horizontal section through skin near surface, midback, adult male sea otter	34
17. Sheared surface showing skin and distribution of pores from which hair bundles emerge	35

	Page
18. Cross section of pelage near midback, adult male sea otter	36
19. Horizontal section through the sea otter skin showing deeper layer	38
20. The shed pelage of an adult male otter was collected from the drain of his pool at 7-day intervals	40
21. Fresh young adult dentition in the late juvenile or early subadult stage of development	44
22. Dentition of newly born male sea otter	45
23. Complete juvenile dentition of a female age 2 to 3 months	46
24. Dentition at birth	47
25. "Old" adult dentition	48
26. Intermediate juvenile-adult dentition	49
27. Dental attrition and bone damage in the adult sea otter	51
28. Cross section of right upper canine tooth of an adult female sea otter	54
29. Favored sea otter habitat in the Aleutian Islands	58
30. Three adult males in typical swimming attitude	61
31. Duration of 87 timed food dives made by a mated pair of otters	65
32. Because the fifth digits of the hind flippers are long, the sea otter walks with a somewhat clumsy rolling gait	70
33. Adult sea otters, startled on a favorite hauling-out beach at Amchitka Island	71
34. Otters usually attempt to find a sheltered kelp bed before sleeping	72
35. A drowsy otter preens its cheeks with its forepaws before going to sleep	73
36. While dozing on the surface of her pool, a captive female sea otter languidly grooms the fur of her chest and sides	75
37. The sea otter curls its long flexible body into a ball and reaches between the hind flippers to groom the tail and lower back	76
38. Using its left paw, a grooming sea otter pulls the loose skin from its right side over the right foreleg in order to press water from the pelage and lick away the moisture	77
39. While grooming, water is squeezed from the fur of the foreleg under pressure and by rubbing with the palm of the paw	78
40. While drying its pelage, a fold of skin is pressed between the palms of the forepaws	79
41. A mother otter rubs the top of her head with one paw and her elbow with the other	80
42. Near the end of a grooming period the sea otter rests belly down at the surface, bends the head to the belly, and vigorously blows air into the fur	81

	Page
43. During the grooming period, before hauling out, the sea otter may beat the water to a froth with the front legs	82
44. After hauling out, the otter usually rests on its back while grooming and drying its fur before sleeping	83
45. A captive adult male sea otter from Amchitka Island pounds a clam, held between his forepaws, against a rock resting on his chest	84
46. A captive otter pounded herring against the cement edge of her pool	85
47. A juvenile sea otter, cornered on an Amchitka beach, prepares to rear backwards	86
48. In the defensive position a sea otter lies on its back	87
49. When closely approached a cornered sea otter hisses, extends its stiffened forelegs, and rears back as far as possible	88
50. After a feeding period and before taking her 3- to 4-week-old pup ashore, the mother sea otter scrubs and grooms her fur with her forepaws	90
51. A captive mother sea otter leads her 3- to 4-week-old pup from the water	91
52. The mother is solicitous of her young for a long period	92
53. The mother sea otter carries her pup high on her chest, clasped by both front paws	95
54. This mother sea otter and her large juvenile were surprised on land	96
55. After dragging her pup onto a rock, a mother sea otter preens and dries her fur while she supports the head of her nursing pup with a hind flipper	97
56. A pup, probably about 2 months old, swims beside its mother	99
57. The mother sea otter has just emerged from a feeding dive	100
58. An immature Glaucous-winged Gull waits expectantly for fish scraps discarded by a feeding sea otter	104
59. A captive sea otter pounds a clam on the cement edge of her pool	107
60. Clams were broken open by pounding one against another held on the chest	109
61. A wild otter accepts a fish head from Innokenty Golodoff	113
62. A captive adult female sea otter clasps one piece of fish to her chest under her left foreleg while she reaches with her teeth to grasp another	114
63. At frequent intervals the sea otter stops eating and rolls about its longitudinal axis through 360°	115
64. Food taken from a sea otter stomach	119
65. Intact sea otter food organisms and partially digested fragments of the same species removed from stomachs	120

	Page
66. Contents of a large sea otter fecal deposit	125
67. Distribution of the sea otter in 1741 and 1965, also showing the locations where remnant colonies survived in 1911	134
68. Beginning in 1957, aerial surveys of sea otter habitat were undertaken	138
69. A group of 157 sea otters resting in a kelp bed in Kagalaska Strait	144
70. Part of a group of 440 sea otters in Kujulik Bay	145
71. The sea otter was exterminated from the Near Islands during the late 1800's or early 1900's	148
72. The Rat Islands group, except Buldir Island, where 15 otters were recorded	149
73. Changes in population density on the north and south coasts of Amchitka Island, 1936-59	154
74. Estimated curve of the Amchitka sea otter population 1909-65	155
75. The Delarof Islands of the western Andreanof Islands were apparently among the few Aleutian areas where sea otter remained in 1911	158
76. The Adak-Great Sitkin Island areas in the central Andreanofs were repopulated during the 1950's and early 1960's	160
77. The colonies on the southern exposures of Atka and Amlia Islands, in the eastern Andreanof Islands, appear to be augmented from the large population in the central Andreanofs	161
78. Populations of sea otters at several Aleutian Islands have increased to maximum size and then crashed between 1936 and 1965	167
79. The colony at Samalga Island and in the vicinity of Cape Sagak, Umnak Island, is a small but permanent one	169
80. The Sanak-Caton Islands and Sandman Reefs areas were last surveyed on 8 April 1962	170
81. This group of 128 otters slept on the open sea about 2 miles off the north coast of Unimak Island	174
82. John Nevzoroff holds an adult female sea otter	201
83. The southeastern end of Amchitka Island showing the most favored male and female hauling grounds	211
84. A group of 39 otters sleeping at St. Makarius Point East, Amchitka Island	212
85. Rifle Range Point, a female hauling ground	213
86. Adult males searching for estrous females in areas habitually frequented by feeding females often swim belly down	216
87. A pair of sea otters rest and groom beside each other shortly after mating	219
88. An adult male and female slept beside each other on a tidal rock	222

	Page
89. Finally aroused, the male moved ahead of the female while she prodded him toward the water	223
90. This adult male was tolerant of a deserted juvenile which slept beside him	224
91. Phases in the reproductive cycle of the female sea otter.....	231
92. Early fetal stages of the sea otter	232
93. Intermediate fetal development	233
94. Estimated period of implanted pregnancy	237
95. The counts and estimates of dead sea otters on Amchitka beaches indicate the order of magnitude of annual mortality	251
96. Observed mortality of sea otters at Amchitka Island, 1955-63	254
97. Mortality of sea otters at Amchitka Island during weekly intervals through period of high mortality in 1959 and 1962	256
98. A moribund juvenile sea otter	256
99. This aged male sea otter sought escape from a high wind in a sheltered cove	257
100. Age and sex of sea otters dying in the winter-spring period of 1961-62	259
101. Age and sex of sea otters dying in the winter-spring period of 1958-59	260
102. Average seasonal mortality of 311 otters found dead on Amchitka beaches 1955-63, and average monthly wind velocities in the outer Aleutian Islands measured by the U. S. Weather Bureau, 1960 through 1963	264
103. Daily record of surf conditions and of otters found dead on the Pacific coast of Amchitka from 14 January through 30 April 1962	265
104. Daily record of observed surf condition and otters found dead on the Bering Sea coast of Amchitka Island from 19 January through 30 March 1962	265
105. After a sea otter was netted, a carrying cage was placed horizontally on the rocks and the otter was allowed to move from the net into the cage	286
106. This 65-lb. male was carried for over a mile in this manner	287
107. In 1955, before it was learned that fur of the sea otter quickly lost its waterproof qualities when otters were carried in dry bedding, these animals were transported from Amchitka to the Pribilof Islands as shown	289
108. This enclosure around a cement pool satisfactorily prevented escape and furnished ideal conditions where otters could be held indefinitely	290
109. The cement pool in the enclosure where otters were maintained in excellent health	291
110. Air temperatures down to +15° F. were withstood with no apparent detrimental effects by captive otters in the outdoor pool	292

	Page
111. On 602 days the amount of food consumed by a captive female sea otter was recorded	296
112. Daily food consumption of a 39-lb. female sea otter (Susie) during a midwinter month and a midsummer month	297
113. Average daily weight of food consumed each month in 1957 by an adult female sea otter weighing about 39 lb.	298
114. Juvenile otters learned begging behavior within a day or two after capture	301
115. A large and unusually light-colored adult female aggressively wrenched a food item from a juvenile otter	302
116. The activities of a captive female sea otter were recorded for each minute from before sunrise to after sunset on 29 August 1957	306
117. Behavior of an adult male sea otter during a mean or average night	308
118. Behavior of an adult female sea otter during a mean or average night	309
119. Seasonal behavior of an adult male sea otter at night	110
120. Seasonal behavior of an adult female sea otter at night	110
121. A mother otter was placed in the pool without receiving a tranquilizer	313
122. The same female and pup as shown in figure 121 about 10 minutes after the mother received an injection of Sparine tranquilizer	314
123. Captive otters held on dry bedding habitually lay on their back or side	318

TABLES

TABLE

1. Weight and length of newborn pups taken at Amchitka Island, Alaska	20
2. Total length and body weight of adult sea otters killed at Amchitka Island, Alaska	22
3. Total length and body weight of adult sea otters killed in areas of sparse population	23
4. Total length and body weight of adult sea otters found dead on beaches at Amchitka Island, Alaska	23
5. Weight loss of 10 adult male sea otters that died in captivity	23
6. Weight loss of seven adult female sea otters that died in captivity	23
7. Intestine length of adult sea otters	26
8. Weights of body organs in nine adult female and six adult male sea otters	27
9. Blood quantity in sea otters	30
10. Observation of sea otters beyond 3 miles from shore in waters off Alaska	68

	Page
11. Volume and classification of food found in 309 sea otter stomachs from Amchitka Island, Alaska	110
12. Sea otter stomachs examined	114
13. Frequency of occurrence of food species in 309 sea otter stomachs from Amchitka Island, Alaska	116
14. Stomach contents of two male sea otters from Simeonof Island, Shumagin Islands, Alaska	122
15. Stomach contents of three sea otters taken in 15-20 fathoms of water in the Bering Sea	123
16. Analysis of 422 fecal samples from Amchitka Island February to April 1959	124
17. Analysis of 75 fecal samples from the Shumagin Islands	126
18. Proximate analysis of important sea otter food species (averages)	127
19. Summary of sea otters observed and estimated in Alaska	140
20. Summary of aerial surveys of sea otters, 1957-65	141
21. Rat Islands group, sea otter population density, estimated from aerial survey counts, 19 May 1959 and 2-3 May 1965	150
22. Rat Island sea otter population density in 30 square miles of feeding habitat	151
23. Amchitka Island sea otter population density in 110 square miles of feeding habitat	153
24. Delarof Island sea otter population density estimated from aerial survey counts of 26 May 1959 and 2-3 May 1965	159
25. Andreanof Islands counts and estimate of sea otters obtained on three aerial surveys to show movement of otters	162
26. Tanaga Island sea otter population density in 83 square miles of feeding habitat	163
27. Kanaga Island sea otter population density in 95 square miles of feeding habitat	164
28. Adak Island sea otter population density in 75 square miles of feeding habitat	166
29. Kagalaska Island sea otter population density in 15 square miles of feeding habitat	166
30. Numbers of sea otters observed and estimated population in the Fox Islands group	171
31. Numbers of sea otters observed and estimated population in the Sanak Islands and Sandman Reefs areas	175
32. Numbers of sea otters observed and estimated population in the Shumagin Islands	177
33. Numbers of sea otters observed and estimated population along the Alaska Peninsula	178
34. Numbers of sea otters observed and estimated population in the Kodiak Islands	179
35. Numbers of sea otters observed and estimated population in the Kenai Peninsula, Prince William Sound, and Kayak Island areas	180

	Page
36. Estimated world population of sea otters	190
37. Changes in sea otter population density in six areas	193
38. Present and projected sea otter populations in certain Alaska areas	194
39. Sea otters tagged at Amchitka Island, Alaska	202
40. Recoveries of tagged sea otters at Amchitka Island	203
41. Prenatal sex ratio at Amchitka Island	206
42. Sex ratio of sea otters killed at Amchitka Island during experimental harvests	207
43. Sex and age of sea otters taken in seven areas frequented mostly by females at Amchitka Island	209
44. Sex and age of sea otters taken in three areas frequented mostly by males at Amchitka Island	210
45. Activities of a mated pair of sea otters during observations on 19, 20, and 21 August 1955	214
46. Adult female sea otter reproductive tracts from Amchitka Island	225
47. Phases of reproduction in the female sea otter as shown by status of ovaries and size of conceptus	226
48. Frequency of primiparous and multiparous sea otters	226
49. Uterine horn of pregnancy	226
50. Weight distribution of embryonic and fetal sea otters	227
51. Reproductive status of adult nonpregnant sea otters	228
52. Sea otters counted along 5.5 km. of shoreline, Kirilof area, at Amchitka Island, Alaska	235
53. Percent of fetuses in each weight class	243
54. Frequency of unimplanted and implanted pregnancy, by season	244
55. Mortality of sea otters, by age and sex, at Amchitka Island, Alaska, 1956-63	255
56. Age and sex of otters found freshly dead on Amchitka beaches	260
57. Abnormal conditions found in sea otters that died on beaches of Amchitka Island, Alaska	262
58. Summary of observations from 83 sea otters found dead at Amchitka Island, Alaska, 1959	262
59. Sea otter mortality in relation to population counts and available habitat, eastern half of Amchitka	266
60. Foods offered to captive sea otters	294
61. Food consumption of a 39-lb. (17.7 kg.) sea otter (Susie) at the Seattle Zoo	295
62. Activity of a captive sea otter in daylight hours, summer (1957) and winter (1960)	304
63. Conditions during sea otter observations at the Seattle Zoo	305
64. Comparison of daily activities of wild and captive female sea otters in summer	307

INTRODUCTION

As early as 1733, Spanish missionaries and explorers bartered for sea otter (*Enhydra lutris*) pelts with the Indians of Upper and Lower California (Ogden, 1941). Apparently the high value of the skins in the Orient was unknown to them.

In 1741 Georg Wilhelm Steller was shipwrecked with the Bering expedition on Bering Island of the Commander Islands. Here he observed the sea otter and gave the western world its first scientific description of the animal and its habits. After the remnant of Bering's expedition returned with valuable furs and news of abundant otters and seals on the islands to the east, fur hunters from Siberia, the Promyshlenniki, soon began exploiting Aleutian sea otter populations.

In 1779, members of Captain James Cook's expedition to the North Pacific sold in Canton otter pelts that they had obtained at Vancouver Island. The high value of the pelts on the Oriental market soon precipitated a flood of fur hunters from America and Europe. Thus began intensive exploitation of otters along the west coast of the United States and Canada. Unregulated hunting throughout the sea otter's range was incessant, and by the end of the 19th century the sea otter was extinct commercially and nearly extinct as a species. Highlights of this period are recounted in context by Miller and Miller (1967).

Management of the sea otter as a valuable natural resource began in 1911 when the remnant population was given Federal protection. It was feared that after nearly 170 years of unregulated exploitation the species might not survive. The initial phase of Government control was one of complete protection.

In 1935, men of the U.S. Coast Guard saw many sea otters at Amchitka Island, and in 1936, U.S. Bureau of Fisheries agents were stationed there to guard against poaching.

In 1936 and 1937, expeditions under Olaus J. Murie of the U.S. Bureau of Biological Survey conducted the first comprehensive biological inventory of what had become, in 1913, the Aleutian Islands Wildlife Refuge (now a National Wildlife Refuge).

These expeditions were the first to reveal that otter populations at a number of islands were growing. During World War II, additional population growth was observed.

On my first brief visit to Amchitka in the late fall of 1947, Dr. V. B. Scheffer and I found dead otters on the beaches. Elmer Hansen, who was stationed there, found and sent us additional specimens. These were mailed wrapped, without preservative, inside weather balloons and, as the assistant who cleaned the bones, I had a strong and unforgettable introduction to the sea otter.

In the 1949-53 period, R. D. Jones, Aleutian National Wildlife Refuge Manager, observed winter "die-offs" at Amchitka. In 1950-51 he led an expedition there to capture and transplant otters to other areas. All captive otters soon died, and it became evident to him that the sea otter adapted poorly to captivity under field conditions. This experience demonstrated that until further knowledge of the animals' biological needs was gained, transplanting attempts would be futile.

As a first step toward a better understanding of sea otter biology, Dr. Robert L. Rausch went to Amchitka to study stranded animals, dead or dying, and Drs. C. M. Kirkpatrick and D. E. Stullken, with the aid of R. D. Jones, F. Wilke, C. J. Lensink, and D. Hooper went there in the winter of 1954 to study sea otter physiology and the responses of otters to captive conditions. Much useful knowledge was gained through these studies, but failure of a further effort to transplant otters from Amchitka to the Pribilof Islands in March and April of 1955 showed that still more knowledge was necessary.

It was now clear that the species was no longer endangered. Anticipating a public request that the resource be utilized, the second or long-term study phase of management was begun by the U.S. Fish and Wildlife Service in 1954 and 1955. An annotated account of field studies is in appendix I. Early in this period it became apparent that several island populations were at or near maximum size and that experimental harvests could be made.

When Alaska became a State in 1959, the statehood act provided that jurisdiction over the exploitation of game and fur-bearing mammals, including the sea otter, should pass to the State.¹ Soon State officials decided to harvest sea otter pelts. The third phase of management began at Amchitka in the winter of 1962 when an experimental harvest was taken by Alaska Department of Game and U.S. Fish and Wildlife Service biologists. Subsequent harvests were taken by State biologists at Amchitka in 1963 and

¹ Federal regulations govern the exploitation of these animals on National Wildlife Refuge lands but not in State waters adjacent to them. Thus, the sea otter is under Federal jurisdiction when it comes on shore on a National Wildlife Refuge and when it goes to sea beyond territorial boundaries.

1967, and at Adak in 1967. One thousand pelts were available for the first public auction (since 1911) on 30 January 1968, at Seattle, Wash.

The harvesting of otters served the dual purpose of furnishing a financial return to the public and making specimens available for biological research. Many of the facts thus obtained are presented in this report.

Biologists of the State of Alaska, particularly K. Schneider, under the direction of J. Vania are progressing in management studies, especially in transplanting otters from areas of abundance to vacant parts of their former range. Concurrently, biologists of the State of California are studying the population there. In the Soviet Union, long continued sea otter studies, principally in the Commander and Kuril Islands, have added much to our knowledge. A comprehensive review of published information on the sea otter is given by Harris (1968).

Wise conservation practices based on biological knowledge will assure not only that the sea otter will once again be an article of commerce, but also that this interesting member of our wildlife community will flourish as an esthetically and scientifically valuable part of our environmental heritage.

SYSTEMATICS

Evolution

It has been supposed that the sea otter derived from an Atlantic Ocean early Pleistocene ancestor *Lutra reevei* (Newton) (Thenius and Hofer, 1960, p. 166). Recent findings in California of sea otter remains from the early and late Pleistocene demonstrate that this supposition is incorrect. Mitchell (1966, p. 1908) studied all available paleontological material. In his exhaustive review of the fossils and literature he stated:

Because these older North Pacific fossils are considered to be conspecific with the living sea otter, it is obvious that the *Lutra reevei* tooth cannot represent a direct ancestor of *E. lutris*. . . . The sea otter may probably be considered as a strict North Pacific endemic autochthon, just as McLaren (1960) has assumed it to be.

Taylor (1914) studied the osteology and aquatic adaptations of the sea otter and the river otter and concluded that the two otters are fundamentally alike and probably descended from a common ancestral form. Because the fossile record is incomplete, it is possible only to speculate where the sea otter originated. Dr. Charles A. Repenning suggests (letter, 3 March 1965):

I would guess that *Enhydra* developed from the otters of the Pliocene of India and eastern Asia and moved northward along the western shore of the North Pacific with the accentuation of global climatic zonality. All of the otters of North America (including *Enhydriodon*) seem to be derived from Asiatic stock and seem to have arrived in North America in the Pliocene and early Pleistocene.

Taxonomy

The sea otter is the only member of the genus *Enhydra*. It is the largest (to 100 lb. [45 kg.]) member of the family Mustelidae, which includes nearly 70 species—river otters, skunks, weasels, and badgers, among others. Unlike other mustelids, it has no functional anal scent glands. The sea otter is the most specialized of the group, being adapted to a narrow ecological zone in the marine environment. Besides being the smallest marine mammal, it is the only one in the order Carnivora. Among mammals it shares the marine environment with the pinnipeds (seals), cetaceans (whales and porpoises), and sirenians (manatees and dugongs).

Miller and Kellogg (1955) and Hall and Kelson (1959) recognize a northern race, *Enhydra lutris lutris* Linn., formerly ranging

from Vancouver Island to the end of the Aleutian Islands chain, and a southern race, *E. l. nereis* Merriam, ranging from the Strait of Juan de Fuca southward, formerly into Baja California, Mexico. The southern race was described on the basis of one skull. Barabash-Nikiforov (1947) reviewed available data and says "we are justified in drawing conclusions on the sea otter based on the slight amount of material we succeeded in collecting." He recognized three races: *E. l. lutris* Linn., "the Commander-Aleutian North American sea otter"; *E. l. gracilis* Bechstein, "The Kuril-Kamchatka sea otter"; and *E. l. nereis* Merriam, "southern California sea otter."

After superficial examination of several hundred sea otters taken at Amchitka Island (as mentioned elsewhere), and after observing the variation in color and body size among animals of this local population, I agree with Scheffer and Wilke (1950). They studied specimens from California and the Aleutian Islands and reviewed the basis for establishing a racial division. They concluded that "Neither on the basis of demonstrable variation nor on the grounds of geographical isolation is there support for a southern subspecies of the sea otter."

A careful study of specimens from the several geographical areas occupied by sea otters is now required before any racial differences in these populations can be recognized. Because of the variation among animals I have seen, the meager specimen material used to date in defining races, and the similarity of habitats occupied by the sea otter throughout its geographic range, it is not possible, without further study, to distinguish racially distinct populations which might exist.

PHYSICAL CHARACTERISTICS

The sea otter's characteristics include the following: (1) A coat of sparse guard hair and dense insulating fur which protects it from cold as blubber insulates other marine mammals. A blanket of air remains trapped at all times among the fur fibers of the sea otter so that the skin is never touched by the water of its chilly environment (fig. 1). (2) Flattened hind feet or flippers for propulsion. (3) Retractable claws on the front feet (fig. 2) (but not on the hind feet), the only member of its family so adapted. The forepaws are used to groom the fur, to gather and grasp food, to break the shells of mollusks and crustaceans against a rock held on the chest, and to pass food to the mouth. (4) A loose flap or pouch of skin under each foreleg, extending partially across the chest, is used to hold food organisms after they are gathered from the bottom until they are consumed while the otter floats on its back at the surface. In the wild it never voluntarily consumes food on land. (5) Flattened and rounded molar teeth having no cutting cusps. These are used to crush the shells, external skeletons, and flesh of food organisms. (6) A horizontally flattened tail aids propulsion. (7) A manner of swimming under water, similar to cetaceans, by means of vertical undulations of the hind flippers and tail. (8) An external ear (fig. 3) that resembles the ear of an otariid or eared seal more than it does the ear of a land carnivore or of its closest relative, the river otter.

The body of the sea otter is relatively long and heavy, making progress on land clumsy and slow. Although highly adapted to the marine environment, the sea otter is specialized to occupy the narrow zone of shallow water near shore. Apparently it cannot (or at least is not known to) obtain pelagic food where the sea is deep. It does not undertake seasonal migrations. If removed from its natural environment, i.e., water, and kept in a dry pen, it shows great distress, perhaps because it instinctively senses that its fur may become soiled and through eventual wetting cause chilling and death. Also, in captivity when water is not available, heat prostration and death may occur unless environmental temperatures are carefully controlled.

At birth the sea otter is covered with dense brownish fur and long silky yellowish-tipped guard hair. The head is a light buff



FIGURE 1.—Pelage appearance shortly after a sea otter emerged from the water and shook himself. Only the tips of the fur are wet and thus stick together to form points. Beneath, the underfur is dry, insulating the otter's skin and enabling it to maintain its body temperature. (KWK 59-8-1)



FIGURE 2.—Front feet of the sea otter. In the relaxed position the claws are retracted (*A* and *B*). The claws are extended (*C* and *D*) during feeding when food is grasped and, with the help of the teeth, torn into small bite-sized chunks. Much grooming is done with the claws retracted, but occasionally during this activity they may be extended. Note that the third and fourth digits are closely joined. The paws are highly sensitive. When an otter grasps a human finger between its forepaws, the mobile digits can be felt moving like fingers inside a mitten. (KWK 64-1-8)



FIGURE 3.—The external ear of the sea otter resembles the ear of an otariid seal. It is cartilaginous and thickened but not as pointed at the tip or as tightly rolled and “valvelike” as the ear of a seal. The ear length (from notch) of an adult male was 32 mm. and of a subadult female 30 mm. While the otter is beneath the water the ears are pointed sharply downward. When the head is above the surface the ears are usually held erect. (KWK 61-42-0)

color (fig. 4). Over a period of several weeks the guard hair grows out, often giving the pup a distinctly yellowish appearance.

The late juvenile pelage is similar to that of the adult, which is typically dark bodied and buffy to light gray headed. The head tends to become whiter with age, and grizzling may appear on other parts of the body. Body color varies from light buff (rare) through shades of brown to nearly black. The sparse guard hair may be dark or silvery white.

IDENTIFICATION OF THE RIVER OTTER AND THE SEA OTTER

The river otter (*Lutra canadensis*) is often seen swimming in salt water in coastal areas of the Pacific Northwest and Alaska.

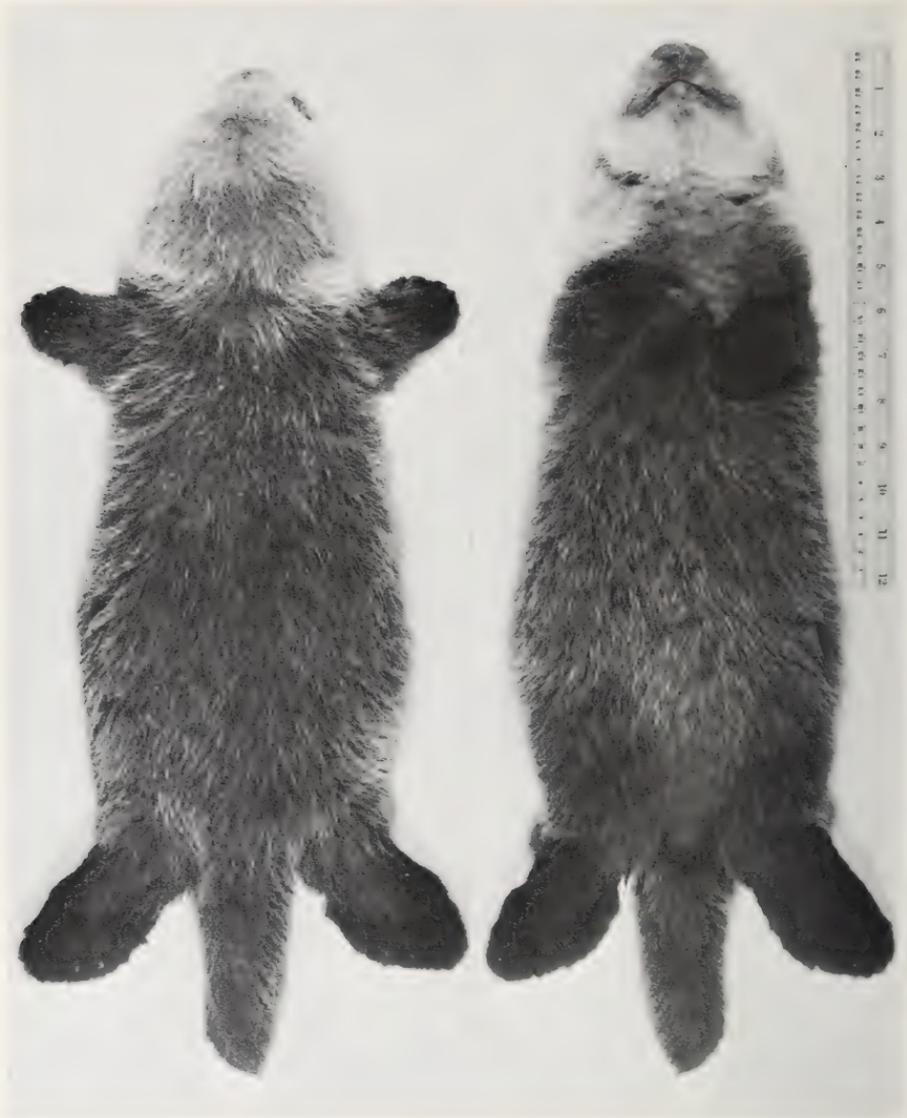


FIGURE 4.—Dorsal (left) and ventral (right) views of a newly born female sea otter taken on 6 April 1949 on Amchitka Island; weight 1,950 g. (4 lb. 6 oz.), length 560 mm. (22 in.); specimen BDM 378. The long, silky, yellowish-tipped natal pelage of the body and typical light buffy head and neck are demonstrated. The nearly black fur of the feet is soft and woolly. (KWK 500 and 501)

For this reason, observers often report the presence of sea otters when they have actually seen river otters. To help in correct identification of these two species, the following comparison of diagnostic physical and behavioral characteristics is presented (see also figs. 5 and 6):

Field observation

Sea Otter

1. Occurs in Alaska from Prince William Sound, along the Alaska Peninsula, in the Aleutians, and near Monterey, Calif. Is currently extending its range and should be looked for in Pacific coastal areas.
2. Found along open-sea coast in salt water only.
3. On surface usually swims belly up, forepaws on chest while paddling with hind flippers. Floats high in water.
4. Clumsy on land, seldom seen on shore except in isolated Alaskan areas.
5. Eats while floating on back, never eats on shore.
6. Sleeps (usually) in kelp beds or calm water while floating on its back (fig. 7).
7. Bears single young which is carried on the mother's chest as she swims on her back.

River Otter

1. Occurs on rivers and along seacoasts in the United States, Canada, and Alaska. Often swims several miles in salt water between islands.
2. Found in salt or fresh water.
3. On surface usually swims belly down, back nearly submerged.
4. Agile and graceful on land, often seen on land.
5. Brings food ashore to eat.
6. Sleeps on land, usually, in dens, never while floating on its back.
7. May have up to four young, does not carry them on chest while swimming.

Specimen Observation

Sea Otter

1. Maximum weight 100 lb.
2. Maximum length 58.25 in.
3. Fur long and soft, guard hair delicate and sparse.
4. Claws of forepaws short and retractile.
5. Hind feet decidedly flipperlike and webbed to tips of toes. Pads visible only at tips of toes (fig. 8) The fifth or outer digit is longest (fig. 9).
6. Tail somewhat flattened and does not thicken markedly at base, less than $\frac{1}{2}$ of body length.
7. Eyes are open at birth.
8. Last upper molariform tooth broad and flattened, about $\frac{3}{4}$ inch or more in greatest width.
9. Baculum of adult about 6 inches in length (fig. 10).

River Otter

1. Maximum weight 30 lb.
2. Maximum length 50 in.
3. Guard hair coarse and dense, covering fur completely.
4. Foreclaws long and not retractile.
5. Hind feet webbed but not flipperlike. Pads cover much of palm and digits. The fifth digit is not elongated.
6. Tail nearly round in cross section and heavily thickened at base, more than $\frac{1}{2}$ of body length.



FIGURE 5.—Adult male river otter. When compared with the sea otter, the river otter's tail is long, heavy at its base, and tapered. The hind feet, although webbed, are relatively small, and the body is less elongate than that of the sea otter. (Specimen VBS 1322, length 122 cm. [48 in.], weight 23.25 lb. [10.5 kg.], taken 8 December 1945 near Forks, Wash.) (VBS 1940)



FIGURE 6.—A small adult female sea otter. White dots mark the umbilicus and mammae. The relatively short, flattened tail of nearly uniform width throughout its length, broadly flattened and webbed hind feet, and elongate body are obvious characteristics which differentiate the sea otter from the river otter. (Specimen KWK 61-2 [Susie], weight in life 40 lb. [18.1 kg.], length 127 cm. [50 in.]. Captured 4 September 1955, Amchitka Island, died 27 October 1961 in Seattle zoo.) (KWK 61-42-16)



FIGURE 7.—Eight sea otters asleep in a kelp bed at Amchitka Island during a midday rest period. In the foreground a large juvenile rests its head on its mother's abdomen. (KWK 55-18-18)

7. Eyes do not open until age 25-35 days.
8. Last upper molariform tooth not broadly flattened and greatest width less than $\frac{1}{2}$ inch.
9. Baculum of adult about 4 inches in length.

FIELD RECOGNITION OF THE SEXES

The sex of a living sea otter in the field may be recognized at a reasonable distance if prevailing weather conditions offer good light and visibility. The fact that the sea otter habitually rests on its back and floats high in the water facilitates recognition of the sexes. If the sea otter is wet, so that the fur is slick, the penial bulge of the male (fig. 11) and the two abdominal mammae of the female (fig. 12) may be visible with binoculars up to a distance of about 100 yards. When the fur is dry and fluffy, these definitive characters are less distinct but are visible at close range.

No instance is known of a male otter carrying a pup on its chest



FIGURE 8.—Plantar surface of the left hind foot of an adult male sea otter. The outer (fifth) digit is longest, a condition not found in other mammals. This adaptation increases efficiency of propulsion by the foot when the otter swims on its back. Pad development at the tips of the toes is minimal. The vestigial pads near the center of the foot are not visible on some individuals. (KWK 62-23-26)

or abdomen. Thus, all animals carrying young are recognized as females. Large juveniles, still with their mothers, may approach an adult male and romp with him. Thus care is necessary during observation to differentiate between the mother and a "visiting" male.

It was shown that the adult male averages larger than the female (see Body Measurements) but because of overlap, size alone is not useful in recognition of the sexes.

The head and neck are heavier and more muscular in appearance in the adult male than in the female. If a mated pair is observed, this difference is apparent. Because of individual variation, however, much observation and field experience is necessary before this relatively slight difference becomes a useful character in the recognition of sex.

In its behavior, the male sea otter is relatively bold. If a human approaches a group of males and females hauled out near each



FIGURE 9.—The skeleton of an adult female sea otter (No. KWK 61-2) shows the general location and shape of the bones. The last joint of each digit was removed with the skin and is missing. The elongate fifth digit of the hind foot is demonstrated. (VBS 4954)



FIGURE 10.—The baculum of an adult male sea otter (No. KWK 60-8). Above, dorsal view; middle, ventral view; below, side view. The baculum is attached to the ischium by a ligament, composed of the ischiocavernosus and bulbocavernosus muscles, which inserts on the left. (KWK 66-15)

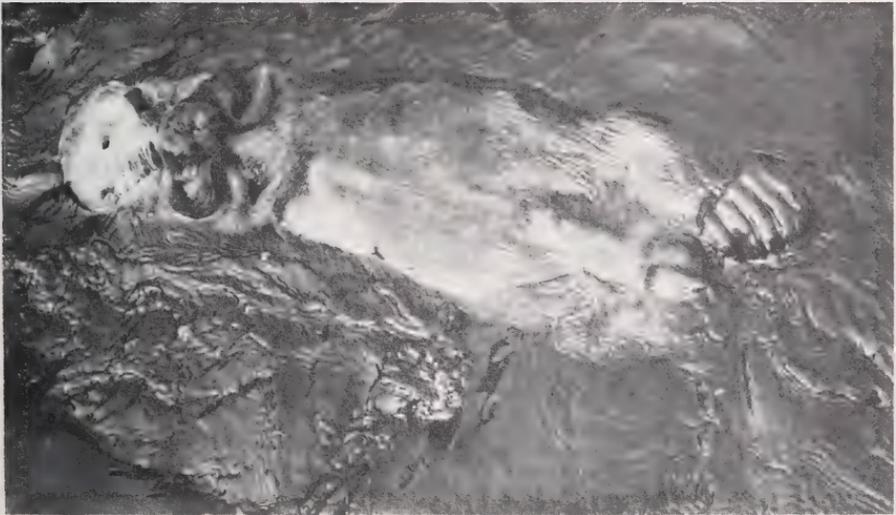


FIGURE 11.—Adult male sea otter. The penial and testicular bulges are evident when the outer pelage is wet and slick. They are less apparent when the pelage is dry and fluffy, making identification of sex difficult in the field. Note loose skin pouches beneath each foreleg. These are used to store food organisms as they are gathered from the bottom, until they are eaten at the surface. (KWK 56-29-11)

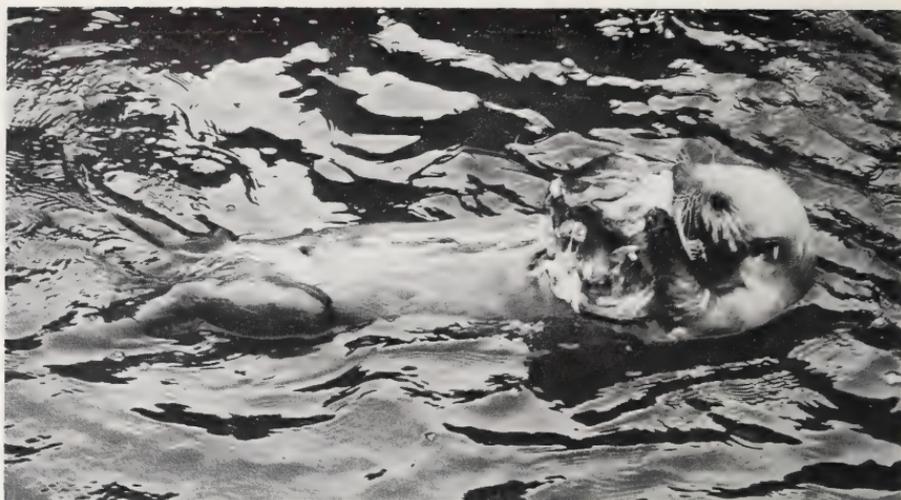


FIGURE 12.—Adult female sea otter eating the head of a large codfish (*Gadus macrocephalus*). Note the two abdominal mammae and that the head and neck are relatively of lighter structure when compared with the male. Also, females float somewhat higher in the water than do males. This is an unusually light-colored animal (albinistic), but the extremities and eyes were normally pigmented. (KWK 59-13-2)

other, the females usually take alarm and depart before the males do.

On several occasions we pursued sea otters in an outboard-powered dory in order to capture them in a dip net. Females attempted to leave the vicinity by making long dives. The relatively fearless males often tried only to avoid the immediate vicinity of the boat. One individual surfaced repeatedly in the same general area. After about an hour of fruitless pursuit, we abandoned the chase and the otter began diving for food near the place we first saw him.

The difference in color between adult males and females was not quantitatively determined. In general, females appear quite black when their fur is dry and fluffy. Males, in general, appear brownish under the same conditions. Black males and brownish females, however, are seen. Both sexes tend to become white headed with age. Dark-headed individuals, however, were examined which had worn teeth, indicating advanced age. Among a group of 10 captive juvenile otters, the animals having the lightest colored heads were males. In general, this difference tends to prevail also in older animals.

Examination of the photographs and this discussion of diagnostic characteristics, indicate that the sex of many otters may

be recognized in the natural environment. Seldom, however, may the sex of all adult or subadult otters seen during a period of observation be positively identified.

During hunting it was demonstrated that recognition of sex in the field is impractical when obtaining skins is the primary objective. Between 31 July and 3 August 1963, officials of the Alaska Department of Game shot 20 sea otters of adult size. Mothers accompanied by pups were omitted from the kill in the hope that a high proportion of males would be obtained. Only one male (5 percent of the kill) was taken in the "female areas" where this collection was obtained.

Body Measurements

Stullken and Kirkpatrick (1955) described some of the physical characteristics of the sea otter and reported on physiological studies of captive otters. My observations are intended to supplement theirs.

Body weights and lengths of sea otters captured or found dead on Amchitka beaches, or shot in waters near Amchitka, and of otters taken in other Alaska areas are discussed in this section. Because no anatomical feature is known to reveal the exact age of a sea otter, juveniles and subadults are omitted and only data from newly born and adult animals are presented. Sea otters were recognized as adults by observations of adult dentition, suture closure and sagittal crest development of the skull, and of the baculum size in males.

Total length was obtained by measuring, with a steel tape, each animal from tip of nose to tip of tail as it lay flat on its back. Only the total length is considered in the following discussion. (The mean tail length was found to be 24.5 percent of the total length. The range in 10 adult males was 22.3 to 29.2 percent and in 10 adult females 22.0 to 26.1 percent.) Some animals killed during the Alaska State harvesting operations could not be measured immediately after death. When an animal in rigor mortis was measured, an attempt was made to stretch it to full length. Some of these, however, were probably measured as being slightly shorter than they would have been when relaxed.

The scales most frequently available were spring scales of 50- and 100-lb. capacity. The data as shown in tables were converted to kilograms. Small young were usually weighed on a 15-kg. capacity balance.

NEWBORN YOUNG

The data on body size of the youngest sea otters obtained are reported in table 1. The umbilical scar was fresh on each individual listed and all showed little or no wear of the fetal claw tips (fig. 13). The two smallest, a male weighing 2.6 lb. (1.2 kg.) and a female weighing 2.25 lb. (1.02 kg.), were both dead when obtained, one from the beach and the other from a mother that was netted on the beach while carrying her dead pup. Among the seven largest fetuses (four males and three females), collected at Amchitka in 1963, the largest, a male, weighed 4.12 lb. (1.869 kg.) and measured 61.0 cm. in length. The mean weight was 3.5 lb. (1.598 kg.) and the mean length 57.3 cm. (22.5 in.). Thus it is probable that the two smallest newborn young were stillborn, being abnormally small at birth. All of the others had received at least some nourishment in the form of milk from their mothers before capture, thus were heavier than when newly born. The living young examined indicate that a healthy newly born sea otter may weigh as little as 3 lb. (1.4 kg.). But the fetal material studied (see Reproduction in the Female) and larger newborn young indicate that larger body size of 4.12 lb. (1.869 kg.) to 5 lb. (2.3 kg.) and 61 cm. (24 in.) in total body length is probably normal.

ADULTS

Analysis of the weights and lengths of 84 adult males and 258 adult females that were shot, are given in tables 2 and 3. Animals

TABLE 1.—*Weight and length of newborn pups taken at Amchitka Island, Alaska*

[The umbilical scar or adhering fragments of the umbilical cord were fresh. All except the two dead pups contained small quantities of milk]

Collection number	Date	Weight	Length
		Kg.	Cm.
Males:			
.....	29 March 1955	1.6	58.0
32-56 ¹	26 May 1956	1.2	47.3
D-6-57	18 November 1957	2.5	62.9
62-178	18 February 1962	1.7	52.8
Mean	1.75	55.25
Females:			
32-56 ²	25 May 1956	1.02	48.4
D-2-57	11 October 1957	1.45	52.1
D-15-57	16 October 1957	2.4	—
(³)	15 Apr. 1959	1.7	—
60-17	8 July 1960	2.35	53.5
60-21	10 July 1960	2.83	61.6
Mean	1.96	53.9

¹ Freshly dead pup taken from the mother when she was netted.

² Freshly dead pup found on beach.

³ Mother and pup netted and released. The pup was not tagged because it was obviously newborn (umbilicus still attached and fresh).



FIGURE 13—At birth the claws are white and curved. Soon after birth the young otter attempts to groom its fur, and the soft tips are lost. (KWK 62-16-21)

found dead on beaches (table 4) and those which died in captivity (tables 5 and 6) are compared and the differences are discussed below.

Scheffer (1951) published information on the body size of three adult sea otter specimens which he measured. The present data confirm that the maximum length of the adult male sea otter is about 148 cm. (58.25 in.), that the adult female is 140 cm. (55 in.). The adult male may reach a maximum weight of about 100 lb. (45 kg.) and the adult female may reach a weight of at least 72 lb. (32.6 kg.).

It is indicated in other sections (see Food and Feeding Behavior, Mortality Factors, and Distribution and Numbers) that at Amchitka Island a dense sea otter population has depleted food resources. Additional evidence for this is revealed by comparing the body weights of Amchitka sea otters (table 2) with animals from a sparse population (table 3).

TABLE 2.—*Total length and body weight of adult sea otters killed at Amchitka Island, Alaska*

Item	Male				Female					
	1959 ¹	1962 ²	1962 ³	1963 ⁴	All	1959 ¹	1962 ²	1962 ³	1963 ⁴	All
Number	13	24	8	39	79	8	99	16	131	254
Maximum weight	38.6	36.3	32.6	38.6	38.6	28.1	26.8	26.8	31.7	31.7
Minimum weight	22.7	22.7	26.3	21.8	21.8	15.4	14.5	15.9	15.4	14.5
Mean weight	28.7	28.2	28.7	28.1	28.3	20.7	20.4	21.9	21.5	21.1
Standard deviation	7.84	7.45	7.58	6.24	7.93	4.13	5.81	5.15	6.81	6.49
Maximum length	145	140	145	142	145	135	136	133	140	140
Minimum length	132	126	132	137	136	124	112	109	107	107
Mean length	139.7	134.5	137.7	133.6	135.0	129.4	125.3	124.7	124.9	125.2
Standard deviation	4.13	3.53	6.67	3.53	4.30	3.29	4.65	5.77	4.64	4.73

¹ Animals netted on beaches, February-May.

² Animals shot, January-March.

³ Animals shot, October.

⁴ Animals shot, March-April. Thirty-four males shown to be subadult by baculum measurements are omitted. Their mean weight was 47.9 lb. (21.7 kg.) and mean length was 123.9 cm. (48.7 in.).

TABLE 3.—*Total length and body weight of adult sea otters killed in areas of sparse population*

[These otters were shot in 1960 in the Shumagin Islands (6), off Unimak Island (2), and Adak Island (1)]

Item	Males	Females
Number	5	4
Maximum weight	44.9	32.7
Minimum weight	34.0	19.9
Mean weight	39.5	25.2
Standard deviation	10.12	13.0
Maximum length	143	139
Minimum length	140	125
Mean length	140.8	129.8
Standard deviation	0.5	6.3

TABLE 4.—*Total length and body weight of adult sea otters found dead on beaches at Amchitka Island, Alaska*

[Weights and measurements could be obtained from relatively few of the total found. All are combined in this table: 1956 (1), 1959 (7), 1962 (20), and 1963 (2)]

Item	Males	Females
Number	13	17
Maximum weight	31.7	18.6
Minimum weight	15.9	12.2
Mean weight	21.4	16.2
Standard deviation	10.20	3.83
Maximum length	145	137
Minimum length	130	122
Mean length	136.5	131.7
Standard deviation	4.39	3.74

TABLE 5.—*Weight loss of 10 adult male sea otters that died in captivity*

[Weight in kilograms]

Collection number	Weight at capture	Weight at death	Weight loss	Percent loss	Days in captivity
II-56	33.6	25.4	8.2	24	15
III-56	32.7	22.5	10.2	31	18
VI-56	33.6	24.0	9.6	28	15
VIII-56	26.3	19.5	6.8	26	8
IX-56	25.8	18.1	7.7	30	47
D-8-57	20.4	17.9	2.5	12	7
D-20-57	30.4	26.3	4.1	13	20
D-21-57	29.5	26.8	2.7	9	13
D-22-57	31.7	20.9	10.8	31	17
D-15-57	28.6	20.9	7.7	27	305
Mean	29.25	22.23	7.03	24	—

TABLE 6.—*Weight loss of seven adult female sea otters that died in captivity*

[Weight in kilograms]

Collection number	Weight at capture	Weight at death	Weight loss	Percent loss	Days in captivity
I-56	21.3	19.3	2.0	9	6
IV-56	23.1	15.0	8.1	35	57
VII-56	24.0	17.0	7.0	29	15
D-7-57	25.4	21.3	4.1	16	6
D-16-57	27.2	23.4	3.8	14	27
D-17-57	22.2	19.7	2.5	11	25
D-23-57	22.5	18.5	2.3	10	10
Mean	23.67	19.17	4.50	19	—

Scheffer (1955) concluded that a reduction in body size was correlated with increasing population or crowding in the northern fur seal (*Callorhinus ursinus*). The data presented below indicate that adult sea otters from a crowded population weigh less than animals from a sparse population. The length of adult otters from sparse populations fell within the length range of otters from the crowded Amchitka population (tables 2 and 3). However, an insufficient number of animals from sparse populations were available to demonstrate a statistically significant difference at the conventional level of 0.05.

Although few adult sea otter specimens (five males and four females) are available from areas where sea otter populations are sparse, the differences in body weight between these animals and the Amchitka collection are noteworthy. Among 79 adult males that were killed at Amchitka, the mean weight was 62.5 lb. (28.3 kg.), and the heaviest weighed 85 lb. (38.6 kg.). Among five that were killed in sparsely populated areas, however, the mean weight was 87.1 lb. (39.5 kg.) and the heaviest weighed 99 lb. (44.9 kg.). The difference between the mean weights of these two samples is 24.6 lb. (11.2 kg.). This indicates that adult males in a sparse population may average about 28 percent heavier than those in crowded populations. The difference is significant at the 0.1 percent level. The mean weight of four females from sparsely populated areas was about 16 percent greater than the mean weight of 254 Amchitka females. When the animals were collected in sparsely populated areas, no effort was made to select large individuals.

The lesser body weights of the Amchitka animals appear to confirm conclusions drawn from food habits and mortality studies that a large population there has created ecological conditions which are below the optimum. Because the sample of adult otters from sparsely populated areas is small, a more thorough statistical evaluation of the apparent differences in mean body weight between crowded and sparse populations must be delayed until more data are gathered.

Most of the sea otters killed at Amchitka were taken during the late winter to early spring period of environmental stress when many of the otters were dying. Thus, it appears appropriate to compare the animals killed at this season with others taken at Amchitka in the fall when body condition would be expected to be optimum. Unfortunately, the only fall (1962) sample of adults is small, consisting of 3 males and 16 females. Comparison of the mean weights of these animals with those taken in the late winter

to early spring period indicates no statistically significant difference in body condition (table 2). The sea otter must maintain a high daily intake of food regardless of season. It is reasonable to suppose that those animals capable of maintaining themselves under the feeding conditions imposed by a maximum otter population would show little seasonal differences in body weight.

WEIGHT LOSS PRECEDING DEATH

Death, in the wild and in captivity, is usually preceded by a period of physical deterioration evidenced by gradual or precipitous loss of body weight. The mean weight of 13 adult males found dead on Amchitka beaches was 47.1 lb. (21.4 kg.) (table 4). The mean weight of 79 adult males that were shot near the same places was 62.5 lb. (28.3 kg.) (table 2). The mean weight difference was 15.2 lb. (6.9 kg.), indicating that preceding death the moribund animals lost 24 percent or about one-quarter of their body weight. Similarly, between 254 adult females that were shot and 17 that were found dead on beaches the mean weight difference was 10.8 lb. (4.9 kg.) (21.1 kg. minus 16.2 kg., tables 2 and 4), or an indicated reduction of about 23 percent.

Seventeen adult sea otters (10 males and 7 females) were weighed at capture and again after they died in captivity. These animals were held captive for periods varying from 6 days to 10 months (tables 5 and 6). Among 10 adult males that died in captivity, the mean weight loss at death was 24 percent of the body weight at capture. Three animals in this group lost 30 percent or more of their body weight (table 5). Data for adult females are similar (table 6).

Massive weight loss preceding death appears to result from (1) evacuation of the gastrointestinal tract, (2) consumption of body fat reserves, and (3) dehydration. The usual terminal symptoms, in wild and captive animals, was excretion of black, tarry feces due to enteritis.

After an adult otter enters a period of physical decline, the restoration of normal vigor and weight may be difficult or impossible by any known means. The afflicted animal may become increasingly lethargic and may consume little or no food. Some emaciated juveniles captured on beaches, however, recovered when given adequate food in captivity.

In summary, there is evidence that among adult otters of about the same body length, those from areas of sparse population may weigh about 16 to 28 percent more than apparently healthy animals from a densely populated area and about 50 percent more

than emaciated individuals which die on beaches in a densely populated area. Animals in captivity, taken in a densely populated area (Amchitka), lost about 25 percent of their body weight at capture, before death.

MISCELLANEOUS MEASUREMENTS

Skin length and body length

The skin of the sea otter is "loose" and stretches considerably after it is removed from the animal, as shown by the following figures:

Specimen	Sex	Body length ¹		Skin length ²		Percent increase	Remarks
		Millimeters	Inches	Millimeters	Inches		
KWK 59-61.....	♀	720	28¾	1,035	40¾	44	Fresh skin.
KWK 59-77.....	♀	1,320	51¼	1,850	72¾	42	Fresh skin.
BDM 128.....	♂	1,478	58	1,715	67½	16	Tanned skin.

¹ Tip of nose to tip of tail flesh.

² Moderate tension applied.

Thus, a skin freshly removed from the animal may easily be stretched 144 percent and a tanned skin 116 percent of the animal's body length. It is concluded that measurements taken from skins are of little use in establishing body size in the sea otter.

Intestine length

Length of intestine in four adult sea otters is shown in table 7. Shortly after death, the intestinal tract was removed, laid on flat ground, and measured. An effort was made to obtain the relaxed length (not the stretched length). The mean length of the small intestine was 9.0 times body length (table 7).

In general, carnivores have shorter intestines than herbivores but the variation among strictly carnivorous mammals is great.

TABLE 7.—*Intestine length of adult sea otters*

[Length in centimeters]

Collection number	Sex	Body length	Intestine length ¹	Small intestine ²	Ratio, small intestine to body length
59-60.....	female.....	124.	1,214 (39.5 feet)	1,154	9.3:1
61-2.....	do.....	127.	1,076 (35.3 feet)	1,016	8.0:1
62-11.....	do.....	128.	1,313 (43.1 feet)	1,253	9.8:1
62-10.....	male.....	136.	1,290 (42.3 feet)	1,230	9.0:1
Mean.....		128.7			9.0:1

¹ From stomach to anus.

² No caecum is present in the sea otter. The small intestine gradually expands into the large intestine. The approximate length of the large intestine is 60 cm. This amount is subtracted from the total intestine length to obtain the approximate length of the small intestine.

Among pinnipeds, which subsist entirely on flesh, the ratio (small intestine length) / nose-tail length ranges from 5.2 in *Monachus* to 42.0 in

Mirounga (King, 1964). The sea otter, which subsists on marine invertebrates and fish, falls within this general range. Apparently animals which feed primarily on warm-blooded vertebrates have relatively shorter intestines. The above ratio is 5 for the dog and cat (King, 1964).

Organ weights

The relative sizes of body organs may give a clue to the adaptations of an organism to its environment. I have undertaken no physiological studies, but the following comparisons of the relative size of selected body organs of the sea otter with those of other mammals indicate that such studies would be interesting and desirable.

Organs were weighed on a balance having a maximum capacity of 15 kg. Sample organ weights were obtained from six adult male and nine adult female sea otters that were shot while apparently in normal health at Amchitka Island and other areas (table 8). Comparison of the organ weight expressed as percent of body weight indicates that in some respects the sea otter is quite

TABLE 8.—Weights of body organs in nine adult female and six adult male sea otters

[Weight in grams. All apparently healthy adults shot at Amchitka Island, except 60-4 to 60-8 which were shot in the Shumagin Islands and off Unimak Island]

Collection number	Body weight	Liver		Heart		Kidney		Spleen	
		Weight	Percent of body weight	Weight	Percent of body weight	Weight	Percent of body weight	Weight	Percent of body weight
Females:									
62-2	21,770	1,219	5.60	182	0.84	409	1.88	65	0.30
62-6	20,410	1,130	5.54	152	.74	340	1.67	59	.29
62-8	19,950	1,135	5.69	130	.65	367	1.84	65	.33
62-11	20,410	1,730	8.48	126	.62	346	1.69	90	.44
62-12	23,130	1,632	7.06	160	.69	425	1.84	90	.39
62-15	21,300	1,226	5.76	135	.63	385	1.81	92	.43
62-19	19,050	955	5.01	134	.70	315	1.65	85	.45
62-20	17,690	1,000	5.65	142	.80	350	1.98	58	.33
60-4	32,500	1,450	4.46	175	.54	470	1.45	150	.46
Mean	21,800	1,275.2	5.85	148.4	.68	378.5	1.74	83.8	.38
Males:									
62-1	29,940	1,479	4.94	185	.62	700	2.34	86	.29
62-10	36,290	2,685	7.39	211	.58	821	2.26	177	.49
60-5	35,500	1,650	4.65	230	.65	870	2.45	100	.28
60-6	45,000	2,390	5.31	270	.60	1,120	2.49	110	.24
60-7	41,300	1,860	4.50	272	.66	997	2.41	113	.27
60-8	41,700	2,086	5.00	227	.54	1,026	2.46	113	.27
Mean	38,280	2,025	5.29	233	.61	922	2.40	116	.31
Mean, all	28,410	1,575	5.67	182.1	.66	596.1	2.01	96.9	.35

similar to other mammals but in other respects it may be unique. Among mammals in general (but with exceptions) total body weight increases at a greater rate than organ weights. It is presumed in the following comparisons that the reader will keep this generalization in mind.

Liver.—To remain healthy the sea otter must consume about one-sixth to one-fourth of its body weight in food daily. Apparently the air blanket in its fur is a less efficient means of insulation in its chilly habitat than the blubber of other marine mammals. The need for a relatively large amount of food indicates an unusually high metabolic rate in the sea otter. Slijper (1962) believes that marine mammals, and particularly cetaceans, have a high metabolic rate. Since the liver is an important organ for the production and storage of energy-producing substances, it is not surprising that the sea otter's liver is relatively very large; the mean is about 5.7 percent of body weight. In this respect it surpasses fur seals of comparable body size (mean 3.1 to 3.5 percent; Scheffer, 1960), porpoises (3.2 percent), and dolphins (2.2 percent; Slijper, 1962), and the river otter (4.85 percent; Jensen, letter, 30 Nov. 1964), although the river otter is a smaller animal.

Heart.—The heart of the sea otter constitutes about 0.66 percent of body weight. The ratio is similar to that of fur seals of comparable size (about 0.6 percent of body weight; Scheffer, 1960), and to dolphins (0.6 percent; Slijper, 1962). As Jensen (1964) points out, sea water gives more support than fresh water and therefore the sea otter may not need as large a heart as the river otter (0.98 percent of body weight).

Kidney.—The marine environment may account for a large difference in relative size between the sea otter kidney, mean 2.01 percent of body weight, and that of the river otter, 0.85 percent of body weight. The sea otter appears to have overcome the physiological problem of the marine environment by developing a lobulate kidney relatively twice as large as that of the river otter. I have observed sea otters in captivity drinking sea water.² A study of the physiology involved has not been undertaken. That the sea otter obtains liquids of appreciably less salinity than sea water from food is improbable, since body fluids of invertebrates,

² The captives were held for 2 months on dry bedding at Amchitka. Frequently when I held a pan of sea water before them they placed their mouths in the water and sucked and lapped it up with their tongues. In their eagerness to drink, they also placed their forepaws in the dish and eventually spilled and splashed so much of the water that I did not measure the quantity that was actually drunk. When given a choice of sea or fresh water they drank either unselectively. Except for one experimental offering of fresh water the captives were given only sea water.

upon which some otters feed almost exclusively, are isotonic, or nearly so, with sea water (Sverdrup, Johnson, and Flemming, 1942, p. 269).

Fisler (1962) demonstrated that even a mouse (*Peromyscus* sp.), that was adapted before capture to a salt marsh environment, survived when given sea water exclusively.

Slijper (1962, p. 314) considers that the kidneys of cetaceans (from 0.44 percent to 1.1 percent of body weight) are, because of great body size, exceptionally large. In general, a large kidney appears to constitute an important aspect of mammalian adaptation to the marine environment.

Spleen.—In the sea otter the spleen is about 0.35 percent of total body weight, which is similar to "0.3 percent in most other mammals" (Slijper, 1962, p. 175). In 62 female fur seals similar in size to the sea otters studied, Scheffer (1960) found that the spleen was from 0.11 to 0.31 percent of body weight. Thus, in the sea otter and river otter (0.46 percent, Jensen, 1964) the spleen is relatively large.

Although the mean percentages of organ size to body weight of all sea otters studied were used in the foregoing general discussion, it appears that in the male, which is larger than the female (see Body Measurements) the kidney is relatively larger than in the female. Also, the spleen of the female is slightly larger than in the male (table 8).

Body temperature

The body temperature of two apparently healthy animals, a juvenile male (59–156) and an adult female (59–157), were obtained when both had lost consciousness after injections of "Lethol" (proprietary name for a compound containing N-amylethyl-barbituate, sodium sec-butylethyl-barbituate, isopropyl alcohol, and sodium carbonate). The deep body temperatures (intracardiac insertion of the thermometer before cardiac activity ceased) and rectal temperatures were the same. The temperature of the juvenile male was 38.0° C. (100° F.) and that of the adult female was 37.5° C. (99° F.).

Body temperature may drop before death under certain conditions. On 1 April 1959, at Amchitka Island, an emaciated adult female (59–98) was lying on a bed of grass above the high tide line, breathing but unconscious. Her intracardiac temperature was 28.0° C. (84° F.). An autopsy revealed extensive enteritis.

During an experimental transplant, observations were made of a juvenile subjected to unusual stress. The otter, a female about

1 year old and weighing 22 pounds, was liberated in cold water (0° C.) on 9 April 1955. The fur had become saturated with filth after 8 days in captivity. Within 1 minute after entering the water the otter uttered loud distress screams and swam toward our dory. After she was retrieved she was placed on dry straw. When we returned to the ship, about 20 minutes later, the otter was unconscious. The rectal temperature was 30.3° C. (86° F.). In a warm room, the fur was vigorously rubbed and dried with a towel and consciousness was restored. At 0700 the following morning the rectal temperature was 38.5° C. (99° F.); the animal appeared weak but ate. She was kept in a warm room (about 22° to 24° C. or 72° to 75° F.) and given almost constant attention until she died on 15 April. During this period her body temperature fluctuated erratically each day from 30° to 36° C. (86° to 96° F.). When her temperature was low, I recorded that she was "almost in a coma." Apparently after chilling, the temperature control mechanism of this otter was upset.

Blood quantity

An approximation of the blood content of sea otters was obtained from five freshly killed animals (table 9). All appeared to be in normal health when killed. The technique used in each case was the same: After capture the animal was given a lethal injection of Lethol. When the animal lost consciousness, it was weighed and measured. The thoracic cavity and heart were opened. The animal was suspended, by means of lines attached to each leg, over a container into which the blood drained. In all cases the heart was still beating when the incisions were made. The blood weight and volume were measured directly.

The percentage of blood weight to body weight of four of the

TABLE 9.—*Blood quantity in sea otters*

[The weight of blood is minimal. The blood was drained from animal directly into a container. No correction was added for the slight amount that was spilled, or for the blood remaining in tissues]

Collection number	Age	Sex	Blood weight	Body weight	Percent, blood weight of body weight
			Grams	Grams	
59-62	Adult	male	2,694	31,297	8.6
59-156	Juvenile	do	767	11,566	6.6
59-48	Adult	female	8,106	28,122	¹ 28.8
59-60	do	do	2,100	20,978	10.0
59-157	do	do	1,531	20,865	7.34

¹ Apparently this animal was abnormal. Pathological conditions such as hydrothorax and heart failure occur in other mammals. The large quantities of fluids that accompany these conditions may be difficult to distinguish from blood.

animals (mean 8.1 percent) fall within the expected range (rabbit, 6.2 percent; dog, 7.2 percent; and horse, 9.7 percent (Dukes, 1943); and walrus, 8.4 percent (Fay, 1958)). In the fifth animal, the blood constituted nearly one-third of the body weight. This animal, when captured, was sleeping on the beach and behaved in a normal energetic way. I noted, however, that it appeared "fat" and the abdomen was round and firm. I suspected then that it was pregnant, but found later that it was not.

There was no food in the gastrointestinal tract. In addition to the blood quantity, the only abnormality found were two cysts (congenital? 1.5x1 cm. and 1.5x1.5 cm.) containing clear, yellowish fluid, on one kidney. The gross appearance of blood was normal. Why this animal retained such a large amount of fluid is unknown. There was no mistake about the quantity of fluid (table 9).

Pelage and Skin

Preliminary descriptive studies of the pelage, skin, and molt have been made.

PELAGE

Victor B. Scheffer (Marine Mammal Biological Laboratory, U.S. Fish and Wildlife Service) has made a cursory examination of pelage samples from three sea otters and has kindly offered the following notes (in letter, 13 August 1964). Unless otherwise stated, the notes are based on a sample from the midback of "Pappy," an adult male, specimen D22-57, which died in Seattle Zoo on 16 December and was autopsied on 17 December 1957.

The pelage is an extremely fine wool or fur with the tips of thinly scattered guard hairs protruding from it. It is light smoky gray near the skin, darkening gradually to smoky brown at the surface of the pile. The *larger guard hairs* are dark; their tips make a layer about 34 mm. (1.5 in.) from the skin. The *smaller guard hairs* are more numerous than the larger ones; their tips make a layer about 28 mm. (1.25 in.) from the skin. The *underfur hairs* are by far the most numerous; their tips make a layer about 23 mm. (1 in.) from the skin. The outer surface of the underfur layer is not distinct; the soft, wavy tips of the fur hairs blend with the tips of the smaller guard hairs (fig. 14).

The *pelage unit* consists of: a bundle of many underfur hairs and one guard hair at or near the anterior side of the bundle (fig. 15); a sebaceous gland on right and left sides of the bundle, joined at the anterior side; a coiled sweat gland beneath and partly adjacent to the follicles of the bundle; and other minor structures. There is apparently no hair-erecting muscle.

The guard hairs vary widely in diameter and length, though they fall into

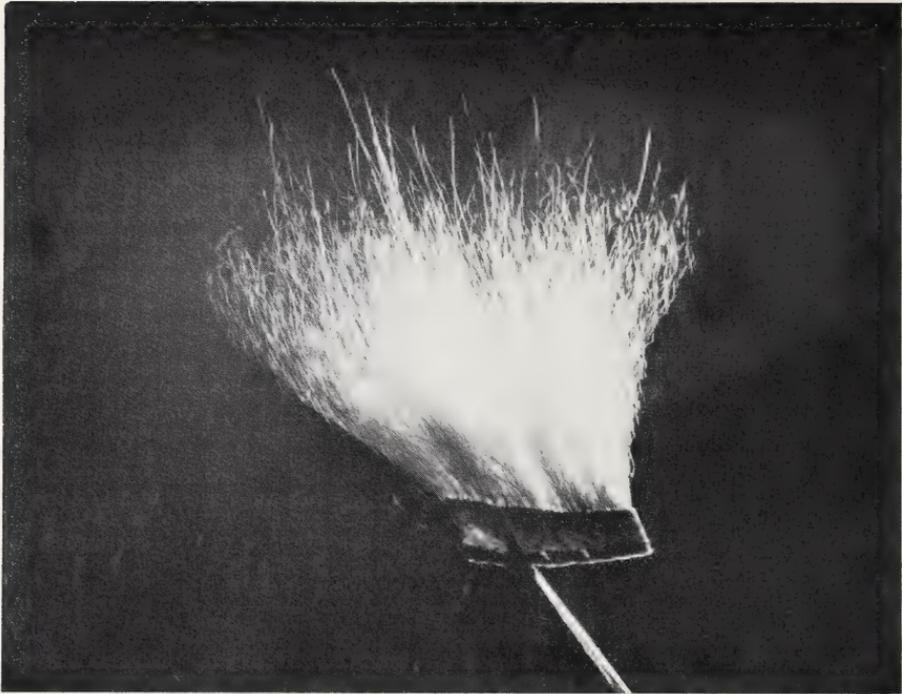


FIGURE 14.—Hair from the midback of adult male sea otter D22-57. The outer surface of the underfur layer is not distinct; the soft, wavy tips of the fur hairs blend with the tips of the smaller guard hairs. (VBS 5710)

two overlapping groups which I call "larger" and "smaller," with few intermediates. For example, here are the diameters of 10 roots in one field of view under the microscope: 14, 15, 16, 18, 20, 25, 26, 33, 38, and 64 microns (cf. fig. 16). Cross sections of the guard hair roots are oval to nearly round in outline; they vary in diameter from 13 to 64 microns (average 25).

In five bundles I count 60 to 80 (average 71) underfur roots per bundle. The counts in two other specimens are: (KWK 59-13, old female, 9 February 1959) 79-110 (average 91); (KWK 59-51, young male, 7 March 1959) 40-45 (average 43). Comprehensive studies of pelage samples from different seasons and different age groups of otters will be necessary before the extent of holdover of pelage hairs can be evaluated. Cross sections of the underfur roots are roundish oval, smooth, fairly uniform, and 6.3 to 8.5 microns (average 7.2) in diameter (fig. 16.)

A disc of skin-with-pelage cut by trephine from the formalin-preserved, mid-back specimen measured 0.4 cm². It contained 520 bundles or 1,400 per cm² (fig. 17). [That there is considerable variability is demonstrated by the finding by J. K. Ling (MS) of 2,176 follicle bundles per cm² on a sample of facial skin.] On the basis of 71 underfur hairs and 1 guard hair per bundle, (hairs per cm² = $72 \times 1400 = 100,800$ or 650,160 per in.²) and an estimated area of 8,000 cm² for the total hair-covered surface of the body, the pelage of an adult male sea otter would contain about 800 million hairs.

Above the surface of the skin, the shaft of each larger guard hair is a typical awn or shield hair, flattened into a blade near the tip. At a level 10

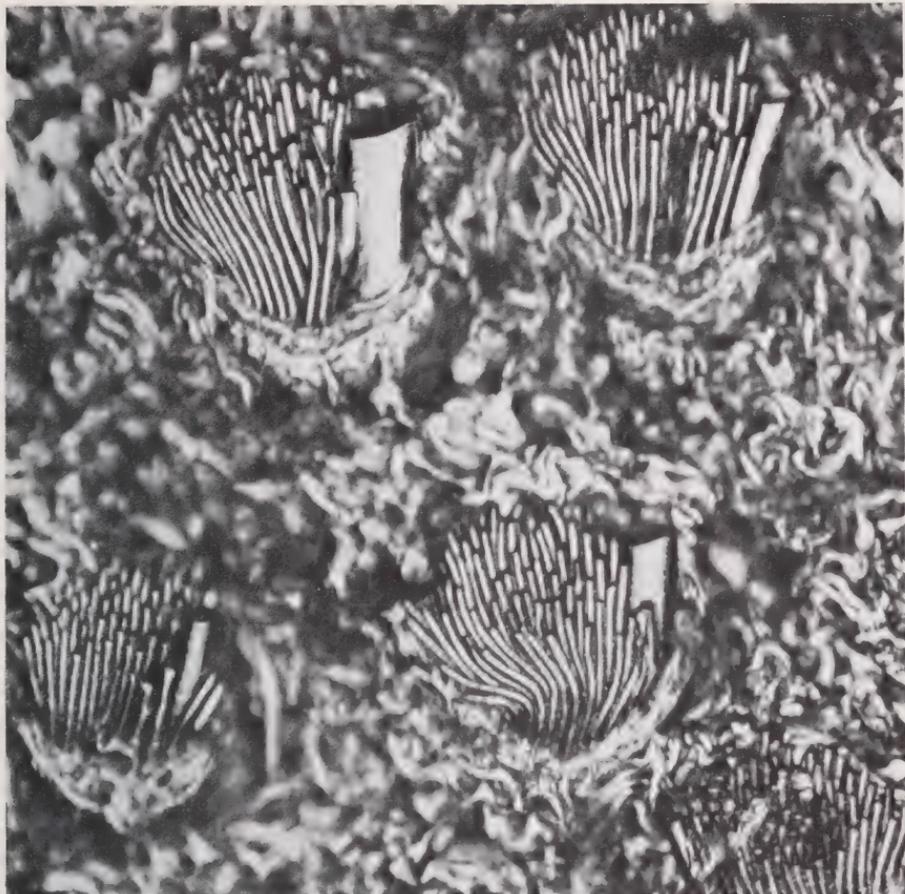


FIGURE 15.—Plastic impression of pelage sheared near skin surface from midback of adult male sea otter D22-57. Anterior at right. Variation in the diameter of guard hairs is demonstrated and their characteristic scapular pattern. Magnification ca. $\times 75$. (VBS 5718)

mm. from the skin, the cross section is oval, slightly wavy in outline, and 55 to 67 microns (average 63) in diameter. The shaft of each smaller guard hair has a small blade. The cross section of the smaller guard hair at the 10 mm. level is 23 to 56 microns (average 42) in diameter. All guard hairs are medullated. Near the surface of the skin, the guard hair root is often displaced from the anterior side of the bundle by pressure of the underfur roots.

The cross section of the underfur hair at the 10 mm. level is irregularly 3- or 4-sided (fig. 18). In this respect it resembles the underfur of the land otter (*Lutra*) (Wildman, 1954, fig. 98b). The underfur shaft is about 7 to 8 microns in cross section diameter, only slightly greater than the root.

In general, the pelage of the sea otter is similar to that of the land otter. The guard hairs seem to be scarcer and more variable in size than those of the land otter, though I have not made a quantitative comparison. The remarkable arrangement of hairs in bundles, outside of which there are no isolated

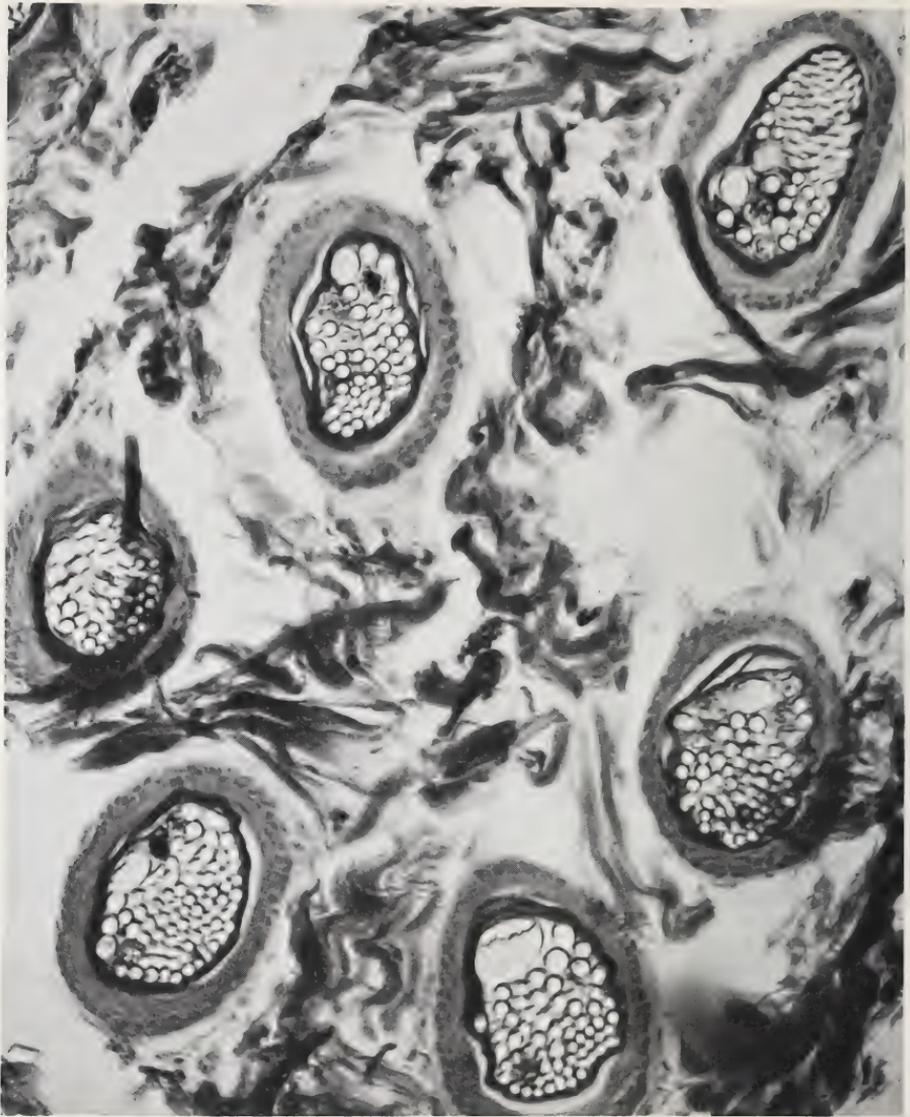


FIGURE 16.—Horizontal section through skin near surface, midback, adult male sea otter D22-57, anterior at top. The large guard hair in each pelage unit may measure 64 microns in diameter. The fur hairs average 7.2 microns in diameter. At this level the hairs are round to slightly oval in cross section. (VBS 5716)

hairs, resembles the pattern in all pinnipeds, especially in the fur seals *Callorhinus* and *Arctocephalus*. Dead underfur hairs probably (?) accumulate from one year to the next in the bundles of older animals as they do in *Callorhinus*. The only evidence is that the count in a young sea otter is 43 as compared to 71 and 91 in two adults. This "reluctant shedding," if actually a feature of sea otter pelage, would help to maintain a heat-insulating coat



FIGURE 17.—Sheared surface showing skin and distribution of pores from which hair bundles emerge, anterior at top. Sample is from midback, adult male D22-57. Magnification $\times 24$. (VBS 5721)

during molt. The underfur hairs seem to be equal in diameter, though twice as long, as those of *Callorhinus* (Scheffer, 1962, p. 22 and 72). On a disc cut from the fresh skin of an adult female fur seal there are 939 bundles and about 50,000 individual hairs (Scheffer, 1964). On a disc of the same area, though from preserved skin, of the adult male sea otter "Pappy" there are 1,300 bundles and about 100,000 hairs. Because of sampling variables, however, it cannot be said conclusively that the fur of the sea otter is twice as dense as that of the fur seal.

SKIN

John K. Ling (Department of Zoology, Massey University, Palmerston North, New Zealand) contributed the following description, based on examination of a small sample of skin from the facial region of one animal (D22-57).

The formalin-fixed skin was sectioned parallel and at right angles to the skin surface along the hair follicle axes and stained with haematoxylin, eosin, and picric acid. Measurements are uncorrected for *post mortem* changes and are to be regarded as approximate only.

The skin is 3 mm thick from the surface to the panniculus carnosus; the epidermis averages 50 microns in thickness, the papillary layer of the dermis

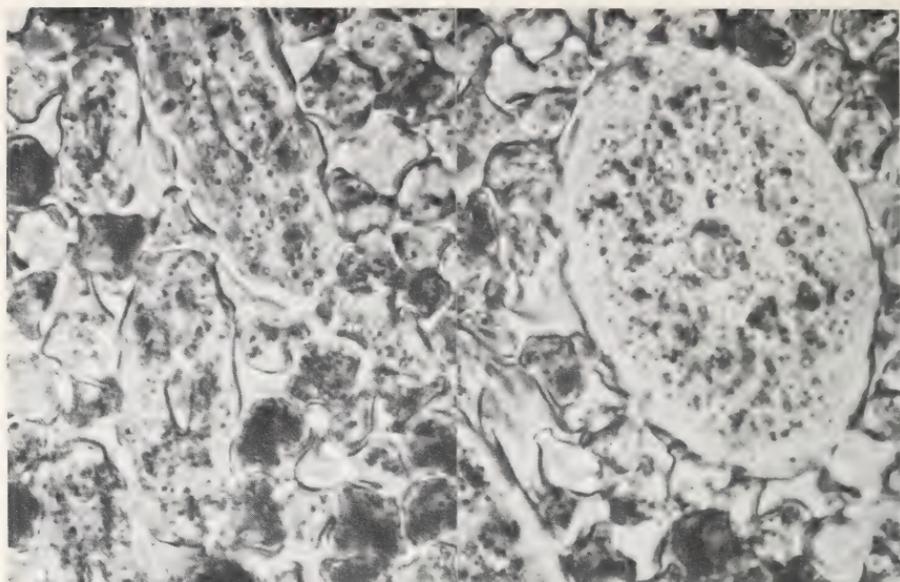


FIGURE 18.—Cross section of pelage (by Hardy device) about 10 mm. from surface of skin, near midback, adult male sea otter D22-57. The large guard hairs are oval in cross section at this level, and their surface is crenulated. The much smaller and numerous fur hairs tend to be 3 or 4 sided. Magnification $\times 430$. (VBS 5712 and 5713)

also 50 microns, and the reticular layer makes up the remainder. The longest underfur hairs measure up to 22 mm in length, of which 19 mm may protrude beyond the surface pore of the hair canals.

Five layers, stratum corneum, stratum granulosum, stratum lucidum, stratum spinosum and stratum germinativum, are recognizable in the epidermis. The granular layer is not uniformly dense throughout and pigment is absent. . . . The epidermis is thrown into a series of folds which are reflected by similar folding of the papillary zone of the dermis. Collagen fibres in the deeper dermis are oriented both randomly and parallel to the skin surface. Arrector pili muscles are absent.

Hair follicles are arranged in bundles and are aligned at an angle of about 70° to the skin surface. Each bundle comprises a guard hair follicle and underfur follicles, which are separated from each other near their base but are held together closely at higher levels. In cross section there is some suggestion of trio grouping with a central guard hair follicle between two other guard hair follicles. The underfur follicles open into the guard hair canal and all hairs emerge at the skin surface through a common pore [fig. 17].

Cutaneous glands associated with each guard hair follicle and opening into the bottom of the guard hair canal comprise a bilobed sebaceous gland and a greatly coiled apocrine sweat gland. The sweat duct opens posterior to, and slightly higher than the common sebaceous duct formed by the union lower down of separate ducts from each gland. Keratohyalin granules abound near

the exterior ends of the cutaneous gland ducts. There are no glands opening into the underfur follicles (fig. 19).

Adaptations of the sea otter integument to an aquatic habit include (1) only periodic occurrence of the granular layer which may confer upon the horny layer different properties from those arising from the continuous presence of granules, thereby contributing to its water-resisting function; (2) the flattened guard hairs; and (3) the absence of arrector pili muscles enabling the hairs to lie close to the skin surface when the animal enters the water. These features are exemplified by the fur seals and they may be common to all semi-aquatic mammals. In common with other densely furred species the sea otter has large functioning apocrine sweat glands associated with each guard hair follicle.

Sensory vibrissae

Sensory vibrissae are in three locations: mystacial, superciliary, and nasal. The numbers of vibrissae are for the left side only of an adult male. There were 8 rows including 62 mystacial vibrissae (i.e., total both sides 124 mystacial vibrissae). The largest was 53 mm. long and the shortest 2 mm. There were four superciliary vibrissae, the largest (dorsal) was 33 mm. and the three others were about 12 mm. long. There were three nasal vibrissae (along the dorsal anterior nasal area), each about 14 mm. long.

The mystacial vibrissae are the most important as sensory organs. They are voluntarily controlled and are frequently extended forward. In this position they are used as sensory aids when walking among rocks or when examining a strange object. Presumably they are used when exploring the bottom of the sea for food. In the wild they are often worn off short but in captivity, where a search for food is not necessary, they may reach a length of 100 to 120 mm.

MOLT

Maynard (1898) wrote that "Their fur is considered equally good at all seasons; hence they are hunted throughout the entire year." Similar statements were made by many other authors.

The lack of an observable molting season may perhaps be explained by analogy with molt in the fur seal. Scheffer and Johnson (1963, p. 32) found that "The number of underfur follicles per bundle in the first adult-type pelage . . . remains unchanged throughout life" but that the number of fibers in each bundle increases with age. "The rise in the fiber count means that up to 60 percent of the fibers are not shed in late molt but remain fast in the bundle."

Scheffer demonstrated earlier in the present report that a young

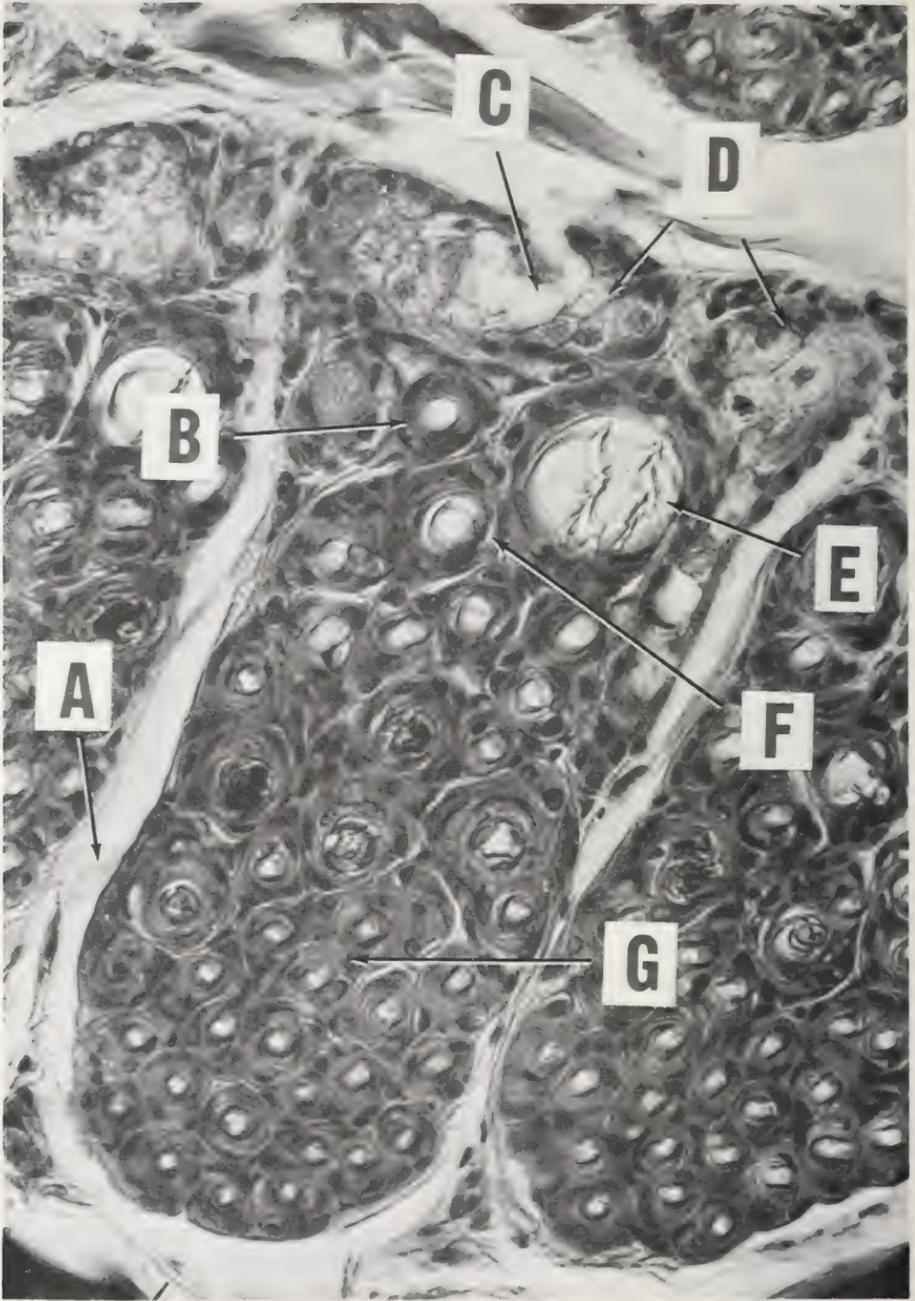


FIGURE 19.—Horizontal section through the sea otter skin showing deeper layer, near hair roots, with one complete pelage unit. *A*—connective tissue, *B*—sweat duct, *C*—sebaceous duct, *D*—sebaceous glands, *E*—large guard hair, *F*—large underfur hair, *G*—smaller underfur hairs. (JKL photo)

sea otter in its first adult pelage had fewer fur fibers (43) per bundle than two adults (adult male 71 and adult female 91). That the fiber population is denser in the sea otter than in the fur seal (adult female 51, adult male 68) is not surprising. Insulation in the fur seal is provided by both blubber and fur but the sea otter, having no blubber, must depend for insulation only on its fur. It seems reasonable to conclude that fur fibers are retained in the sea otter as they are in the fur seal, thus "masking" the period of molt.

John Vania, Leader, Marine Mammal Studies, Alaska Department of Fish and Game, visited the Marine Mammal Biological Laboratory in Seattle from 8 to 19 November 1966 to work with V. B. Scheffer on the examination of skin samples from sea otters. Of 26 sea otters taken in winter and 20 taken in summer, all showed evidence of molt in some of the fiber roots. This evidence is puzzling; the molt deserves further study. A tentative conclusion is that, throughout the year, at various places on the body, individual fibers are in molt while others are at rest.

Observations of captive sea otters also suggested that the period during which fur is shed is prolonged. In all seasons fur fibers were seen on the paws of otters during grooming activity and quantities of fur accumulated at the drain of their pool.

To estimate the periods of maximum and minimum molt, Cecil Brosseau, Director, the Tacoma Aquarium, collected samples of fur for me from a screen over the drain of a pool that held an adult male sea otter (Gus). The uniformly collected samples consisted of the accumulation of fur and guard hair for a 15-hour period at 7-day intervals from October 1967 through October 1968. The samples were dried, cleaned manually (fish scales, fragments of bone, and other debris were removed), and weighed on a beam balance to the nearest 0.01 g. The mean weights of the samples for each month show that shedding is maximal in late spring and summer (mean of 4 August samples = 59 cg.) and minimal in midwinter (mean of 4 January samples = 25 cg.) and that appreciable shedding occurs in all months (fig. 20).

This study suggests that the sea otter exhibits one period of maximal follicular activity (molt) annually in the spring and that it may be similar to the European otter (*Lutra lutra*) which is said to molt almost imperceptibly during a prolonged period (Novikov, 1956), as does the polecat (McCann, 1955).

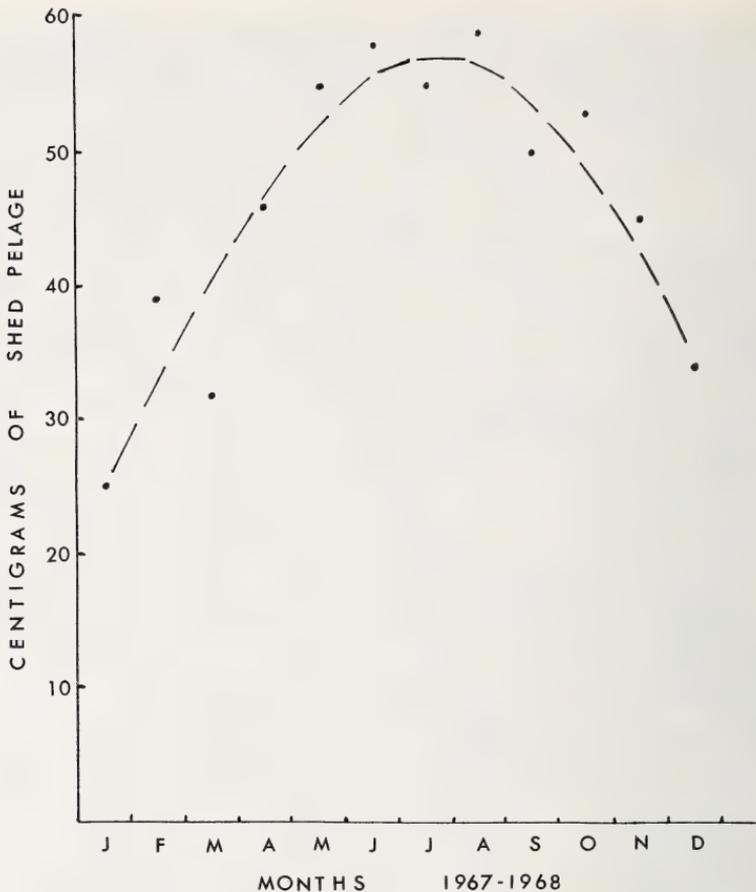


FIGURE 20.—The shed pelage of an adult male sea otter was collected from the drain of his pool at 7-day intervals from October 1967 to October 1968. The mean weights in centigrams of three to five samples (four samples were discarded) collected each month are indicated by dots. The curve shows maximal and minimal periods of shedding during the year and suggests one annual maximal period of molt.

THE PELT IN COMMERCE

Processing

Concerning the processing of sea otter skins, Poland (1892) stated: "The skins are occasionally smoked, and are also dyed or topped." To clarify the meaning of this statement I wrote to Dr. J. L. Stoves of Martin-Rice Ltd., fur processors, London, England, and received the following information (letter, 7 May 1963):

Sea otter fur was dressed in the 19th Century by the conventional method, i.e. fatty tissue was removed by scraping or fleshing after which the skins were smeared with grease or oil (butter rejected for human consumption

was also used). The greased skins were then trampled underfoot in large barrels or tubs (so called 'tubbing'). Excess grease was removed by tumbling the skins in sawdust contained in revolving drums ('drumming'). After this the leather was reduced in weight by cutting down or shaving (by hand or by machine). The guard hairs were not removed. . . .

With regard to the quotation from Poland's book, he is referring to the colour of the fur. Poor quality furs were sometimes up-graded (temporarily!) by hanging the skins in smoke from a smouldering, smoking fire whereupon a thin film of soot and tarry matter deposited on the fur turned light yellowish fur into a darker richer brown. The effect was purely temporary but was an unethical way of up-grading fur prior to sale.

The remarks on "dyeing or topping" refer to more lasting improvement of colour (after the raw skins have been auctioned) by deliberate use of dyes. These could be applied by immersing the skins in solutions of the metallic mordants and vegetable dyes then used, or alternatively the materials could be applied to the fur only by brushing, i.e. "topping", a method which left the leather undyed and the article then looked more like a better grade skin which had been dressed only.

Skins taken in recent years were tanned by modern conventional methods. In describing the color, a fur dealer who examined several typical specimen pelts used the following terms: "dark brownish underwool," "brown wool," "very silvery-good top hair," "brownish with a greenish cast."

Value of pelts

Fisher (1941a) summarized information on prices paid for sea otter skins from the time of Bering to 1940: In the mid-1700's skins sold for 20 rubles (about \$10) in Kamchatka to 100 rubles (about \$50) at the Chinese frontier. During the 1880's prices on the London market ranged from about \$105 to \$165. By 1903, when sea otters had become scarce, extra rich, large skins sold for as much as \$1,125. Fisher was unable to verify or find the source of the statement by Evermann (1923) that during the 1920's (after the sea otter received protection) the prices paid for sea otter pelts ranged from \$2,000 to \$3,000 each. Among 54 confiscated sea otter skins sold at auction for the account of the U.S. Government from 1924 to 1940, the most valuable brought \$465. Only 3 skins were sold for more than \$400, 7 for \$300 to \$350, 7 for \$200 to \$295, 12 for \$105 to \$190, and the remaining 25 for less than \$100. The average price per skin was \$148.54.

On 12 April 1957 at public auction, 117 dressed skins sold for the account of the U.S. Government brought an average price of \$22.88 per skin (F. G. Ashbrook, letter 29 April 1957).

On 1 January 1968 the first collection of sea otter skins taken for commercial use since 1911 was offered for sale at the Seattle Fur Exchange, Seattle, Wash. The auction was held for the ac-

count of the State of Alaska. Among 1,000 available skins, 905 were considered acceptable for commercial use and were offered for sale.

To prepare them for sale the skins were cased (skinned through a single slit along the hind legs from heel to heel) and dried on frames. The pelts were cleaned and brushed and displayed fur side out. They were divided into 197 lots. The lots ranged in size from one to eight skins matched according to size and color. The bid price for a single skin determined the price for all skins in that lot.

Skins taken in 1962 and 1963 and held since then were less valuable, because of depreciation of quality in storage, than pelts taken in 1967. The earlier collection sold for an average price of about \$80 each. The more recently taken skins averaged \$280 each. One lot of four skins was sold at the maximum price of \$2,300 per skin.

The auction was attended by buyers representing 33 companies from 7 states and 6 foreign countries. All skins offered for sale were sold.

Feeding Mechanisms

Dr. Robert P. Scapino, Department of Oral Anatomy, University of Illinois, has undertaken continuing study of the jaw mechanics and feeding behavior in carnivores. He accomplished a preliminary study of the skull and musculature of the sea otter and kindly contributed an anatomical description, excerpts from which are quoted below (letters, 1963 and 1964). He plans an extensive publication on his studies of carnivore feeding mechanisms.

MASTICATORY MUSCLES

I have completed gross dissection of the masticatory musculature in *Enhydra*. The descriptive terminology used is somewhat different than what you will find in works on *Lutra* (Fisher, 1942; Schumacher, 1961), however, the terms used to designate the various muscles are perfectly acceptable and, in my view, the most useful. My division of the superficial temporal muscle into superior and inferior heads is somewhat unusual and later, when I have examined the muscle in a sufficient number of other mustelids, I may decide to label it differently. But right now the separation seems warranted, at least from an anatomical standpoint.

The masseter muscle of carnivores is usually described as having incompletely distinct superficial and deep parts, but in the sea otter these divisions are even more indistinct than usual.

The anatomy of the jaw muscles in *Enhydra* is essentially the same as in

other carnivores. Two features of the temporalis, however, are noteworthy. The superficial temporalis in most other carnivores arises from the entire undersurface of the superficial aponeurosis and is not confined to the anterior part as in *Enhydra*. Of the carnivores I have examined the only two that are like *Enhydra* in this respect are the mink and river otter.

The inferior head of the superficial temporalis is well developed in *Enhydra* and distinct from the superficial head. In other carnivores this muscle seems relatively smaller and blends with the superior head. The functional significance of these differences is not clear.

MANDIBULAR JOINTS

Most carnivores have three jaw joints. The two temporomandibular joints are obvious, but the third, the symphyseal joint has escaped the serious attention of comparative morphologists. My studies indicate that the latter joint has crucial functions in carnivore jaw mechanisms.

The morphology of the temporomandibular joints in carnivores is distinctive. The condyle of the lower jaw takes the form of a transversely oriented cylinder that articulates more or less snugly in a trough-like glenoid fossa. The temporomandibular joint of *Enhydra* does not appear significantly different from that of other carnivores.

The symphyseal joint of carnivores is more varied. This joint consistently shows high mobility (i.e., high mobility for carnivores) in those large carnivores that are powerful crushers. The mobile type of symphysis typically has relatively flat articulating plates that are separated by a well-developed fibrocartilagenous cushion along their anterosuperior borders. The symphysis of *Enhydra* fits this model. Also in *Enhydra*, the articulating plates are bound together by stout cruciate ligaments below and behind the fibrocartilage.

The mobile type of symphysis seems to function to facilitate fitting the teeth to the object that is to be crushed and the fibrocartilage cushion as a shock absorber to reduce the biting force that is transmitted to the skull when the resistance of the object is overcome (Scapino, 1965). The cruciate ligaments allow symphyseal movement, but stabilize the joint by preventing direct lateral separation of the articulating plates.

The teeth and symphysis of *Enhydra* appear to be primarily adapted for crushing hard objects. The sea otter easily cracks the shells of mollusks with its posterior teeth (Kirkpatrick *et al.*, 1955). The combination of a loose symphysis with bunodont teeth in this animal is also observed in other large carnivores that are crushers.

DENTITION

The teeth of the sea otter, particularly the molars, are flattened and rounded. They are not adapted to cut or shear flesh but to crush invertebrates, the preferred food. Even the canines are rounded, having a blunt point and no sharp edge (fig. 21). Because these are used to open the valves of such organisms as the rock oyster (*Pododesmus*) the tips are often worn or broken. Fisher (1941b) described the dentition of the sea otter on the basis of fragmentary material (particularly from younger ani-

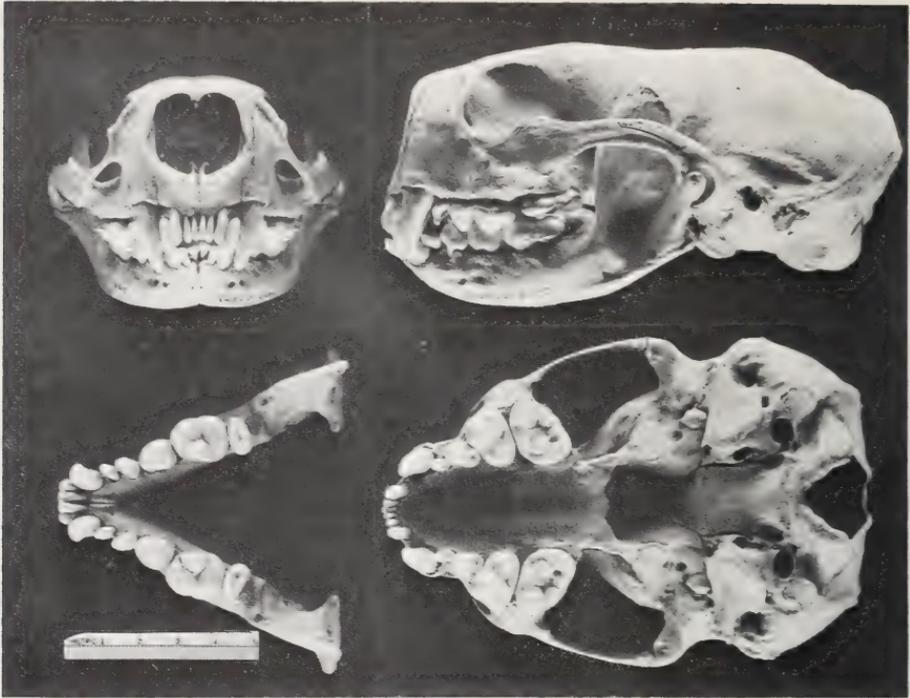


FIGURE 21.—Fresh young adult dentition in the late juvenile or early subadult stage of development. Note the rounded, blunt canines and spade-shaped lower incisors which are used to scoop invertebrate organisms from their shells. Found dead on the beach, 5 March 1962, Amchitka Island, Alaska, weight 24 lb. (10.9 kg.), length 1,005 mm. (KWK 66-9-9)

mals) then available. For this reason, the present description of premature dentition differs somewhat from hers.

In the following discussion, the terminology of Scheffer and Kraus (1964, p. 296-298) is used. The ages at which individual teeth erupt are approximations and are based primarily on body size. A limited number of specimens was studied to determine the progression of tooth eruption from birth to the adult dentition. A detailed study of dental development remains to be undertaken.

In a newborn sea otter (fig. 22), weight about 1.7 kg. (3.7 lb.), the four canine teeth, two upper incisors and two lower first and second pairs of postcanine teeth are erupted from the gums. At birth there are a total of 26 deciduous teeth of which 10 are visible (see formula). The fate of the fetal teeth that are erupted from the bone at birth but are not gingivally erupted is not known, but it appears that they are exfoliated without becoming functional.

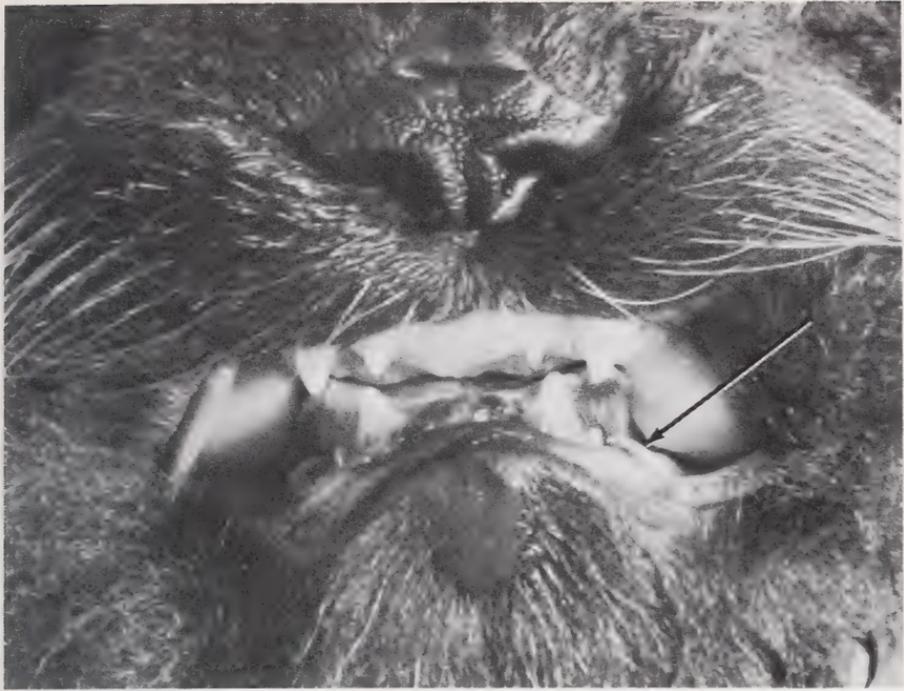


FIGURE 22.—Dentition of newly born male sea otter (62-178), taken at Amchitka Island, 18 February 1962, weight 1.7 kg. (3.7 lb.), length 528 mm. The canines and one pair of upper incisors are clearly shown. The barely erupted first postcanine is visible and the second postcanine is indicated by an arrow. The young sea otter pup probably receives most of its nutrition from mother's milk but soon after birth its mother gives it soft bits of solid food. (KWK 62-14-28)

The complete juvenile dentition (fig. 23), consisting of 44 teeth of which 26 are gingivally erupted, is obtained within about the first 2 to 3 months after birth when the young otter has reached a body weight of about 4 kg. (8-9 lb.). This mixed or transitional dentition is retained for several months.

The complete permanent or adult dentition (fig. 21) consisting of 32 teeth is attained toward the end of the first year of life and before sexual maturity is attained.

The dental formulae given below were determined from skulls that appeared to be typical of the stages of development. These skulls were chosen after examining several dozen specimens.

Dental formulae

Figures represent the number of teeth present on one side; those in parentheses are not yet gingivally erupted. Lower case=deciduous tooth;

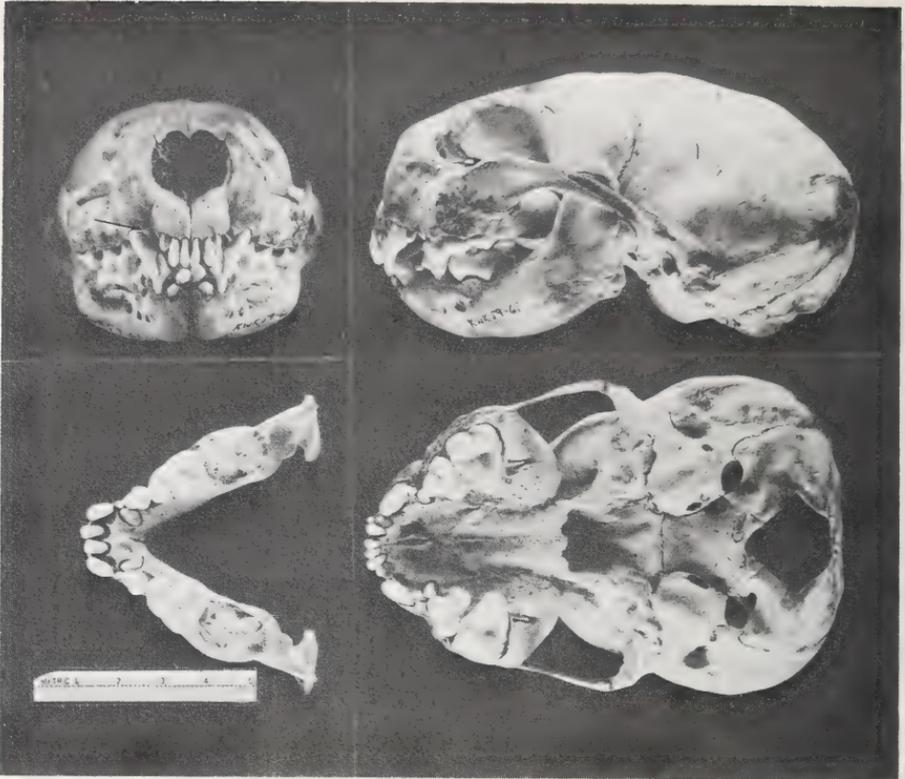


FIGURE 23.—Complete juvenile dentition of a female aged 2 to 3 months, weight 8.75 lb. (3.9 kg.), length 720 mm., captured 12 March 1959. The permanent incisors have all erupted and the permanent first postcanines are erupting and displacing their fetal antecedents. The second and third pairs of deciduous postcanines are well developed. No indication of molar eruption is visible but the tips of the erupting canines are visible (arrow). (KWK 66-11-11)

upper case=permanent tooth, (I=incisor; C=canine; PC=postcanine; M=molar).

Newborn (fig. 24 and fig. 22):

$$i \frac{1+(2)}{(2)} \quad c \frac{1}{1} \quad pc \frac{(3)}{2+(1)} = \frac{2+(5)}{4+(2)}$$

Total on one side, 4+(9); total teeth, 26.

Juvenile (mixed or transitional) (fig. 23):

$$\begin{array}{rcccccccc} I & 3 & C & (1) & PC & 1+(2) & M & (1) & & 4+(4) \\ i & - & c & \frac{1}{1} & pc & \frac{2}{2} & - & - & = & \frac{3}{3} \\ i & - & c & 1 & pc & 2 & - & - & & 3 \\ I & 2 & C & (1) & PC & 1+(2) & M & (2) & & 3+(5) \end{array}$$

Total on one side, 13+(9); total teeth, 44.



FIGURE 24.—Dentition at birth. The tiny fetal teeth are not erupted from the gums. The canine teeth, a pair of upper incisors, and the first and second pair of lower postcanine teeth are erupted from the gums at birth. Female, captured with mother, Amchitka Island, Alaska, weight 1.5 kg. (3.2 lb.), length 521 mm., umbilical cord attached. (KWK 66-11-2)

Adult (fig. 21) :

$$I \frac{3}{2} \quad C \frac{1}{1} \quad PC \frac{3}{3} \quad M \frac{1}{2} = \frac{8}{8}$$

Total on one side, 16; total teeth, 32.

Incisors

At birth the deciduous caniniform incisors (No. 3 pair) are erupted (fig. 22). These are the first functional teeth to be lost, and are replaced after the two central pairs of permanent upper incisors and the two pairs of permanent lower incisors have erupted gingivally at about 2 or 3 months after birth. The four pairs of central incisors are the first permanent teeth. Their ante-

cedents are small and nonfunctional; they are probably shed when the permanent incisors erupt.

As Hildebrand (1954) has pointed out, the spade-shaped and somewhat protruding permanent lower incisors are used to scoop food organisms from their shells when the sea otter is feeding. In older animals they show wear (fig. 25).

The sea otter is the only member of the order Carnivora with only two pairs of lower incisors. In this respect, it resembles the pinnipeds, most of which also have only two pairs of lower incisors. The walrus has no lower incisors in the adult dentition.

Canines

At birth the deciduous canines are erupted. They are shed and replaced following the loss and replacement of the deciduous caniniform incisors at about 5-6 months of age.



FIGURE 25.—“Old” adult dentition. No method of determining chronological age has been found, but animals with severely worn teeth like this were classified as “old.” The worn lower incisors and canines and severely eroded postcanines and molars result when hard-shelled organisms are crushed by the teeth. This male, weight 55 lb. (25 kg.), length 1,420 mm., was captured on a beach at Amchitka Island, 14 March 1959. (KWK 66-12-10)

Postcanines

The deciduous lower 1st and 2d postcanines are erupted at birth. The other four pairs erupt a few weeks later. The postcanines are the last deciduous teeth to be replaced by permanent teeth, at an estimated age of 8 to 12 months. The 2d and 3d permanent postcanines erupt in the last quarter of the first year of life. These are the last of the permanent teeth to erupt. As they push upward the deciduous postcanines are raised above their neighbors but remain anchored to the alveolar bone for a considerable period. This condition results in poor occlusion of all tooth surfaces (fig. 26).

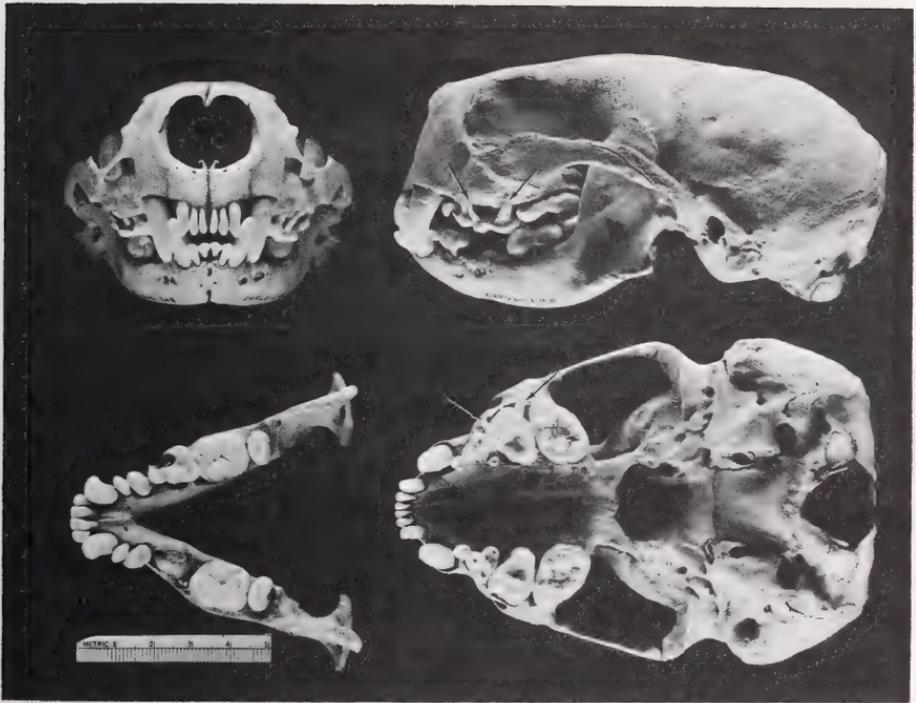


FIGURE 26.—Intermediate juvenile-adult dentition. At this stage the incisors, two pairs of lower postcanines, one pair of upper postcanines, and molars of the adult dentition are almost fully erupted. The remaining postcanines of the juvenile dentition, however, are still held in place by their extended roots (arrows) above the erupting permanent teeth. The upper photographs demonstrate that these teeth prevent occlusion of the molars and incisors. Many young at this stage are found dead of starvation on beaches. Note abrasion-caused attrition of juvenile teeth. (Juvenile female 62-208, weight 22 lb. (10 kg.), length 1,000 mm., found dead on beach, 5 March 1962. (KWK 66-10-15)

Molars

The upper and lower molars have no antecedents. They erupt in the late juvenile period somewhat later than the permanent canines and somewhat earlier than the permanent postcanines.

Many young are born in the late winter-spring period. In the following late winter and early spring period of stress, the food intake of these large juveniles is inhibited by the eruption of the permanent postcanine teeth and the accompanying loss of deciduous teeth. In the crowded Amchitka population where food resources are heavily exploited, such young, still dependent on their mothers for much of their food, are deserted and die at this time. Apparently, the mothers are unable to supply the food needs of both themselves and their large young during this season of stress.

Because poor occlusion, as described above, was observed in many young otters found dead of starvation on beaches, it was assumed that this condition was a factor in their failure to survive (see Mortality Factors).

Dental attrition

The teeth of many sea otters at Amchitka Island show severe tooth wear (fig. 27). In order to learn something of the nature of this damage, sample skulls with worn teeth were sent to Dr. David B. Scott, Chief, Laboratory of Histology and Pathology, National Institute of Dental Research. After he and his associates had examined the teeth they contributed information in a letter of 23 May 1963. Excerpts are quoted:

None of us feels that the pitted and worn areas have the requisite characteristics of dental caries. The alterations are quite curious. Since we were not familiar with the dentition in the otter, we removed an unerupted permanent tooth and uncovered two others from under the deciduous teeth of a juvenile male (KWK 59-105), and also removed one of the more interesting atypically pitted ones from an adult female (KWK 59-11). One of the former teeth split well enough for us to get an idea of the enamel thickness; taken together with the appearance of the other permanent teeth in this young skull the impression is gained that deep pitting is not a feature at the outset.

The most interesting and confusing configuration in the pitting of the type found in the tooth from KWK 59-11, is the tips of the cusps. As seen in the sectioned tooth, the hole in the underlying dentin is actually broader than the opening through the enamel, resulting in a sort of undermining. [Examination of many teeth indicate to me that these pits are formed when a piece of hard sand is pressed into a newly formed break in the enamel. Movement of the sand grain and pressure on it when food is chewed cause it to rotate and create a cavity in the dentin larger than the hole through which it entered.] This is not expected in attrition, but all of us feel that the classical signs of caries are not present. There is quite a deposit of secondary dentin

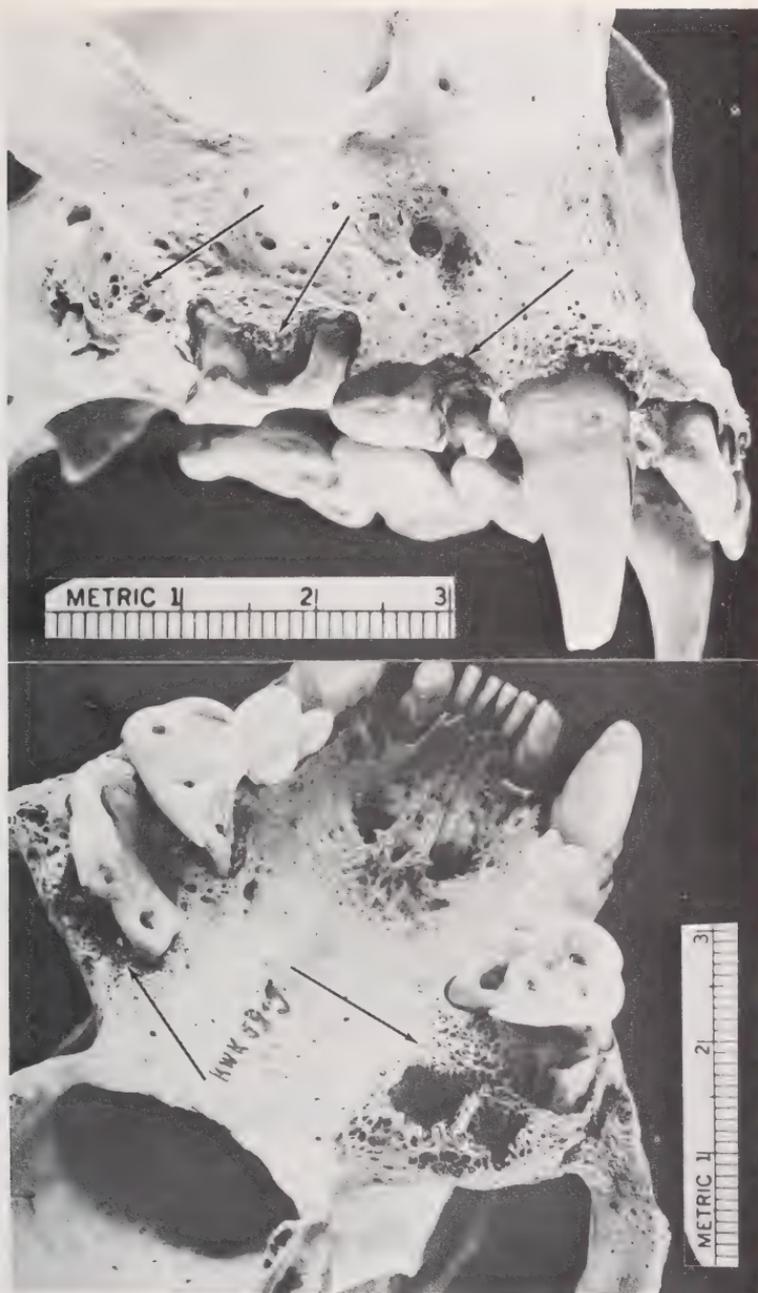


FIGURE 27.—Dental attrition and bone damage in the adult sea otter. Adult otters found dead on beaches at Amchitka Island often have severely worn teeth. Bone resorption (indicated by arrows) and periapical abscesses accompany severe tooth attrition. All teeth showing severe wear were loose. The crushing of hard-shelled organisms, such as mussels and sea urchins, is a suggested cause of severe tooth wear. (KWK 66-14-10 above, 66-13-20 below)

in the pulp chamber beneath the large pit that has resulted in obliteration of the pulpal horn. This phenomenon is ordinarily considered as a defense reaction against trauma or caries. Looking at these pits and the more advanced damage in the other skulls, we are tempted to conclude that some sort of peculiar attritional sequence is represented. The later flattening can be more easily explained in the usual terms of wear and tear. I suspect that a rather large-scale study would be required before the facts could be ascertained as to how the early pitting occurs.

There is a good bit of calculus on the teeth. The bone resorption in an adult female (KWK 59-153) suggests that there may have been periapical abscesses in the lower left molar region, probably as a result of pulp exposure from the attrition. The bone damage in the upper left posterior region could be explained in the same way, or equally well as an outcome of periodontal disease. There are also other areas of bone damage.

Tooth attrition and its relationship to feeding habits and mortality at Amchitka Island are discussed elsewhere. It is apparent that a dense otter population at Amchitka has resulted in a shortage of soft-bodied invertebrate food species. Hard-shelled forms are eaten in large quantities. Sea otters often chew mussels (*Mytilus*) and sea urchins (*Strongylocentrotus*). The sounds of shells crushed by the teeth are often audible for many meters. Also, sand is ingested with food organisms and sand grains are often found imbedded in teeth.

Dental attrition is less prevalent in sea otters from areas having uncrowded populations than from the crowded Amchitka area. A captive female sea otter that was fed primarily on soft foods showed no dental attrition when she died at the age of about 7 years. It is thus concluded that dental attrition of the kind found at Amchitka is the result of a diet that includes many hard-shelled organisms with which abrasive sand, and even rocks are taken (see Food and Feeding Behavior).

Age Determination

The chronological ages of certain wild animals may be ascertained from anatomical specimens. In pinnipeds the teeth show rings or annuli (Scheffer, 1950a) which are related to cyclical annual phases of fasting and feeding. Similar growth layers are found in the ear plugs and baleen plates of whales (Ichihara, 1966) and in bones (Chapskii, 1952). To a limited degree of accuracy, eye lens weights may indicate age in long-lived mammals, such as the fur seal (Bauer, Johnson, and Scheffer, 1964).

In any study of age determination in mammals it is desirable to have a collection of known-age specimens. The isolation of sea

otter populations, problems yet unsolved in keeping a captive colony, and the fact that a regular annual harvest of wild animals has not been taken, have prevented the accumulation of known-age specimens.

Lacking such basic material, but drawing on his experience in the study of teeth for indications of growth layers and age estimation, V. B. Scheffer studied a number of sea otter teeth from young and old animals. Techniques that reveal growth layers in teeth of other mammals revealed nothing that could be related to the annual growth cycle in the sea otter.

Dr. A. F. Forziati and Mrs. M. P. Kumpula, Research Division of the American Dental Association, National Bureau of Standards, Washington, D.C., undertook a study of sea otter teeth. Teeth were sectioned and subjected to techniques such as X-ray photography and exposure to ultraviolet radiation. These and other techniques useful in revealing growth layers in other mammalian teeth showed faint lines (fig. 28) but gave no useful indication of annual growth layers.

In a further effort to "mark" stages of tooth growth, three captive sea otters on Amchitka Island were injected periodically during a 3-month period with alizarin red S dye. It was hoped that visible growth lines would be formed. When the teeth of these animals were studied by Dr. Forziati and Mrs. Kumpula, however, no consistent markings were revealed. Further studies of structures that may indicate age in the sea otter are reserved for the future.

Karl Schneider, Alaska Department of Game (letter, Nov. 1968), tells me that he experimented with a number of different stains and techniques and is now able to differentiate cementum layers which appear to indicate age.

The sea otter is a permanent resident in a relatively uniform environment. It requires a daily food intake of uniform amount (a captive consumed 15 lb. [6.8 kg.] of food per day during all seasons). There is no abrupt molt or distinct period of fasting. In the absence of marked seasonal environmental changes or periodic metabolic changes during the sea otter's life, it is not surprising that the usual indicators of chronological age are not evident.

One captive otter (Susie) was about 1 year old when captured and died of abnormal causes after 6 years in captivity. Her teeth and bone structure at death appeared to be those of a young adult. On this basis it is estimated that in ideal habitat a wild sea otter might be expected to live for from 15 to 20 years. A captive river

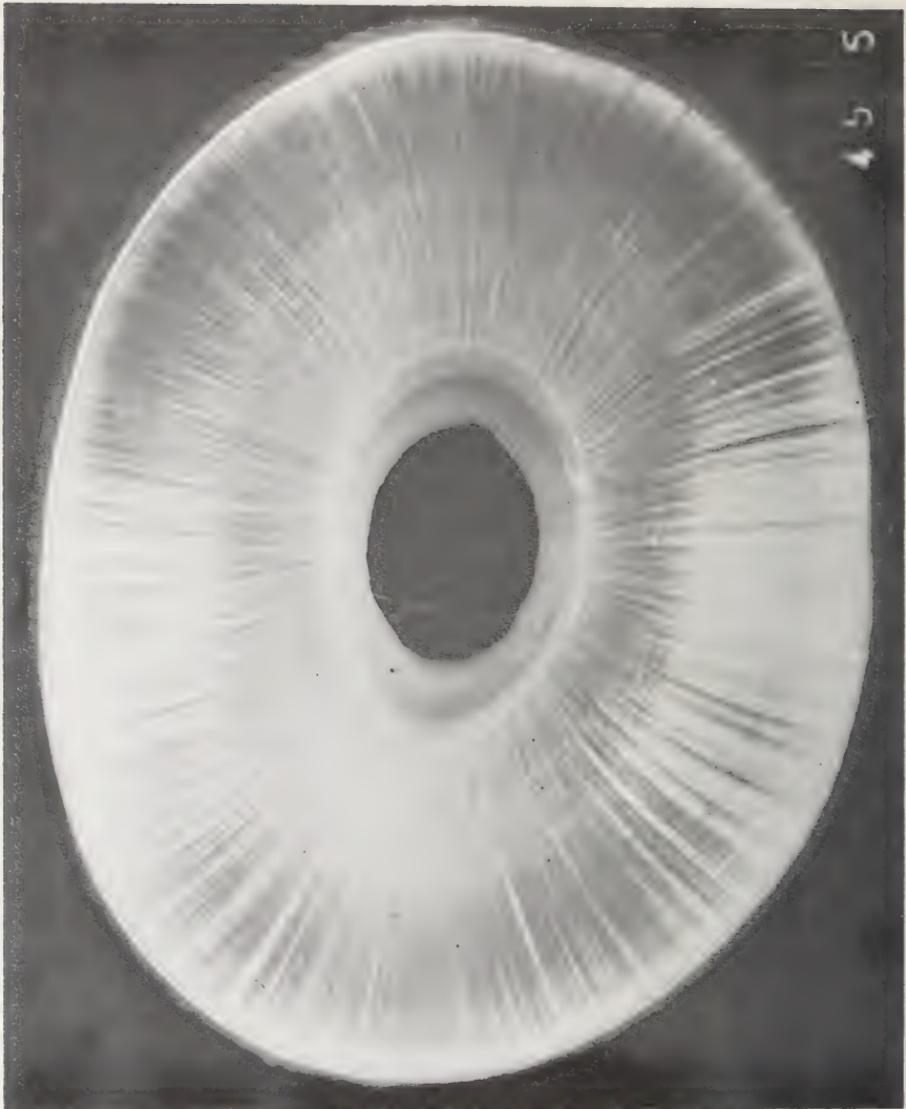


FIGURE 28.—Cross section of the right upper canine tooth of an adult female sea otter, weight 47 lb. (21.3 kg.) taken at Amchitka Island, 12 June 1956. Although various zones and lines are revealed by refracted light in this thin section, no series or rhythm of growth layers relating to the annual cycle could be defined. No technique is yet developed to reveal chronological age from a study of the teeth. (National Bureau of Standards photo 45-56)

otter lived to the age of "14 years and 4 or 5 months" (Scheffer, 1958).

The Senses

The various senses are mentioned or discussed in context under different subject headings in other parts of the text. A brief summary of observations of the use of the senses is given below.

SIGHT AND SMELL

The sense of sight appears moderately well developed but, on land at least, is less important than smell as a warning sense. The following observation illustrates this:

I approached a dispersed group of 25 otters sleeping on the rocks. The S. W. breeze of ca. 4-6 knots was such that I could approach cross wind. I moved quietly to within about 10 feet of a group of six sleeping animals and made a noise to awaken them. The animals looked at me but were not alarmed. After taking photos I made some quick movements and they became mildly alarmed and went slowly to the water which was in a channel about 15 feet wide among the rocks. Here they preened—not alarmed. Then they swam slowly to a point directly down wind of me. As they got my scent, all dived in great alarm and swam frantically away under water.

One old male awoke of his own accord and walked leisurely over the rocks on my upwind side. He was only 3 feet away. He looked at me with no recognition—I moved slowly and took a picture, the click startled him but he was not alarmed and ambled around behind me, to a point downwind of me. When he caught my scent he took extreme alarm and scrambled frantically over the rocks, dived into the water, and did not come up until 100 feet away. (Field notes, 12 March 1962, East Cape, Amchitka Island, Alaska.)

When otters feeding or resting in the water are approached by a human observer and the wind is blowing from the observer to the otters, they become restless. Feeding and resting animals rise high in the water and sniff the air. Although there is no rapid movements or indication of alarm, it is generally true that all animals will leave the area within about 10 minutes after the observer's arrival. In the same locations, when the wind blows from the otters toward the observer, the otters remain unconcerned even though the observer moves about on land in clear view.

As mentioned under "Food and Feeding Behavior," sight under water may be useful in finding food. Gentry and Peterson (1967) demonstrated that a sea otter was capable of quite a high degree of accuracy in distinguishing, under water, the size of experimental disks.

HEARING

No observation that I know of demonstrates that the sense of hearing is either particularly acute or poor. The sound of a camera shutter clicking at a distance of 3 to 5 m. usually causes an otter to glance alertly about, but does not cause alarm. Both wild and captive otters soon become accustomed to routine sounds of human activity.

TASTE

Captive otters, when given a variety of foods, often licked each item, then went back to eat first the food which they apparently considered most tasty. Certain foods were obviously preferred, presumably because of their taste.

TOUCH

The forepaws and vibrissae appear to be very sensitive, and they are important in finding food (see Food Gathering and Sensory Vibrissae).

HABITAT REQUIREMENTS

Sea otters inhabit waters of the open coast of the North Pacific Ocean. Although they enter bays on outer sea coasts, there is no evidence that they ever occupied inland waters far from the sea, such as Puget Sound and the extensive inside passages of the Alexander Archipelago of Southeastern Alaska.

They obtain food from the ocean bottom and are seldom seen in waters deeper than 30 fathoms (54 m.), indicating that this may be the approximate limit of their feeding habitat.

Since sea otters are often seen sleeping and diving for food in and near kelp beds (*Alaria*, *Macrocystis*, and *Nereocystis*), it has often been assumed that kelp beds are a habitat requirement. That this is not true is demonstrated by the fact that a large, permanent sea otter population remains throughout the year in the Bering Sea off Unimak Island and off the western tip of the Alaska Peninsula. There are no kelp beds here and in certain other areas occupied by permanent sea otter populations.

In general, however, sea otters favor waters adjacent to rocky coasts near points of land, or large bays where kelp beds occur. Coasts adjacent to extensive areas of underwater reefs are particularly attractive. In such areas, especially where large rocks or islets are located near shore, some feeding and resting areas are sheltered from wind and storm waves regardless of their direction (fig. 29).

In the Aleutian and Shumagin Islands sea otters regularly haul out on land and they may do so elsewhere. Rocky points are favored but sand beaches, islets, or spits are sometimes used. When a sea otter comes ashore it usually remains within about 1 to 6 m. of the water. Where human disturbance is minimal, as on some Aleutian islands, I have found them sleeping in grass (*Elymus*) as far as 50 to 75 m. from the water. Sea otters tend to concentrate and form colonies in areas which offer an abundant invertebrate bottom fauna and sheltered feeding and resting areas.



FIGURE 29.—Favored sea otter habitat in the Aleutian Islands is characterized by having extensive underwater reefs to a depth of about 20 fathoms, kelp beds, and points of land or offshore rocks that give shelter during storms. This photograph shows an example of favored habitat on Kirilof Bay at Amchitka Island, Alaska. (KWK 55-16-35)

GENERAL BEHAVIOR

Observations of the habits and characteristic behavior of sea otters were obtained in their natural habitat and in captivity. Quantitative studies of behavior and experimental studies were undertaken in only a limited way (Gentry and Peterson, 1967; and in section "In Captivity"). Certain characteristic habits and behavioral traits are discussed in context as they relate to various subjects in other sections of this report.

Daily Cycle of Activity

It was shown in the section "In Captivity" that when an abundant food supply was available a captive animal spent relatively little time feeding as compared to a wild otter. It appears that the abundance of food in the wild also strongly influences the daily cycle of activity of otters in different areas of the Aleutian Islands.

In general, at Amchitka, otters begin to dive for food within the first hour after sunrise. Feeding, interspersed with short periods of grooming and rest, then continues until mid- or late-morning. Sometime between 1100 and 1300 the otters sleep or doze, usually while floating on their backs in a kelp bed. The duration of this rest period usually varies from about one-half to three-quarters of an hour. One mated pair rested from 1225 to 1302 (37 minutes). After this nap, feeding, interspersed with short rest periods for preening and grooming the fur, continues until mid-afternoon when the otters may sleep soundly, usually while floating, but in male areas a number of animals may haul out for the afternoon nap. This nap usually continues for about an hour. The same pair mentioned above rested from 1446 to 1548 (62 minutes).

After this rest period, feeding again occurs and may continue until sunset or after. At dark or shortly before, some animals haul out to sleep, usually within a meter or two of the water but on rare occasions as far as 75 m. up on the beach. Others spend part or all of the night sleeping in a kelp bed while floating on the back.

In areas where populations are less crowded than at Amchitka, and presumably food is more abundant, general observations in-

dicating that rest periods are of longer duration because food needs may be satisfied in a relatively short time.

Mothers accompanied by young, especially large young at Amchitka, often continued to dive for food long after all other otters in the general vicinity had retired for the night. On several occasions I watched mothers feeding until they were obscured by darkness. This is another indication that food species in the Amchitka habitat have been overutilized by that local population. To obtain sufficient food for herself and her young, a mother must search for it after other otters have retired.

The general daily cycle of behavior described above continues throughout the year. When prolonged storms create violent wave action, the daily cycle is disrupted and animals unable to obtain sufficient food die (see Mortality Factors).

Locomotion

SWIMMING

Methods of swimming

Taylor (1914, p. 491) pointed out that the outer or fifth digit of the sea otter's hind foot is the longest (fig. 8). In this respect the sea otter differs from its nearest relative the river otter, from seals, and from most if not all land carnivores. He considered that "extra support" (presumably in walking) is furnished by this unusual feature. Howell (1930, p. 284-287), however, after studying the musculature of the pelvic limbs, surmised that the sea otter swims by means of vertical undulations of the posterior part of the body; that it uses the hind flippers held in the horizontal plane, palms up, in combination with the tail to "present in a satisfactory degree the lunate rear border theoretically desirable." Thus, "the long fifth toes would form the outer borders of the swimming organ." He was unable to confirm this theory by observation. He felt some doubt as to its validity because "It is true that no other mammal is known ever to have employed this method of swimming."

On many occasions, from boats and cliffs, and in captivity, I have watched sea otters swimming in clear water beneath the surface. Howell's deductions were entirely correct.

While the sea otter is swimming beneath the surface or diving, vertical undulatory movements of the body, as described above, furnish propulsion. While near the bottom, maneuvering and

searching for food, stroking or paddling movements of the hind flippers are also used.

Unlike other marine mammals, the sea otter habitually swims on the surface when it is moving from one area to another. It usually swims on its back and paddles with alternate strokes of its hind flippers (fig. 30). In this position the long fifth digit dips most deeply into the water and in combination with the other webbed digits produces forward motion.

Thus, the fifth digit is a useful adaptation to two unusual methods of swimming in a mammal: (1) Progression beneath the surface through undulations of the hind flippers and tail in the vertical plane, and (2) progression on the surface by paddling while resting on the back. Whether the fifth digit became elongated as an adaptation to swimming beneath the surface or as the dominant member used in surface propulsion is difficult to surmise.

The sea otter infrequently swims belly down at the surface, with the head and shoulders above the surface (fig. 86). At such



FIGURE 30.—Three adult males in typical swimming attitude. The forepaws are folded across the chest or pressed palmside down against the chest. Forward progress is obtained by alternate strokes of the hind flippers. Maximum sustained surface speed is about 2.5 km per hour (1.5 knots). (KWK 62-27-14)

times the hind feet are used to deliver paddling strokes similar to the stroking movements employed when swimming on the back. Progress on the surface appears to be slower when swimming on the belly than while swimming on the back.

The front feet are not used in swimming either on the surface or beneath it. They are pressed palmside down against the chest or folded across the chest when not in use to manipulate food or to preen the fur or hold young (fig. 30).

The tail is flattened in the horizontal plane and tapers only slightly, so that it presents a broad surface for most of its length. The tail of an adult female measured 317 mm. long, 44 mm. thick, and 64 mm. wide near its base. In addition to its use in conjunction with the hind flippers in underwater swimming, the tail is used as a "sculling oar." Slight alterations of positions are made when the otter is floating on its back. Frequently I observed resting otters floating in this position with front and hind feet folded on the chest and abdomen. Normally the tail floats on the surface while the otter rests, but if it wishes to make slight movements, for example to face away from a light breeze, the tail is projected downwards and by means of circular sideward movements the body is rotated in the desired direction. Also, when captives were eating and they wished to pivot about on the surface to avoid food pilferage by other otters, the tail was used in sculling to assist the stroking hind flippers.

Swimming speed and agility

The sea otter is a slow swimmer but it moves more rapidly beneath the water than on its surface. Two methods were used to measure swimming speed: (1) From the shore, otters traveling from one area to another were timed as they passed beach points. The distances were then measured on nautical charts and the speed computed. (2) Otters were pursued with a motor-driven dory while they swam beneath the surface. In clear water the otters could sometimes be seen as they attempted to escape pursuit. Presumably, at such times they moved at maximum velocity. The speed of the dory was measured by timing its passage over a known distance.

Examples, surface speed: (1) An adult female swam parallel to the coast of Kirilof Point on a nearly windless day. For the most part she swam on her back but occasionally she rolled over and "porpoised" (exposing the back, but not leaving the water) for 10 to 15 yards. During the observation period she made one food dive and when she emerged ate the several urchins she had

gathered while she continued on course at the surface. In 44 minutes she covered exactly 1 nautical mile, thus her speed was 2.3 km. per hour (1.4 knots). (2) An adult female, carrying a sleeping pup on her chest, moved hurriedly and steadily on the surface from an area where a rising wind caused rough water. The wind was from her side, so she was neither swimming with or against it. She passed over a measured distance of about 800 m. in 20 minutes, or at the rate of 2.4 km. per hour (1.5 knots). (3) After emerging from a food dive with a fish (weighing about 0.5 kg.), an adult male swam on his back while he consumed the fish and moved with moderate speed to another area. His departure from the feeding area was apparently prompted, to some degree at least, by the presence of three Glaucous-winged Gulls (*Larus glaucescens*) which swam beside or flew above him while they retrieved discarded fish scraps. The otter was able to outdistance the birds that alighted beside him on the water. In 675 seconds he traversed a measured distance of 300 m. at an average speed of 1.6 km. per hour (0.9 knots).

The top speed of our dory was approximately 11 km. per hour (6 knots). On many occasions we chased sea otters in order to catch them in a dip net. When the water was clear and smooth, we could watch the otters swimming beneath the surface as they attempted to escape. It appeared that their top speed for brief intervals, less than 1 minute, was not more than 9.25 km. per hour (5 knots) and probably somewhat less. When we were unable to see otters beneath the surface, we often overran them. Occasionally during escape attempts, otters would porpoise clear of the water ahead of the boat. When this was done they were most readily captured.

Thus it appears that when an otter moves from one area to another on the surface, its near maximum sustained rate of travel may approach 2.5 km. per hour and the underwater, briefly maintained (up to about 1 minute), maximum escape speed is about 9 km. per hour. This compares with a near maximum, briefly sustained (3 to 5 minutes), escape speed of the northern fur seal, which we pursued in a vessel having a maximum speed of 26 km. per hour (14 knots), of about 18.5 km. per hour (10 knots). A Pacific bottlenose porpoise (*Tursiops gilli*) sustained a speed of 29 km. per hour (16.1 knots) for 7.5 seconds (Lang and Norris, 1965).

Although a slow swimmer, the sea otter is remarkably agile. On one occasion I plunged the dip net directly in the path of an otter as it swam just ahead of the dory and at a depth of about $1\frac{1}{2}$ m. The otter, unable to avoid entering the net, rolled forward,

completed a 180° reversal of course, and escaped before I could pull the net from the water.

DIVING

Duration of food dives

In water depths ranging from about 2 to 25 m. food dives were timed with a stop watch from observation points on the cliffs of Amchitka. Several factors render such observations somewhat difficult to obtain and evaluate. Usually several otters were diving for food in an area under observation. Although an otter may make several food dives in a rather limited area, perhaps 15 m. in diameter, the animal may unexpectedly move 100 m. or more beneath the surface to a new feeding location. Also, a nearby otter may move to the vicinity of an animal that is being timed, causing confusion. The positive identification of the sex of a diving otter is sometimes difficult to ascertain at the distances and with the frequent poor visibility caused by weather conditions.

General observations indicate that the duration of food dives by adult males exceeds that of adult females. The following data probably exaggerate this difference because the females' dives were, to a greater extent than the males', in shallow water:

	Number of animals observed	Duration of food dives (seconds)			
		Timed food dives	Average duration of dives	Maximum duration	Minimum duration
Adult male	4	20	100	160	72
Adult female	6	41	49	82	15

The few observations presented are not strictly comparable, because water depth varied and the animals under observation may have had differing food preferences which caused some of them to search longer for a particular item. Males feed on fish to a greater extent than females. Among 50 stomachs of adult males which contained food, 82 percent contained fish, and 62 percent of 178 stomachs of adult females contained fish. The search for and capture of fish would probably require more time than the gathering of invertebrates.

The best data on the duration of dives of the female were obtained on 20 and 21 August 1955. On these two days a mated pair of otters remained in a small cove at Amchitka and no other otters fed in the area. During the period of mating the two otters dived and emerged from their food gathering dives simultaneously. Because the male followed the female closely, the duration of her

dives appeared to determine the duration of his. The mean duration of food dives was 65 seconds and the extremes were 20 and 95 seconds. The majority of the dives (69 percent) lasted between 50 and 80 seconds (fig. 31).

In generalizing on the duration of food dives in the usual foraging depths, between 10 and 25 m., it may be said that the adult female usually stays beneath the surface for about 1 minute and the adult male for about $1\frac{1}{2}$ minutes.

The number of dives in a feeding period varies. In 9 hours and 8 minutes when records were kept the mated pair spent 4 hours and 45 minutes in feeding activity, making 87 dives in water approximately 23 m. deep. Nikolaev and Skalkin (1963) report observations of 63 dives in 1 hour and 18 dives in 12 minutes. Presumably these data were obtained from animals feeding in shallow water.

Duration of escape dives

The sea otter, however, is capable of dives of long duration. This was demonstrated when we pursued a female otter for 50 minutes on 10 July 1960 in the Bering Sea off Unimak Island. During the chase she made 13 dives averaging 120 seconds beneath the sur-

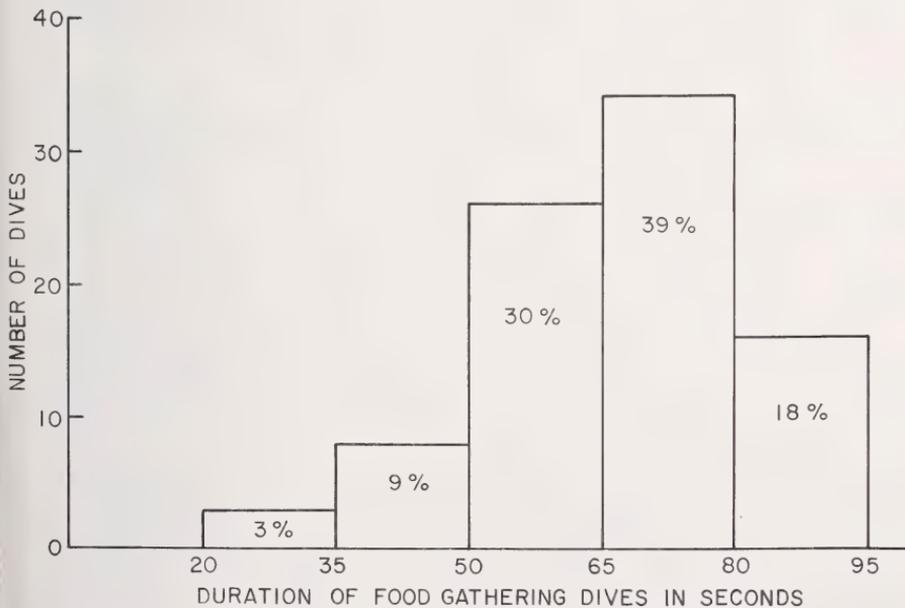


FIGURE 31.—Duration of 87 timed food dives made by a mated pair of otters. The water depth was 23 m. The male followed the female closely, both in submerging and emerging.

face. The longest dive lasted for 250 seconds (4.2 minutes) and the shortest 30 seconds. The last timed dive of 205 seconds indicated that the animal had not become exhausted and we abandoned the chase as futile. Barabash-Nikiforov (1947) says that "the longest time that the sea otter can submerge is not more than 6 minutes." My conclusion is that the maximum duration of a dive is probably less than 6 minutes.

Depth of diving and distance from shore

The maximum depth to which a sea otter may descend to gather benthic food organisms is not definitely known. Consideration of the historical record along with modern observations and data, however, indicate certain tentative conclusions.

The greatest diving depth I find in the historical record is quoted from Chase Littlejohn, a sea otter hunter of the 19th century. He said "There is a [place] . . . about 50 fathoms deep where they go to the depth of the water to feed" (Hall, 1945). Other otter hunters indicate lesser diving depths. Snow (1910, p. 281) stated that the sea otter appears to prefer to get its food at depths of 10-25 fathoms.

Captain C. L. Hooper (1897) studied the sea otter and problems of conserving it in Alaska during the latter part of the 19th century. It was his conclusion that "banks of 30 fathoms of water are its feeding grounds." Further, he concluded—

that the principal parts of the present sea otter grounds are already within the territorial waters of the United States. . . . suitable regulations by the United States Government, properly enforced, will furnish ample protection for the sea otter, as not enough can be taken outside of these limits to encourage hunting to any extent.

This statement implies that otters seldom ventured to depths greater than those found relatively near shore.

Modern observations tend to confirm the early sea otter hunters' information, except that in certain areas where shallow water is found far from land sea otters appear to find suitable feeding grounds beyond the 3-mile limit.

During seven seasons (April through August, 1957-63) A. C. Hartt and B. F. Jones recorded all sea otters sighted beyond 3 miles from shore. Their primary mission was offshore fisheries investigations during which their ships operated near various Aleutian islands, in the passes between them, and as far as 200 miles from land in the North Pacific and Bering Sea.

Their observations of otters over deep water (table 10) are of interest, because in each case the otters were near areas where

shallower water was only a few miles distant. Also, the observations were in areas where strong tidal currents are prevalent. These could quickly move an otter sleeping on the surface several miles from a feeding area.

The observation of two otters 32 miles west of Kiska in the 55-mile wide pass between Buldir and Kiska Islands on 27 May 1959 (A. C. Hartt, letter, 1960) is of particular interest. Their presence there may be explained by the fact that they were near an underwater mountain ridge, Buldir Reef, which is about 20 nautical miles long and over a mile wide, and which offers considerable area having depths of from 17 to 30 fathoms.

The only available authentic record of an otter far from shore and away from passes between islands was recorded by G. T. Joynt (letter, 1957). While flying as a naval aviator in the Aleutians in the spring of 1943, Joynt saw an otter—

a little over 50 miles due south of East Cape on Amchitka Island. On this particular day the open ocean was as smooth as a mill pond . . . This animal was observed at very close quarters and identity was certain because of the rarity of anything on the surface making a wake so far from land. I have often conjectured that this particular animal could have been a victim of an unintentional ride in a large free-floating kelp raft. Whenever sea otter were observed more than a half-mile from the nearest kelp patch it was usually a single animal and they were most frequently in the straits between two of the larger islands. On these occasions they were usually headed to one island or the other and not aimlessly swimming about.

Joynt was a trained biologist before becoming a naval aviator and gathered much useful information about sea otters in the Aleutians.

The large amount of time spent by the several observers (table 10) in offshore areas and the dearth of observations of sea otters at an appreciable distance from depths of 20 to 30 fathoms, demonstrate the tendency of otters to remain in shallow water.

On 10 July 1960, an adult female sea otter (KWK 60-19) was shot 9 nautical miles north of the Alaska Peninsula ($55^{\circ}20' N.$ lat., $163^{\circ}11' W.$ long.) in water 20 fathoms (120 ft.) deep. The stomach contents (see Food and Feeding Behavior) consisted of benthic organisms. During aerial surveys of the area off the north coast of Unimak Island and south of Amak Island on 8 April 1962, the majority of 811 otters recorded were seen between 3 and 10 miles from shore in water from 10 to 25 fathoms deep. The majority were near or inside the 20-fathom curve. The 20-fathom curve where this large number of otters were seen ranged from 5 to 8 miles from the north shore of Unimak Island. I presumed that

TABLE 10.—*Observation of sea otters beyond 3 miles from shore in waters off Alaska*

Date	Number of otters	Nautical miles from land	Location	Water depth (fathoms)	Observer	Remarks
Spring 1943	1	50+	S. of E. Cape, Amchitka	2,000+	GTJ ¹	Aerial observation.
31 July 1957	Groups	6-7	S. W., Cape Sujaka Tanaga I.	200-300	J ²	Floating kelp patches present.
15-19 Aug. 1957	do.	ca. 8	S., Little Kiska I.	70-90	H ³	Seen while en route from Kiska I. to fishing grounds.
27 May 1959	2	32	W. by N. of Sirius Point, Kiska I.	ca. 900	J	Floating kelp patches present; otters 25 yards from vessel.
11 May and 23 June 1960	Several	ca. 7	Sitkin Sound	40-60	H	Scattered otters seen en route Adak I. to Great Sitkin I.
10 July 1960	2	5	Bering Sea, S. of Amak I.	20-22	K	Specimen collected had food in stomach.
8 April 1962	811	3-10	Bering Sea, N. of Unimak I.	10-25	S & K ⁴	Otters seen singly and in groups; feeding observed.
3 July 1963	2	6	S. by E. of Kagalaska Strait	ca. 100	J	Resting on surface.
9 July 1963	1	17	N. of Unimak I.	31	F ⁵	Resting on surface.

¹ G. T. Joynt, Naval Aviator on patrol from Amchitka I.² B. F. Jones, Fisheries Research Institute.³ A. C. Hart, Fisheries Research Institute.⁴ D. L. Spencer and K. W. Kenyon, Bureau of Sport Fisheries and Wildlife.⁵ C. H. Fiscus, Bureau of Commercial Fisheries.

light-colored objects seen on the chest of some of these animals were food items.

Aerial observations of most of the Alaskan areas populated by sea otters indicate that otters prefer to feed in depths of 5 to 15 fathoms and that most of them, except off Unimak Island, are within about one-half mile of the shore. Weather conditions and lack of time prevented aerial examination of all shallow banks far from land where otters might be expected. On 3 May 1965, however, Tahoma Reef (51°51' N. lat., 175°50' E. long.), Middle Reef (52° N. lat., 176° E. long.), and Buldir Reef (52°10' N. lat., 176°30' E. long.), respectively, 30, 20, and 20 miles from the nearest land (Buldir Island) and having considerable water areas from 3 to 20 fathoms in depth, were examined. Observation conditions were excellent. We saw a number of birds and sea lions, particularly in the kelp beds over Tahoma Reef, but sea otters were absent.

Numerous observations of feeding otters near Amchitka Island, at all seasons, indicate a preference there for depths of 5 to 20 fathoms. Also, during rough winter weather otters are inclined to search for food to a greater degree near shore. When the weather is mild they tend to move offshore to the vicinity of submerged reefs.

Several otters were observed over deep water and far from shore in the vicinity of drifting patches of floating kelp. This suggests that the otters could obtain food organisms that gathered in the shelter of the kelp. It is known that pelagic fishes accumulate under and around floating objects in the sea. That sea otters might rarely adapt to pelagic feeding is intimated by Snow (1910, p. 280):

On one occasion I found the stomach of an otter I killed some 8 or 10 miles offshore filled with the remains of a quantity of small fish with no signs of the remains of any crustaceans.

He does not, however, identify the area or state the depth of water where this otter was taken. Marakov (1965, p. 214) also reports sea otters up to "15 miles from the coast in comparatively deep places." No authentic record, however, indicates that the sea otter is capable of adapting itself to the capture of pelagic organisms where great depth prevents food gathering from the bottom.

In consideration of all the data available, it is my conclusion that sea otters feed in shallow water (1 to 15 fathoms deep) when sufficient food is available there. When food resources are more abundant offshore and particularly in mild weather, they move to feed in depths of 20 or, rarely, 30 fathoms. Food dives to depths

as great as 50 fathoms for food may be possible but otters are rarely seen in water as deep as 30 fathoms (180 ft.). No specimen is available to give positive evidence of food gathering at depths greater than 20 fathoms (120 ft.).

Our observations tend to confirm the conclusion of Barabash-Nikiforov (1947) that "the greatest depth to which it can go is 50 meters [164 ft.]"

WALKING AND RUNNING

Progression on land is similar but less agile than in other mustelids. The long, outer 5th digits of the hind flippers, which particularly aid progression when the otter swims on its back, hinder progress on land. Snow (1910, p. 275), however, exaggerated this hindrance when he wrote:

The use, however, of the hind limbs is very limited, the toes appear to lack all muscular power, and the otter cannot place its hind-feet flat upon the ground; when it attempts to walk, the toes are doubled back under the soles.

As figure 32 illustrates, Snow's statement is not true. He probably received his impression from otters that were cornered



FIGURE 32.—Because the fifth digits of the hind flippers are long, the sea otter walks with a somewhat clumsy rolling gait. It moves somewhat more slowly than normal human walking speed. (KWK 62-10-29)

on land and trying frantically to escape the clubs of hunters. His impression that the toes of the hind flipper were doubled back under the foot when walking was so strong a conviction that he figured this unnatural position in the frontispiece of his book.

When the sea otter walks unhurriedly on land, it moves with a rolling gait, raising one foot at a time and with the back arched (fig. 32).

When animals some distance from the water are startled, they arch the back and bound or hop, moving both forefeet then both hind feet forward in rapid succession (fig. 33). Juveniles and young adults are more agile than large, heavy adults. Some large animals seem unable to raise their bodies from the ground and slide, with the help of the feet, across the beach on the belly.

Sleeping

The sea otter may sleep while floating on its back (fig. 34) or when hauled out on shore (fig. 84).



FIGURE 33.—Adult sea otters, startled on a favorite hauling-out beach at Amchitka Island, bound toward the water in a typically mustelid manner. Speed of movement is somewhat less than the running speed of a normally agile man. (KWK 1027)

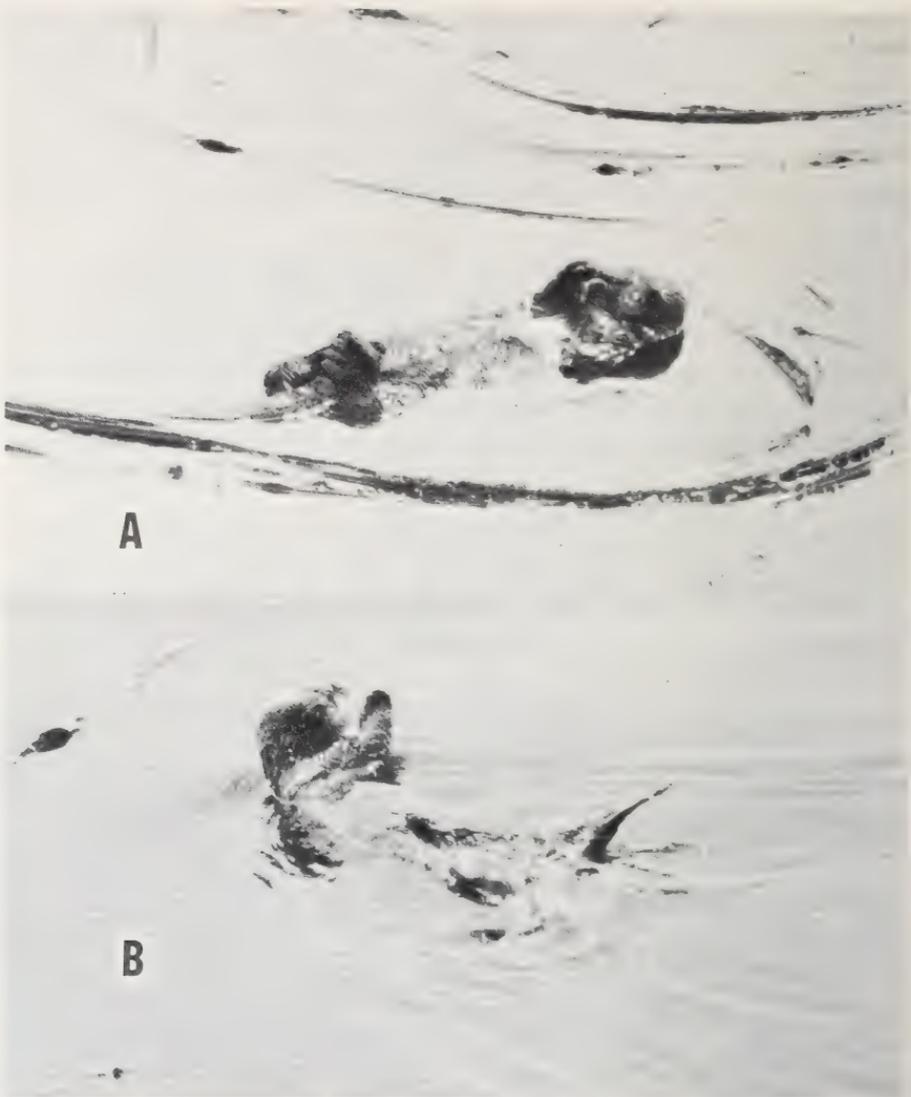


FIGURE 34.—A—Otters usually attempt to find a sheltered kelp bed before sleeping. After grooming is finished, the hind feet are folded on the abdomen. The forepaws may be placed over the eyes or against the side of the head or folded across the chest while sleeping. (KWK 56-4-4) B—This recently awakened otter is swimming languidly from its resting place while attempting to keep the head and forepaws dry. After awakening, otters appear reluctant to immerse the feet and head. (KWK 56-4-19)

Where kelp beds are available, the otters sleep in their protection. When surrounded by strands of kelp, the sleeping otter is protected from rough water and from movements by wind and water currents. Often, before going to sleep the otter uses its forepaws to pull one or several strands of kelp over its body; or it may make a shallow dive under the kelp strands, emerging with the strands in place over its body (fig. 35). In certain areas, for example off the north shore of Unimak Island, no kelp beds occur. In that area otters gather in large groups to sleep on the open sea (fig. 81).

Before going to sleep, otters scrub and groom their fur for about 5 to 15 minutes in the water. Then, if they haul out to sleep, the fur is preened and rubbed dry before sleeping.

On land the otter may sleep in many positions, from lying on the back as when sleeping in the water to stretching out flat on the belly or curling up nose-to-tail (fig. 84).

When otters awaken, they appear reluctant to get wet. If floating, they hold the feet, head, and tail aloft while rolling the body from side to side. Often they roll completely over, arching the back to avoid wetting the extremities. The head and forepaws are



FIGURE 35.—A drowsy otter preens its cheeks with its forepaws before going to sleep. The hind flippers and tail protrude beyond strands of kelp (*Macrocystis*) that lie across its chest and belly and prevent movement by wind or current while the otter sleeps. (Photographed near Monterey, Calif., by Wm. F. Bryan)

usually the last to be immersed as the otter swims leisurely from its resting place (fig. 34).

When sleeping on land, an otter usually spends a variable time languidly preening its fur before entering the water. Then it may follow the procedure described above to delay wetting the feet, head, and tail.

Grooming

Pelage care is of primary importance to survival in the sea otter. Grooming is essential to maintain pelage cleanliness and waterproofness, and thus insulation against the chilly marine habitat. A blanket of air remains trapped among the dry underfur fibers which serves as insulation. A captive female sea otter spent 48 percent (about 7.5 hours) of the daylight hours grooming her fur and a wild female, observed for about 7½ hours, spent 11 percent of the time in grooming activity (table 64, Comparison of daily activities of wild and captive female sea otters, see In Captivity).

Grooming takes place either in the water or on land. Energetic grooming is done before rest periods and languid grooming (fig. 36) at intervals during a resting period and at the end of a rest period. Grooming may be divided into two primary phases, (1) washing the fur and (2) drying the fur.

Grooming is accomplished primarily by rubbing the fur with the palms of the forepaws, but the hind flippers may be rubbed together or against the fur of the abdomen and sides. The fur of all parts of the body is rubbed by the forepaws. To accomplish this and reach remote parts of the body, the otter may twist and squirm within its loose-fitting skin, so that areas of the mid-back can be reached. The flexible body may be rolled in a ball so that the forepaws reach beyond the root of the tail to the lower back (fig. 37). Also, loose skin of the sides and belly may be rolled over a foreleg while water is pressed from the pelage and removed with the tongue (fig. 38).

Water may be pressed from the fur by the palms of the forepaws (fig. 39). A fold of skin and fur may be pressed between the forepaws, squeezing water from the fur and the moisture removed with the tongue (fig. 40). The fur may be rubbed in a circular motion or by rapid strokes in many directions. The retractile claws (fig. 2) (see Physical Characteristics) are occasionally extended to aid in grooming but usually they remain retracted. Figure 41, illustrates a typical grooming posture.



FIGURE 36.—While dozing on the surface of her pool, a captive female sea otter languidly grooms the fur of her chest and sides. (KWK 61-10-34)

The fur is washed by rubbing submerged parts of the body with the forepaws and by rolling, head first, over and over at the surface. Rolling may be accomplished just prior to sleep on the water's surface. It smooths the fur and leaves a thin film of water in the outer pelage tips.

In the final stages of a grooming session the otter may rest belly down at the surface, the head bent under the body while blowing air into the fur. Simultaneously the sides and belly are rubbed vigorously with the forepaws (fig. 42). The fur may also be aerated by a rapid churning motion of the forepaws, beating the water to a foaming froth (fig. 43).

If the otter intends to rest on land, it swims to a point near the desired resting place. Here it goes through a 5- to 10-minute grooming routine before leaving the water. After hauling out, the otter energetically rubs and dries its fur (fig. 44).

In general, females tend to be more thorough than males in grooming their pelage. I sometimes saw males, but not females, after hauling out, that failed to thoroughly groom and dry their fur before sleeping.



FIGURE 37.—The sea otter curls its long flexible body into a ball and reaches between the hind flippers to groom the tail and lower back. (KWK 1028)

Casual observers of grooming sea otters often misinterpret grooming for "scratching" and ask if sea otters have lice. They do not.

Voice

BABY CRY

This cry is uttered from birth until the large juvenile stage is passed. The pup cries when in distress or when it wants attention from its mother. The sound: a sharp, high pitched "waah-waah." This may be repeated constantly for long periods if the pup is



FIGURE 38.—Using its left paw, a grooming sea otter pulls the loose skin from its right side over the right foreleg in order to press water from the pelage and lick away the moisture. Moisture in the tips of the fur give the pelage a slick, wet appearance except on the head where dry, light-colored underfur is exposed by parting of the wet tips. (KWK 61-10-19)

separated from its mother and no tranquilizer is given. The sound resembles the cry of a young gull. The mouth is open wide when the cry is uttered.

SCREAM

This is uttered (1) when an adult is in severe distress—as when held in unsatisfactory captive conditions. Often it indicates that the animal is near death. It is not uttered when an animal is captured. (2) When a female has lost her young, as when the pup strays behind a rock, she screams repeatedly. This cry is the adult version of the baby cry. It is earsplitting at close quarters and can be heard at a distance of $\frac{1}{4}$ to $\frac{1}{2}$ mile in the wild and as far away as 200 meters when an animal is in a closed building. The mouth is open wide when the otter screams.

WHISTLE OR WHINE

This is uttered to denote frustration or mild distress. Captives



FIGURE 39.—While grooming, water is squeezed from the fur of the foreleg under pressure and by rubbing with the palm of the paw. (KWK 61-10-25)

whistle when the feeding schedule is delayed, and when they are carried on a truck or aircraft. The sound is uttered by adults and subadults primarily and to a lesser degree by juveniles. The whistle is loud enough to be heard to a distance of about 200 meters. It is a high pitched vocal sound that resembles a human whistle and is uttered with the mouth slightly open. "Wheeee wheeee" repeated often and of varying duration.

COOING

Females coo during premating and postmating behavior and also when grooming and fondling young. The coo appears to come from the throat and to denote satisfaction and contentment. Females coo while eating if the food is particularly pleasing. The mouth appears to be closed when it is uttered. Cooing can be heard up to a distance of about 15 to 30 m. on a quiet day. The sound "ku-ku-ku" may be continued for considerable periods either steadily or intermittently.

SNARL OR GROWL

This sound appears to originate deep in the throat and is uttered



FIGURE 40.—While drying its pelage, a fold of skin is pressed between the palms of the forepaws. Water expelled from the fur is removed with the tongue. (KWK 61-10-10)

when a newly captured animal is attempting to escape from a net. The snarl or growl is audible only a few meters away.

HISSING (NONVOCAL)

Females hiss during capture, after capture, and before becoming tame. The sound is similar to a cat's hiss (as noted by Steller in his *Journal*) but more explosive and of short duration. The sound is characteristic primarily of females and juveniles. If a person appears unexpectedly near a caged otter the hiss may be uttered in the first moment of fright.

GRUNTING

When a hungry animal is eating voraciously it utters soft grunting sounds that appear to denote satisfaction. In the male this appears to be equivalent to the cooing of the female.



FIGURE 41.—A mother otter rubs the top of her head with one paw and her elbow with the other. Both paws are in constant motion during grooming. After grooming her own fur, the mother took her pup onto her chest and groomed and dried it before allowing it to nurse from her two abdominal nipples. (KWK 57-29-14)

BARK

A yearling male during pool cleaning, while trapped in the empty pool and resenting thus being "cornered," uttered a staccato bark which trailed off into the whistle, apparently to denote frustration.

COUGHING, SNEEZING, AND YAWNING

Sounds as in other animals.

Handedness

During many hours of watching wild sea otters feeding, I noted that when the animals emerged from a food gathering dive the food items were carried to the surface under the left forelimb. Only if a large quantity of food was brought to the surface, i.e.,



FIGURE 42.—Near the end of a grooming period the sea otter rests belly down at the surface, bends the head to the belly, and vigorously blows air into the fur. At the same time it scrubs the fur on both sides with the forepaws. Note bubbles of exhaled air on water and splash caused by scrubbing paw. (KWK 61-10-26)

too much to be held under the left forelimb, did the otters place food under the right forelimb.

I have watched through calm, clear water while both captive and wild otters gathered food from the bottom. In all cases the right paw appeared to be used dominantly in gathering food and placing it under the left forelimb. Both paws were used to pick the food from the bottom, then with the right paw the food was pushed under the left forelimb.

When food was eaten on the surface, the food item was retrieved from the "chest pouch" under the left forelimb by the right paw, aided by the left paw, then held between both paws while being eaten. The teeth were usually employed to break the shells of small sea urchins. Before a large hard-shelled green sea urchin was eaten, however, the top of the urchin was cradled in the left paw while pressure was exerted by the heel and sometimes the toes of the right paw to crush the test around the oral opening of the urchin. The urchin was rotated against the left palm, so that the



FIGURE 43.—During the grooming period, before hauling out, the sea otter may beat the water to a froth with the front legs, perhaps aerating the fur to some degree. (KWK 55-19-3)

test was broken completely around the oral orifice before the teeth were employed to remove the broken shell.

From these observations I have concluded that the sea otter is right-handed. In hundreds of animals observed I have never seen food items brought to the surface under the right forelimb unless the quantity was too great for the left limb to accommodate.

Handedness in other animals is variable. Warren (1953) demonstrated that in the Rhesus monkey the right and left hands are used with about equal frequency. Lane (1946) indicated that birds of prey tend to be left-footed, and parrots (Friedman and Davis, 1938) are similar. Pigeons, Fisher (1957) concluded, tended to be right-footed.

Further study under experimental conditions may reveal if sea otters invariably exhibit right-handedness.

Tool-using

The use of a rock or hard-shelled mollusk held on the chest as an "anvil" for breaking the shell of a clam held in the forepaws is discussed under Food and Feeding Behavior. Chest pounding with the forepaws commonly occurs as an apparent expression of frus-



FIGURE 44.—After hauling out, the otter usually rests on its back while grooming and drying its fur before sleeping. (KWK 57-32-4)

tration, as when an otter has been robbed of its food by another otter. Perhaps the pounding of a hard-shelled mollusk against another originated because of frustration when the otter could not break, with its teeth, the shell of a food organism. At Amchitka, where the shells of mussels are crushed by the post-canine teeth, food pounding behavior is not observed. Where feeding was observed in Alaska, hard-shelled clams were not eaten and mussels (*Mytilus*) do not grow as large as those in California where they are commonly pounded against a hard object (Hall and Schaller, 1964).

When captive otters from Amchitka were presented with clams that could not be broken with the teeth or crushed between the paws, they broke them against a rock or another clam on the chest (fig. 45) or by pounding them on the cement edge of the pool (fig. 59). A female also pounded smelts (*Osmeridae*), and herring (*Clupeidae*) which she did not particularly relish (fig. 46), and she pounded a rock on the edge of her pool. Thus, animals that came from an area where food organisms were not observed to be broken by pounding, used this technique when frustrated by

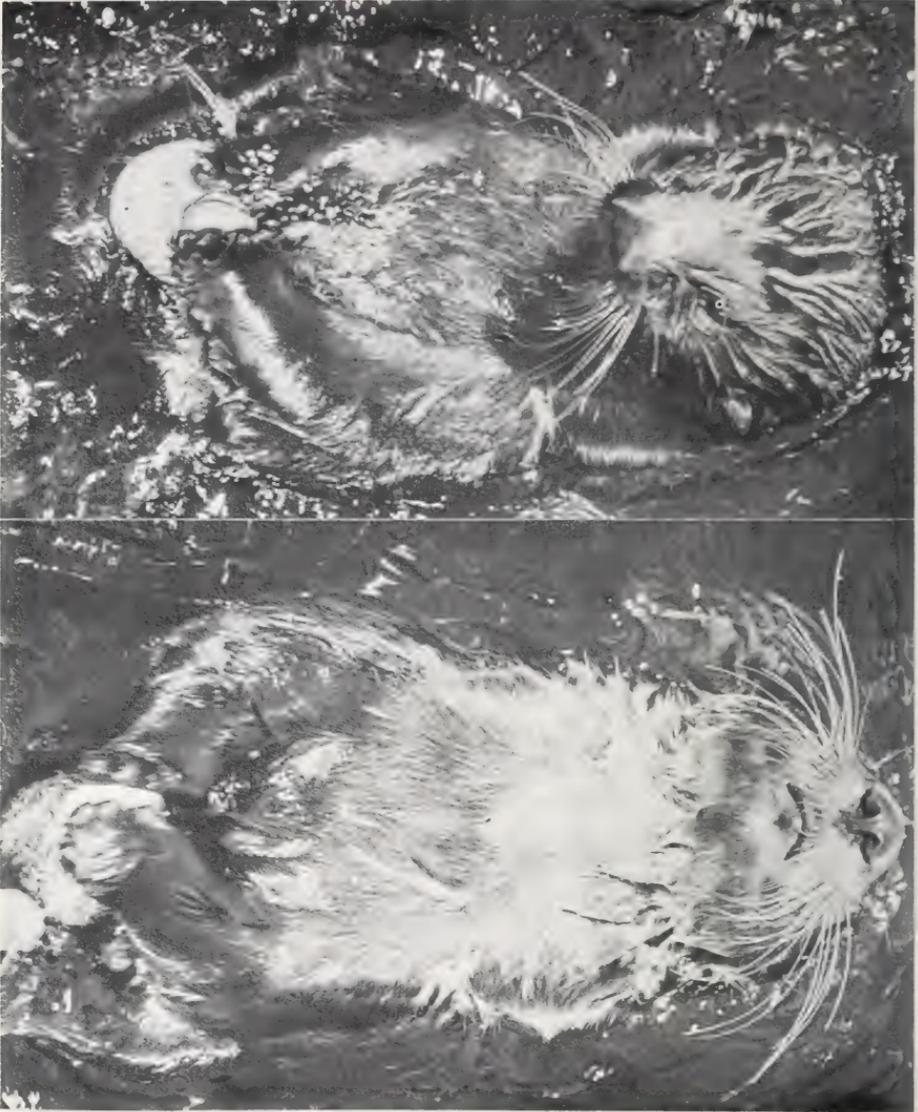


FIGURE 45.—A captive adult male sea otter from Amchitka Island pounds a clam, held between his forepaws, against a rock resting on his chest. Usually the head is held erect (above) but not infrequently it is extended during food pounding behavior (below). (KWK 67-15-7 above, 67-14-30 below)

hard-shelled organisms or by fish they did not care for. Also (Kenyon, 1959), a sea otter pounded a drain cover with a rock when the cover frustrated a desire to explore the drain. I consider the sea otter's tool-using behavior, as derived from chest-pounding,



FIGURE 46.—A captive otter pounded herring (*Clupea*) against the cement edge of her pool. The otter did not particularly relish this species as food, and the pounding behavior appeared to denote frustration when more appetizing food was not available. The irregular surface of the pool edge shown was produced when the otter pounded this area with a rock, cracking away the finishing layer. Rock pounding behavior appeared to express frustration when food was not available in the pool. (KWK 61-10-27)

frustration behavior. Also, I agree with the statement of Hall (1965) that the pounding behavior in the sea otter is—

but a behavioural adaptation that has no special relevance to the evolution of the sort of intelligent, anticipatory skills which are most highly developed in man and which he uses for the manufacture of a standard set of tools to be kept in store and used on different occasions for various purposes.

Thus, tool-using behavior in the sea otter might be likened to the use of gravity by gulls and ravens. These birds commonly

break the shells of clams and mussels by carrying them aloft and letting them fall on a rocky beach.

Defense and Escape

ON LAND

When a sea otter on shore finds itself cornered and cut off from escape to the sea it stiffens, faces the approaching intruder, and begins to rear backward (fig. 47). If the intruder continues to approach, the otter flops onto its back (fig. 48). If it is approached more closely, it may hiss and the stiffened forelegs are extended (fig. 49). The animal may attempt to bite any object extended toward it, while using the forepaws to push it away. I have never seen a cornered animal attempt aggressively to attack human intruders. Defense and escape are the only reactions.

IN THE WATER

When a sea otter is surprised at close quarters by an intruder it first rises high in the water. It faces the intruder and extends



FIGURE 47.—A juvenile sea otter, cornered on an Amchitka beach, prepares to rear backwards to assume the defensive posture illustrated in figure 48. (KWK 62-10-10)



FIGURE 48.—In the defensive position a sea otter lies on its back, faces the source of danger, and is alert to repel an attack. If an advance is made to touch an animal in this position, it attempts to bite and to push the adversary with its forepaws. The forepaws may also be used to aid in bringing the teeth into contact with the adversary. (KWK 62-10-26)

its forelegs, stiffly, palms of the forepaws outward toward the intruder. It then submerges vertically, pushing the forelegs above the head. It sinks backward beneath the surface, rather than plunging forward as in a normal dive.

Maternal and Filial Behavior

DURATION OF DEPENDENT PERIOD

The place of birth is discussed under "Reproduction in the Female." In her paper on the "Early life of a sea otter pup," Fisher (1940a) described many aspects of the behavior of mother and pup. Other writers have remarked on the unusual care of the mother for her young.



FIGURE 49.—When closely approached, a cornered sea otter hisses, extends its stiffened forelegs, and rears backwards as far as possible. No aggressive behavior is displayed. (KWK 59-8-6)

The period of dependence is unusually long. This was not ascertained directly from known individuals, but indirectly through various observations at Amchitka. Female reproductive tracts from there indicate that the majority of young are born from early spring to summer (see Reproduction in the Female). In the fall and early winter, large juveniles are numerous. During the late winter and early spring period of high mortality (March to May), most of the juveniles that die weigh 20 to 30 lb. (9 to 14 kg.). At the end of the annual "die-off" few large juveniles can be found alive. Observations during this period of juveniles crying and swimming about, apparently in search of their mothers, plus data compiled under "Mortality Factors" and "Home Range" indicate that most of these young animals are abandoned by mothers in the period of stress caused by storms and depleted food resources.

It is assumed that this group of young, most of which were dead by May, were the young that were born in the previous spring

and early summer, in which case they would be 10 to 12 months old at time of death. Young that were born in the fall and winter were small (5 to 10 lb., 2.3 to 4.5 kg.) during the period of stress, and being less a burden to their mothers were cared for during this season. These were the young that survived to augment the population.

During summer, some dependent juveniles were larger than those that were deserted and died during the season of stress, indicating that they were probably more than a year old. Thus, I believe that the period of dependence of the young is normally at least a year and probably somewhat longer. Young somewhat less than 1 year old and in the 15 to 25 lb. (7 to 11 kg.) group do not usually survive in the wild if premanently separated from their mothers, particularly if separation occurs shortly before or during the season of stress.

At birth the pup is helpless and remains so for several weeks. When the mother dives for food the pup is left floating on its back at the surface, where it usually sleeps. If the pup awakens while its mother is diving, it may squirm and move its hind flippers about in an uncoordinated way. A very young pup appears unable to roll over onto its belly, which the pup apparently attempts to do by twisting the forward half of its body (fig. 50).

The ages of pups in the wild are estimated on the assumption that during the first year of life a pup grows at a nearly constant rate from about 5 lb. (2.3 kg.) at birth to about 30 lb. (14 kg.) when mother and young may separate. The sizes of pups are estimated by visually comparing pups in the wild with animals of similar body size that are weighed. On this basis, it is estimated that the pup remains nearly helpless during the first month, although it is able to crawl weakly for a meter or so on land (fig. 51) and swim weakly in an uncoordinated fashion.

SOLICITUDE

Much has been written of the solicitude of the mother sea otter for her young. Snow (1910, p. 142) noted the reluctance of a mother to abandon her pup.

For two hours we chased this otter, pursuing her between the rocks. The pup had been killed during the first hour, but she was holding it as firmly as ever, until a shot, striking one of her paws, made her drop it; and in trying to regain it she was once more wounded. Again and again she made the attempt, all the time giving utterance to the most plaintive and sorrowful cries . . .

After retrieving the pup, which the mother was unable to pick



FIGURE 50.—(Above) After a feeding period and before taking her 3- to 4-week-old pup ashore, the mother sea otter scrubs and grooms her fur with her forepaws. The pup at this stage is unable to swim. By aimless strokes of its hind flippers it may move about in a circle or attempt to roll over (as shown here) to grasp a kelp strand. While she washes and grooms, the mother seldom moves more than a meter from her pup and usually stays close beside it (below). She watches it constantly. (KWK 55-19-7 and 9; 11 September 1955)



FIGURE 51.—A captive mother sea otter leads her 3- to 4-week-old pup from the water. This appeared to be a “walking lesson.” At other times the mother carried her almost helpless pup from the water in her mouth. (KWK 57-27-8)

up because of her wounds, the hunters started to return to their ship and later that same night, Snow wrote:

We had traveled some distance, when all at once, right under our stern, we heard the most unearthly crying imaginable; . . . another cry alongside showed us the dark form of the otter we had been chasing. It was now following the boat, lamenting the loss of her offspring.

The possessiveness of the mother sea otter is evident from birth until the young one is one-half to nearly two-thirds the mother’s size (fig. 52). Virtually the only time that the mother is apart from her pup is while she is diving for food, while preening, or when swimming beside the pup. On one occasion I watched a mother with a juvenile nearly as large as she. They rested together on a rock until the energetic young one began to explore nearby. When it went to the water as if to depart, the mother rolled forward, grasped the juvenile’s hind flipper in her teeth, and did not release it until the young one turned and resumed its position near her.

Many observations of mothers and young at Amchitka indicate that the ties between them may be strong but that the strength of the mother-young bond varies with each individual.



FIGURE 52.—The mother is solicitous of her young for a long period. *A*—A large juvenile, probably weighing about 20 lb. (9 kg.) and about 8 months old, nurses while its mother preens its fur. *B*—Alarmed by the photographer, the mother grasps her young one by the side of the head and, *C*, plunges with it into the water. (KWK 62-19-31, 32, and 37)

On 6 May 1959, a juvenile (about 16 lb., 7 kg., in weight), sleeping beside its mother on rocks near deep water, was captured in a dip net after the mother awoke and escaped. Three times within the next 5 minutes, while a metal tag was being attached

to the pup's flipper, the mother partially emerged from the water, grasped the net in her teeth, and attempted to drag it and her pup away.

A captive mother and her very young pup were held in a high-walled enclosure. During the windy night of 28 November 1957, the enclosure door blew open and the mother escaped. When I arrived soon after sunrise, I found her swimming about in the surf near shore and shrieking repeatedly. On entering the enclosure I found her pup still sleeping soundly. When I awoke the pup and carried it outside, it began to cry in answer to its mother's calls. In response, she rushed ashore and was easily recaptured.

The fearlessness of a mother in coming to the aid of her pup is often less strongly expressed than in the above two examples. During tagging operations we frequently netted mothers with large young. Usually when the mother was liberated in advance of her pup, she swam 50 to 100 m. from shore where she uttered repeated shrieks until joined by her pup.

Whenever a mother with a small helpless pup was captured, we attempted to return the pup to its mother as she was liberated. Usually, the mother grasped the side of the pup's head in her teeth and swam rapidly away. Occasionally, however, the frightened mother failed to take her young one. On 5 April 1959 a mother and her pup were captured and tagged on an Amchitka beach. In my field notes I recorded:

The mother of the newborn pup (Tag. No. EL 12938) was released close to her helpless pup so that she brushed over it as she ran to the water, but she failed to pick it up. This was at 1445. I watched from a hiding place until 1720 (2 hrs. and 35 min.). During this time, the mother swam about in a 200 m. radius, screaming frequently. She made 13 approaches to the beach, then swam out among the reefs, and continued to utter loud screams. On the 4th and 8th trips toward the beach, she approached to within 3-4 m. of the pup, then became frightened and swam out. Three other otters hauled up on the beach near the pup but the mother was not reassured and would not come out onto the beach. When I left, because of cold, she was still in the vicinity screaming.

Because of the possible loss of the young during tagging operations, the capture of mothers with helpless pups was discontinued.

A young otter may also demonstrate concern for its mother, as suggested by my field notes (27 February 1962):

A mother and her 15-pound male pup were captured as they slept side-by-side on the beach today at St. Makarius Pt. W. (Amchitka Island). They were caught in separate nets. The pup was tagged first and released. Instead of heading for the water he ran to his struggling mother, put his forepaws on her side and began tearing at the net with his teeth and tried to climb up on her side. He had to be dragged away while a tag was placed on the mother's

flipper. As soon as she was released, he rushed to her side and then followed her to the water. After a dive of about 50 meters, the two came up. The pup immediately clasped his mother about the neck and she pulled him toward her with her forepaws. This was a healthy, energetic pup.

Fright during capture may temporarily upset the normal behavior of a pup towards its mother (Field notes, 27 March 1962):

Today we captured in the same net a mother with a large pup as they slept beside each other on the cobble beach at Rifle Range Point (Amchitka Island). After the net was placed over them, they both began to struggle violently and the pup attacked the mother, biting her wherever it could. The mother paid little attention to the pup except that when its head came near hers she attempted to grasp the back of its neck in her teeth—as if to carry it off with her. We removed the pup from the net and tagged it. It was released about 2 feet from the struggling, still netted mother. It rushed to her and bit her on the side in several places. The mother ignored the bites and struggled on with the net. After tagging, the mother was released. As she ran to the water, the pup followed her. The mother swam rapidly for about 100 m., then stopped and the pup surfaced beside her and put its forepaws around her neck while both looked back at us before swimming out together—their fright apparently forgotten.

ATTENTION TO DEAD YOUNG

Mothers were occasionally seen carrying dead pups. I watched a mother carrying a dead, watersoaked pup while she emerged from the water and rested on kelp-covered rocks. For nearly an hour she licked the water from the pup's pelage and groomed its fur with her forepaws. When it was fluffy and dry, she went to sleep with it on her chest. How long a mother will attend a dead pup is not known but one was observed in which patches of skin and hair were slipping from the body, indicating that it had been dead for several days. A dead pup was removed from beside a sleeping captive mother after she had carried the carcass with her for 31 hours. On several occasions we attempted to take dead young from mothers seen resting on tidal rocks. Mother otters, however, are wary and in each instance, the mother escaped, carrying the carcass with her.

Although mother otters carry their pups beneath the surface during escape dives, they normally leave the young one floating on the surface when they dive for food. Dead pups, however, were carried by the mother while food diving. Unanswered questions are: Did the pup die because the mother carried it while diving for food? or did the mother carry it to avoid its loss because the fur became watersoaked causing it to sink after the pup died?

MOVING YOUNG

While swimming on her back, the mother sea otter carries her pup clasped between her forepaws (fig. 53). After a feeding or preening period, when the pup floats near its mother, she may grasp the pup with her forepaws and lift it onto her chest or she may roll on her side, clasp the pup to her chest and then roll again onto her back. If a mother with a pup is frightened or pursued, she holds the pup tightly with her forelegs and grasps the side of its head in her teeth as she turns to dive. Small young may drown during escape dives if the mother must dive repeatedly at short intervals (see Diving).

On land the mother otter grasps the side or back of the pup's head in her teeth and drags it. The pup is limp and relaxed, as if dead, while it is being dragged. Large juveniles usually walk beside the mother when they haul out but if alarmed, the mother grasps the youngster by the head and drags it. Although a juve-



FIGURE 53.—The mother sea otter carries her pup high on her chest, clasped by both front paws. White scar tissue was seen frequently on the noses of adult females but rarely on juveniles or adult males. It is presumed that these scars are inflicted by the male during mating when the nose of the female is grasped by the male's teeth, usually causing it to bleed. (KWK 57-29-27)

nile weighing 15 to 20 lb. (7 to 9 kg.) may be at least as agile on land as its mother, it relaxes completely when grasped by the mother and allows itself to be dragged, even over rough terrain, making no effort to assist in its own progress (fig. 54).

NURSING

The mother sea otter nurses her pup from two abdominal nipples, usually while floating on her back. Nursing may also take place on land (fig. 55). When the pup is small it usually rests on the mother's chest and abdomen while nursing, both on land or while the mother is floating. If the pup becomes hungry and cries while its mother is feeding, she grasps it around the chest with her forepaws and rolls it onto her chest, then turns it around, pushing it headforemost toward her abdominal nipples, allowing it to nurse.

As the pup grows larger it nurses while floating belly down, its body at right angles to that of its mother. Nursing periods are short, lasting 2 to 5 minutes. The pup kneads its mother's abdomen while nursing. It was difficult to time the duration of the nursing period because pups often fell asleep within 5 minutes and the actual duration of the nursing period was in doubt.



FIGURE 54.—This mother sea otter and her large juvenile (estimated weight 20-22 lb., 9-10 kg.) were surprised on land. Although the pup was capable of running at least as fast as the mother, she grasped the side of its head in her teeth and dragged it. On the rough terrain the pup bounced and caught in crevices but it remained relaxed and limp. When the two reached the water the pup was allowed to swim free of its mother's grasp. (KWK 62-17-37)



FIGURE 55.—*A*—After dragging her pup onto a rock, a mother sea otter preens and dries her fur while she supports the head of her nursing pup with a hind flipper. *B*—After drying her fur, the mother takes her pup on her chest and while she preens its fur with her forepaws she allows it to nurse from one of her two abdominal nipples. *C*—After the pup has nursed for 3 to 5 minutes the mother turns it around and fondles and plays with it. *D*—Mother and pup sleep, their fur dry and fluffy. This pup is probably a month to 6 weeks old. Its natal coat, particularly the long yellow guard hairs have grown considerably since birth. During the approximately 30-minute period when this sequence was taken, the mother frequently made soft chuckling or cooing sounds. (KWK 55-20-36, 55-934, 936, and 938)

Large juveniles often attempt to nurse. When the mother is reluctant, she rolls over. If the young otter is persistent and clasps her firmly with the forelegs, she may roll on a horizontal axis rapidly through 5 to 10 rotations, which usually dislodges it.

SWIMMING

At an early age, while the pup is still nearly helpless, the mother occasionally lifts it from her chest, places it in the water, then swims slowly away from it. The pup swims belly down paddling clumsily with all four feet. During these early swimming sessions, the pup frequently cries. The mother may remain just beyond the pup's reach for 50 m. or more before she allows it to overtake her when she again rolls or lifts it onto her chest. By the time the pup reaches an estimated age of 2 to 3 months, swimming ability is improved and it appears more at ease, crying less when swimming. When the mother swims near the pup it does not attempt frantically to reach her but swims quietly beside her (fig. 56). At this stage the pup apparently has not learned to swim on its back. Swimming on the back appears to develop slowly. While the mother is resting the pup often plays, swimming and making shallow dives near her. During these periods the pup appears to develop the ability to swim on its back.

DIVING AND FOOD GATHERING

After a pup learns to swim, it attempts to dive. Its first dives barely take it beneath the surface and considerable effort over a period of time is required to overcome the buoyancy of its air-filled fur. When the pup finally learns to reach the bottom in shallow water it brings up starfishes, bits of kelp, and pebbles. Seldom does it obtain edible items. Even after the pup is nearly a year old and about three-quarters as large as its mother, and may obtain much of its own food by diving, it continues to depend on its mother to satisfy its food needs.

From the time of birth the young otter is able to consume solid food which its mother gives to it. In the early weeks of life, however, stomach examinations indicate that milk predominates in its diet. After the pup is a month or two old it frequently pesters its mother for food. When she emerges from a food dive, the pup climbs onto her chest to beg for and receive part of the food she has brought to the surface (fig. 57). Large juveniles, able to dive well but unable to satisfy their food needs, may snatch food forcibly from the tolerant mother while she is floating on the surface and eating.



FIGURE 56.—This pup, probably about 2 months old, swims beside its mother. The mother removed the pup from her chest, placed it in the water, then swam slowly away while the pup followed. Swimming sessions, such as this, were seen often at Amchitka. They usually lasted for from 3 to 5 minutes and terminated when the mother again lifted the young one onto her chest. (KWK 1022)

SLEEP

Resting and sleeping are more frequent on the water than on land but mother otters may bring their young ashore to sleep. Newly born young often sleep while pressed against the mother's neck, under her chin. As the pup grows, it usually sleeps sprawled farther down on her chest or abdomen. When the young has reached a weight of about 10 lb. (4+ kg.), the mother holds the sleeping juvenile's head on her chest or abdomen (fig. 7) while its body floats at right angles to hers. Large juveniles sleep floating close beside and parallel to the mother. When mother and young rest on land, sleeping positions are similar (fig. 55).

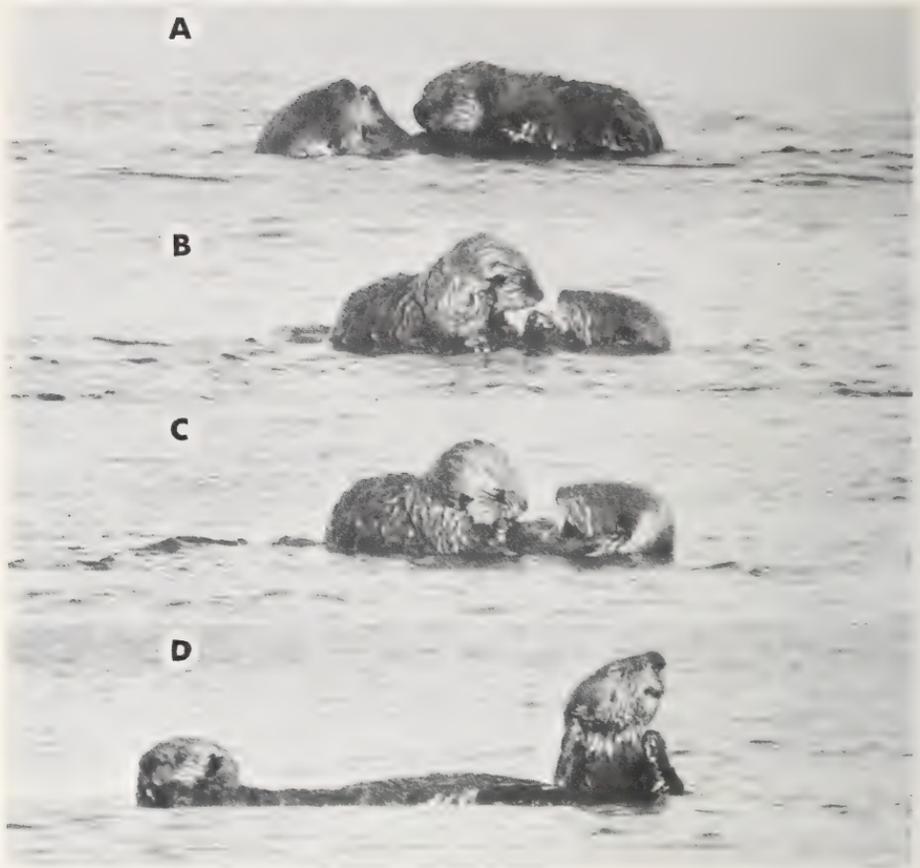


FIGURE 57.—*A*—The mother sea otter has just emerged from a feeding dive. While she eats, her pup (about 2 to 3 months old) crawls onto her belly. *B*—The pup tries to take food from the mother's paw. *C*—The mother reaches forward, placing food (a sea urchin) in the pup's mouth and paws. *D*—After finishing her food the mother rises vertically in the water while inhaling before rolling forward in another food dive. The pup continues to eat the food obtained from its mother. (KWK 65-24-13, 14, 15, and 16; 31 October 1965)

GROOMING

Shortly after birth the sea otter pup makes uncoordinated attempts to rub and groom its fur. Young animals are, however, dependent upon their mothers to keep their fur fluffy and dry. After a feeding period and before resting, the mother otter first grooms and washes her own pelage thoroughly while her pup floats nearby (figs. 41 and 43). When she has finished, she either takes her pup on her chest to preen and dry its pelage or drags it ashore. She licks the pup's fur thoroughly, then fluffs it and rubs it

dry with her forepaws. When the pup defecates, the mother cleans it by licking the fur in the anal region—often while doing this she holds the pup's hind flippers above her head with her forepaws. Mothers may continue to groom the fur of large juveniles to some degree even after these animals are capable of caring for their own pelage (fig. 52).

PLAY

Large pups frequently play. If two mothers with large young are feeding in the same area, the two pups may wrestle and chase each other. Frequently the mothers disapprove of such play as one or the other will break up the playing pair, take her young one onto her chest, and swim to another feeding area.

During a feeding period the mother sea otter satisfies her pup's food needs before she satisfies her own. While the mother continues to dive and eat, her pup explores the vicinity. If the pup sees an adult sleeping in floating kelp, it approaches quietly, then rising high in the water descends with both forepaws on the adult's chest or abdomen. Adults are tolerant of such behavior and usually indulge in a period of rolling and chasing play before abandoning the activity to leave the vicinity and continue resting.

ADOPTION

Juvenile otters, lost from their mothers, may join company with a tolerant adult, either male or female. Such pairs may be confused for mothers with pups. Figure 90 shows an adult male and juvenile. The two had been sleeping close to each other. The young animal was first to become alarmed by my presence. Besides retreating behind the adult, it placed its paws on the adult's back and sides. When the adult eventually was aroused and moved into the water, the juvenile followed him closely and remained in company with him as he swam to deep water.

On 16 February 1964, a newly captured adult female (which had been given a mild injection (1 cc.) of Sparine) was placed in an enclosure with an orphaned juvenile female several months of age (wt. 18 lb., 8.2 kg.). Within a few minutes the juvenile approached the adult and was allowed to nurse. Two hours later the adult clasped the juvenile around the neck with her forelegs when I entered the enclosure and alarmed them. Similar nursing and protective behavior was repeated but at increasingly long intervals until 24 February. By this time the adult pushed the juvenile away when it attempted to nurse and when fish were given to each animal at feeding time, robbed it of food. During rest periods,

however, the two slept in close proximity and when alarmed by a human visitor or unexpected noise they clasped each other with their forelegs.

An adult female and two juveniles of about the same size were netted together on a beach at Amchitka Island on 2 April 1955. The adult showed maternal attention to one pup and tolerated the other, allowing both to nurse. The adult, however, groomed only one juvenile and my conclusion was that the other was a stray or an orphan that had joined company with the mother and pup. Additional evidence that this may have been the situation was observed on 9 April. The pup presumed to be the mother's offspring died shortly before this group of sea otters was to be liberated at the Pribilof Islands. The surviving juvenile and the adult female were liberated together. In the water, the juvenile attempted to climb onto the adult but she ignored it and swam quickly away. We then retrieved the screaming juvenile.

The above observations indicate to me that under certain conditions a tolerant adult otter might contribute to the survival of an orphaned juvenile. It appears, however, that under conditions of stress and during times of food shortage an adult might give little more than companionship toward the survival of an "adopted" juvenile.

Relation to Other Animals

Within its usual habitat, which includes the beach, offshore rocks, and water out to a depth of about 30 fathoms (60 m.), the sea otter is often near other mammals and birds. Two species, the Bald Eagle and killer whale, are discussed under "Predation."

Harbor seals and sea otters often haul out on the same rocks and rest or sleep near each other. Each species appears to ignore the other; no interspecific strife of any kind was ever seen. In general, harbor seals and sea otters appear to prefer slightly different resting places. At St. Makarius Point on Amchitka several large rocks are located a few meters offshore. Some of these were habitually used by sea otters and others by harbor seals. If a sea otter found a harbor seal on a favorite resting spot, it selected another place. On several occasions a harbor seal was seen to cause a sea otter to move. When the moving seal jostled the sea otter in attempting to pass, the otter got up and moved.

Interspecific competition for food is probably negligible. The harbor seals at Amchitka feed primarily on octopus and Atka mackerel (Kenyon, 1965a). Both of these species may be taken

by sea otters but our fishing operations indicated that fish populations at Amchitka are large. Also, sea otters tend to feed on sedentary fish that were not found in seal stomachs.

Steller sea lions seldom chose places that were favored by sea otters for resting on land. When sea lions passed near sea otters that were diving for food, the otters usually raised themselves high in the water to stare at the sea lions. Otherwise the two species ignored each other.

Parasitic worms (*Terranova decipiens*, for example) which commonly infest the harbor seal and sea lion, enter the encysted stage in fishes. Sea otters that eat fish also become infested. *Halarachne miroungae*, a nasal mite commonly found in harbor seals, were rarely found in wild sea otters. These may have been picked up by the sea otters at a location commonly used by the two species. In the wild these pinniped parasites seemed not to seriously affect sea otters.

Glaucous-winged Gulls frequently obtained scraps from otters while they fed on fish. I did not see gulls attempt to take fish away from a feeding otter but they swam close to feeding otters or hovered above them ready to take scraps (fig. 58). When we were searching for sea otters during census studies, we found that gulls were a useful indicator of the location of feeding otters. A group of gulls sitting together on the water usually marked the location where an otter would emerge from a food-gathering dive.

Unlike many other mammals, sea otters at Amchitka did not appear to recognize the calls of birds as possible indicators of approaching danger. On a number of occasions, Black Oystercatchers (*Haematopus bachmani*) and Emperor Geese (*Philacte canagica*) were alarmed by our approach when we were stalking sea otters that were hauled out on the beach. Although the calling birds sometimes flew directly over the otters, they appeared to pay little or no attention to them.

Rats (*Rattus norvegicus*) introduced to Amchitka during World War II often entered the sea otter enclosure to search for food scraps. On one occasion a rat approached a sea otter that was grooming its fur while resting on its back beside the pool. After sniffing at the sea otter's side, the rat suddenly jumped onto the otter's chest. Quickly the otter struck the rat with its forepaw, knocking it a distance of nearly a meter.

In general, it did not appear that the sea otter was in serious competition with other mammal and bird species within its environ-



FIGURE 58.—An immature Glaucous-winged Gull waits expectantly for fish scraps discarded by a feeding sea otter. Groups of two or three gulls sitting together on the surface in the Aleutian area usually indicated the location of a sea otter feeding on fish. While the otter was beneath the surface the gulls waited near the location where they expected it would emerge from a food-gathering dive. (KWK 57-31-2)

ment at Amchitka or that any interspecific strife existed. Perhaps in periods of food scarcity, survival of gulls is enhanced through their utilization of the otters' discarded food scraps.

FOOD AND FEEDING BEHAVIOR

In this section, methods of food gathering and consumption, the kinds and quantities of foods eaten, and the food requirements of sea otters in the wild and in captivity will be discussed. This information was gathered by means of field observation, quantitative and qualitative studies of stomachs and feces, and data gathered from otters held on Amchitka Island, the Woodland Park Zoo, Seattle, and the Tacoma Aquarium.

The amount of food required by the sea otter is greater than that of most animals of comparable size. The sea otter stores body fat but it does not accumulate fat in quantities comparable to the blubber stored by most marine mammals. Because it lacks an insulating blubber layer, the sea otter is dependent for warmth in its chilly habitat upon its fur and upon the rapid metabolic use of energy from food. Passage of food through the gastrointestinal tract is rapid. Food marked with red dye passed through an otter in about 3 hours (Dr. James A. Mattison, personal communication).

Periods of fasting which are characteristic of other marine mammals, such as certain cetaceans and pinnipeds, would prove fatal to the sea otter. Its vitality is maintained by a relatively high and constant consumption of food.

Studies comparable to ours in Alaska were conducted in the Kuril Islands by Soviet biologists Nikolaev and Skalkin (1963) and Nikolaev (1965b).

Feeding location

Sea otters habitually gather their food from the bottom or near it in salt water ranging in depth from a few feet, in the intertidal or littoral zone, to about 20 fathoms (40 m.). This is the greatest depth from which we took an otter having food in its stomach. The majority of otters feed within about one-half mile of shore. In certain areas, particularly off the north shore of Unimak Island in the Bering Sea, where shallow water extends far from shore, they commonly range 3 to 10 miles offshore and one was seen in this area about 17 miles from shore in water about 30 fathoms (56 m.) deep (see table 10).

That certain individual animals would learn to feed on pelagic forms and thus divorce themselves from the necessity of remaining in relatively shallow water is improbable. Observations indicate that the sea otter subsists only on benthic organisms. Wide, deep passes between islands, which prevent bottom feeding, appear to act as a barrier to the spread of sea otter populations. (See Distribution and Numbers.)

Food Gathering

Many observations indicate that the sea otter uses its forepaws primarily to gather food and that the tactile sense is important in locating food organisms. A captive female with good eyesight was offered food in a bucket about half full of turbid water. In one instance the bucket contained about 200 small crabs (*Pachygrapsus*), 4 blue mussels (*Mytilus edulis*), and a number of pebbles of various sizes. The otter had eaten both organisms before but showed a preference for mussels. When the bucket was presented to her, she immediately reached to the bottom with both forepaws, her chin on the edge of the bucket, and within a few seconds retrieved the four mussels. She made no attempt to place her head in the bucket or to look into it. Thus, she demonstrated a high reliance on her tactile sense in selecting the mussels from among pebbles and crabs.

Numerous observations of Susie, during the 6 years that she lived at the Woodland Park Zoo, indicated that she relied heavily on her tactile sense while retrieving food placed in her pool. She was blind in her right eye when captured and blind in both eyes for over a year before death. During this period of total blindness she continued to find food and to select the most desired kinds, using her paws to select it. I have observed several healthy wild otters that were blind in one eye but have seen only one that was apparently blind in both eyes. This animal was emaciated and near death. Existence without sight among breakers in the harsh coastal environment would probably be impossible even if food could be found.

Wild otters normally terminate feeding activities before dark and do not begin morning feeding until after sunrise. Mothers which must provide for their young, however, may continue diving for food after dark. I watched a mother diving one evening until darkness prevented further observations. During the period shortly before visibility was lost, the otter continued to bring food items (mostly sea urchins) to the surface in the usual quantities.

I thus inferred that she relied primarily on her tactile ability to find food.

Sight under water, however, is apparently sometimes used in locating food. Captive otters on Amchitka often searched the bottom of their pool by swimming on the surface, head submerged. Food items on the bottom were quickly located visually in this manner and retrieved.

The vibrissae may also aid in the search for food. Captive otters, having an abundance of easily located food, abrade the vibrissae to a minor degree; they may reach a length of 10 to 12 cm. (fig. 59). The vibrissae of wild otters may be worn off short, to a length of about 1.5 to 2.5 cm. Presumably the abrasion occurs during the search for food among rocks.



FIGURE 59.—A captive otter pounds a clam (*Protothaca*) on the cement edge of her pool. This otter came from Amchitka where breaking shells of food organisms by pounding was not observed. The whiskers of captive otters grow long, as illustrated here. In the wild the whiskers are usually abraded and short. Presumably wear occurs during the search for food among rocks. (KWK 57-24-16)

It would appear that under usual circumstances the sea otter does not use its teeth under water. On many occasions I have seen sea otters come to the surface clasping living fish to their chests with their forepaws. After surfacing, each otter grasped the fish's head in its jaws and killed it, suggesting that the teeth are not used to kill fish beneath the surface.

That otters may use their teeth beneath the surface when necessary to obtain food was demonstrated at Amchitka. In Constantine Harbor the otters apparently learned that our net floats marked an abundant supply of fish. We often saw an otter on the surface, eating, near the floats. When we pulled the nets, we found fish that the animals were unable to remove but which they had partly eaten underwater. Usually about half the fish was left, but occasionally only the head and pectoral girdle remained. The fish were not bitten off cleanly; they were chewed, leaving strips of skin and tooth-marked shredded flesh attached to the entangled portion. The frequency with which we saw otters eating fish on the surface near the nets indicated that they were able to remove a considerable number. Rarely did otters become entangled in the nets and drown.

The stomach of one adult male contained a number of large clam siphons. The siphons, with adhering fragments of mantle and muscle tissue, appeared to have been ripped from the clams by the otter's paws or teeth. Visceral material from these clams was lacking in the stomach. Presumably the siphons protruded from the sea's floor and the remainder of the clam was not dug out.

Fisher (1939) postulated that the sea otter used either a rock or its canine teeth to remove abalones from the bottom. Cox (1962) presents convincing evidence that the sea otter uses a rock to break the abalone shell; that the otter then removes the viscera and, after the abalone dies and releases its hold on the rock bottom, brings it to the surface where it eats the muscle from the remainder of the shell. The behavior of a captive otter, which persistently pounded a rock against an underwater drain cover until it was able to damage the fastening and remove it (Kenyon, 1959), lends strong support to the use of a rock rather than the teeth in obtaining abalones. The canine teeth are probably not of sufficient strength to remove any but small abalones from the bottom.

A unique habit related to feeding in the sea otter, that of pounding hard-shelled mollusks against a stone or other mollusk held on the chest, has been given much attention, most recently by Hall and Schaller (1964). Although this habit is frequently observed

in California sea otters, it is rarely observed in the parts of Alaska where I have watched sea otters feeding or in Soviet waters (Barabash-Nikiforov, 1947). At Amchitka, I have twice observed subadult otters pounding a chunk of coralline algae held between the forepaws against another resting on the chest. This behavior appeared, however, to be play as the animals did not attempt to find food in the algae after breaking it but discarded the material after a few minutes of intermittent pounding.

That Alaska sea otters are capable of using the pounding technique was demonstrated by a captive taken at Amchitka Island. Soon after Susie had become accustomed to captive conditions at Seattle, several small stones and whole butter clams (*Saxidomus*) were placed in her pool. Although she used a stone as an anvil on which to break the clams, she used it in other ways too. The stone was also held in the paws and used as a hammer. Also, if a large number of clams were given to her she often neglected to obtain the stone but pounded the clams against each other (fig. 60). Clams, sea urchins, fish, and rocks were pounded against the cement-constructed side of the pool (fig. 59).



FIGURE 60.—Clams (*Saxidomus*) were broken open by pounding one against another held on the chest. If a rock was handy, this captive otter pounded clams against it. Clam meats are scooped from the shell with the tongue and lower incisors. (KWK 57-22-32)

What Food is Eaten

The food of the sea otter consists predominantly of benthic invertebrates and fish. At Amchitka Island fish predominate (50 percent by volume), mollusks are second in importance, and echinoderms (mostly sea urchins) third (table 11). In other areas, mollusks and echinoderms are found to predominate.

That the feeding habits of the sea otter vary in different areas, in accordance with the abundance of food organisms, is indicated by the statements of Snow (1910), who claimed to have examined hundreds of stomachs. He stated that he did not find clams among the food species eaten by the sea otter and that—

I have never noticed any traces of the shells of clams, or limpets, or mussels in the stomachs I have examined, but found as a rule, the remains of crabs, sea urchins, sea-squirts, and what looked like fish spawn.

He also said that he very seldom found any remains of "ordinary fish, the bones of which would immediately prove its presence." He adds that the sea otter "finds no difficulty in chewing up good-sized crabs, which judging from the contents of the many stomachs I have opened and examined, appear to be its chief food." Mr. H. P. Hansen, a king crab (*Paralithodes platypus*) fisherman told me (1964) that in the Andreanof Islands he "often sees sea otters eating king crabs, sometimes quite large ones."

Although a large variety of organisms is eaten, individual otters appear to have certain food preferences. "Individual sea otters often prefer a certain food in the assortment of food characteristic to them" (Barabash-Nikiforov, 1947). Some adult males at Amchitka subsist primarily on fish and rarely eat sea urchins. In general, at Amchitka it appears that the otters fall into two groups—those eating mostly fish and those eating mostly invertebrates. The fish eaters, as would be expected, show a higher degree of infestation with certain parasites (principally *T. decipiens*)

TABLE 11.—*Volume and classification of food found in 309 sea otter stomachs from Amchitka Island, Alaska*

[Only stomachs containing food are considered. The samples include 107 stomachs collected in January and February 1962, 20 stomachs collected in October 1962, and 182 stomachs collected in March and April 1963]

Food item	Total volume (milliliters)	Percent of total volume
Annelid worms	929	1
Crabs, shrimp, etc.	467	<1
Mollusks	34,895	37
Echinoderms (mostly sea urchins)	10,020	11
Tunicates	363	<1
Vertebrates (fish)	46,518	50

than those subsisting primarily on invertebrates. Also, the bones of "fish-eaters" are white but the bones of those otters utilizing invertebrates—including many sea urchins—are stained purple by the biochrome polyhydroxynaphthoquinone (Scott, *in* Fox, 1953, footnote p. 195).

Much indigestible material is swallowed incidentally in the consumption of nourishing food. Part of the test of almost every sea urchin eaten is crushed by the postcanines and swallowed. Many stomachs contain scraps of red and brown algae. Seaweeds, as Barabash-Nikiforov (1947) and Fisher (1939) indicate, cannot be considered an otter food. This material appears in the feces unaltered in appearance, except for the wear and abrasion encountered during passage. I have often seen such scraps of kelp eaten when entangled among the spines of sea urchins. Its occurrence in stomachs is accidental.

Small pebbles, gravel, and bits of hard clay occurred in 14 percent of 475 stomachs from Amchitka. One stomach contained 325 small stones. Stones are also commonly found in the stomach of fur seals and sea lions (*Eumetopias* and *Zalophus*) and no sure explanation of their presence is known. Although the "gastroliths" of pinnipeds are usually waterworn or smooth, the stones we found in sea otter stomachs often looked as if they had been freshly broken apart; they were seldom waterworn or smooth. No reason for the swallowing of this indigestible material is known.

After food has been selected from the substrate, it is stored for transportation to the surface in folds of loose skin (fig. 11) which extend from the axilla across the chest (see Kirkpatrick et al., 1955; Barabash-Nikiforov, 1947). If only enough food is gathered to fill the pouch on one side, it is stored under the left foreleg and paw. If a large quantity is gathered, it may be stored and carried in the chest pouches under both forelegs.

When an otter captures a large octopus or fish and satisfies its appetite before it consumes the entire organism, it often sleeps on the water's surface with the remains of such an uneaten meal clasped to its chest. After sleeping for awhile, the otter awakens and continues to eat. Uneaten food, however, is not retained for an extended period. After the animal has nibbled its food intermittently for perhaps 2 hours, and then begins to groom, the food is forgotten and allowed to sink. Captives retrieve discarded food and again eat after grooming and resting.

On occasions when we have pursued otters with an outboard motor-powered dory we have interrupted their feeding. When this

occurs, the otters do not relinquish food remaining in the chest pouches. In one instance we interrupted a feeding adult male and pursued him for nearly 2 hours. He invariably evaded us by surfacing at unpredicted places. We finally abandoned as futile our effort to capture him and he immediately continued to eat the sea urchins he had carried under his left foreleg during the entire chase.

When captive otters are given food on land, the items are transferred to the chest pouch under the left foreleg with the assistance of the right paw. The otter then walks on three legs to return to the water with the food. If the quantity of food exceeds the capacity of the pouch under the foreleg, additional food may be grasped and carried in the jaws.

A captive, resting on her side near her pool, was able to place 18 clams (*Protothaca*), ranging from about 3 to 4 cm. in greatest diameter, under her left foreleg. When a 19th was added, most of the others fell out. Eight clams were easily carried under the left foreleg while the otter walked on three legs about 3 m. to the pool.

Where Food is Eaten

Sea otters normally bring food items to the surface and, using their forepaws, pass the food to the mouth and eat while floating on their backs. Hooper (1897) probably misinterpreted a statement by Steller (1751) when he stated that "the otter haul out upon the land to feed on the sea urchins and the other shellfish exposed at low water." Wild sea otters do not carry food from the water to exposed rocks or beaches and normally do not emerge from the water to obtain food. I know of no record of a wild otter voluntarily consuming food on land.

A wild otter that habitually frequented the inshore water near our fish-cleaning platform quickly learned to take fish scraps from our hands. After several weeks he often left the water to beg for food while following us about. Even though he accepted pieces of fish as far as 25 m. from the water (fig. 61), he always carried the food back to the water before eating it.

Captive otters, if they are denied access to water, will eat while lying on a dry surface, but usually reluctantly. Captives having free access to water and dry areas, voluntarily leave the water to obtain food when they are hungry (fig. 62) but return to the water to eat it.

Periodically (usually at intervals of 20 to 30 seconds) while consuming food at the surface, the sea otter stops eating and rolls



FIGURE 61.—A wild sea otter accepts a fish head from Innokenty Golodoff. This otter frequented the area where we discarded fish scraps. He soon became tame and emerged from the water to follow us as far as 25 meters from the water to beg for food. He never consumed food on shore but carried it in his mouth or under the left foreleg to the water where he ate while floating on his back. (KWK 57-34-31)

over (fig. 63). This action washes food scraps from the chest where they were either purposely discarded or accidentally dropped.

Stomach Analyses

The best information available on food habits of the sea otter was derived from the examination of 475 stomachs from otters most of which were shot at Amchitka Island (table 12). Previously Wilke (1957) studied stomachs from five otters taken there. Also, we examined a number of stomachs of otters found dead or dying on beaches.

Stomachs were removed from sea otters as soon as practicable, usually within 2 to 3 hours after death. They were then injected with a 10 percent formalin solution and immersed in a large container of formalin solution, where they soaked for several days.



FIGURE 62.—A captive adult female sea otter clasps one piece of fish to her chest under her left foreleg while she reaches with her teeth to grasp another. After receiving all the food she could carry under the foreleg and in her teeth, she returned, walking on three legs, to the water before she consumed her food. The long outer or fifth digit of the hind foot is illustrated. (KWK 59-13-10)

TABLE 12.—*Sea otter stomachs examined*

[This listing includes animals presumed to be healthy. Most of them were shot. Animals found dead and dying on beaches are excluded]

Date	Location	Stomachs empty		Stomachs with food		Total examined
		Number	Percent	Number	Percent	
6-10 June 1960	Shumagin Islands	4	67	2	33	6
8-10 July 1960	Bering Sea ¹	2	50	2	50	4
22 Jan.-9 March 1962	Amchitka Island	32	23	107	77	139
26-29 Oct. 1962	do	4	17	20	83	24
14 March-2 April 1963	do	119	39	183	61	302
Total		161	34	314	66	475

¹ Otters were taken at sea off the north coast of Unimak Island.



FIGURE 63.—At frequent intervals, while floating on the surface and consuming food, the sea otter stops eating and rolls about its longitudinal axis through 360°. This action washes food slime and scraps from the chest. It is an important behavioral characteristic that helps to keep the fur clean and waterproof. Food slime destroyed the water-resistant and insulating qualities of the fur of captive otters that were not given access to water. In nature, sea otters eat only in the water—never on shore. (KWK 1021)

After removal from the pickling bath, they were packed in wide-mouthed, 5-gallon cans and shipped to the Seattle laboratory. After removal from the stomach, the weight and volume of the contents were measured, the food species were identified, the percentage composition of each species was evaluated, and all pertinent data for each specimen was entered on a 3-by-5 card. A collection of identified invertebrates and fish, accumulated at the Seattle laboratory for the study of marine mammal food habits, aided identification of food species. Food organisms that could not be identified locally were sent to specialists who examined them and made identifications whenever this was possible.

If a feeding otter swallows the test, shell, or bony parts of a food organism, the identification of food species may not prove difficult. Such hard parts are usually not crushed sufficiently to obliterate all diagnostic characteristics. Often, however, the feeding otter discards most or all of the hard parts, making identi-

fication of food species difficult or impossible. As the stomachs were examined, a collection of unknowns was accumulated. Food organisms found in various stages of mutilation in different stomachs eventually furnished material that made possible the recognition of small fragments or badly mutilated food in other stomachs. The food species found in sea otter stomachs taken at Amchitka are shown in table 13 and a general account of these organisms and the sea otter's habits relating to their consumption follows.

Annelid worms were usually torn into pieces several centimeters long and the pieces swallowed with minor damage from mastication. Considerable slimy mucus accompanied annelid remains.

Crabs were torn to pieces and usually the carapace was not among the stomach contents. The larger legs and chelipeds were usually thoroughly crushed.

Among the mollusks that were found, various techniques of ingestion were indicated. Small chitons were slightly crushed and often swallowed nearly intact. Large ones (*Cryptochiton stelleri*) were thoroughly crushed and torn, reducing them to small pieces. The flesh of limpets was scooped from the shell and swallowed nearly intact and the shell discarded. Rarely was a fragment of limpet shell swallowed.

TABLE 13.—Frequency of occurrence of food species in 309 sea otter stomachs from Amchitka Island, Alaska

Food organism	Number of stomachs having item—			Total	Percent
	Of 107 stomachs February–April 1962	Of 20 stomachs October 1962	Of 182 stomachs March–April 1963		
Annelida			5	5	
Ribbon worm <i>Emplectonema</i> sp.....	1	—	—	1	
Sand worm <i>Nereis</i> sp.....	2	—	—	2	
Lug worm <i>Arenicola</i> sp.....	5	—	—	5	
Total.....	8	—	5	13	2
Arthropoda:					
Crustacea:					
Olive green isopod <i>Idothea (Pentidotea)</i>	6	—	3	9	
Amphipods (probably incidental).....	5	—	6	11	
Shrimp <i>Sclerocrangon boreas</i>	1	—	—	1	
Hermit crab <i>Pagurus</i> sp.....	3	3	9	15	
Crab:					
<i>Cancer</i> sp.....	1	5	—	6	
<i>Telmessus cheiragonus</i>	1	1	—	2	
<i>Paralithodes?</i> (larval).....	2	—	—	2	
<i>Placetron wosnessenski</i>	5	—	1	6	
<i>Haplogaster</i> sp.....	—	—	5	5	
Unidentified.....	—	—	4	4	
Shrimp unidentified.....	—	—	1	1	
Total.....	24	9	29	62	7

TABLE 13.—Frequency of occurrence of food species in 309 sea otter stomachs from Amchitka Island, Alaska—Continued

Food organism	Number of stomachs having item—			Total	Percent
	Of 107 stomachs February– April 1962	Of 20 stomachs October 1962	Of 182 stomachs March– April 1963		
Mollusca:					
Amphineura:					
Lined chiton <i>Tonicella</i> cf. <i>T. marmorea</i>	1	—	—	1	
Mossy chiton <i>Mopalia</i> sp.....	1	—	—	1	
Giant chiton <i>Cryptochiton</i> <i>stelleri</i>	4	5	8	17	
Chiton unidentified.....	—	—	2	2	
Gastropoda:					
Limpet <i>Acmaea</i> sp.....	5	5	10	20	
Snail:					
<i>Thais</i> sp.....	1	—	4	5	
<i>Natica clausa</i>	1	—	—	1	
<i>Buccinum</i> sp.....	10	—	7	17	
<i>Argobuccinum</i> <i>oregonensis</i>	6	—	8	14	
Gastropod unidentified.....	—	—	3	3	
Pelecypoda:					
Cockle <i>Clinocardium</i> <i>ciliatum</i>	2	—	1	3	
Clam:					
<i>Liocyma viridis</i>	1	—	—	1	
<i>Serripes</i>	1	—	—	1	
<i>Macona</i> sp.....	—	—	3	3	
Unidentified.....	—	—	2	2	
Mussel:					
<i>Musculus vernicosa</i>	10	12	24	46	
<i>Volsella volsella</i>	22	6	21	49	
Pearly monia <i>Pododesmus</i> <i>macrochisma</i>	28	2	20	50	
Cephalopoda: <i>Octopus</i> sp.....	12	4	14	30	
Mollusk unidentified.....	—	—	3	3	
Total	105	34	130	269	31
Echinodermata:					
Asteroidea:					
Blood star <i>Henricia</i> sp.....	15	2	11	28	
Six-rayed star <i>Leptasterias</i> sp.....	29	—	28	57	
Starfish <i>Ceramaster</i> sp.....	6	—	6	12	
Brittle star Ophiuroidea.....	1	—	13	14	
Echinoidea: Green sea urchin					
<i>Strongylocentrotus</i> <i>drobachiensis</i>	71	17	92	180	
Holothuroidea: Sea cucumber					
<i>Cucumaria</i> sp.....	17	4	5	26	
Total	139	23	155	317	37
Chordata:					
Tunicata: Tunicate (2 species)					
	4	1	6	11	1
Vertebrata:					
Osteichthyes:					
Sablefish <i>Anoplopoma</i> <i>fimbria</i>	1	—	—	1	
Rock greenling <i>Hexagrammos</i> <i>supercilius</i>	5	1	9	15	
Atka mackerel <i>Pleurogrammus</i> <i>monopterygius</i>	4	2	3	9	
Red Irish lord <i>Hemilepidotus</i> <i>hemilepidotus</i>	18	4	14	36	
Globefish <i>Cyclopterichthys</i> <i>glaber</i>	22	—	87	109	
Cottidae unidentified.....	1	—	—	1	
Fish and fish eggs unidentified.....	5	—	—	5	
Total	56	7	113	176	22
Grand total				848	100

Snails were recognizable in stomachs because the tough muscular foot was usually little affected by chewing and often the chitinous operculum remained intact and attached to the foot. The shells of small snails (*Buccinum* sp.) were often swallowed but those of large ones (*Argobuccinum oregonensis*), except the operculum, were not.

Clam shells, except those from small individuals, were seldom present in the stomach. One stomach contained about 2 liters of clam meats, the foot and viscera of many almost intact, but not one scrap of shell. The shell of thin-shelled clams (*Serripes groenlandicus*) were fragmented and swallowed in considerable quantity.

The small mussel *Musculus vernicosa*, which was consumed in large numbers, was usually swallowed whole. Individual mussels may appear in the feces with the valves still intact. Many fragmented shells of larger mussels, such as *Volsella volsella*, sometimes appeared in feces. Often, however, stomachs having a number of mussels contained little or no shell. The viscera were recognizable by their orange color and attached byssus.

The pearly monia (*Pododesmus macroschisma*) appeared in 50 stomachs, often in considerable quantity but only a few tiny fragments of shell were found. Observations of feeding otters revealed that, after slightly loosening the valves with one canine tooth, the two valves were twisted horizontally past each other between the paws so that the viscera could be quickly scooped with the lower incisors and tongue from the half shell to which it adhered. Seldom are the shells broken during this procedure. Since few hard parts of this species are ingested, it is not revealed as an important food species in fecal examinations.

Octopuses are eaten with particular enthusiasm by captive otters and wild otters also appear to relish them. Because of its size (commonly 2 to 4 lb.), the octopus constitutes an excellent food source at Amchitka. Apparently otters are not disturbed by the writhing tentacles of this mollusk. Pieces of arms are bitten off and eaten when one moves within range of the paws and mouth. Other tentacles wrap themselves about the otter's head, legs, and body while the otter continues to tear off and swallow chunks of flesh (fig. 64). Occasionally a sucker attaches itself to the otter's palate but it is quickly torn loose by the extended claws of the forepaws. A large octopus may furnish sufficient food for more than one feeding period. The chitinous beak of the octopus may or may not be swallowed. Even if it is, fecal examinations do not reveal the importance of this food species.



FIGURE 64.—Food taken from a sea otter stomach: *A*—fragment of octopus jaws; *B*—small pebbles; *C*—octopus tentacles and mantle; *D*—ascarid worms (probably *Terranova decipiens*); *E*—fins, skin, and opercular spines of the red Irish lord (*Hemilepidotus hemilepidotus*). The sea otter's teeth are not adapted to cutting; the tough octopus flesh is swallowed in chunks that show little effect of chewing. (The pencil is 12 cm. long.) (KWK 1013)

A captive otter was fed 5 lb. (2.3 kg.) of squid (*Loligo*) daily. Before beginning to eat each squid he removed the pen by grasping its tip between his incisors and drawing it from the mantle. He then discarded it over his left shoulder by turning his head quickly to the side.

Starfish of several species are of minor value as a sea otter food. Although a number of stomachs (111) contained starfish remains, the volume was small. I have seldom observed a feeding otter that ate an entire starfish. The otter usually tears off and eats one or two arms of a starfish, then loses interest and discards the remainder.

Fecal and stomach examinations indicate that the green sea urchin (*Strongylocentrotus drobachiensis*) is frequently eaten and this food has been considered the most important, if not essential, item in the diet of the sea otter. With captive sea otters, Shidlovskaya (1947) stated that "Longer interruptions than 5 days in

feeding sea urchins should not occur." Evidence that this assumption is not always true is presented under "Relative Values of Sea Otter Foods."

The method of ingesting green sea urchins varies according to the size of the sea urchin and also somewhat according to the habits of individual otters. Stomach examinations and observations of feeding otters indicate that some animals habitually ingest more of the test than others. Small urchins are crushed by the molars and usually at least part of the test is swallowed (fig. 65). Large urchins may first be bitten with the postcanines on one side,



FIGURE 65.—Intact sea otter food organisms are shown at the top of columns A to E, and partially digested fragments of the same species removed from stomachs are shown below. A—six-rayed star (*Leptasterias* sp.); B—green sea urchin (*Strongylocentrotus drobachiensis*); C—sea cucumber (*Cucumaria* sp.); D—pearly monia (*Pododesmus macroschisma*); E—mussel (*Mytilus edulis*); F—fragments of marine algae. Algae, which is voided undigested in the feces, is not a food species but is eaten accidentally. (KWK 1011)

fracturing the test. Then, with the aid of paws and teeth, the otter is able to open the test and with the lower incisors and tongue to scoop out the exposed viscera and gonads (Hildebrand, 1954). Large urchins may also be opened primarily with the paws. The top of the urchin is cradled against the palm of one paw while the digits and palm of the other exert pressure on the test surrounding the urchin's oral opening, crushing it inward. The urchin may be rotated to facilitate application of pressure. When the test is sufficiently weakened the teeth are used to remove the broken test so that the contents may be scooped out. The empty test may be tossed aside with the paws or dropped on the chest or belly while another item is eaten.

Sea cucumbers appear to be of minor importance in the diet of the sea otter, they appeared in only 26 stomachs. They are tough and showed relatively little mutilation from chewing (fig. 65). We did not give them to captive otters but Shidlovskaya (1947) says that they were eaten reluctantly by her captives.

Tunicates, having a tough leathery covering, do not appear to be an important food. A few individuals were in 11 stomachs.

Fish, particularly the globefish (*Cyclopterichthys glaber*), contributed the greatest food volume (50 percent of all food volumes combined) among stomachs taken at Amchitka. It is evident that this food source, along with mollusks, is of major importance.

The identification of fish species eaten is sometimes difficult because sea otters often discard diagnostic bony plates from the heads of fish. Also, the bones that are swallowed may be severely crushed during mastication. The variety of fish eaten is not large and a series of specimens was accumulated during stomach examinations that enabled us to identify most fish remains.

The fish taken are usually bottom-inhabiting forms and are somewhat sedentary or sluggish. The red Irish lord (fig. 64) and globefish, both sluggish species, occurred in 75 percent of the stomachs containing fish. Information obtained from hundreds of trammel net hauls at Amchitka, as well as data from the stomachs of harbor seals taken there, indicate, however, that the rock greenling and Atka mackerel may be more abundant than the red Irish lord or globefish. However, they are more active than these two species and possibly for this reason are less frequently captured by the otters.

The sea otter does not appear to be well adapted to the capture or consumption of fish. The dentition is very unlike that of seals and porpoises. All marine mammals that eat fish, except the sea otter, capture them with their teeth and swallow them without

mastication (seals and sea lions may, however, tear chunks from a fish that is too large to swallow intact). The sea otter apparently captures fish with its paws and all fish flesh found in stomachs had been torn into chunks that were crushed before swallowing. No fish were swallowed whole.

Thus, the sea otters' manner of capturing and eating fish is unique among marine mammals. After the fish was brought to the surface and killed by a crushing bite at or near its head, it was held in the paws and chunks were torn from it, masticated to a moderate degree and swallowed. Some chunks of fish found in stomachs measured about 3 x 4 x 5 cm. Eating usually began at the fish's tail and often all or most of the head (particularly of the cottids) and viscera were discarded. Strong adult males clasped the fish body firmly with the forepaws and extended claws, then, starting at the anterior end ripped the skin with the canines and incisors from first one side, then the other. The flesh and bones were then rapidly eaten like a candy bar. Globefish, being scaleless and having soft bones, were consumed almost in their entirety.

In the Shumagin Islands four adult male and one adult female sea otters were taken on 6 and 7 June 1960 at Simeonof Island and one female on 11 June at Little Koniuji Island. Four stomachs were empty. The stomach contents of two males are shown in table 14.

Of interest is the fact that among the contents of the two stomachs which had a combined volume of 3.48 liters (3.7 qt.), mostly clam meats, there were no scraps of clam shell. For this reason, the species eaten could not be positively identified. Dr. G. D. Hanna did, however, tentatively identify the large siphons as belonging to the Washington clam (*Schizothaerus nuttallii*). Perhaps this large clam was not removed from the sand bottom or the shell could not be broken or opened by the otter. About 1 inch of the siphons appeared to have been bitten or ripped from the clam bodies. A captive otter demonstrated that clams, even large horse clams (*Schizothaerus*), are cracked either against a

TABLE 14.—Stomach contents of two male sea otters from Simeonof Island, Shumagin Islands, Alaska

Specimen and food item	Volume (milliliters)	Individuals
KWK 60-6: Clam feet.....	2,425	155+
KWK 60-8:		
Large clam siphons.....	844	59
Small clam feet.....	206	17
Horse mussel.....	5	1
Whelk operculum.....	trace	1
Total.....	3,480	233

rock or against another clam resting on the otter's chest (fig. 60). It is thus inferred that clams which are buried are not dug from the bottom.

In the Bering Sea on 8 and 10 July 1960, one adult male and two adult female otters and two pups were taken 31½ miles off the north shore of Unimak Island in a depth of 15 fathoms and 9 miles north of the Alaska Peninsula in 20 fathoms. The food habits of these individuals are of particular interest because no other stomach specimens of otters which habitually remain offshore are available. The foods found in three of the stomachs are shown in table 15. All food items (clams, crabs, and a hexagrammid fish) are benthic forms. This indicates that here, as in other areas, the sea otter is predominantly a bottom feeder (see Diving). The lack of feces on the beaches of nearby Amak Island in July 1961 and 1963 indicates that otters in this area seldom come ashore.

Fecal Analyses

Studies of sea otter food habits prior to 1962 were based primarily on analyses of fecal remains (Williams, 1938; Murie, 1940; 1959; Jones, 1951). All of these studies indicated that the sea urchin was the dominant food species.

About 95 percent of 422 fecal samples I examined at Amchitka contained sea urchin remains (table 16). Stomach examinations, however, as well as other studies discussed elsewhere (see Relative Values of Sea Otter Foods), indicate strongly that mollusks and fish are essential foods and that in some areas sea urchins may be of relatively minor importance and then primarily during their season of reproduction.

The examination of feces may contribute certain qualitative

TABLE 15.—Stomach contents of three sea otters taken in 15–20 fathoms of water in the Bering Sea

Specimen and food item	Volume (milliliters)	Individual
Adult female (KWK 60-16):		
<i>Clinocardium ciliatum</i>	75	ca. 4
<i>Musculus</i> sp.?.....	trace	?
Surf clam (<i>Spisula alaskana?</i>).....	50	1
Fish (<i>Hexagrammos</i> sp.?).....	125	1
Pup (KWK 60-18):		
Clam, unidentified.....	20	ca. 4
Milk curd.....	10
Adult female (KWK 60-19): ¹		
Clam (<i>Serripes groenlandicus</i>).....	427	ca. 20
Tanner crab (<i>Chionecetes bairdi</i>).....	48	1
Hermit crab (<i>Pagurus</i> sp.?).....	150	several
Crab, unidentified.....	trace
<i>Musculus niger</i>	trace

¹ Both stomach and intestinal contents included.

TABLE 16.—*Analysis of 422 fecal samples from Amchitka Island, February to April 1959*

[The samples were examined on seven habitually used hauling-out beaches]

Food organism ¹	Number of occurrences (frequency) ²	Percent of fecal samples having item
Arthropoda:		
Crabs (Crustacea).....	67	16
Mollusca:		
Chitons (Amphineura).....	26	6
Snails (Gastropoda).....	11	3
Limpets <i>Acmea</i>	10	3
Horse mussel <i>Volsella volsella</i>	89	21
Mussel <i>Mytilus edulus</i>	1	<1
Varnished horse mussel <i>Musculus vernicosa</i>	48	11
Pearly monia <i>Pododesmus macrochisma</i>	1	<1
Clam (Pelecypoda).....	5	1
Pecten (Pelecypoda).....	1	<1
Octopus (Cephalopoda).....	3	1
Subtotal.....	195	46
Echinodermata: ³		
Sea urchin <i>Strongylocentrotus drobachiensis</i>	401	95
Chordata:		
Fish.....	63	15
Total.....	726	

¹ Nonfood material, clay, gravel, etc., was found in seven fecal samples.² Frequency refers to the number of samples having the item, not the number of individuals present.³ Starfish were probably broken into fine pieces and thus not detected.

information concerning the food habits of sea otters but, because hard parts of some food species are not ingested, information derived from fecal examination contributes distorted information on both the qualitative and quantitative aspects of food habits.

Otters must defecate on land if fecal samples are to be studied. In many areas otters defecate on land infrequently or not at all. Weather conditions, geographical features (such as sheltered beaches above the tide line), and the presence of a human population appear to influence the frequency with which sea otters haul out on land. Like all other marine mammals, and unlike many terrestrial ones, the sea otter is not selective in choosing a defecation site. When sleeping or resting on land, the otter usually rises to its feet and expels the feces at the edge of its resting place. As it changes position for comfort during several hours on shore, feces may be deposited in several locations around the resting spot and the animal may, in changing position, lie in its own feces. Defecation in the water is also a random function and may occur while the animal is eating, swimming, or resting on its back on the surface. Although, as noted above, defecation on land is frequent, I have often noted that captive otters, after a rest period beside their pool, may defecate immediately upon entering the water.

Where otters habitually use certain hauling-out areas, as they do at Amchitka Island, a large number of fecal deposits may accumulate. Because these are composed primarily of the hard parts of marine organisms (fig. 66), they may remain in recognizable form for a number of weeks or, in well-protected locations, for months.

The analysis of fecal deposits from the Shumagin Islands and from Amchitka are presented in tables 16 and 17. The fact that sea urchins appeared in 95 percent of the droppings found on Amchitka and only in 4 percent of those from the Shumagins is significant. Sea urchins are available in the Shumagin Islands. It thus appears that the sea otter may feed selectively. No evidence,

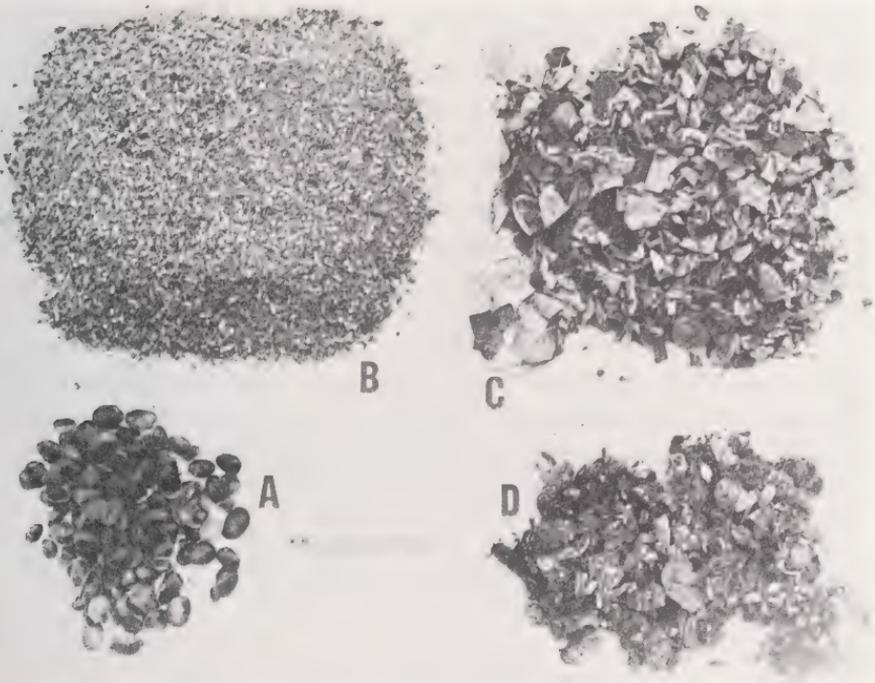


FIGURE 66.—Contents of a large (286 g. dry weight) sea otter fecal deposit: *A*—more than 100 varnished horse mussels (*Musculus*) (10 g.); these are usually swallowed whole, the viscera are digested, and the valves pass intact through the gastrointestinal tract. *B*—fragments of the tests, spines, and Aristotle's lanterns of an unknown number of green sea urchins (*Strongylocentrotus*) (159 g.). *C*—broken shells and *D*—byssus threads, of more than 40 horse mussels (*VolSELLA*) (117 g.). Sea urchins and large mussels are crushed by the teeth, and parts of the test or shell are swallowed. Specimen was collected on an Amchitka beach, 21 July 1956. The rule is 5 cm. (KWK 68-13-4)

TABLE 17.—*Analysis of 75 fecal samples from the Shumagin Islands*

[15 samples were taken at Simeonof Island, 5-9 June 1960 and 60 at Eagle Harbor, Nagai Island on 16 June 1960]

Food organism	Number of occurrences (frequency)	Percent of fecal samples having item
Arthropoda:		
Crabs (Crustacea)	12	16
Mollusca:		
Snails (Gastropoda)	4	5
Horse mussel <i>Volsella volsella</i>	3	4
Mussel <i>Mytilus edulus</i>	58	77
Clam (Pelecypoda)	6	8
Subtotal	71	94
Echinodermata:		
Sea urchin <i>Strongylocentrotus drobachiensis</i>	3	4
Chordata:		
Fish	8	10
Total	94	

such as high winter mortality, indicates that the sea otter population has approached its maximum size in the Shumagin Islands as it has at Amchitka. It might therefore be concluded, in the light of all available evidence (see Relative Values of Sea Otter Foods), that the sea otters of Amchitka consume a large number of sea urchins because other food resources have been depleted. In areas where otter populations have not yet approached maximum size, food species more nourishing than sea urchins are still abundant and the sea urchin may be eaten to a minor degree.

The fecal analyses presented here give useful qualitative information on food habits. They show that the food habits of otters in a crowded population differ from those in areas where crowding is not a factor. It is, however, evident that stomach analyses are necessary to reveal the food habits in their proper perspective. A discussion of the method of ingestion of each group of food organisms indicates in more detail why fecal examinations are of only limited use in food habits studies of the sea otter.

Food Quantities Required

The food requirement of the sea otter is great. Captive juveniles held on Amchitka Island during the 1957-59 study periods required from 25 to 30 percent of their body weight of food per day.

The quantity of food consumed by captive adult otters did not vary according to season. The required amount for an adult male and female was similar, about 20 to 23 percent of the body weight per day. The data are discussed in the section on the sea otter "In Captivity."

Relative Values of Sea Otter Foods

Miss Neva L. Karrick, Assistant Laboratory Director, Food Science Pioneer Research Laboratory of the Bureau of Commercial Fisheries at Seattle, has furnished proximate analyses of certain representative sea otter foods (table 18). From these data and the known quantities of food consumed by captive otters and data obtained from stomach examinations, it is evident that the sea urchin is seldom as important a food item as previously supposed and that the sea otter is primarily dependent for survival on other foods with more calories and higher protein content.

A captive sea otter weighing about 40 pounds required an average of about 8.4 lb. of food, primarily rockfish, per day (24-hour period). This diet supplied about 3,400 calories (about 89 calories per 100 grams of fish). Sea urchins with gravid gonads can supply roughly 58 calories per 100 grams of gonads and 16 calories per 100 grams of viscera. If large gravid sea urchins were available, about 200 would be required to supply 3,000+ calories to a sea otter in a 24-hour period.

Most of the sea urchins now available at Amchitka are small. The reason appears to be that a large sea otter population is over-utilizing this food resource (see Depletion of Food Resources). Mature gravid green sea urchins, weighing about 115 g. each, were obtained for analysis from an area at Cold Bay, Alaska, where there are no sea otters. At Amchitka, the size available in greatest quantity weigh about 6 to 10 g. These are consumed in large numbers, particularly by juvenile otters. The gonads in these immature sea urchins are almost microscopic. The amount of visceral material available in them is small and is a poor

TABLE 18.—*Proximate analysis of important sea otter food species*

[Averages. These data were furnished by Bureau of Commercial Fisheries Technological Laboratory, Seattle, Wash.]

Species	Moisture (percent)	Oil (percent)	Protein 6.25 × % N. (percent)	Ash (percent)	Calories per 100 grams ¹
Dungeness crab meat <i>Cancer</i> <i>magister</i>	77.2	0.90	20.8	1.61	91
Butter clam <i>Saxidomus nuttalli</i>	83.0	1.30	13.3	1.9	63
Octopus ²	85.7	0.86	12.1	1.3	56
Sea urchin <i>Strongylocentrotus</i> <i>drobachiensis</i> :					
Gonads.....	85.9	2.70	8.4	2.51	58
Viscera.....	92.2	0.72	2.3	3.72	16
Rockfish <i>Sebastes</i> sp.....	79.0	1.50	19.0	1.18	89

¹ Calories per 100 grams = average percent oil × 9 plus average percent protein × 4.

² Sea otters usually discard most or all of the viscera of octopus; therefore only the flesh was analyzed.

nutritional source. Because of the general depletion of invertebrates and the apparent inability of juvenile otters to obtain an adequate number of fish and mollusks, these young animals are compelled to eat the abundant and easily obtained immature sea urchins. An otter would have to consume nearly 6,500 of these immature urchins daily to supply the 3,000+ calories which appear to be required.

Depletion of Food Resources

The requirement for large amounts of food by sea otters has been discussed. Feeding grounds are limited by depth to relatively shallow waters and tag returns indicate that individual sea otters do not range widely along the coast (see Home Range). Because of these circumstances which concentrate feeding activities in rather limited areas, it appears probable that a large population of sea otters could seriously deplete food resources within their home range. Evidence is available that this does in fact occur.

SEA URCHIN DEPLETION

McLean (1962) presents convincing evidence that the sea urchin *Strongylocentrotus franciscanus* has been nearly exterminated in a particular area on the California coast which is occupied by a considerable number of sea otters. Of the area he studied he says (p. 101) "the large sea urchin was totally absent, although spines and test fragments were present in gravel samples."

Indirect evidence from Amchitka Island, where a large sea otter population exists, indicates that sea otter predation has drastically reduced certain food species there. Small green sea urchins are abundant. It is not possible, however, to find large individuals in the intertidal zone and I seldom saw an otter eating an urchin that approached in size the large individuals which are abundant in other Aleutian areas where the sea otter is scarce or absent. Bottom samples obtained by R. D. Jones, while diving with SCUBA equipment, both at Amchitka and in comparable areas at Adak (where at the time few sea otters occurred), showed that sea urchins at Amchitka are relatively scarce and small.

In a recent letter (16 December 1966), Jones reported on a subsequent visit to the Adak area he had explored prior to the time that it was occupied by a large number of sea otters:

In 1957 the green sea urchin was numerous and obvious in this area, and this time I saw none. I have no quantitative data because I had neither the equip-

ment nor time to gather it. This same thing is reported to have happened in the Sandman Reefs and Sanak Reefs when the sea otters reappeared in numbers.

John Nevzoroff, a native of the Aleutian Islands who worked with me on Amchitka in 1962, told me that in the early 1930's, when he trapped foxes on Amchitka with his father, sea otters were considerably less numerous, particularly along the Bering Sea coast, than they are today. He also said that he found large sea urchins ("sea eggs") abundant along the shores of Constantine Harbor where we were unable to find them in the 1955-63 study period.

Tons of fragments of large sea urchin tests are contained in kitchen middens at Amchitka Island. These indicate that in pre-historic times large sea urchins were abundant there. Presumably the aboriginal human population was able to obtain these large sea urchins because the sea otter population had been utilized and reduced. Thus, the sea urchin resource was not overexploited by the otters as it is today, and the urchins were allowed to grow to maximum size.

It is evident that at Amchitka, where mature sea urchins are scarce, the diet of the sea otter must be supplemented by other foods, such as fish and mollusks, to prevent starvation. That starvation does, in fact, occur in winter and early spring, particularly among young otters, is discussed in the section on Limiting Factors.

THE ABALONE-SEA OTTER PROBLEM IN CALIFORNIA

J. H. McLean writes (letter, December 1964):

20 miles of coastline below San Simeon which formerly produced abalone year after year under continuous commercial exploitation has been completely ruined for abalone as a result of the southern migration of the California herds. It has nothing to do with the number of divers now working because the otters take the entire population, not just those of legal size. The fact is that otters, urchins and abalones do not coexist and the entire commercial abalone fishery is very seriously threatened by possible southern expansion of range.

Cox (1962), who has conducted comprehensive studies of the abalone (*Haliotis*) along the California coast, says (p. 57) "all evidence indicates they [sea otters] pose a threat to human exploitation [of the abalone] when the two are competing in the same area." Data gathered in Carmel Cove and Stillwater Cove before and after the areas were occupied by sea otters demon-

strated that the local abalone beds were seriously decimated but not entirely eliminated by sea otter predation.

In a public statement, additional information was given by Cox (California Senate, 1963):

In 1956 we went into Shelter Cove right off Monterey and over a period of several days tagged 513 abalone. One year later we came back in the area and we spent approximately three days searching and we found five abalone . . . one of which had a tag. The area where we were able to collect five hundred abalone in an hour we couldn't find any. On one dive I brought up over two dozen broken shells . . . characteristic of broken ones of the sea otters. We were told . . . by the caretaker, that a herd of sea otters had spent the winter in this cove . . . I had been called to task for not reporting this. . . . However, I felt this was not an adequate experiment.

In a recent study of sea otter feeding habits on the California coast, Ebert (1968) concluded that "sea otters exert a profound influence upon benthic communities."

During 1963, abalone fishermen in San Luis Obispo County, California, complained that sea otters were destroying the abalone resource of that area. Claims of spectacular damage to abalone beds appeared in many newspapers. In response to these complaints a hearing was held at the City Hall, San Luis Obispo, on 19 November 1963. At this hearing Mr. Harry Anderson, Deputy Director of the California Department of Fish and Game, presented testimony to the California Senate Fact Finding Committee on Natural Resources. He compared commercial landings of abalones in certain areas before and after sea otters were present in these areas. In 1961 when sea otters were present "the catch was over 1,550,000 pounds, by far the largest catch of any year in the 10-year period." He indicated further that competition among abalone fishermen has increased greatly. In 1928 there were 11 licensed commercial abalone fishermen in California. The number has increased to 505 in 1963. Since the abalone resource is limited, it becomes apparent that the individual fishermen can expect to obtain fewer abalones than when competition among them was less. It was concluded that "all the evidence we have indicates that the sea otter has not seriously harmed or threatened the abalone resource."

The data indicate that the depletion of food resources at Amchitka has resulted in an abnormally high winter die-off of sea otters as well as a population of undersized animals (see Mortality Factors and Body Measurements). Evidence from California reveals that when sea otters feed for an extended period in a limited area they may seriously deplete local populations of their prey species.

Unusual Food Items

BIRDS

On 27 March 1962, at Amchitka Island, I watched an adult female sea otter through a 50-power telescope while she consumed what appeared to be a shearwater (*Puffinus*) or Fulmar (*Fulmarus*). When first seen she was carrying the carcass on her chest. She stopped in the shelter of an islet to groom, leaving the bird floating beside her. After about 5 minutes of grooming she picked up the bird and tore flesh from the breast. She alternately groomed and ate for about 30 minutes. While she ate, the bird's intestines streamed out across her chest and feathers littered the water around her. After apparently satisfying her appetite she swam away carrying the carcass, bloody sternum erect, on her chest.

On 13 November 1957, I found sea otter feces at East Cape, Amchitka Island, which consisted of feathers, skin, fat, and flesh (breast muscle) of what appeared to be a cormorant (*Phalacrocorax pelagicus*). The chunks which were torn from the bird showed little indication of having been affected by passage through the digestive tract.

Hungry captive otters consumed Emperor Goose (*Philacte canagica*) flesh (Kirkpatrick et al., 1955) but Jones told me that the meat passed undigested through the alimentary tract.

It appears that the flesh of birds is eaten only under the stress of hunger, particularly in winter. Also, the sea otter, adjusted to a diet of fish and invertebrates, seems unable to derive nourishment from the flesh of birds.

MISCELLANEOUS

On several occasions sea otters were seen to eat unusual food items that zoo visitors threw into their pool. These included a slice of white bread, a marshmallow, and peanuts. The animals appeared to suffer no ill effects from ingesting these items but the keeper reported that the peanuts passed through the animal undigested.

Conclusions

It is evident that fecal examinations give less adequate information about sea otter food habits than similar studies for other species. Certain food species (clams and certain fishes) may not

appear in recognizable form at all in droppings because shells are not swallowed and the bones of some fish (*Cyclopterichthys*) are soft and are digested. On the other hand, when sea urchins are eaten some part or all of the test may be swallowed. The important quantities of high protein food contained in mollusks and fish cannot be evaluated by the examination of feces.

It has been wrongly assumed that sea urchins held first-rank importance as a sea otter food. Barabash-Nikiforov (1947) believed that sea urchins were essential to survival. There can be no question but that where and when mature gravid sea urchins are available they are an important food source. That they are not essential to sea otter existence is demonstrated by: (1) A captive sea otter was given no sea urchins for a period of 4 years and remained in good health; (2) numerous captives held on Amchitka refused to eat urchins after being introduced to a diet of fish; (3) each winter many juvenile sea otters (apparently incapable of obtaining fishes) died of enteritis (probably induced by shock or stress accompanying starvation) and were found to have the remains of considerable numbers of sea urchins in the intestines; (4) feces and stomachs of sea otters taken, for example, in the Shumagin Islands, contained few, if any, sea urchin remains (although sea urchins occur there).

My conclusion is that sea urchins may, during their season of reproduction in areas of abundance, rank high in importance as a sea otter food source. Where an abundance of mollusks and fish may be obtained, however, the sea urchin is at no time an essential food species. The food value of the sea urchin may vary from poor to good, depending on maturity and the season of reproduction. Mollusks and fish, however, when available and to those animals able to obtain them, furnish an adequate and consistently nourishing diet. Mollusks (37 percent) and fish (50 percent), relatively high in calories, account for 87 percent by volume of the sea otters' food at Amchitka.

DISTRIBUTION AND NUMBERS

Original

The sea otter originally ranged at least as far south as Morro Hermoso (27°32' N. lat.) on the Pacific Coast of Lower California (Ogden, 1941, p. 7). Scammon (1870) noted that it occurred at Cedros Island, about 30 miles north of Morro Hermoso, and at Guadalupe. From these locations its distribution continued northward along the coast of North America to Prince William Sound and westward through the Aleutian, Pribilof, and Commander Islands to the coast of Kamchatka and south through the Kuril Islands at least to northern Hokkaido and southern Sakhalin (Barabash-Nikiforov, 1947) (see map, fig. 67).

ICE AND THE NORTHERN LIMIT OF RANGE

The northernmost permanent sea otter population in the Western Hemisphere is in Prince William Sound (60°30' N. lat.) where the sea does not freeze. In the Bering Sea the aboriginal population on the Pribilof Islands (57° N. lat.) and that along the northwest extremity of the Alaska Peninsula (55° N. lat.) overlap the southern limit of winter drift ice. That the sea otter is able to survive limited winter ice conditions is also indicated by the fact that the aboriginal Pribilof population was apparently a large and permanent one, and that on occasion the sea freezes there for brief periods. Winter drift ice reaches the southeastern Kamchatka coast and Kuril Islands where early sea otter populations were apparently prosperous and are today increasing. Nikolaev (1965b) found in the Kuril Islands that when sea otters were unable to move to ice-free locations in winter they died of starvation. When closed in by ice they crossed its surface or even went overland in search of open water.

Bee and Hall (1956) record two unsubstantiated sight records of sea otters far north of their usual range in the Arctic Ocean. One was reported in 1951 at Cape Halkett, 70°49' N. lat., 142°16' W. long. and another at Atigaru Point, 70°35' N. lat., 151°50' W. long. C. H. Fiscus, who obtained these reports from other observers, told me in 1964 that he is now doubtful of their authenticity.

Barabash-Nikiforov (1947) and Nikolaev (1960) indicate that on the east coast of Siberia the sea otter may have ranged to 64° N. The records, however, are vague. Gulin (1952) photographed the skin of a sea otter said to have been taken by local hunters at Lavrentiya (65°08' N. lat., 171° E. long.) near Bering Strait on the Chukotsk Peninsula. No date or other specific data are given. Such a casual report in a popular magazine of a sea otter so far north of the usual range must be regarded with skepticism.

Specific records as far north as 64° do not appear to be available. Gribkov (1963) says that the known boundary of the sea otter's range is 57° N. on the east coast of Kamchatka but mentions that in 1960 sea otters "were bagged" north of this point.

The occurrence of a permanent sea otter population in the northern Bering Sea or Arctic Ocean where the sea freezes is quite unlikely. That a stray otter might have traveled north with pack ice in spring from the lower limit of winter drift ice in southern Bristol Bay and the southeastern shore of Kamchatka, is a possibility. Retreating winter ice might account for the presence of three sea otters at the Pribilofs in 1889, 1892, and 1896 (Preble and McAtee, 1923) long after they were extirpated there. A sighting in Norton Sound (64° N.) in June 1941, was reported by Frank Glaser (*in* Lensink, 1958).

In general it is true today, as it was in early times, that the prosperous sea otter colonies are south of areas where sea ice forms regularly and remains for long periods in winter months.

The environmental factors that control the southern limit of distribution, other than predation by man and environmental pollution caused by him today, are unknown. Additional sources of information on aboriginal distribution are cited by Barabash-Nikiforov (1947).

POPULATION REDUCTION THROUGH EXPLOITATION

Intensive exploitation of the sea otter by Europeans began with the voyage of Vitus Bering in 1741 and continued unregulated for 170 years. Exploitation was halted and protection was given to the sea otter by international treaty in 1911.³

³ Convention between the United States, Great Britain, Russia, and Japan for the preservation and protection of fur seals. Proclaimed 14 December 1911 and approved 24 August 1912. Article V of this Convention extended protection to the sea otter. Further protection was extended by the "Presidential Proclamation for the preservation and protection of fur seals and sea otter," signed by Woodrow Wilson on 31 May 1913, and an "Executive order regarding the protection of fur seals and sea otters," signed by Calvin Coolidge on 14 January 1929 (U.S. Bureau of Fisheries, 1929).

The sea otter was then commercially extinct and nearly extinct as a species. The number of sea otters that were taken during the period of unregulated exploitation is not known because proper records were not kept. Most records are vague concerning where skins came from, except that they came from the New World. Fisher (1940b) states that her summary is not complete but lists records of 359,375 skins taken between 1740 and 1916. Between 1745 and 1867, "260,790 sea otter skins were reported as having been shipped from Alaska" and from 1868 to 1905 the take was 107,121 skins (U.S. Bureau of Fisheries, 1906). From 1906 to 1910, 240 skins are recorded taken by U.S. and Canadian hunters (U.S. Bureau of Fisheries, 1907 through 1911). Thus the total recorded number of skins taken in waters off Alaska, prior to 1911, was 368,151. Skins taken by hunters of other nationalities are not recorded. Lensink (1960) presents figures and broad estimates which place the take of sea otters from Alaska at over 906,500 animals.

POSTULATED SIZE OF ABORIGINAL POPULATION

From data gathered during recent studies, some idea of the possible take may be postulated. Today it appears that about 30,000 sea otters occupy approximately one-fifth of the original lineal coastal range of the sea otter. Some of the presently occupied habitat is of superior quality. Islands contribute more usable habitat than do unbroken continental coastlines. Thus, it is probable that the population of sea otters in 1740 may have been no more than five times the present number, probably between 100,000 and 150,000 animals. If the annual increment that could be cropped on a sustained yield basis was about 2.5 percent per year (the approximate annual yield of the Pribilof fur seal (*Callorhinus ursinus*) herd is 5 percent per year and fur seals normally bear one pup each year; 2 years elapse between sea otter pups), then the take in 170 years could have been between 425,000 and 637,500 if cropping had been rational. The killing of sea otters, however, was unregulated and for periods of many years the take was at the expense of the population "capital." Probably certain populations were wiped out during an early part of the exploitation period. Thus the yield over the entire period was less than it would have been if only the annual increment had been taken. Reasoning on this basis, it appears that the probable take of sea otters between 1740 and 1911 was less than a million and more likely about a half million animals.

In the following section, sea otter population studies in Alaska

are reviewed and a summary of information on the past and present world populations is presented. Field counts of living sea otters (omitting pups carried by mothers) furnish the information on which this study of population and distribution is based. To obtain a knowledge of population dynamics, studies of mortality, reproduction, food habits, and movements of sea otters were also undertaken.

Modern

ALASKA POPULATIONS

The greatest population of sea otters in the world today is in the central to outer Aleutian Islands (table 36). This is also the area where repopulation of available habitat, from which the sea otter was extirpated before 1911, is apparently occurring the most rapidly. It is also the location where most of our studies were concentrated.

Data were made available by individuals who visited or worked in Alaska during the 1930's and 1940's. Additional data were obtained, particularly after 1955, by observers who made extensive aerial and surface surveys. During these studies, areas occupied by sea otters as well as areas to which otters have not yet returned were surveyed.

The Aleutian Islands chain consists of five named groups of islands from west to east (subgroups are in parentheses): the Near (Semichi Islands), Rat, Andreanof Islands (Delarof Islands), the Islands of Four Mountains, and Fox Islands (Krenitzin Islands) (see map, fig. 68). Important island groups which furnish suitable sea otter habitat are separated from each other by passes up to 55 miles wide, hundreds of fathoms deep, and swept by swift tidal currents. These wide passes appear to hinder seriously the movements of otters from a heavily populated area to a neighboring island group having vacant habitat.

Today (1968), a sea otter "population explosion" is occurring in the Andreanof Islands. The early expansion of this population was sketchily documented during the late 1930's and early 1940's. More thorough observations were made in the 1950's and until 1965. A similar "population explosion" in the Rat Islands apparently reached a climax in the mid-1940's. The historical data on these two populations are reviewed below and compared with modern findings.

The locations in which sea otters survived the 1741-1911 period

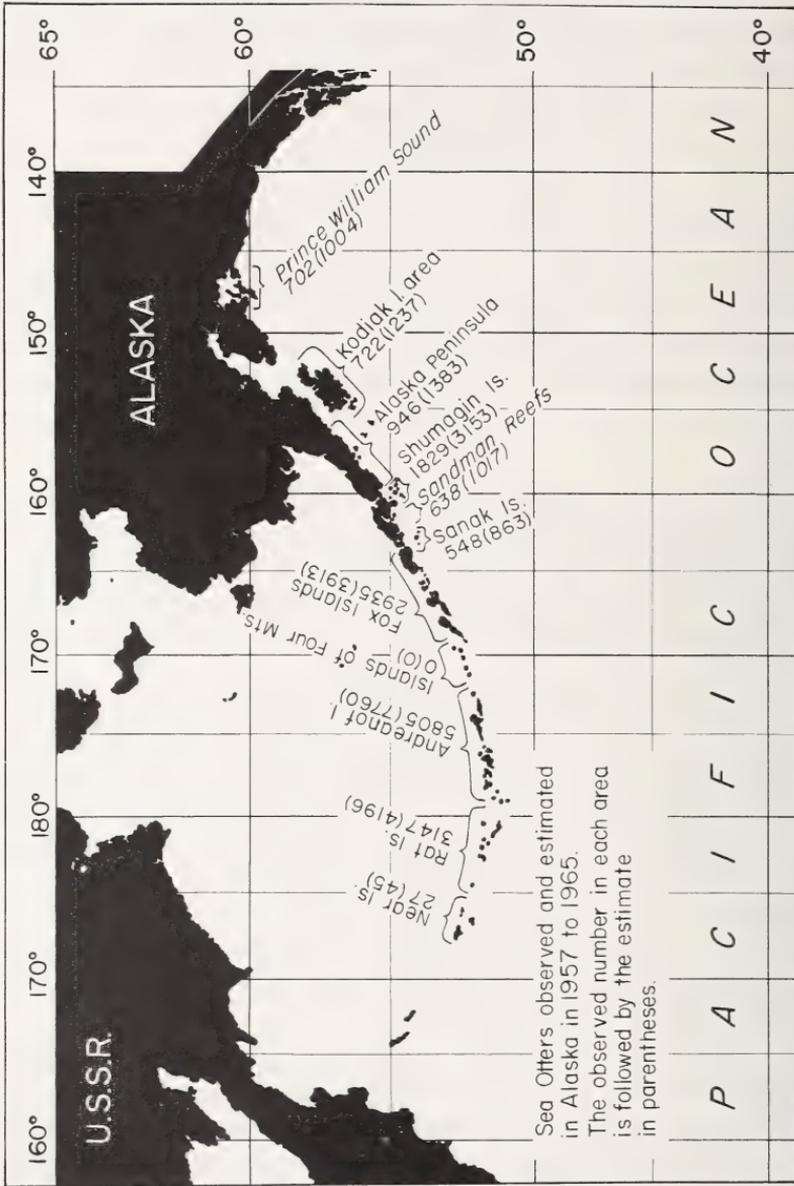


FIGURE 68.—Beginning in 1957, aerial surveys of sea otter habitat were undertaken (see appendix 1). From the recorded counts of otters, calculated estimates of the various populations were derived. Because the figures on this map were taken from tables in the text, they are not rounded.

of unregulated hunting are indicated by (1) areas where large populations are found today, and (2) areas where sea otters were taken shortly before and after 1911. Fragmentary data on otters that were taken between 1906 and 1936 are reviewed briefly below.

Records of the U.S. Bureau of Fisheries (1907-37) indicate that at least 302 otters were taken in Alaska from 1906 through 1936. Of these, 240 were taken between 1906 and 1911 and 62 from 1912 to 1936. For 213 skins (186 before 1911 and 27 after 1911) no location of origin is given, but many apparently came from the Aleutian, Sanak, and Kodiak Islands areas. The specific locations of origin of the remaining skins were often not stated clearly. It appears, however, that the remaining 89 skins may be allocated to the following areas: Aleutians, 7 (4 in 1910 and 3 in 1929); Southern Bristol Bay and Bering Sea north of Unimak Island, 15 (all before 1911); Alaska Peninsula, south coast (about 56° N.), 6 (1918, 2; 1929, 2; 1931, 2); Sanak Island area, 3 (1926, 2; 1934, 1); Shumagin Islands, 1 (1910); Kodiak area, 52 (31 before 1911 and 21 after 1911); Prince William Sound and Kayak Island area, 5 (1910, 3; 1924, 2). Within these areas otters probably survived along exposed coasts that offered few if any anchorages and where offshore reefs made hunting hazardous. Such areas also offered otters feeding habitat well offshore.

The map (fig. 68) and table 19 summarize modern field counts and estimates of sea otter populations in Alaska and indicate that most of the population is concentrated in an area about 500 miles long which includes the Rat and part of the Andreanof Islands (9,605 observed, 1965, table 19). From the present spearhead of population expansion in the central Andreanofs eastward to the next small colony at Atka (228 observed, 1965, table 25) is about 75 miles. The next colony (159 observed, 1965, table 25) is 50 miles farther east, near the east end of Amlia. Moving eastward 30 miles, the next colony (28 observed, 1965, table 25) is at Seguam. From here to the small Samalga-Umnak colony (9 observed, 1965, table 30) is 140 miles. The next small colony (32 observed, 1965, table 30) is at Tigalda Island 175 miles to the east. From here to the Unimak-Amak-Port Moller colony (2,892 observed, 1965, table 30) is 75 miles. Along the south side of the Alaska Peninsula and northeastward to the Kayak Island area, a distance of about 800 miles, the colonies (5,748 observed, table 36) are not separated by any known geographic barriers.

After the publication of population and distribution studies by Usink (1960) considerable field work was undertaken. The data

TABLE 19.—*Summary of sea otters observed and estimated in Alaska*

[See tables in sections for counts by islands. Most areas have now been surveyed several times. The highest counts which were made under optimum conditions were selected for this summary. Three observers, D. L. Spencer, C. J. Lensink, and K. W. Kenyon gathered most of these data]

Area	Aerial surveys		Estimated total otters ¹	Estimated total 1965 ²
	Year	Otters observed		
Near Islands.....	1965	27	45	45
Rat Islands.....	1965	³ 3,147	4,196	4,196
Delarof Island.....	1965	³ 653	871	871
Andreanof Island.....	1965	³ 5,805	7,760	7,760
Islands of the Four Mountains.....	1965	0	0	0
Fox Islands.....	1965	2,935	3,913	3,913
Bogoslof Island.....	1962	0	0	0
Sandman Reefs.....	1962	638	879	1,017
Sanak Island area.....	1962	548	746	863
Shumagin Islands.....	1957	1,829	2,724	3,153
Pavlov Islands.....	1962	4	8	12
Alaska Peninsula.....	1962	949	1,317	1,383
Semidi Islands.....	1957	5	10	12
Kodiak area.....	1957-59	722	973	1,237
Prince William Sound and Kayak Island.....	1959	702	1,004	1,004
Total.....		17,964	24,446	25,466

¹ See Aerial Surveys for method of estimating.

² Projected in the regions where growth was observed on the assumption that the increase is at the rate of 5 percent per year.

³ Total 9,605.

now available indicate that in significant areas sea otter populations have declined and are less than the estimates which Lensink computed on the basis of figures then available to him. Lensink (1960) considered that sea otter feeding habitat included waters to a depth of 50 fathoms, but no evidence is available that they descend to this depth (see Diving). Because of this assumption a greater area of available habitat and greater population potential was postulated by Lensink than is indicated by information now available. Also, Lensink's (1960) estimates for a large sea otter population at Amchitka do not agree with the modern or historical data for this area. The rate of population growth which he postulated is greater than indicated by the data now available. In addition, as shown later, the Amchitka population "crashed" in the 1940's and now fluctuates annually near a population about one-half its maximum size.

Aerial surveys

The most extensive aerial surveys consumed about 200 hours of flight time in a DC-3 aircraft (table 20). Air speed was maintained at 120 knots and flight altitude varied from 200 to 400 feet, depending on winds and nearby terrain. Two observers counted otters from the aircraft's cockpit. Some groups were so large that

TABLE 20.—*Summary of aerial surveys of sea otters, 1957-65*

[Before these surveys, organized surveys were not undertaken]

Date	Method	Hours of flight time	Observers	Areas surveyed (inclusive)
1957: 6 May-28 Sept.	A variety of air and surface craft used	(?)	C. J. Lensink, D. L. Spencer, R. D. Jones, W. A. Troyer, F. Wilke	Various areas, Cook Inlet to Kanaga Island (Aleutians).
1958: August	Aircraft	(?)	W. A. Troyer	Shuyak area.
1959: 21-27 May	DC-3 aircraft	56.8	D. L. Spencer, K. W. Kenyon	Attu Island (Near Island group) to Herbert Island (Island of Four Mountains).
13 July	UF-2 aircraft (U.S. Coast Guard)	3	K. W. Kenyon	Outer coast, Olympic Peninsula, Washington.
July	Aircraft	(?)	C. J. Lensink	Kodiak area.
August	Cessna 180 aircraft	(?)	C. J. Lensink, R. Pirtle	Prince William Sound, Kayak-Wingham Island.
1960: 3-5 March	DC-3 aircraft	28	D. L. Spencer, K. W. Kenyon, D. W. Rice	Herbert Island to Amak Island.
1961: 27 March	DC-3 aircraft	4	D. L. Spencer, K. W. Kenyon	Amak area (failed because of fog).
27 October	UF-2 aircraft (U.S. Navy)	1.8	L. W. Croxton, K. W. Kenyon	Adak area (all data lost in crash of survey aircraft).
1962: 29 March-10 April	DC-3 aircraft	53.6	D. L. Spencer, K. W. Kenyon, J. J. Burns	Rat Islands to Amak I.; Sanak, Sandman Reefs, Shumagin Is., Alaska Peninsula.
1965: 19 April-9 May	DC-3 aircraft	49.2	D. L. Spencer, K. W. Kenyon, E. G. Klinkhart	Aleutian Is., Alaska Peninsula (part), Cook Inlet (part).
Total		196.4+		

all individuals could not be counted in the time available. In such groups we counted a sample of 10 to 50 animals. We then visually divided the remainder of the group into sectors equivalent to the counted sector to obtain an estimate of the total number of animals. Aerial photographs were taken of unusually large groups to ascertain the accuracy of the field estimates (see Aerial Photography). The flight path was divided at the center line of the aircraft. One observer stood behind the pilot and the other behind the copilot. Otters were seen to a distance of at least 1 mile on each side of the aircraft during excellent survey conditions and to at least $\frac{1}{2}$ mile under good conditions.

The width of the survey track was ascertained by flying at survey height over an air strip of known length. In this way each observer obtained a reference point on the wing of the aircraft, which from his position in the aircraft during surveys delimited a known distance on the surface.

Observation conditions were evaluated during the surveys and were classified as follows:

Excellent—no wind, high overcast (water glassy and no glare).

Good—light wind (to 6 or 8 knots) and overcast; or no wind (glassy water) but sun glare present.

Fair—light wind to 10 knots and surface glare or wind 8 to 15 knots and sky overcast.

Poor—winds over 10 knots and glare on water, or wind over 15 knots regardless of sky cover.

When possible, survey operations were suspended during fair or poor conditions, because too few otters could be seen and the errors in the census could not be properly evaluated.

Observations were recorded by one of the biologists, or by a third person assisting him. Each observation was immediately plotted on a U.S. Coast and Geodetic Survey chart.

Several aerial surveys which supplemented the comprehensive surveys were conducted from single engine aircraft and from a Grumman Widgeon. Also, the U.S. Navy cooperated by sending Fish and Wildlife observers on survey flights in a UF-2 Grumman Albatross aircraft.

Data were gathered in 1959 to provide a factor for computing estimated total sea otter populations from aerial counts.

In an effort to ascertain as nearly as possible the number of sea otters occupying a particular coastal area at Amchitka Island, inshore and offshore surface surveys were repeatedly conducted by dory. A total of 17 survey counts were made along a 13-mile section of coast from (and including) Crown Reefer Point

(51°28' N. lat., 179°11' E. long.) to (but not including) East Cape (51°22'32" N. lat., 179°27'45" E. long.) The surveys were conducted in February, March, and April of 1959 (see Kenyon and Spencer, 1960).

These surface surveys differ from the others because an intensive effort was made in a limited area to observe, by repeated trips, the available sea otter habitat at close range in locations familiar to the observer. The mean number of otters observed was 254. On an aerial survey of the same section of coast in May 1959, 192 otters were counted. Thus, approximately 76 percent of the number seen from the surface was observed from the air.

If only the highest surface counts for the section of the coast are considered, the total count for the area is 295 otters. This figure would indicate that on the aerial survey about 65 percent of the otters in the survey area were seen $\left(\frac{192 \times 100}{295}\right)$.

Based on the premise that the maximum number of otters seen on surface surveys failed by 15 percent to include all those present, an aerial survey would reveal 50 percent of the otters present. This correction factor was used previously (Kenyon and Spencer, 1960).

The correction factor indicating that about 75 percent of the otters were seen is a conservative one and is used to estimate total populations in the following discussion for these reasons: (1) Tag recoveries at Amchitka revealed that the home range of a sea otter may include about 10 miles of coastline. It therefore appeared reasonable to use the mean of counts for each part of the area studied. In this way some compensation is made for the movements of individual otters in and out of the study areas during intervals between surveys. (2) Many observations during aerial surveys, when the same locations were flown over repeatedly, indicated to us that, in general, under excellent conditions we saw at least 75 percent of the otters present. In some places, having a minimum number of rocks and kelp breaking the surface, where the shoreline was even and the band of water furnishing available feeding habitat was narrow, we felt reasonably certain that, in calm weather, we saw more than 75 percent of the otters present. (3) We found that water depths as shown on USCGS charts constituted a dependable guide to locations inhabited by sea otters. A large majority occur within the 20-fathom curve (waters less than 120 feet in depth). Rarely do sea otters occur in water as deep as 30 fathoms. Therefore we consider that no significant number of sea otters was missed during the aerial surveys.

Future studies may show that we were unable to estimate the

error in our counts accurately. Nevertheless, the results of the surveys are comparable and they establish the order of magnitude of populations in the locations that were surveyed. For the purpose of this report, comparability of field observations in different areas is more important than an estimate of absolute population magnitude.

On calm days, when the sea was glassy and a floating otter could be seen at a distance of more than a mile on each side of the aircraft, we carefully examined many extensive offshore areas between islands. Where the water is shallow and otters occur in numbers well offshore (as off the north shore of Unimak Island) we systematically flew sectors through the area covering most of the sea's surface where otters occurred.

In areas of dense population, the otters tend to gather in groups or "pods" of variable size numbering from 10 to 30 animals. Groups of 100 or more animals were infrequent (fig. 69) and rarely were more than 200 otters together (the maximum observed was 440, fig. 70). In sparse populations, relatively fewer groups



FIGURE 69.—A group of 157 sea otters resting in a kelp bed in Kagalaska Strait (between Adak and Kagalaska Islands), Aleutian Islands, Alaska. Flight altitude about 150 feet, air speed 120 knots; 6 April 1962. (KWK 62-35-19)



FIGURE 70.—Part of a group of 440 sea otters in Kujulik Bay on the south shore of the Alaska Peninsula. This was the largest group observed on the aerial surveys. Flight altitude 200 feet, air speed 120 knots; 10 April 1962. (KWK 62-39-13)

of animals were seen; most animals were scattered. Because it is easier to see a large group of animals than scattered individuals, we realized that, in our aerial surveys, we saw a greater proportion of the animals where populations were dense than where they were sparse. For this reason, a sliding scale based on numerous field observations was chosen to compute an estimate of total populations in various areas.

<i>Otters counted</i>	<i>Estimation factor to obtain total</i>
1-15.....	Estimate 50 percent were seen
16-100.....	Estimate 60 percent were seen
Over 100.....	Estimate 75 percent were seen

Aerial photography

Aerial photography is a useful censusing tool when views of animal concentrations may be obtained. A large majority of sea otters are scattered as individuals or gathered in small groups of 5 to 20 animals, which may be counted directly. Therefore we have used aerial photographs primarily to assist us in improving our technique of estimating occasional large concentrations of otters. The mean of 1962 and 1965 data listed below shows that

the field estimates of large concentrations were 12 percent below the number counted on photographs. The 1965 field estimates, made after studying earlier results, however, averaged only about 2 percent below the counts from photographs. Relatively few groups as large as 100 animals were seen, therefore no general correction factor is applied to the field count, as this would not materially affect the overall estimate.

Date	Location	Field estimate	Photo count	Percent error in field estimate
6 Apr. 1962	Kagalaska Str.	150	157	-5. }
10 Apr. 1962	Kujulik Bay	250	387	-35. }
25 Apr. 1965	L. Tanaga I.	300	334	-11.0 }
25 Apr. 1965	Umak I.	275	274	+0.4 }
25 Apr. 1965	Box I.	450	440	+2.0 }
Total		1,425	1,592	12.

¹ Average.

Surface surveys

Surface surveys were made in limited areas from an outboard motor-driven dory and by observers using binoculars and telescope from shore (Lensink, 1958; Kenyon and Spencer, 1960).

A review of observations of sea otters from 1933 through 1962 in many Alaska areas indicates that observations of numbers of animals made from the surface are generally less useful than aerial observations. When a local otter population is small, surface observers may miss the animals altogether. For example, on aerial surveys in 1959, 1962, and 1965 Spencer and I were able to count 8 to 10 otters in the vicinity of Samalga Island and Cape Sagak, Umnak Island. Reports from Aleut hunters at nearby Nikolski Village during the past 10 years indicate that this population, though small, is permanent. In 1961, R. Thomas and in 1963, G. Baines, fur seal research biologists, Bureau of Commercial Fisheries, visited Samalga. They each spent a 24-hour period on or near Samalga and looked specifically for sea otters. Neither saw otters or any indication on beaches that they were present.

Lensink (1958) counted otters in the Shuyak and Barren Islands in the summer of 1957, first from the surface and then from the air. The surface count was 211 otters. On an aerial survey of the same area he recorded 515 otters, indicating that at least 59 percent of the otters in an area may be missed on a surface survey. On the basis of these surveys, a correction factor of 60 percent is applied to certain surface counts that are discussed.

Area of habitat

Sea otter feeding habitat was ascertained to consist of waters

30 fathoms or less in depth (see Diving). Where population and distribution surveys were made, the area of available habitat was measured on U.S. Coast and Geodetic Survey charts. A modified acreage grid, 64 dots per square inch, was used to obtain measurements which were converted to square miles of available habitat. Estimates of populations (exclusive of pups carried by mothers) were applied to the square miles of habitat to obtain the population densities that are presented in the following discussion and tables.

The entire Aleutian Chain, waters adjacent to the Alaska Peninsula, the Sanak Islands and Sanak Reef area, the Sandman Reefs, and the Shumagin Islands were surveyed one or more times under good to excellent observation conditions during our comprehensive 1959, 1960, 1962, and 1965 surveys. During these surveys and those by other individuals in different Alaska areas, 17,964 (table 19) otters were observed. The highest count obtained in each area surveyed was used to obtain this total.

As the aerial surveys and surface studies proceeded, it became evident that the population of sea otters in the various geographically separated areas exhibited different stages of population development. For example, in the Rat and Delarof Islands a crowded population heavily exploited available food resources (see Food and Feeding Behavior), and in certain of the Andreanof Islands dense local populations were expanding into adjacent areas of vacant habitat. These observations are discussed in the perspective of available data from earlier observers under the geographical headings that follow.

The Near Islands

This Aleutian group (fig. 71), the western extremity of U.S. territory, is separated from Buldir, the westernmost of the Rat Islands by 55 miles of open water. Attu and Agattu are the largest islands but Shemya is today more important because of its airfield and military base. A small military base has been maintained on Attu since World War II. Early in the war, the native Aleut population was removed from Attu by the Japanese and was never reestablished there (Golodoff, 1966).

In the early years of sea otter exploitation, the Near Islands yielded many furs. The Alaska survey expedition of the U.S. Navy Department in 1932 searched for sea otters at Attu but found none. Information was received, however, that "the Chief of the Attu natives assured the commander of the expedition that there were a few [sea otters] at Agattu which would soon be gone because the Japanese come frequently to take them" (Hutchinson, 1935).

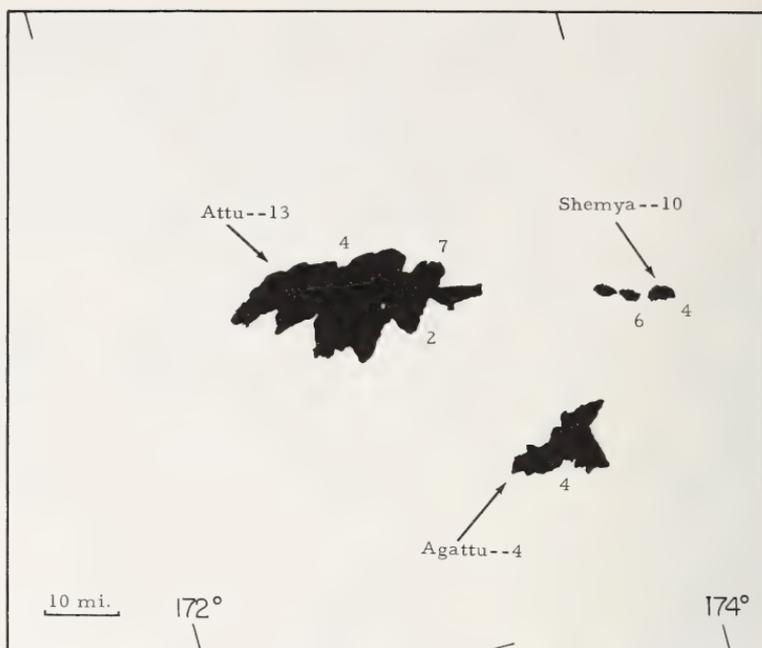


FIGURE 71.—The sea otter was exterminated from the Near Islands during the late 1800's or early 1900's. Probably because wide passes separate these islands from the heavily populated Rat Islands, it was not until July 1964 that the first authentic observations of otters were obtained in the Near Islands. Our aerial survey of 2 May 1965 revealed that at least 27 otters are now established there.

Whether the remnant population was exterminated before 1911, or by poaching in later years, is not known. Beals (1943) visited the Near Islands but was unable to find any clue that the sea otter existed there. That the aboriginal sea otter population of the Near Islands was in fact extirpated is beyond doubt.

In 1956, Refuge Manager R. D. Jones moved five otters to Attu from Amchitka on a U.S. Navy ship and liberated them. It is not known whether any of these survived. Before our 1959 aerial survey, no surface observer had reported seeing otters.

Our aerial survey of 19 May 1959 included all of the Near Islands and was conducted under excellent conditions. We made repeated sweeps to inspect areas appearing to offer ideal sea otter habitat but we saw no sea otters.

B. F. Jones, while a biologist with the Fisheries Research Institute, told me that on 12 June 1959 he sighted one otter one-fourth of a mile off Chirikof Point at the eastern extremity of Attu. An additional report from R. D. Jones (letter, 25 March 1964) states

that a warrant officer stationed at Shemya "is convinced he has seen a sea otter several times" there. In July 1964, R. D. Jones (1965) saw eight otters in the Near Islands and obtained skeletal remains of another at Agattu. On an aerial survey, 2 May 1965, we saw 13 otters at Attu, 4 at Agattu, and 10 at Shemya. These observations indicate that the Near Islands population is now established. The Near Islands were probably repopulated by otters from the heavily populated Rat Islands. The statement by Nikolaev (1960) that "movements occur... from the Commander to the Aleutian Islands" is not documented, and the present study indicates that such movement across 185 miles of open sea is improbable.

The Rat Islands

The Rat Islands (fig. 72) extend 160 miles from Buldir eastward to Semisopochnoi. During World War II large military installations existed on Kiska and Amchitka, with small outposts on several other islands. Since about 1948 none of these was occupied, except for brief and intermittent military occupation of Amchitka, par-

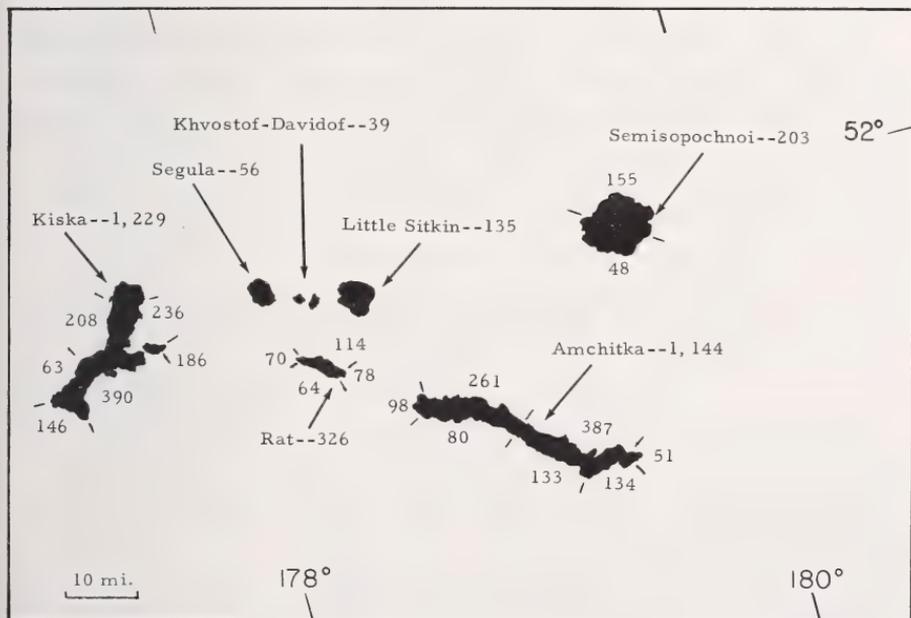


FIGURE 72.—The Rat Islands group, except Buldir Island, where 15 otters were recorded. The aerial survey was conducted on 2 and 3 May 1965 under good to excellent survey conditions. The numbers near the islands indicate the approximate distribution of the 3,147 otters that were observed.

ticularly in 1964 and 1965, and present day Defense Department-Atomic Energy Commission weapons testing activity.

The Rat Islands are noteworthy because it was at Amchitka Island that the first indication of substantial recovery of a sea otter population was noted in 1935. An aerial survey covering all of the Rat Islands was conducted in 1959. Attempts to repeat the survey in 1962 failed because of prolonged harsh weather, but a successful survey was made 2 May 1965. The survey data are recorded in table 21.

Individual islands from which data of particular interest are available are discussed below.

Buldir Island.—This island is 55 miles west of Kiska and is the most isolated of the Rat Islands group. Apparently, for this reason it was the last to be repopulated. No otters were seen during an aerial survey 19 May 1959, but this survey was unsatisfactory because of poor weather conditions (wind and fog). The first modern report of sea otters at Buldir was made by R. D. Jones (1963). He saw an adult male and three females with young there during a visit, 25–28 June 1962. In 1963, between 7 and 19 July, our party recorded five mothers with young and four lone adults on a partial surface survey which included the north coast of the island.

On 2 May 1965 aerial survey conditions were fair (wind 10–15 knots and sun glare) and 15 otters were seen. Numerous sea lions were also present, making observations somewhat difficult. It seems probable to us that the total sea otter population does not exceed 30 animals.

Murie (1940 and 1959), and Williams (1937) did not find sea

TABLE 21.—*Rat Islands group, sea otter population density, estimated from aerial survey counts, 19 May 1959 and 2–3 May 1965*

Island	Otters counted		Estimated total		Square miles of habitat ¹	Otters estimated per square mile	
	1959	1965	1959	1965		1959	1965
Buldir ²	—	15	—	30	13	—	2
Kiska, L. Kiska, Tanadak I. and Pass	1,127	1,229	1,503	1,652	78	19	21
Segula	47	56	63	75	7	9	11
Pyramid, Davidof, Khvostov	33	39	44	52	8	5	7
Little Sitkin	50	135	66	180	15	4	12
Rat	270	326	360	435	30	12	15
Amchitka	1,560	1,144	2,078	1,525	110	19	14
Semisopochnoi	393	203	524	271	32	16	8
Total	3,480	3,147	4,638	4,220	293	12	11

¹ Square nautical miles of water 30 fathoms or less in depth.

² At Buldir Island in July of 1963, 9 otters were counted from the surface along 4 miles of the 10-mile shoreline. The estimated total in that year was 25 otters.

otters at Buldir. The present breeding population probably became established there in recent years. This fact is important because the sea otters must have crossed 55 miles of open water to reach Buldir from Kiska. Buldir reef, a 20-mile strip of relatively shallow water, extends 20 miles west of Kiska to 15 miles east of Buldir. It offers depths of less than 30 fathoms where food might be found en route, and otters were seen in this area on 27 May 1959 (A. C. Hartt, letter, 1960).

The observed absence of sea otters at Buldir after intensive exploitation ended in 1911, and their reappearance there in 1962, furnishes another example that, given time, sea otters will find their way from one island group to another across broad expanses of deep open water.

Rat Island.—The available observations of numbers of sea otters at Rat Island are listed in table 22. These data indicate that population changes at Rat Island followed a pattern similar to the changes observed at Amchitka during the same period and in more recent years in the Andreanof Islands. No observations are available from Rat Island to indicate that population reduction there was caused by mortality. Presumably, though, as was observed at Amchitka, mortality at Rat Island caused population reduction from a high of 31 otters per square mile of habitat to 12 to 15 per square mile in recent years.

Amchitka Island.—A number of surface and aerial counts and estimates of the Amchitka sea otter population have been made since 1935. Estimates of the total population, because of the variety of methods used in obtaining the basic field data, are approximations and are given to represent an order of magnitude. That these approximations are within reasonable limits is indicated by the fact that they reveal a history of population growth, decline, and stabilization (with annual fluctuations) that is typical of animals when a "seed population" is given complete protection in ideal vacant habitat.

The first observation of significant recovery of a sea otter popu-

TABLE 22.—*Rat Island sea otter population density in 30 square miles of feeding habitat*

Year	Count	Estimate of total	Otters per square mile	Authority and survey method ¹
1943.....	705	² 940	31	F. Beals and G. T. Joynt, aerial count-estimate.
1949.....	234	312	10	R. D. Jones, aerial survey.
1959.....	270	360	12	Spencer-Kenyon, aerial survey.
1965.....	326	435	15	Spencer-Kenyon, aerial survey.

¹ All unpublished reports in U.S. Fish and Wildlife Service files.

² Estimate based on the assumption that 75 percent of the otters were recorded.

lation was reported at Amchitka Island by Lt. H. B. Hutchinson, U.S.N., Commander, Aleutian Islands Survey Expedition, in a memorandum of 21 June 1935. The investigation by Naval personnel at Amchitka was in response to a request by the U.S. Department of the Interior. Hutchinson (1935) stated "there are more than one thousand (1,000) adult animals and half that number of pups on the waters surrounding the island." Possible poaching of sea otters by the Japanese was suspected when a vessel believed to be the *Hakuyo Maru* was observed attempting to enter Constantine Harbor, Amchitka Island, on 24 June 1935 (Hutchinson, 1935).

Also, unidentified men were seen on the island in August 1936 (Swicegood, 1936). Accordingly, buildings were erected on Amchitka by the U.S. Bureau of Fisheries in July 1937 (U.S. Bureau of Fisheries, 1938). Sea otter wardens were stationed there intermittently during parts of each year from 1937 through 1940.

During World War II, specific observations of sea otters were recorded by G. T. Joynt (1957) and Beals (1943). Beginning in 1949, many observations were obtained from Amchitka. Selected population counts and estimates that were made are shown in table 23. Other estimates not based on field counts are omitted.

The tendency of a sea otter population to expand to new areas primarily at the periphery of a dense population is illustrated by observations from Amchitka.

Lt. Cdr. S. P. Swicegood (1936), commanding officer of the *Chelan*, conducted field counts of otters at Amchitka on 14-16 August 1936. Although 804 otters were counted along 24 miles of the Pacific coast of the island, only 10 were seen on the Bering Sea coast. A similar condition was observed in the summer of 1937 when C. L. Loy and O. A. Friden (1937) counted 1,241 otters along the Pacific coast of Amchitka and only 80 along the Bering Sea coast. The aerial count by Beals (1943) when he recorded 2,198 otters along the Pacific coast and 1,219 along the Bering Sea coast indicates that between 1937 and 1943 a movement of otters from the Pacific to the Bering Sea coast of the island occurred, probably because the large Pacific coast population caused food depletion along that side of the island.

A review of the field counts at Amchitka between 1936 and 1965, summarized in table 23, demonstrate that a dense population existed on the south side of the island in 1936 (42 otters per square mile) while a sparse one (3 otters per square mile) occupied the north side. Emigration was not rapid but it was appreciable by the year 1939 (south side 40 otters per square mile, north side 14

TABLE 23.—*Amchitka Island sea otter population density in 110 square miles of feeding habitat*

[Only the counts that included all or substantial areas of Amchitka, are included. Area measurements from USCGS charts show 72 square miles of feeding habitat on the Pacific (south side) and 38 square miles on the Bering Sea (north side) of Amchitka. Habitat is considered to be water 30 fathoms or less in depth.]

Year	Counts			Estimates				Otters per square mile			Authority and survey method
	North side	South side	Total	North side	South side	Total	North side	South side	Total		
1936	10	804	814	1 100	3 000	3 100	3	42	28	Swicegood (1936) ²	
1937	80	1 241	1 321	³ 200	3 102	3 302	5	43	30	Loy and Friden (1937) ²	
1939	217	1 138	1 355	³ 542	2 845	3 387	14	42	31	Loy (1940) ²	
1943	1 219	2 198	3 417	4 1 625	2 931	4 556	43	41	41	Beals (1943) ⁵	
1949	528	559	1 087	704	745	1 449	19	10	13	Jones (1949) ⁵	
1959	537	1 023	1 560	716	1 364	2 080	19	19	19	Kenyon and Spencer (1959) ⁵	
1965	720	424	1 144	960	560	1 520	25	8	14	Kenyon and Spencer (1965) ⁵	

¹ Estimates made by Swicegood on the basis of counts made along 24 miles of coast and other observations at Amchitka.

² Surface surveys.

³ The estimate given by Loy and Friden in 1937 was 1,760, and by Loy in 1939 was 1,700. Both estimates are given above on the assumption that about 60 percent of the otters are not seen on a surface survey (Lenskink, 1958).

⁴ Beals did not give a calculated estimate of the totals. This estimate, like other aerial surveys is based on the assumption that about 75 percent of the otters present were recorded.

⁵ Aerial survey.

otters per square mile). By 1943 the population density was high on both north and south sides of the island but nearly equal (43 and 41 otters, respectively, per square mile). The difference observed in 1949 (10 otters per square mile of habitat on the south side of the island and 19 on the north side) probably resulted from mortality and emigration caused by depletion of food species that must have occurred in earlier years when the population on the south exposure was very dense (42 otters per square mile). By 1959 the population reached a condition of relative equilibrium with the population evenly distributed (19 otters per square mile) on both north and south shores of the island (fig. 73). By 1965 considerable divergence again occurred, the density on the north side increasing to 25 otters per square mile and on the south side decreasing to 8. Additional detailed studies over a period of years will be necessary to understand the observed population fluctuations. It is possible that significant numbers of otters might move across Oglala Pass to Rat Island.

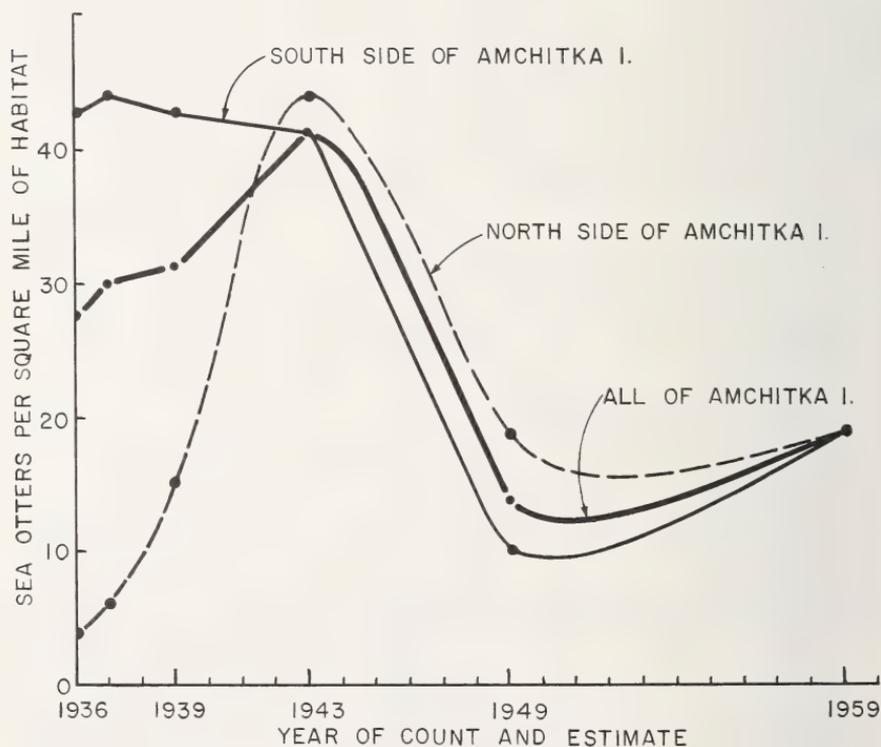


FIGURE 73.—Changes in population density on the north and south coasts of Amchitka Island, 1936-59. Estimates of the population density are based on field counts (see table 23).

Available information indicates that in the 1909–11 period the Amchitka sea otter population may have numbered about 100 animals (fig. 74), and that this population reached maximum size of about 4,500 otters in the early 1940's and then "crashed" to about 1,500 animals by 1949. A gradual increase to about 2,000 otters apparently occurred between 1949 and 1959, but mortality in the winter-spring period of environmental stress caused the population to stabilize or possibly to decrease in the early 1960's.

A curve based on field counts and population estimates is shown in figures 73 and 74. An estimated rate of increase of 10 percent

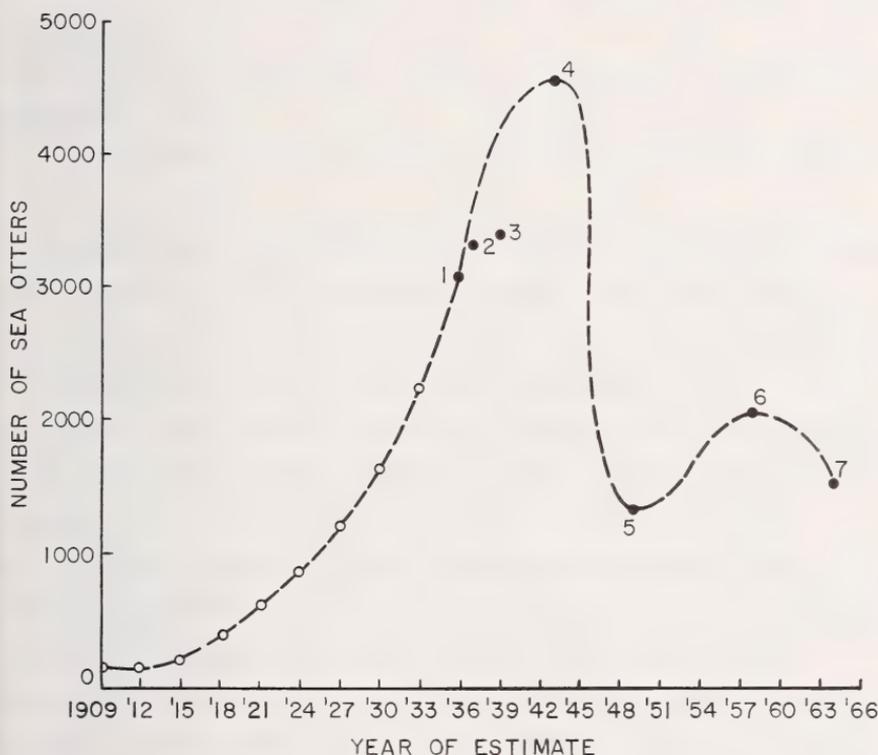


FIGURE 74.—Estimated curve of the Amchitka sea otter population, 1909–65. No data are available before 1936. The curve from 1909 to 1936 is a projection back from the estimated 1936 population, assuming that the population increased in this period at an exponential rate of 10 percent per year (see section on Seguam Island). Point 1: Population estimate by Swicegood (1936) based on extensive surface counts and observations. Points 2 and 3: Population estimates based on the surface counts of Loy and Friden (1937) and Loy (1940). Point 4: Estimate based on aerial count by Beals (1943). Point 5: Estimate based on aerial count by Jones (1949). Points 6 and 7: Estimate based on aerial counts by Kenyon and Spencer (1960) and Kenyon (1965).

per year in early stages of growth (fig. 74) is based on the observed growth rate in a part of the Andreanof Islands (Seguam Island) where conditions seemed similar to the Amchitka area. The field counts of otters by Loy and Friden (1937) and Loy (1940) are projected to estimated totals on the basis of Lensink's (1958) data indicating that about 60 percent of the otters present may not be seen on a surface survey. These estimated totals assume logical positions (Points 2 and 3) on the curve between the estimated totals of Swicegood (1936), Point 1, and Beals (1943), Point 4. The observations of mortality which occurred after the Amchitka population reached a density of at least 42 otters per square mile are discussed under Limiting Factors.

Lensink (1960) estimated the total population of sea otters at Amchitka on the basis of a field count of otters obtained during a period of weeks in the summer of 1956. His count was 2,568 otters on the eastern half of the island and his total estimate was 6,000 to 8,000 animals.

Our 1959 and 1965 aerial surveys for all of Amchitka were made under excellent observation conditions and our total counts were 1,560 and 1,144 otters, respectively. Why were our total counts much less than Lensink's partial count? Two reasons are suggested: (1) The number of otters at Amchitka may have been reduced between 1956 and 1959. General field observations and observed high winter-spring mortality indicated that population reduction may have occurred. Emigration may also have occurred. (2) Lensink made many trips to different contiguous counting areas during a period of weeks. It is possible that otters moved in the time between counts and the same animals were included in more than one count. If Lensink's (1960) estimate of 6,000 to 8,000 otters at Amchitka is accepted, it would mean that the population there was 55 to 73 animals per square mile of feeding habitat. All other observations and studies made at Amchitka and in other areas indicate that this estimate is very high—nearly twice as large as the indicated maximum population observed by Beals (1943).

In summary, our studies conducted since 1955 and intermittent surveys made since 1935 have indicated that the sea otter population on Amchitka Island grew to a large size, causing overutilization of food resources during the mid-1940's. Population reduction through starvation was then observed and a fluctuating population in balance with the habitat resulted.

It was not surprising, therefore, that our 1965 observation of 1,144 otters at Amchitka was less than our 1959 tally of 1,560, a

reduction of 416 animals, or 27 percent. It is interesting to note that during the interval between surveys 637 otters were killed, either by the Alaska Department of Game for their pelts (502 in number) or by the Fish and Wildlife Service for research. Apparently reproduction during the 1959-65 period compensated only partially for the natural and artificial mortality that occurred. It may be concluded that either the habitat limited the otter population below the 1959 level, or the slow rate of reproduction prevented compensatory population growth.

A summary of the probable history of the rise and fall of the Amchitka sea otter population, as deduced from field studies at Amchitka and by analogy with observed rates of growth in other populations, is given below:

1. The 1911 population of otters, at Amchitka, was about 100 animals.

2. At a rate of growth of about 10 percent per year, this population increased to about 3,000 animals in 1935.

3. In the 1935-43 period, the south side of the island was overpopulated and otters moved to the north side. The rate of increase decreased because of mortality caused by overuse of food resources.

4. By 1943 both the north and south shores were crowded by a total population of over 4,000 otters (more than 40 otters per square mile of habitat) and mortality increased.

5. By 1949 field observations indicated that the population had crashed to less than one-third of its 1940-43 maximum. Mortality rather than emigration apparently accounted for much of the decline.

6. Since about 1949 high mortality annually among juveniles and old adults in the late-winter, early-spring season of stress has caused the population to fluctuate within the range of about 1,500 and 2,500 animals (exclusive of dependent young).

Semisopchnoi.—Available information indicates that the sea otter was exterminated at Semisopchnoi during the pre-1911 period of unregulated exploitation. They were vulnerable to hunters because the island is relatively small, the band of feeding habitat along the shore is narrow, and there are no offshore reefs.

No mention is made that sea otters were seen there during the 1936-38 expeditions by Murie (1959) and his assistants. V. B. Scheffer told me in 1964 that sea otters were not seen when he landed on Semisopchnoi on 4 July 1937.

Beals (1943), speaking of military pilots who developed much interest in the distribution and abundance of sea otters while stationed on Amchitka, says "These same pilots have made many

scouting flights around Semisopochnoi Island and report that they have never seen sea otters in that vicinity."

On the aerial survey of 19 May 1959, when observation conditions were excellent, we saw 393 otters (16 per square mile of habitat) at Semisopochnoi Island. It thus appears that the animals moved from Amchitka across nearly 30 miles of open water to this island after 1943, when the Amchitka population approached maximum size and population pressure stimulated emigration. By 1965, the population at Semisopochnoi had decreased to an estimated 8 otters per square mile of habitat (table 21).

Delarof Islands

This small group (fig. 75) is technically part of the Andreanof group (U.S. Board on Geographic Names, 1963), but is treated as a separate unit here. The group includes a distance of about 33 miles from east to west and is separated from Tanaga Island

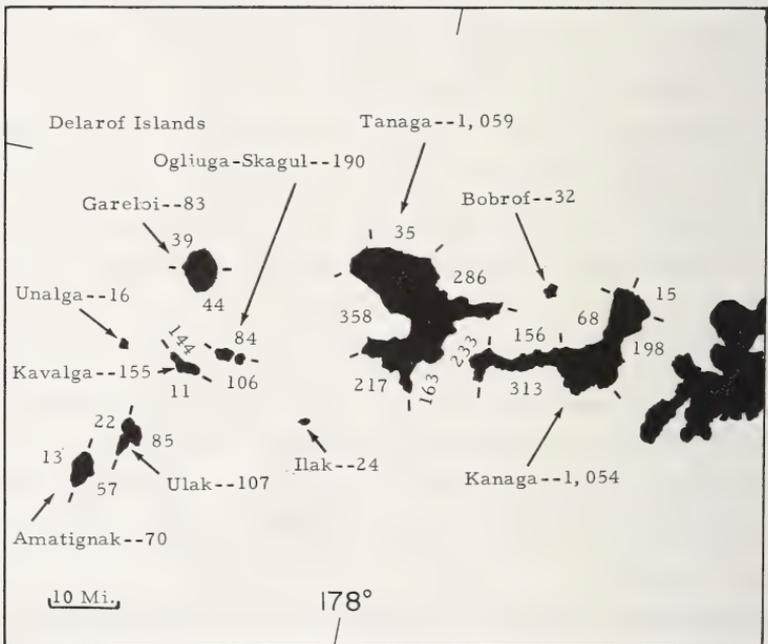


FIGURE 75.—The Delarof Islands of the western Andreanof Islands were apparently among the few Aleutian areas where the sea otter remained in 1911 when it was given protection. A large population developed here and at Kanaga and Tanaga Islands by the late 1940's, but population pressure did not cause repopulation of nearby Adak until the mid-1950's. The number of otters observed on aerial surveys of 2 and 3 May 1965, as shown on this map, was 2,790.

on the east by 14-mile-wide Tanaga Pass and from the Rat Islands on the west by 50-mile-wide Amchitka Pass. The Delarofs have no human inhabitants.

Murie (1940) found a thriving sea otter population at Ogliuga in 1936. Joynt (1957) says of his 1943 aerial observations that—

The most densely grouped of any pod of sea otter observed was on one end of the sand bars exposed at half tide that lies between Kavalga Island and Ogliuga Island in the Delarof Islands group.

Data from the 1930's, as cited above, indicate that the Delarof and Rat Islands populations approached maximum size at about the same time. Because of the width of Amchitka Pass (50 miles), it appears probable, as pointed out by Lensink (1960), that remnant populations remained in 1911 in both the Rat and Delarof Island groups. The habitat at Amchitka and in the Ogliuga-Kavalga Islands areas, is similar in having extensive shallows dotted by submerged or partially submerged reefs. Although these offered feeding habitat and a place of refuge to the sea otter, they presented considerable hazard to early sea otter hunters and were probably instrumental in preserving the species.

On 26 May 1959, our aerial observations (table 24) revealed that the number of otters per square mile of habitat in the Delarofs was the highest of any island group that we surveyed. This condition is of particular interest because the Delarofs were among the first Aleutian islands to be repopulated. By May 1965, our observations indicated that the Delarof population had dropped by approximately 50 percent (table 24).

It may be postulated that after the population peak, which probably occurred in the 1930-40 period, emigration to Tanaga

TABLE 24.—*Delarof Islands sea otter population density estimated from aerial survey counts of 26 May 1959 and 2-3 May 1965*

Island	Otters counted		Estimated total		Square miles of habitat ¹	Otters estimated per square mile	
	1959	1965	1959	1965		1959	1965
Gareloi.....	41	83	68	111	9	8	12
Unalga.....	51	16	85	27	8	10	3
Kavalga.....	275	155	367	207	529	52	10
Ogliuga.....	112	144	149	192			
Skugul-Tag-Ugidak.....	281	46	375	77	260	20	13
Gramp Rock.....	134	32	179	53			
Ilak.....	49		82				
Ulak.....	352	107	469	143		30	
Amatignak.....	102	70	136	117			
Total.....	1,397	653	1,910	927	89	Av. 21	10

¹ Includes water of 30 fathoms or less in depth as measured from U.S. Coast and Geodetic Survey charts.

² Closely associated islets and islands.

took place. After the Tanaga population exceeded the carrying capacity of the available habitat, otters moved westward to the Delarofs again as well as eastward to Kanaga and Adak. Thus, we observed a second population peak in the Delarofs in 1959. This resulted in food depletion and a subsequent "population crash" bringing the population density from 21 down to about 10 otters per square mile by May 1965 (table 24). Whether oil from the San Patrick, which was wrecked on the south shore of Ulak Island during the winter of 1964-65, was a factor in population reduction is not known.

Andreanof Islands

The Andreanof Islands (figs. 76 and 77) (excluding the Delarof group) extend for a latitudinal distance of about 230 miles from Tanaga on the west to Seguam on the east. Human populations in this group are at the U.S. Naval Station on Adak, and Atka

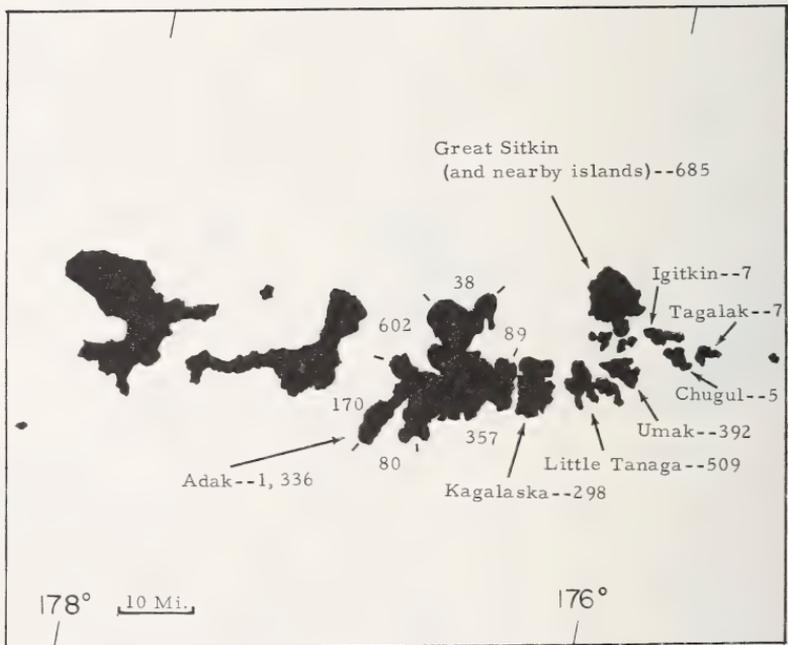


FIGURE 76.—The Adak-Great Sitkin Island areas in the central Andreanofs were repopulated during the 1950's and early 1960's by otters from the Delarof and Kanaga and Tanaga Islands. No otters were found on a survey of Adak in 1952, but on an aerial survey in 1954 a count of 48 was obtained, and by 1965 the count increased to 1,336. On aerial surveys of 25 and 26 April 1965, 3,239 otters were observed in the area shown.

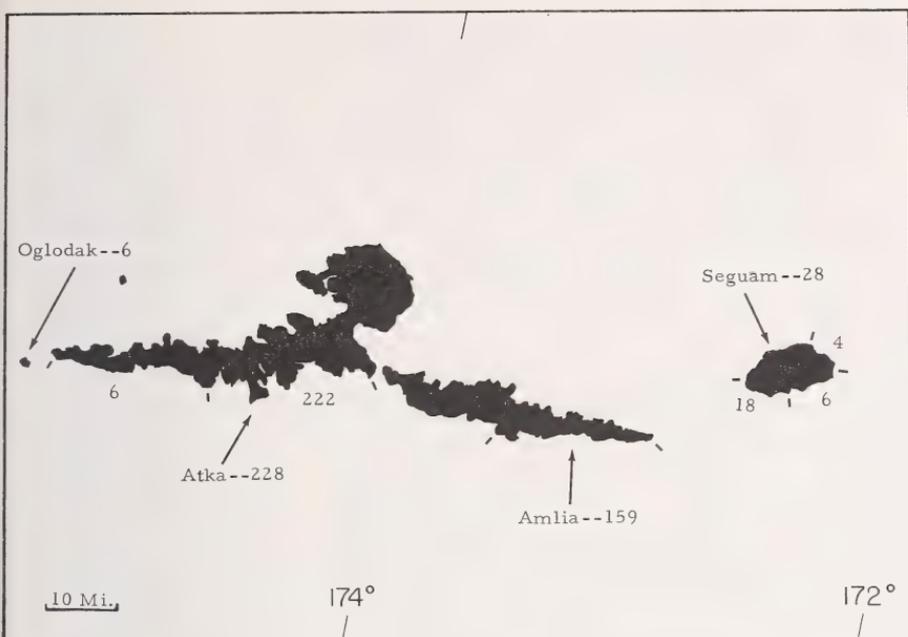


FIGURE 77.—The colonies on the southern exposures of Atka and Amlia Islands, in the eastern Andreanof Islands, appear to be augmented from the large population in the central Andreanofs (Adak–Great Sitkin area). Repopulation is proceeding at Atka and Amlia as it did at Amchitka, where a large population developed on the south side of the island before the north exposure was repopulated. On aerial surveys of 21 April and 6 May 1965, 421 otters were observed in the area shown.

Village on Atka Island. Several other islands were occupied by the military during World War II.

The group is of special interest because detailed observations on population growth and range extension of sea otters were obtained there. Aerial surveys of the entire group were conducted in late May 1959, early April 1962, and early May 1965. In all significant areas these surveys were conducted with excellent observation conditions and by the same observers (D. L. Spencer and Kenyon). The surveys offer the best comparable data available. Field observations, population estimates, and population density are summarized in table 25.

Analyses of observed population growth and of population fluctuations are presented for individual islands on the following pages and a discussion of the group as a unit is presented below.

The sea otter populations at islands from Tanaga on the west to Seguam on the east (exclusive of Bobrof Island, which is small

TABLE 25.—*Andeanof Islands counts and estimates of sea otters obtained on three aerial surveys to show movements of otters*

[Surveys were made on 25-27 May 1959, 5-6 April 1962, and 19 April to 8 May 1965. The islands are listed in geographical sequence, top to bottom from west to east. Counts made at small islets closely associated with large ones are combined with the count for the large island].

Island	Otters counted			Otters estimated			Square miles of habitat			Otters per square mile of habitat		
	1959	1962	1965	1959	1962	1965	1959	1962	1965	1959	1962	1965
Tanaga.....	902	898	1,059	1,203	1,197	1,412	83	14	17	14	—	17
Bobrof ¹	57	—	82	76	—	53	2	—	26	38	—	26
Kanaga.....	1,822	846	1,064	2,429	1,128	1,405	95	12	15	26	12	15
Adak.....	1,718	2,260	1,336	2,291	3,013	1,781	75	40	24	31	40	24
Kagalaska.....	1	251	298	1	335	397	15	22	26	<1	22	26
Little Tanaga.....	0	214	509	0	255	679	22	9	31	0	13	31
Umak.....	0	94	392	0	157	523	9	17	58	0	17	58
Anagaksik.....	0	14	0	0	28	0	1	28	0	0	28	0
Great Sitkin ²	0	325	710	0	433	947	80	5	12	<1	5	12
Atka.....	33	50	228	44	83	304	200	<1	1.5	0	<1	1.5
Kasatochi.....	0	0	NS	0	0	—	5	0	—	0	0	—
Koniuji.....	0	0	NS	0	0	—	1	0	—	0	0	—
Amlia.....	83	91	159	111	152	212	150	1	1.4	<1	1	1.4
Sequiam.....	14	23	28	28	38	47	28	1	2	<1	1	2
Total.....	4,630	5,066	5,805	4 6,183	6,849	4 7,760	766	—	—	—	—	—

¹ Bobrof is a small island and was not surveyed in 1962. It is omitted from certain calculations based on this table.

² In addition to Great Sitkin the counts made at 12 small islands from north of Umak to Atka are included.

³ NS = no survey was conducted.

⁴ When Bobrof Island is excluded the total becomes 6,107 in 1959 and 7,707 in 1965.

and was not surveyed in 1962) increased from 6,107 otters in 1959 to 6,849 in 1962 (table 25), a gain of 742 otters or 12.1 percent in 3 years. In the next 3-year period (1962-65) the same area gained 858 otters (7,707 minus 6,849, table 25) or 12.5 percent.

Within the Andreanofs, emigration occurred when islands became densely populated. For example, the Kanaga population lost 1,301 otters (2,429 minus 1,128, table 25) between 1959 and 1962, while nearby islands (Adak, Kagalaska, Little Tanaga, Umak, Anagaksik, Great Sitkin, and adjacent islets) increased from 2,292 to 4,269 (table 25), a gain of 1,977 otters or 86 percent. Because immigrating otters may have moved into the available vacant habitat surrounding the above named islands from Tanaga as well as Kanaga, it is not possible to separate the increase representing reproduction from that caused by immigration in these areas. The conclusion is indicated that in the Andreanofs the total sea otter population may grow at a rate of about 4 to 5 percent per year and that in the 1975 to 1980 period the population there may number over 12,000 otters or about 14 animals per square mile of habitat.

Tanaga Island.—The repopulation of Tanaga Island appears to have been well underway by the mid-1930's. Williams (1937) mentions it along with Amchitka and Ogliuga as being one of the "most productive" islands. D. Hooper (*in Jones, 1953*) indicated that the otter population there was large in 1953. Until our aerial surveys, no comprehensive quantitative assessment of the otter population at Tanaga was made. Available population data are summarized in table 26.

The few observations available indicate that population overflow from the Delarof Islands repopulated Tanaga during the 1930's, and that during the late 1940's or early 1950's the local population reached maximum size. During the mid- or late-1950's, the population density probably became reduced through emigration to Kanaga Island and remained stabilized from 1959 to 1962 at about 14 otters per square mile of habitat. The increase to about 17

TABLE 26.—*Tanaga Island sea otter population density in 83 square miles of feeding habitat*

Year	Count	Estimate of total	Otters per square mile	Authority and survey method
1937.....	(7)	150+	2	O. J. Murie and V. B. Scheffer, surface survey.
1953.....	1,000 (ca.)	1,000+	12+	D. Hooper, surface survey (<i>in</i> Lensink, 1960).
1959.....	902	1,203	14	Spencer and Kenyon, aerial survey.
1962.....	898	1,197	14	Spencer and Kenyon, aerial survey.
1965.....	1,059	1,412	17	Spencer and Kenyon, aerial survey.

otters per square mile in 1965 may have resulted from emigration from densely populated Kanaga.

Kanaga Island.—The Murie expedition visited Kanaga in 1936 and Williams (1937) states that no sea otters were seen. Natives reported to him, however, that otters did “occur occasionally or sparingly” there. By 1943, Kanaga was apparently only sparsely repopulated. Joynt (1957) says that in 1943:

A few stray animals were observed along the south shore of Kanaga but I do not recall ever observing more than 6 or 8 animals on the three or four flights over this area.

By 1953 the population had increased greatly. In June of that year D. Hooper (*in Jones, 1953*) spent 21 days on Kanaga. He walked 40 miles of beach and counted 575 otters. After examining a number of inshore areas at Tanaga he estimated that the otter populations of Kanaga and Tanaga Islands were large, “probably numbering several thousand” animals.

Data obtained on the 1959 and 1962 aerial surveys indicate that the Kanaga population was near maximum size in 1959. The precipitous population drop from an observed total of 1,822 otters in 1959 to 846 in 1962 indicates that the estimated 1959 population of 26 otters per square mile of available feeding habitat may have depleted food resources and precipitated substantial emigration (and mortality?) during the elapsed 3-year period. By 1965 a slight increase, probably resulting from crowding at nearby Adak, had occurred (table 27).

On a dory survey in 1957 along a 19-mile sample of coast, Lensink (1960) recorded 566 otters. Along the same coastal sample on our 1959 aerial survey we recorded 549 otters and in 1962 the aerial count there was 404. The similarity of the 1957 surface

TABLE 27.—*Kanaga Island sea otter population density in 95 square miles of feeding habitat*

Year	Count	Estimate of total	Otters per square mile	Authority and survey method
1943	6-8	few	(?)	G. T. Joynt (1957) flew repeatedly over area.
1953	575	many	(?)	D. Hooper (<i>in Jones, 1953</i>) walked 40 miles of beach and counted otters.
1957	566	¹ 3,000-5,000	32-53	C. J. Lensink (1960), dory survey along 19 miles of coast.
1959	1,822	2,429	26	Spencer and Kenyon, aerial survey, entire island.
1962	846	1,128	12	Spencer and Kenyon, aerial survey, entire island.
1965	1,054	1,405	15	Spencer and Kenyon, aerial survey, entire island.

¹ Because this estimate was made from data gathered along the south shore, where more habitat is available than along the north shore, the estimated upper limit may be somewhat high.

and 1959 aerial observations indicate that the total populations in these two years were at least similar, or perhaps larger in 1957, since aerial counts usually include a higher percentage of animals present. The number of otters seen along different parts of the coast on aerial surveys when correlated with the distribution of available feeding habitat around the island, indicate that the distribution of otters along the shores of the entire island varies according to the amount of habitat available.

The coastal zone of sea otter habitat is narrow along much of the north shore of Kanaga. In 1959, along 30 miles of the north shore, we observed 415 otters (14 otters per mile of coast), while along 45 miles of the mostly southern and eastern coast, where the habitat zone is wider, we recorded 1,407 otters (31 per mile of coast).

These data suggest that Lensink's (1960) "somewhat conservative" estimate of 3,000 to 5,000 otters at Kanaga (32 to 53 otters per square mile of feeding habitat) based on his sample count along the south shore may have been quite realistic (table 27).

Adak Island.—The U.S. Naval Station, Adak, was established in the early 1940's. It remains today the most important center of human population in the Aleutian Islands and furnished facilities for sea otter studies in the outer Aleutian area.

The Murie expeditions did not find sea otters at Adak and obtained no information from natives that they were observed there in recent years (Williams, 1937).

Although 14 otters were seen in 7-mile-wide Adak Strait between Kanaga and Adak in 1943 (Lensink, 1960), few if any crossed the strait and became established at Adak during the 1940's.

When I visited Adak on 31 October to 5 November 1947, I saw no sea otters and could find no report of an observation there. Neither did R. D. Jones see any otters (table 28) on a complete circuit of Adak by dory in 1952. The first indication that sea otters had become established at Adak was an observation of 48 animals during an aerial survey in 1954 by Lensink (1960).

The influx of otters that began from Kanaga to Adak in the early 1950's proceeded rapidly and was documented during the 1959 and 1962 aerial surveys. It appears that emigration from Kanaga (26 otters per square mile in 1959) to Adak (31 otters per square mile in 1959) continued during this period and that a large population at Kanaga during a period of years had depleted food resources there. Adak, on the other hand, was repopulated only recently (in 1959) and serious food depletion did not occur until the

TABLE 28.—*Adak Island sea otter population density in 75 square miles of feeding habitat*

Year	Count	Estimate of total	Otters per square mile	Authority and survey method
1947	0	0	0	Kenyon field notes. No otters seen or reported seen.
1951.....	0	0	0	R. D. Jones, surface survey, west side only.
1952.....	0	0	0	R. D. Jones, surface survey entire island.
1954.....	48	80	1	C. J. Lensink (1960), air survey. All otters seen on west side of island.
1954.....	1	—	—	R. D. Jones. First recorded sighting at Adak Naval Station, on east side of island.
1957.....	399	997	13	C. J. Lensink (1960) and R. D. Jones, surface survey. Most otters on west side of island.
1959.....	1,718	2,291	31	Spencer and Kenyon, aerial survey.
1962.....	2,260	3,013	40	Spencer and Kenyon, aerial survey.
1965.....	1,336	1,781	24	Spencer and Kenyon, aerial survey.

1962–65 period. All available observations are listed in tables 27 and 28.

Kagalaska Island.—Kagalaska is uninhabited by man. Most of the island is precipitous. Although its coastline is about 35 miles long, the band of shallow water surrounding it and offering sea otter feeding habitats is relatively narrow. As at nearby Adak, sea otters were apparently exterminated at Kagalaska before 1911.

On the 1959 aerial survey we recorded one otter there. Between then and the 1962 survey the influx from nearby Adak was rapid and had apparently passed its peak in 1965 (table 29 and fig. 78).

Atka Island.—The village of Atka is the farthest west location of a small Aleut population today. The village is on Nazan Bay near the eastern end of the 55-mile long island.

Both R. D. Jones and I were told repeatedly by Aleuts living at Atka that during the 1940's sea otters were occasionally seen at Vasilief Bay near the east end of Atka. The 1959, 1962, and 1965 aerial surveys confirmed that a small and growing sea otter colony is resident in this area (table 25).

Vasilief Bay offers ideal sea otter habitat. The main body of the bay is dotted with rocks and islets. Numerous channels among them and irregular shores offer many areas that are sheltered

TABLE 29.—*Kagalaska Island sea otter population density in 15 square miles of feeding habitat*

Year	Count	Estimate of total	Otters per square mile	Authority and survey method
1954.....	0	0	0	Lensink, aerial survey.
1959.....	1	2+	<1	Spencer and Kenyon, aerial survey.
1962.....	251	335	22	Spencer and Kenyon, aerial survey.
1965.....	298	397	26	Spencer and Kenyon, aerial survey.

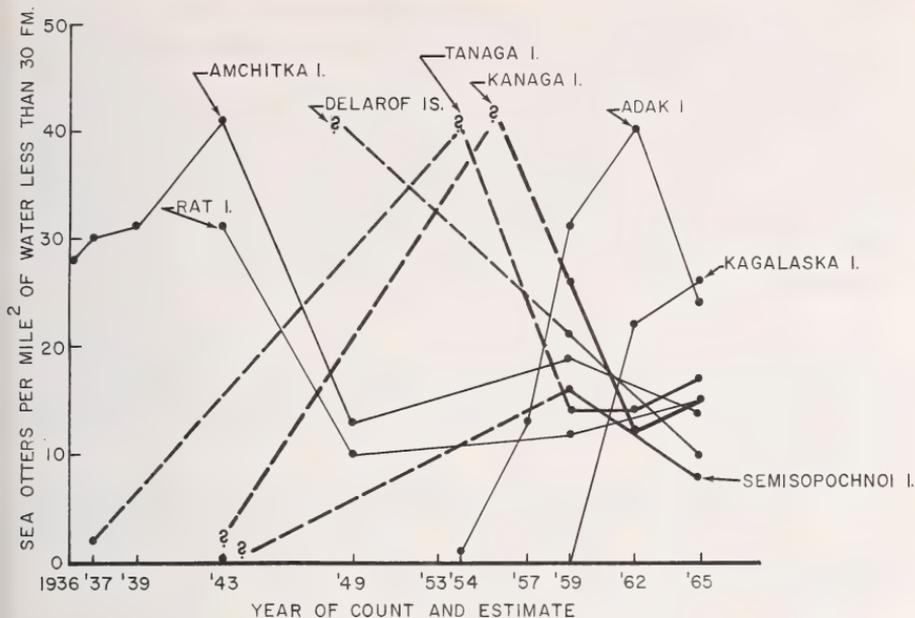


FIGURE 78.—Populations of sea otters at several Aleutian Islands have increased to maximum size and then crashed between 1936 and 1965. Estimates of otters per square mile of habitat (waters within the 30-fathom curve), which are based on extensive field counts, are shown as dots which are connected by solid lines. Observations of "few," or "many," or "thousands" are shown by question marks and connected by broken lines. (For data, see tables 21-29.) Population peaks apparently occurred between aerial surveys at Adak and Kagalaska Islands.

from wind and rough water in storms. This habitat apparently attracted the occasional otter that wandered eastward from the large population in the western Andreanofs, causing the colony to form and to be augmented by further immigration. In the 1959 to 1962 period, the colony increased by 86 percent and between 1962 and 1965 by 375 percent. Repopulation of the north side of Atka had not begun in 1965.

Amlia Island.—It is 40 miles long, has no human inhabitants and except near the west end is seldom visited by the Aleutian natives of nearby Atka Village. The U.S. Coast and Geodetic Survey has not as yet (1965) issued a chart showing soundings of Amlia's inshore waters. The area of sea otter feeding habitat (table 25) was estimated on the basis of measurements taken at Atka because the two islands appear similar.

Vague reports that I received from the hunters of Atka during the 1940's and 1950's indicated that a small number of sea otters

was resident at Amlia for a number of years. The 1959 aerial surveys revealed that a small population occupied the south side of the island, the greatest number being near the eastern extremity (fig. 77 and table 25). The 1962 survey confirmed that this population is resident but time was not available then to resurvey the north coast. In 1965 the entire coastline was surveyed but otters were seen only on the south coast. The increase between 1962 and 1965 from 111 to 212, a doubling of the population, may in large measure be attributed to immigration from the west.

If repopulation of this island proceeds in a way similar to population spread observed in other areas (Amchitka and Adak, for example) the north coast can be expected to repopulate after the present population on the south coast has increased considerably.

Seguam Island.—This is the easternmost island in the Andreanof group (U.S. Board on Geographic Names, 1963). It is separated from Amlia by Seguam Pass, 16 miles of deep water and strong currents. It has no human inhabitants.

The Murie expeditions did not find sea otters at this island but information from Aleutian natives indicated that otters had been seen there (Williams, 1937). The first specific evidence that sea otters occupied Seguam was found on our 1959 aerial survey. The 1962 and 1965 surveys confirmed that the small population is resident and is growing slowly. An increase of approximately 10 percent per year (from 28 to 47 otters in 6 years) may represent the rate of increase due to reproduction in an isolated, uncrowded population.

Because the population today is so small (table 25), it seems unlikely that otters survived the period of unregulated exploitation in this location. It appears more probable that wanderers from the larger populations in the west reached Seguam in recent years and remained there either because the habitat is desirable or because the width of Amukta Pass discouraged emigration to the Islands of Four Mountains. The relatively slow rate of increase, however, indicates that immigration is, as yet, not appreciable at this rather isolated location.

Islands of the Four Mountains

From Amukta Island northeastward to Kagamil Island on Samalga Pass is about 70 miles. There is no human population in this island group, therefore few surface observations are available. The survey of 3 March 1960 covered all coastlines and was made under excellent conditions. On 7 April 1962, survey conditions

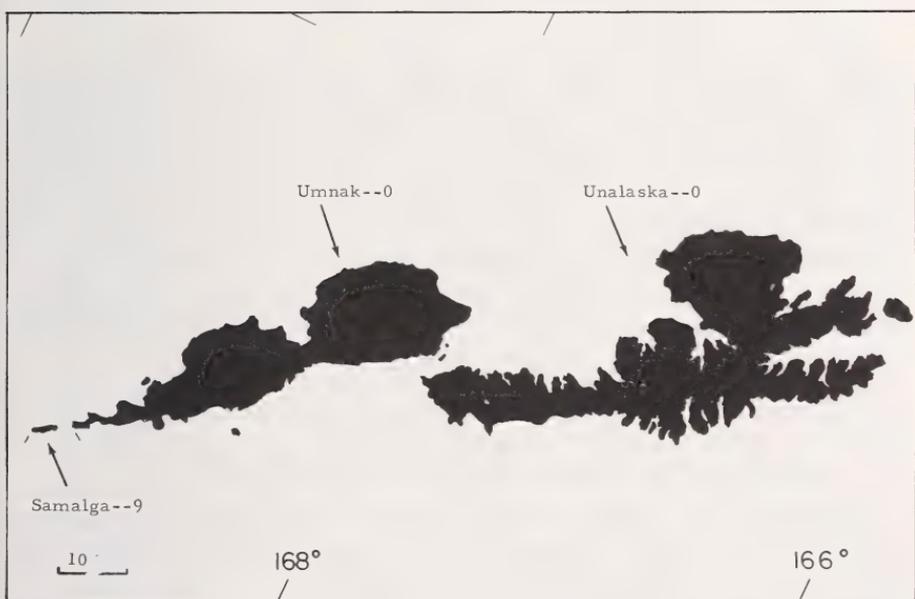
were fair and only about 50 percent of the coastline of each of the main islands was surveyed. On neither survey were otters seen. It is probable that no sea otters occupy this group at present.

The available sea otter habitat around the seven steep-sided islands in this group is 88 square miles. When compared with Gareloi, a similar island having a sea otter population of 8 otters per square mile of habitat, the estimated future population in the Islands of Four Mountains may be about 700 otters.

Fox Islands

This group (figs. 79 and 80) includes the islands in the 240-mile sector of the Aleutians between Samalga Pass and Isanotski Pass at the western extremity of the Alaska Peninsula. Amak Island, off the north coast of the Alaska Peninsula, although not one of the Fox Islands, is included in this discussion because of its proximity to Unimak Island.

Among the Fox Islands at present there are two small, widely



FIGURES 79.—The colony at Samalga Island and in the vicinity of Cape Sagak, Umnak Island, at the western extremity of the Fox Islands, is a small but permanent one. Otters were observed there during aerial surveys in 1960 (6), 1962 (10) and, as shown on the map, in 1965. This is the most isolated Aleutian colony. Complete surveys of Umnak and Unalaska Islands were made in March 1960 and April 1962. Only the south exposures were surveyed on 8 May 1965.

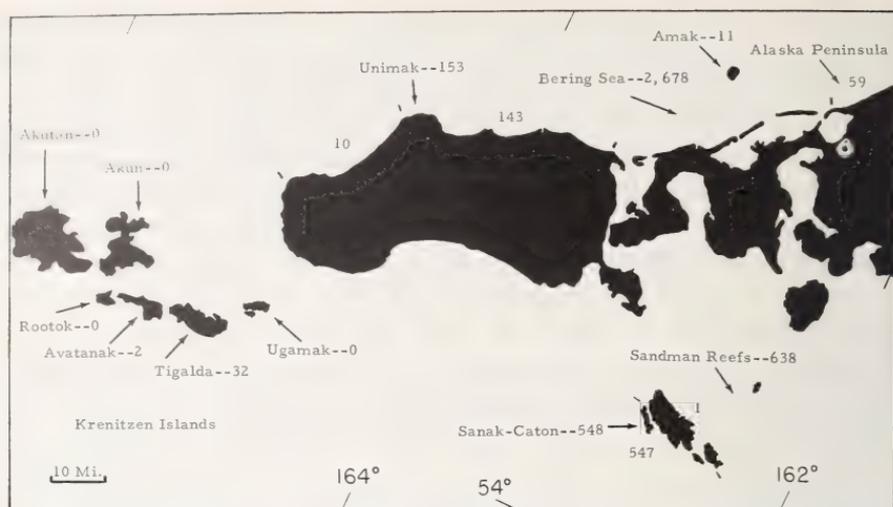


FIGURE 80.—The Sanak-Caton Islands and Sandman Reefs areas were last surveyed on 8 April 1962. All other surveys of the eastern Fox Islands shown on this map were made on 8 May 1965. The total number of otters observed on these two surveys in the areas shown is 4,121.

separated, but apparently permanent, sea otter colonies and one large population, but most of the available habitat is unoccupied. The small Samalga-Cape Sagak colony and the other on the northeast coast of Tigalda are apparently growing slowly. The large Bering Sea population off the north coast of Unimak Island and the western Alaska Peninsula, already of considerable size, is possibly augmented by an influx of otters from the Sanak-Sandman Reefs areas in the North Pacific Ocean. R. D. Jones (letter, 10 April 1964) reports that he—

observed an adult otter right smack in the narrows of the north end of False Pass [Isanotski Strait]. I've never seen one there before. He was at the time being swiftly carried into Bering Sea by the tide.

The available sea otter habitat in the Fox Islands is at present sparsely populated. Because of the large extent of this area, repopulation will probably require many years.

The western Fox Islands.—Human settlements include Nikolski Village, a sheep ranch, and a DEWline site near the south end of Umnak Island, and a sheep ranch and Reeve Aleutian Airways' installation near Cape Tanak on the north end of 65-mile long Umnak. On Unalaska Island the village of Unalaska is the largest of the extant native Aleutian settlements. There is also a DEWline site at Driftwood Bay on Unalaska Island. Counts of otters from

several sources and estimates of all otters in this area are summarized in table 30.

Several Aleutian natives who hunt and fish in the waters off the south end of Umnak and near the east end of Unalaska have given me verbal reports over a period of several years (1950-62). Fred and Antone Bezezekoff of Nikolski Village, Umnak Island, have told me of repeatedly seeing a small number of otters in the vicinity of Samalga Island and Cape Sagak at the southwest end of Umnak Island. Their highest count was 14 otters (F. Bezezekoff, letter 13 March 1961). The three aerial surveys of the Fox Islands indicate that the small colony at the western extremity of Umnak Island is permanent but no increase is indicated. Apparently few wanderers enter this extensive western Fox Islands area which is isolated from other populations.

No one at Unalaska reported a sea otter sighting in the 1950-62 period. That sea otters are now repopulating Unalaska is indicated by a recent report. On 19 and 20 July 1968, C. H. Fiscus, A. M. Johnson, and H. Kajimura (personal communication) saw an otter in Kismaliuk Bay, on the north coast of the island, and another off Tiderip Point at the island's southwestern extremity.

The available sea otter habitat adjacent to the islands from Samalga Island to Akutan Pass is about 570 square miles. If this habitat can support about 12 otters per square mile, the estimated future population of this area may eventually be about 6,800 otters.

Krenitzin Islands.—The Krenitzin Islands occupy a 45-mile sector of the Fox Islands from Akutan Pass on the west to Unimak Pass. The village of Akutan, on Akutan Island, is the only human settlement in the Krenitzins. Occasional otter sightings near Akutan are reported by native Aleut fishermen (Lensink, 1958).

TABLE 30.—*Numbers of sea otters observed and estimated population in the Fox Islands group*

[The many islands, islets, and rocks where no sea otters were observed are omitted]

Island and year	Otters counted	Estimated total
Samalga-Umnak:		
1962.....	10	20
1965.....	9	20+
Egg and Old Man Rocks: 1957 ¹	1	2
Tigalda:		
1960 ²	11	22
1965.....	32	53
Unimak-Amak:		
1962.....	811	1,081
1965.....	2,892	3,856
Total (highest counts).....	2,935	3,931

¹ Lensink (1958) aerial survey.

² Surface survey of June 1960.

On 23 August 1962, R. Thomas (fur seal research biologist) sighted one otter in Akutan Bay (personal communication).

On 3 and 4 March 1960, D. L. Spencer and I surveyed this island group in detail under good weather conditions. On 7 and 8 April 1962 and again on 8 May 1965, wind permitted us to make only an inadequate survey of a small area off Tigalda Island, the only place where sea otters were previously seen. Only three otters were sighted in 1959 and 1962. In addition to the aerial survey data, I obtained information during surface surveys by dory on 26–29 June 1960 when I counted 11 adult otters and 6 young with mothers at Tigalda Island. During the 1965 survey, in spite of wind and rain, we sighted 32 otters there (table 30).

During May and June of 1960 and 1962, C. H. Fiscus (fur seal research biologist) spent considerable time in the Krenitzins while conducting pelagic sealing investigations in Unimak Pass and Bering Sea. The sealing vessel anchored on numerous occasions in different bays and bights and Fiscus went along the shore by dory in several areas. These included Avatanak Strait, Akun, Serekka, and Trident Bays at Akun Island; Rootok Strait, Durbin Strait, Durbin Bay at Tigalda Island; Ugamak Strait, Ugamak Island; and the south shore of Akutan. Although a careful search was always made for sea otters, Fiscus told me that none was observed. It therefore appears probable that the small colony along the northeast shore of Tigalda Island is the only one in the Krenitzin Islands and that otters reported occasionally from Akun Strait are wanderers.

The area of sea otter habitat adjacent to the Krenitzin Islands is about 200 square miles. If it may support about 12 otters per square mile, the future otter population may be about 2,400.

Unimak and Amak Islands.—Unimak Pass separates Unimak Island from the Krenitzin Islands. The distance from Unimak Pass to Amak Island is about 100 miles. A Coast Guard Station at Cape Sarichef is the only human settlement in the study area.

The greatest number of sea otters in this area inhabit the shallow waters of the Bering Sea off Izembek Bay in the vicinity of Amak Island and off the north central portion of Unimak. Depths of 20 fathoms or less extend to about 8 miles from shore and the 30-fathom curve extends to about 15 miles from shore. The majority of the 811 otters observed on the 8 April 1962 aerial survey were seen near the 20-fathom curve. Observation conditions were good to excellent during this survey and sectors were systematically covered between 1 and 15 miles from the shore of Unimak Island and the tip of the Alaska Peninsula. In addition, I conducted

surface investigations in these waters with C. H. Fiscus and his crew of biologists from 7 to 10 July 1960 while on board the M/V *Windward*. Otters were found over waters as deep as 23 fathoms. An investigation of about 2 miles of beach on Amak Island in 1960 revealed no remains of sea otters or droppings. While walking the same beach in 1963, Fiscus found the remains of two adult sea otters but saw no living animals on shore. It appears that this population leads a predominantly offshore existence. Some observers (Lensink, 1958) speculate that this group of otters migrate seasonally. No evidence to support this supposition is available.

During aerial surveys of walruses on 27 March 1961, the Amak Island area was visited. Fog, however, prevented a satisfactory survey. A few otters were seen through gaps in the fog northeast of Amak Island, north of Izembek Bay, indicating that a number were present. It seems reasonable to conclude that, as in other areas, otters are resident there throughout the year. Where they bear their pups is unknown.

In 1963, R. D. Jones and C. P. McRoy (Jones, letters Dec. 1963 and March 1964) found five dead sea otters in April, June, August, and November on the Kudiakof Islands which separate Izembek Bay ($55^{\circ}20' N.$ lat., $162^{\circ}30' W.$ long.) from the Bering Sea. They also saw several living otters in Izembek Bay, 17–19 December 1963. These observations and the lack of similar ones in past years indicated a population increase in the southwestern Bristol Bay area which was confirmed during the 1965 aerial survey.

One of the significant observations we obtained during the 1965 aerial survey was of the very large number of otters occupying shallow water north of the Alaska Peninsula and Unimak Island (table 30). Many of these animals were gathered into large rafts well outside the surf line, apparently sleeping on their backs at midday when we made our survey (fig. 81). Scattered individuals were feeding. Although the 1965 survey showed that the majority of the otters in this area were within the 3-mile limit, the 1962 survey demonstrated that numbers of them may feed in waters near the 20-fathom curve, which in this area is from 5 to 8 miles from shore. A possible reason that more otters were near shore during the 1965 survey was that a north wind of approximately 30 knots had blown steadily for several days before our survey. At the time of the survey, the wind had dropped to 10–15 knots but was still from the north.

The indicated great increase in the otter population from Fox Islands to Port Moller may probably be attributed primarily to



FIGURE 81.—This group of 128 otters slept on the open sea about 2 miles off the north coast of Unimak Island, Alaska. No kelp beds are found in this offshore location. Available evidence indicates that animals in this area rarely come ashore. (KWK 65-17-8)

three factors: (1) An influx of otters from the Sanak Island-Sandman Reefs area. (2) A north wind of several days' duration before and during our 1965 survey may have concentrated large numbers of otters near shore from their extensive offshore feeding grounds. During the 1962 survey of this same area, we found otters more scattered than in 1965. In 1962 they were spread over many square miles of open water. Possibly we failed to see many of them in 1962. (3) A large number of mothers carrying young were observed during both surveys—obviously reproduction accounted for some but certainly not all of the observed population increase in this area.

If the habitat (more than 1,000 square miles) may be populated as densely as some of those of the Aleutian Islands, the population might reach from 10,000 to 15,000 otters. No quantitative study of the marine invertebrate fauna of southwestern Bristol Bay has been made. A qualitative study by McLaughlin (1963), however, revealed a variety of crustaceans and molluscs in this area and suggests that it is rich. The large numbers and variety of aquatic birds and marine mammals there indicate that food species are abundant.

We extended the 1965 survey along the north shore of the Alaska Peninsula about 10 miles northeast of Port Moller but found no sea otters beyond the mouth of that bay. Our observations

suggest that Port Moller (56° N. lat., 160°50' W. long.) is near the northeast extremity of the sea otter's range in Bristol Bay. A sea otter taken "... near the Naknek River ..." at about 58°40' N. lat., in northeastern Bristol Bay "... where they are rarely to be found" (U.S. Bureau of Fisheries, 1911, p. 56) was probably a wanderer from southwestern Bristol Bay.

Sanak Island and Sandman Reefs

Sanak Island (fig. 80), which supports a small village, is approximately 20 miles southeast of the eastern extremity of Unimak Island. Between Sanak Island and the Alaska Peninsula the Sandman Reefs consist of extensive shallows having a number of exposed rocks and islets.

Sea otters were reported in the Sanak Island-Sandman Reefs area as early as 1922 (McCracken, 1957), but must have been very scarce at that time (Lensink, 1962). The Murie expedition received reports of otters in this area in 1936 but found none (Williams, 1937). Aerial surveys in 1957 and 1962 indicate that a substantial population now in this area is increasing (fig. 80 and table 31).

Aerial surveys in 1957 by Lensink (1958) and my observations obtained on dory surveys of 20-23 June 1960 indicated that few sea otters occupied waters surrounding Caton Island and that the animals were more numerous among the reefs off the southeast coast of Sanak. Aerial surveys of 10 April 1962, during excellent weather conditions, confirmed these observations. The majority of the otters observed on both aerial surveys were concentrated among reefs and islets off the southwest coast of Sanak Island

TABLE 31.—Numbers of sea otters observed and estimated population in the Sanak Islands and Sandman Reefs areas

Area	Aerial surveys		Estimated total in 1962
	1957 ¹	1962 ²	
Sanak area:			
Sanak Island and associated reefs	236	525	700
Caton Island and associated reefs	15	23	46
Total	251	548	746
Sandman Reefs:			
Cherni Island	271	259	345
Clubbing Rocks	33	2	4
Little Goose Island	76	82	137
Deer Island and all reefs not named above	123	295	393
Total	503	638	879
Total both areas	754	1,186	1,625

¹ Aerial survey by Lensink (1958) on 19 July 1957.
² Aerial survey by D. L. Spencer and Kenyon on 10 April 1962.

within the 20 fathom curve. Lensink (1958) saw no otters in the relatively deep waters off the northeast shore of Sanak and only one was seen there during the 1962 survey.

Flights over the Sandman Reefs on 10 April 1962 were undertaken when conditions were excellent. We viewed the exposed rocks and islets and examined most of the open water. Otters could be seen on the glassy surface within a track about 2½ miles wide.

Because of the irregular bottom topography of this area, it is difficult to measure from charts the amount of available sea otter habitat. The approximate measurements obtained, however, indicate that the Sanak Island-Sandman Reefs area may furnish nearly 900 square miles of feeding habitat. With about two otters per square mile of habitat this area appears underpopulated.

Since the surveys of 1957 and 1962 were undertaken under excellent observation conditions, they may be comparable. If the total count in the Sandman Reefs area is projected forward at an increase of 5 percent per year (see Andreev Islands) the estimated 1962 count would be 637. The aerial count of 1962 was 638 otters. The 1957 survey may have missed a number of otters in the Sanak Island area, since Lensink's (1958) figures when projected to 1962 at 5 percent per year fall short of the count obtained in 1962.

Shumagin Islands

This group lies 100 miles east of the tip of the Alaska Peninsula and reaches its southern extremity at Chernabura Island about 100 miles south of the Peninsula's south shore.

Sea otters apparently survived the 1741-1911 period of exploitation in the Shumagin area where offshore feeding areas offered them refuge. Japanese poachers worked the area until at least 1910. An estimate of 4,000 otters in the southern Shumagins was made in 1920, but this population was certainly reduced when a tanker and a freighter were wrecked and spilled oil in this area during World War II (Kenyon, 1964).

A small human population lives at Unga Village on Unga Island and another at Sand Point on Popof Island. Reports from surface observers at these locations indicate that occasional otters wander to the vicinity of these two islands but that no sizable population exists there. About half of Unga Island was surveyed in 1962 and only four otters were seen, confirming reports of surface observers. The sea otter population of the outer Shumagins is, however, large (table 32). Many shallow areas with underwater reefs, particularly

TABLE 32.—Numbers of sea otters observed and estimated population in the Shumagin Islands

Island	Aerial survey		1962 estimate of total
	1957 ¹	1962 ²	
Unga	2	4	8
Nagai	149	338	676
Near	3	14	28
Bird	160	38	76
Chernabura	132	79	158
Simeonof	455	294	588
Little Koniuji	430	255	510
Big Koniuji	220	222	444
Peninsula	0	3	6
Spectacle, Bendel, and Turner	268	105	210
Popof (plus rocks)	2	—	4
Andronica	1	—	2
Twins	7	—	14
Total	1,829	1,352	2,724

¹ Complete aerial survey, 20 to 24 July 1957 (Lensink, 1958).

² Aerial survey, 10 April 1962, by D. L. Spencer and Kenyon. The survey of shallow areas offshore was incomplete. Therefore all 1962 field enumerations are increased by a factor of 50 percent to obtain the estimated total. If Lensink's 1957 count is used, the estimated total in that year is 2,440 (assuming 75 percent were seen). If population growth is considered to be 5 percent per year the 1962 population was 3,045 otters based on Lensink's field count.

between Chernabura and Simeonof Island, furnish sea otter habitat well offshore.

Surface observations at Simeonof Island between 4 and 10 June 1960 did not give an adequate indication of the number of sea otters inhabiting this area. On 8 June a dory survey around Simeonof Island yielded a count of only 75 adult otters.

When the aerial observations of 1957 and 1962 are compared (table 32) it appears that many of the 1962 counts are substantially less than those obtained in 1957 (Lensink, 1958). I believe that, because of the very calm weather conditions prevailing before and during the 1962 survey, many otters had moved to shallow offshore feeding areas, as they were observed to do in June 1960, and were thus not seen. Lack of time prevented a comprehensive survey in 1962 of rather large offshore shallow areas.

U.S. Coast and Geodetic survey charts indicate that water depth is not known in much of the Shumagin Islands area. A careful measurement of available sea otter habitat could therefore not be made. The available soundings suggest that large shallow areas exist. I have estimated that about 700 square miles of habitat are available around the islands and that in 1962 the population density was about four otters per square mile of habitat.

Alaska Peninsula

The south shore of the Alaska Peninsula, which offers considerable sea otter habitat, extends for over 400 miles from False

Pass to Cape Douglas at the mouth of Cook Inlet. The north shore of the peninsula is discussed under "Unimak and Amak Islands."

D. L. Spencer has flown over the coastal waters of the peninsula many times. Because of his previous knowledge of sea otter distribution and because of a shortage of time, our 1962 survey included primarily those areas where a significant number of sea otters was known to exist.

Otters were counted in the Cape Kumliun-Sutwick Island area in 1951 and 1957 (table 33). This area appears to be the center of the population along this coast. The 1962 survey was made from Cape Kumliun northeastward. The greatest concentration of sea otters was in Kujulik Bay and around Sutwick Island. One large group which was photographed (fig. 70) contained 440 otters, by a count from the photograph, the largest assemblage that was seen on the aerial surveys up to that time. From this area northeastward the number of otters seen decreased as shown in table 33. In 1957 Lensink (1958) found none east of Chiginagak Bay. Our observation of five otters east of this point in 1962 indicates a slow population spread eastward.

The difference in distribution of otters in the area between Cape Kumliun and Cape Kunmik, including Sutwick Island, between the 1957 and 1962 surveys, probably indicates that this rather large local population shifts about in this area in response to weather or food supply.

It is not possible from available charts to measure the square miles of sea otter habitat along the southeast coast of the Alaska Peninsula. We believe, however, that the increasing population may fill much vacant habitat in future years before maximum population is reached.

TABLE 33.—Numbers of sea otters observed and estimated population along the Alaska Peninsula

Area	Surveys			Estimate of total ⁴
	1951 ¹	1957 ²	1962 ³	
Univikshak Island area	13	180	86	143
Kujulik Bay (C. Kumlik)	12	103	684	912
Sutwick Island area	355	581	109	145
Aniakchak Bay and Amber Bay (C. Kunmik)	8	6	47	78
Cape Kunmik to Cape Igvak (55 miles)		19	22	37
Cape Igvak to Cape Kuliak (70 miles)		0	1	2
Total	388	889	949	1,317

¹ Aerial surveys during the May to August period by R. D. Jones (*in* Stiles, 1953).

² Aerial survey, 25 July 1957 (Lensink, 1958).

³ Aerial survey, 10 April 1962, by Kenyon and Spencer.

⁴ Estimated population as of April 1962.

Kodiak Island to Cook Inlet Area

From the Trinity Islands, off the south shore of Kodiak, to the Barren Islands, in the mouth of Cook Inlet, is about 180 miles.

Records of confiscated sea otter skins in reports of the U.S. Bureau of Fisheries (1912 to 1936) and the observation of four otters near Afognak Island in 1922 (Eyerdam, 1933) indicated that sea otters survived after 1911 in the Kodiak area.

Lensink (1958; 1960; 1962) conducted both aerial and surface surveys in this area and reviewed the numerous reports available from various individuals who lived in or visited the area during a period of many years. The historical record of 18th and 19th century otter hunters, as well as midden excavations reported by Laughlin (1963), reveal that the sea otter was once numerous in the Kodiak area. Today repopulation is proceeding slowly. The majority of observations of otters come from waters off the north coast of Afognak Island and nearby Shuyak Island or from the Barren Islands. Lensink (1958) says of the few Kodiak Island reports that "The observations of otters on Kodiak are believed to be stray animals from the Shuyak area."

During the 1957 surveys Lensink did not find otters in the Trinity Islands but reports that R. Lopp observed 14 in 1957 (Lensink, 1958). The results of surveys by Lensink and W. Troyer are shown in table 34. D. L. Spencer has flown over and visited on the ground much of the coastal Kodiak area in recent years. He told me in 1962 of reports from many local inhabitants. These all indicate that the Kodiak area has not been repopulated to a significant degree.

On the west side of Cook Inlet, in Kamishak Bay, Spencer (letter, 1957) observed 40 otters at Augustine Island and one at Shaw Island.

Kenai Peninsula, Prince William Sound, and Kayak Island areas

The distance from the tip of the Kenai Peninsula to Kayak

TABLE 34.—Numbers of sea otters observed and estimated population in the Kodiak Islands

[Data for 1957 and 1959 are from Lensink (1962), except the estimates based on field observations; 1965 data is from aerial survey by Spencer and Kenyon]

Island	Survey date	Otters observed	Estimate of total
Augustine and Shaw Islands and Cape Douglas area	April 1965	120	200
Barren	July 1959	272	363
Shuyak	July 1959	395	527
Trinity	July 1957	14	28
Total		801	1,118

Island off the coast is about 250 miles. Sea otters are scarce along the coast of the Kenai Peninsula. The center of the sea otter population in this area is in Prince William Sound.

Many reports of otters, particularly from Prince William Sound, were made during past years by personnel of the U.S. Fish and Wildlife Service, the Alaska Department of Fish and Game, and the U.S. Coast Guard (Lensink, 1962). That the population is a long-established one is indicated by the seizure by the Government of two illegally taken skins at Seward in 1924 (U.S. Bureau of Fisheries, 1925).

Aerial surveys made in 1959 by Lensink (1962) furnish the best modern information on sea otter populations in this region (table 35). We did not conduct an aerial survey of the Kenai Peninsula but a number of biologists have visited this coast. The lack of sea otter observations by them and by residents indicates that no significant population of otters occupy this area.

The long-established Prince William Sound sea otter population may have reached maximum size some years ago followed by a decrease in recent years, or, possibly the surveys are not comparable (table 35). The reason for the indicated decline is a matter of speculation. It may be that ecological conditions are marginal. Much of the coastal area is precipitous, furnishing only a narrow zone of shallow water where sea otters may obtain food. The Prince William Sound population, being the most northerly in Alaska, may suffer during severe winter weather. Available food species may be heavily infested with parasites to which the sea otter is poorly adapted. F. H. Fay found an individual more massively infested than any animals taken from other areas (see Parasites and Miscellaneous Diseases). Lastly, it is possible that the relatively

TABLE 35.—*Number of sea otters observed and estimated population in the Kenai Peninsula, Prince William Sound, and Kayak Island areas*

Area	Aerial survey observations		Estimated populations	
	1959 ¹	1964 ²	1959 ³	1964
Kayak-Wingham Islands	138	24	184	40
Hinchinbrook Island	58	167	93	223
Montague Island	349	42	465	70
Green and Little Green Islands	42	116	70	155
Latouche and Erlington Islands	87	1	145	2
Other, including unsurveyed areas	28	42	47	70
Total	702	392	1,004	560

¹ Data from aerial surveys made in April and August 1959 using a Cessna 180 aircraft.

² John Vania, letter of 30 October 1964. Aerial surveys made 1 and 2 October 1964.

³ Estimates, although similar to Lensink's estimate of 1,000 to 1,500 (1962), are not taken from his report. For the sake of uniformity in this report they were computed on the same basis as other estimates.

large human population of the Kenai Peninsula and Prince William Sound area may in some way inhibit sea otter population growth.

The Prince William Sound area was greatly affected by the earthquake of 27 March 1964. An expedition to discover the effects of the earthquake was undertaken by the U.S. Geological Survey in May and June 1964. An indication of the damage to some of the sea otter habitat is told in letters of 4 June and 20 July 1964 from Dr. G. Dallas Hanna who was a member of the expedition.

The destruction of animal and plant life in the former intertidal zone where we have been is catastrophic. Not a living thing is left on the upraised section. I think it will be many years before a new zone is formed.

Sea otters have been the most common of the marine mammals thus far. Usually we are in small boats close in shore or on land in daylight hours and opportunity for observation has not been the best. . . . Where the rise was greatest (7 to 33 feet) the kelp beds were destroyed so the animals seem to range out in the channels.

Dr. Hanna recorded 70 otters observed by himself and other members of the expedition in the vicinity of Hinchinbrook, Latouche and Montague Islands.

Further studies will be required to determine if the reduced number of sea otters observed in 1964 (table 35) was related to the March 1964 earthquake.

Earthquake caused disturbances have drastically affected sea otter populations. Voronov (1967) observed starvation and changes in distribution of sea otters in 1963 and 1964 following massive destruction of bottom fauna by tsunami in the Kuril Islands.

Pribilof Islands

The sea otter was numerous at the Pribilofs at the time of their discovery in 1786. Elliott (1875) says—

when the Prybilov Islands were first discovered, two sailors, Lukannon and Kaiekov, killed at Saint Paul's Island, in the first year of occupation, *five thousand*; the next year they got less than a *thousand*, and in six years after not a single sea otter appeared, and none have appeared since.

Lutke (1835), however, indicates that in the first 2 years [ca. 1786–88] the take was "plus de 200 loutres" and by 1828 "il n'y eut bientôt plus une seule loutre." The number taken during Pribilov's short visit to the Pribilof Islands is given by Nozikov (194?) as 2,325.

I. Veniaminov (*in* Elliott, 1875) indicates that the species was not exterminated at the Pribilofs until about 1840. Records of the sighting of two sea otters and of "one which had been crushed by the ice" in 1889 and 1896 are recorded by Preble and McAtee

(1923). As previously suggested (Lensink, 1960) these may have reached the Pribilofs on drifting ice from the Unimak-Amak Islands area. Preble and McAtee (1923) mention the finding of skulls in subsequent years. I presume that these, like the ones several other biologists and I have found since 1947, had remained buried under sand dunes since the 1700's or even earlier.

The area of available feeding habitat—water 30 fathoms or less in depth—around St. Paul Island is about 395 square miles. If the population there was as dense in 1786 as that now found at certain of the Rat and Delarof Islands (about 16 to 19 otters per square mile), the total population at the Pribilofs could have been about 6,300 to 7,500 in 1786. This estimate indicates that Elliott's (1875) statement is plausible.

In April 1954 we attempted to transplant sea otters by ship from Amchitka Island to the Pribilofs. All 19 animals apparently died soon after liberation on 9 April. None was subsequently seen. Another transplant of seven otters by aircraft on 20 May 1959 was successful in that at least some of them survived. Residents of the Pribilof Islands, believed to be reliable observers, reported the occasional sighting of one or two otters until the spring of 1961. Although the sightings could not be verified, they do indicate the possibility that at least some otters survived for 2 years (see Transplant Attempts).

Isolated as this island group is by 240 miles of open sea from the nearest population, near Unimak and Amak Islands and the tip of the Alaska Peninsula, there is probably little chance that natural repopulation will occur in the near future. The possibility exists that eventually otters associated with floating ice may reach the Pribilofs from the Unimak-Amak-Alaska Peninsula area.

Other western Alaska areas

The Pavlov Islands (55° N. lat., 161°30' W. long.) are south of the Alaska Peninsula and northeast of the Sandman Reefs. In 1957 (Lensink, 1958) and again in 1962 the group was partially covered during aerial surveys. On each survey four otters were seen near outer Iliasik Island. As the Sandman Reefs population grows, otters will probably move from that area into the Pavlov Islands.

The Semidi Islands (56°10' N. lat., 156°45' W. long.) lie about 20 miles south of Sutwik Island. In the summer of 1957 Lensink (1958) recorded five otters there. This isolated group was not subsequently surveyed.

Chirikof Island (55°50' N. lat., 155°35' W. long.) is about 40

miles southwest of the Trinity Islands and was not included on sea otter surveys. D. L. Spencer told me in 1962 that he flew around Chirikof and saw no sea otters there.

Southeastern Alaska

Observers occasionally report sea otters from the vast complex of islands, passes, and straits of Southeastern Alaska. Enforcement Agent J. A. Klingbeil, Jr., (letter, 14 October 1950) reported four animals seen at Nakwasina Bay on 2 September 1950, which he believed to be sea otters. He also reported a single otter seen at Silver Bay, Baranof Island (*in* Lensink, 1958). The possible observation of sea otters near Ketchikan was reported by J. Ditcher in 1945 (*in* Lensink, 1958) and by L. W. Croxton in 1961 (letter, 1962). No observation, however, has been confirmed by other observers. It appears that until 53 were transplanted to the area by the Alaska Department of Game in 1965 and 1966 few, if any, sea otters existed in Southeastern Alaska.

Dall (1870) indicates that exploitation of the sea otter in the Alexander Archipelago was intensive. Apparently this population was wiped out before 1900.

Maynard (1898) indicates that otters were most abundant "along the coast as far as Sitka. South of that point they were less numerous and were taken mostly from Queen Charlotte Islands."

There is no record that sea otters occurred in the inland passages of Southeastern Alaska and apparently they also shunned parts of the outer coast.

BRITISH COLUMBIA

The sea otter apparently became extinct on the British Columbia coast during the 1920's.

In a conversation, in 1962, A. W. F. Banfield told me of a sea otter skull, deposited in the National Museum of Canada, that was found by Patch in the Queen Charlotte Islands in 1919. Later he wrote (letter, 1963):

I discussed the specimen with [C. A.] Patch some years ago and was under the impression it was a fairly fresh skull, when he picked it up. . . . The National Museum of Canada sponsored an expedition to the north end of Graham Island during the summer of 1919. . . . Concerning the sea otter he [Patch, 1922] writes (p. 103): "I found a sea otter skull in a deserted cabin near Rose Spit. Chief Harry Wiah said that about a year before our visit an Indian shot at a sea otter which was resting on kelp near North Island. He also said that about thirty years ago his father, his wife's father and other Indians—a total of nineteen boats—got twenty-one sea otters in a forenoon and six in the afternoon.

The most recent record is of a sea otter taken at Grassie Island, Kyuquot, in 1929 (Cowan and Guiguet, 1956). Concerning this specimen Guiguet wrote in a letter (1958) that—

We have one specimen record (skin) of an adult sea otter taken at Kyuquot Sound (Grassie Island) in the autumn of 1929 and donated to the Provincial Museum by the B. C. Game Commission. There are few details, the animal was not sexed, measured or the skull preserved. Since that time we have no authentic report, but many "sight" records, and of those investigated all proved to be river otter. . . . As far as we know, the sea otter has yet to re-establish on the British Columbia coast.

WASHINGTON

The last authentic record of sea otters on the Washington coast is of "several" being killed at Willapa Harbor in 1910 (Scheffer, 1940).

The river otter is frequently seen in salt water along the outer coast and among the islands and inland waterways of Washington State. Observers often report these to us as sea otters. To date, all sightings that could be investigated proved to be of river otters. C. Vandersluys of Friday Harbor, Wash., who is familiar with the inland waters, wrote (letter, 1963):

We did see a group of otter last summer, off the San Juan Islands. In fact, this animal seems to be increasing in number in this area each year. Locally we call them land otter, and to my knowledge, I have never seen a sea otter around here.

I have searched the outer coast of Washington many times during the past 10 years but have never confirmed any report of sea otters there (Kenyon and Scheffer, 1962).

Although originally numerous on the outer coast of Washington, it is doubtful whether the sea otter ever occurred on inland waters at any distance from the open-sea coast. Scheffer (1940) says, "There are no authentic records of the sea otter in Puget Sound or the San Juan Islands." Dr. E. Gunther (letter, 1963) told me:

Peter Puget's Journal of the exploration of Puget Sound, May 7 to June 11, 1792 [from] Pacific Northwest Quarterly, vol. 30, no. 2, April 1939 . . . commented on the absence of sea otters in Puget Sound (p. 200). . . . [From] Menzie's Journal of Vancouver's Voyage: "We saw but few sea otter skins amongst them [the natives] which shows that these animals do not much frequent the interior channels."

Dr. R. E. Greengo, Professor of Anthropology at the University of Washington, told me in 1963 that he and his students have carefully examined about 30 midden sites in the Puget Sound area. Among the many bones found, only two, from *Sucia* Island in the

San Juan group, were from the sea otter. Comparison with specimens in the U.S. Fish and Wildlife Service collection showed them to be phalanges, one from a front and one from a hind paw (University of Washington collection no. 455J105). Dr. Greengo estimates that the remains were deposited at the site 1,500 years ago. Sea otter bones occur quite frequently in midden sites on the outer coast of Washington. It appears that during the time of human occupation, the sea otter was extremely scarce or absent within the enclosed waters of Puget Sound. Certainly the "great numbers of sea otters" in the Columbia River as far up as Celilo Falls recorded by Lewis and Clark (see Burroughs, 1961) were not sea otters but, as Bailey (1936) and Scheffer (1964) point out, harbor seals (*Phoca vitulina*).

OREGON

Bones found in middens along the Oregon coast indicate that the sea otter was once abundant there, but Bailey (1936) records that after 1876 the species was not again reported from Oregon. Mrs. V. F. Martin (letter, 12 August 1965) told me of an unconfirmed report that may represent the last of the original sea otter population in Oregon:

In answer to my query to Otter Rock, Oregon, a correspondent (signed C. Jones) wrote me on July 29, 1965: "Frank Priest of Newport, Oregon (now deceased) told me several years ago that the last otter taken here was by he and Joe Biggs (deceased) of Agate Beach, Oregon. That was in the year of 1906, and they sold it for \$900.00. (Rich Chinese in San Francisco were the otter buyers for local people.)"

A recent sighting about 30 miles north of Tillamook Bay, near Neahkahnie, at about 45°44' N. lat. (Pedersen and Stout, 1963) has not been confirmed by other observers.

It is a matter of speculation that occasional otters may wander down the coast from Prince William Sound, as far as the outer coast of British Columbia, Washington, and Oregon, or that stray animals move northward from the well-established California population. A linear distance along the Pacific Coast of approximately 2,000 miles separates the sea otter colony at Kayak Island, Alaska, from the central California population.

CALIFORNIA POPULATION

Although reports of fish and game wardens recorded the continual presence of a small herd of sea otters during early years of the present century, it was not until 19 March 1938 that their

presence near the mouth of Bixby Creek, Monterey County, became generally known (California Senate, 1965).

The permanent population of sea otters on the California coast is between Point Conception ($34^{\circ}27'$ N. lat.) and Monterey Bay ($36^{\circ}33'$ N. lat.). Here, during an aerial survey on 27 August 1957, Boolootian (1961) observed 638 otters. Because of predation by the sea otter on abalones (*Haliotis* sp.) the opinion was expressed that sea otters were shot or killed with spears by fishermen (H. Shelby, in California Senate, 1963). To ascertain the number of otters presently on the California coast, aerial surveys were conducted by the California Department of Fish and Game. The surveys included the areas surveyed by Boolootian (1961). During the first, 26 to 29 January 1964, 236 otters were observed (Commercial Fisheries Review, 1964a). During the second, 13 February 1964, the counts by two observers were 339 and 351 (Commercial Fisheries Review, 1964b). The most recent survey was on 8 June 1966 when 618 otters were counted (J. G. Carlisle, Jr., letter, July 1966). [For recent information see page 200 and footnote 5, table 36.]

These surveys indicate that the California sea otter population has not increased in recent years. Other observations, however, suggest that the population in the area surveyed did not increase because otters wandered to other areas.

R. G. Prasil searched National Park Service files on the Channel Islands and found the following reports (J. C. von Bloeker and R. M. Bond, letter 28 May 1940):

Kenneth E. Stager saw a sea otter asleep in the rocks on the northwest side of Santa Barbara on March 17th [1940]. He approached to within 30 feet of it before it awakened and took to the water. He is familiar with these animals off the Monterey County coast (as I am also) and I see no reason to doubt his record.

Another report was obtained by L. Sumner and R. M. Bond (letter) during a survey at Anacapa Island in 1950. They interviewed a long-time island resident named Raymond (Frenchy) Ladreau and wrote:

Ladreau told us that in 1943 two sea otters came to the kelp beds of the West Island and to the landing area nearby where he has his shack. He said they were quite tame and unafraid and remained there for 2 or 3 days before disappearing. This is the second recent record of sea otters in the Channel Islands area and indicates that if undisturbed they may be expected to increase in that general region. Perhaps some day, if protected from poachers, they will remain permanently around Anacapa and neighboring islands.

Allanson (1955) reported seeing two otters at San Miguel Island in the Channel Islands (34° N.) in 1954.

On 17 and 18 March 1958, I visited Santa Rosa and San Miguel Islands aboard the M/V *Trinity* and observed the inshore waters of both islands from a dory. Much ideal sea otter habitat was examined but no otters were seen. This survey and reports from other visitors to the Channel Islands indicate that, as yet, no substantial sea otter population has developed there.

Orr and Poulter (1964) recorded several observations at Año Nuevo Island (37°7' N. lat.) in the summer of 1963; and Bentley (1959) noted two near Trinidad Head (41° N.) in December 1956, indicating that individual otters are moving northward.

LOWER CALIFORNIA, MEXICO

The aboriginal population of sea otters reached its southern limit at least as far south as Morro Hermoso (27°32' N. lat.) (Ogden, 1941) and Natividad and Cedros Islands (27°50' N. lat.) (Anthony, 1925; Scammon, 1870). Anthony indicates that the last remaining colonies "in the region of certain kelp beds south of Ensenada" were wiped out when about 50 were killed in 1897 and an additional 28, "eight or nine years later at the same point." The last record he gives is of one being "killed by fishermen in 1919, at San Benito Island."

In April and May 1946 and in January and February 1965 I visited many of the islands and inshore water areas along the coast of Lower California from Natividad Island to the U.S. border. I found no information that sea otters might still exist along the coast and saw nothing to indicate their presence. The species was probably extirpated on the Mexican coast in 1919.

SOVIET UNION POPULATIONS

Barabash-Nikiforov (1947) summarizes information on the distribution of sea otters in the Soviet Union. Information on modern sea otter populations in areas under Soviet control became available only recently. The drowning of Scientist S. D. Pereleshin at Paramushir Island in the Kuril Islands in 1959 probably retarded sea otter studies. Pereleshin's successor, Scientist A. N. Belkin, accidentally shot himself in 1965 (pers. comm., V. A. Arseniev) but some of his work was published posthumously.

Commander Islands

Data obtained on a visit to the Commander Islands in July 1961 and the available published information is summarized.

Geologically the Commander Islands (Komandorskie Ostrova)

are part of the Aleutian Chain. They are separated from Attu, westernmost of the Near Islands, by about 185 miles of open sea. Permanent human settlements are Preobrazhenskoe (population about 300) on Copper Island (Ostrov Medny) and Nikolskoe (population about 500) on Bering Island (Ostrov Bering).

Exploitation of the sea otter began at the Commander Islands in 1741 when Vitus Bering's second expedition discovered them. Barabash-Nikiforov (1947) stated that in 1902 the sea otter population there was "at least 2,000 head" but because of excessive killing "the herd numbered 700 head in 1904." The number at Medny "in the winter 1911-1912 . . . was 63 head." After 1924 he says that "Importation of animals was begun and still continues" and the number rose to "over 200 head in 1930." He also says that "An increase in the number of sea otters around Bering Island was observed after the autumn of 1931."

Information now available contradicts some of the data given by Barabash-Nikiforov (1947). The current information is presented.

Marakov (1963) says of the Commander Islands that the sea otter became rare early in the 19th century and then "disappeared entirely, first on Bering Island and then also on Medny Island." They reappeared on Medny toward the end of the century but have never reappeared on Bering Island. "Hunting continued on Medny Island until 1924. When it was completely banned, no more than 350 individuals were left." The herd showed little or no increase during the following 30 years. Marakov believes that various human activities, including the spilling of petroleum products in the sea, prevented population growth. Marakov (1965) states that "the herd of otters on Medny Island numbers more than 1000 adult individuals."

I obtained additional information during a visit to the Commander Islands from 9 to 23 July 1961.

We saw six sea otters (five adults, one pup) during our visit. We found these near the southeast end of Medny Island along about 3.5 miles of coast. Reefs projecting from the shore, outlying rocks, and extensive kelp beds provide excellent habitat in this area. The green sea urchin is abundant at the locations we visited on Medny and Bering Islands. Two sea otter droppings found among the rocks at Medny consisted entirely of sea urchin tests.

Certain of our hosts, the late Dr. S. V. Dorofeev, G. A. Nesterov (biologist), and E. P. Skripnikov (supervisor of sealing activities at Medny and a resident of the Commander Islands for about 25 years—15 years on Bering Island and 10 years on Medny Island)

gave us the following information: Hunting of sea otters at the Commander Islands continued until the 1917-22 period. By that time, when protection was enforced, otters had been extirpated at Bering Island. They have never become reestablished there.

Sea otter studies were carried on at the Commander Islands by Barabash-Nikiforov during the late 1920's. The animals were captured in nets set in the water and were held captive for study purposes. During the 1950's, Biologist Fedorof and Scientific Worker Danielov held a male and female captive on Bering Island. The animals were captured at Medny.

Kuril Islands and the Kamchatka Peninsula

In 1943 Nikolaev (1961) estimated that the sea otters in the Kamchatka Peninsula area numbered about 300, and Klumov (1957) estimated from field observations made in 1951, 1955, and 1956 that the Kuril Islands population numbered "at least 1,500 head." Belkin (1966) reviews various studies of sea otters in the Kuril Islands and presents the results of his own work from 1962 to 1964. His count of otters at 22 islands yielded a total of 4,300 animals (3,300 adults and about 1,000 young).

WORLD POPULATION

The preceding sections present the data on the world population of sea otters that were gathered during a period of many years. The most recent estimates derived from field observations, when projected at the observed growth rate (for those populations still growing) of one population (about 4 to 5 percent per year), give a computed estimates of about 33,000 sea otters (table 36) extant in the world in 1965.

On the basis of the historical record and field observations presented in foregoing pages, it appears that sea otters survived at the close of the 1741-1911 period of unregulated exploitation in the following 11 geographical areas: (1) Kuril Islands, (2) Kamchatka Peninsula, (3) Commander Islands, (4) Rat Islands, (5) Andreanof Islands, (6) The Unimak and Sanak Islands-Sandman Reefs area, (7) Shumagin Islands, (8) the Kodiak to Prince William Sound area, (9) near Monterey, Calif., (10) the Queen Charlotte Islands, British Columbia, and (11) the San Benito Islands, Baja California. From the last two locations, however, they were soon extirpated.

TABLE 36.—*Estimated world population of sea otters*

Area	Date of observation	Sea otters observed	Estimated total ¹	Estimated total in 1965 ²	Authority
Soviet Union:					
Kurul Islands.....	1962-64	(?)	4,300	4,700	Belkin (1966).
Kamchatka.....	(?)	(?)	1,000+	1,200	Marakov (1965).
Medny Islands.....					FWS aerial surveys.
Alaska:					
Near Islands.....	1965	³ 27	45	45	Do.
Rat Islands.....	1965	³ 3,147	4,196	4,196	Do.
Delarof Islands.....	1965	³ 653	871	871	Do.
Andreanof Islands.....	1965	³ 5,805	7,760	7,740	Do.
Fox Islands.....	1965	³ 2,935	3,913	3,913	Do.
Sanak-Sandman Reefs.....	1962	⁴ 1,186	1,625	1,880	Do.
Shumagin Islands.....	1957	⁴ 1,829	2,724	3,972	Do.
Pavlov Islands.....	1962	⁴ 4	8	10	Do.
Senidi Islands.....	1957	⁴ 5	10	16	Lensink (1958).
Alaska Peninsula.....	1962	⁴ 949	1,317	1,525	FWS aerial surveys.
Prince William Sound.....	1959	⁴ 702	1,004	1,004	Lensink (1962).
Kodiak Island area.....	1957-59	⁴ 722	973	1,237	Do.
California ⁵	1966	618	600	600	J. G. Carlisle, Jr., letter, 1966.
Total.....		18,582	30,346	32,909	

¹ At time of observation.² Projected from the year of the original estimate on the basis that in underpopulated areas growth will be at the rate of 5 percent per year. Where field observations indicate that little or no growth is occurring, no projection of growth is shown.³ Aleutian Islands total is 12,567. This also includes S.W. Bristol Bay.⁴ Total 5,397. The total for all of Alaska is 17,964 (5,397 + 12,567).⁵ In a series of aerial and surface censuses begun in August 1968, the highest count of sea otters was 1,014 (Peterson and Odemar, 1969).

DISCUSSION

In the foregoing section, observations of sea otter populations obtained between 1935 and 1965 in several geographic areas were reviewed. The data included aerial and surface counts, total population estimates based on them, measurements of available habitat, and population densities in different areas. The field observations and the conclusions derived from them are discussed below.

Rate of population increase

Two methods may be used to ascertain the approximate rate of increase in a sea otter population: (1) The annual rate of reproduction and mortality in a population may be studied; or (2) otters in an isolated population may be counted at intervals and the increment found directly. The first method is treated elsewhere. The results obtained by the second method are discussed below.

Because movements of large numbers of otters from one island to another were recorded, it was evident that the area included in population surveys must be sufficiently large to include locations where both emigration and immigration occurred. The population surveys in the Andreanof Islands furnish the best available information on which to base a study of population growth. On the east, this otter population is isolated from the small population of the Umnak-Samalga Islands by 120 miles, which includes Amukta Pass and the unpopulated Islands of Four Mountains. On the west, the study area is separated from the Delarof Islands by 14-mile-wide Tanaga Pass.

This sample area, about 210 miles in length, includes densely populated islands adjacent to others having unoccupied habitat. Aerial surveys of the Andreanofs in 1959, 1962, and 1965 were conducted under comparable conditions by the same observers. The small, semi-isolated populations at Atka and Amlia at the eastern end of the sample area showed a larger rate of increase than did the total Andreanof population. Probably these colonies were augmented by wandering individuals that formed the vanguard of the massive eastward moving population of the Kanaga-Adak-Kagalaska Islands segment of the sample area.

The rate of the Andreanof population increase of about 12+ percent in each of two 3-year periods or over 4 percent per year, is less than the rate of increase postulated by Soviet biologists. The rate of increase was at first presumed to be 10 to 12 percent per year by Barabash-Nikiforov (1947) but he finally concluded that this rate was not in accord with his field observations and

placed the annual rate of increase of a population at 7 percent. In the Commander Islands, however, even this rate appeared somewhat high when compared with his "on the spot observations." Lensink (1962), on the basis of his surveys, concluded that the rate of increase of the Andreanof Islands population was 10 to 15 percent per year. The more comprehensive data gathered in the same areas after his studies were completed, however, indicate that the total population within the Andreanof group is now increasing at a lower rate, probably because of density-caused mortality in the heavily populated areas.

In a local area of sparse population, the 1959-65 data indicate the population may have increased during that period at an annual rate of at least 10 percent. For example, the estimated population at Seguam, the easternmost island of the sample area, increased from 28 to 47 otters (table 25) in the 6-year period 1959-65 or at a mean annual rate of a little more than 11 percent. This conclusion is based on the assumption that Seguam Pass is a fairly effective barrier to immigration.

After a large population is produced, as it was, for example, at Adak (in the Andreanof Islands) in the 1954-62 period (table 28), the overall annual increase of the Andreanof population was at the rate of about 4 percent.

The observed 4 percent annual rate of increase is a generalized figure. At islands where the population exceeded the carrying capacity of the habitat, i. e., more than 10 to 15 otters per square mile of habitat (see table 25), population regression was observed. Stress mortality (starvation), as well as emigration, probably accounted for the local population decreases. Evidence to support this view was found on 28 April 1965 during a brief examination of one otter hauling ground at Shagak Bay, Adak. There I found a large juvenile otter dead on the beach. It exhibited all the characteristics of starvation that I observed at Amchitka. Probably the rate of mortality during the winter-spring season of stress at Tanaga, Kanaga, and Adak in the 1962-65 period was considerably greater than at the relatively sparsely populated islands east of Kagalaska during this same period.

Thus, the rate of population increase varies according to population density and its relation to ecological conditions and may be quite different from the rate of reproduction. Elsewhere it is shown that about 16 young may be born annually per 100 independent animals of both sexes and all ages.

In general, it is concluded that an isolated population having ample unused habitat may grow through local reproduction (no

immigration) at a rate of about 10 to 12 percent per year. In a region that includes both densely populated areas (where winter-spring mortality occurs) and adjacent unpopulated habitat, the rate of growth may be about 4 to 5 percent per year.

Optimum population density

No study has yet been undertaken to indicate the productivity of the sea otter habitat or to show what critical differences in food productivity exist in different habitats. Because such studies are not available it is not possible to compute, on the basis of food resources available, the number of sea otters that any particular habitat may support.

On the basis, however, of the observed behavior of several island populations of sea otters it is possible to reach tentative conclusions as to the approximate optimum population density and which areas are overpopulated or underpopulated.

At five locations (Rat, Amchitka, Tanaga, and Kanaga Islands, and the Delarof group) we observed large otter populations which subsequently became greatly reduced (table 37 and fig. 78). The figures available do not necessarily represent absolute maximum and minimum populations because of the infrequency of observations. From these data it appears, however, that a growing sea otter population in an unexploited habitat may reach a temporary maximum density of 40 or more animals per square mile of habitat. After such a high density is attained, a period of population reduction occurs, either through emigration, a high rate of mortality, or both concurrently during seasons of stress. That a depleted feeding habitat may support about 10 to 15 otters per square mile is indicated by the observation that the five densely populated areas dropped to that level.

TABLE 37.—*Changes in sea otter population density in six areas*

Island	High population		Low population		Interval years	Means of reduction ²
	Date	Number ¹	Date	Number ¹		
Rat.....	1943	31	1949	10	6	Mortality (?).
Amchitka.....	1943	41	1949	13	6	Mortality.
Delarof.....	1959	21	1965	10	6	Mortality (?).
Tanaga.....	1953	(³)	1959	14	6	Emigration.
Kanaga.....	1959	26	1962	12	3	Emigration.
Adak.....	1962	40	1965	24	3	Emigration and mortality.
Mean.....		30		12		

¹ Otters per square mile of feeding habitat (waters 30 fathoms or less in depth).

² It is known that emigration took place because rapid population increase in nearby areas was observed. Mortality was observed and documented only at Amchitka. At Rat Island and in the Delarofs a condition similar to that at Amchitka would be expected.

³ Unknown but presumed to be high on the basis of reports that otters there numbered in the thousands (Hooper, in Jones, 1953; Lensink, 1960).

The Kanaga data indicate that this level may be maintained for at least a 3-year period. The Amchitka data indicate that after the initial population "crash" a period of slow increase, or adjustment, occurred (table 23). During the recovery period the population approached a density of about 20 otters per square mile of feeding habitat. That this is not an optimum population density is indicated by the continued annual occurrence of heavy mortality among juveniles and old adults (see Age Specific Mortality), by comparatively small body size (see Body Measurements), by excessive dental attrition, and by the fact that by 1965 the population had fallen to a density of 14 otters per square mile of habitat.

Optimum population density in the Aleutian area, after a depleted habitat has recovered from the damage caused by overutilization of food resources, may be postulated at about 10 to 15 otters per square mile of habitat. Table 38 shows predicted populations in certain Alaska areas based on data now available. More data are needed, however, to properly estimate optimum population density.

Geographic barriers

Passes between areas of feeding habitat around islands, may act to a varying degree as barriers to the spread of sea otter populations. For example, Buldir, Semisopchnoi, and the Near Islands were not repopulated for a number of years after the islands nearest to them supported high populations. The 55 miles of open water between Buldir and Kiska was an effective but not a permanent barrier. A few otters reached Buldir from Kiska between 1936 and 1961. Kiska was densely populated by 1959 and perhaps before that, but not until the 1959-65 period were small colonies established in the Near Islands, 65 miles west of Buldir.

TABLE 38.—*Present and projected sea otter populations in certain Alaska areas*

[Only the areas that have been most intensively studied are included. The projections of future populations are based on the assumption that a population of about 10 to 15 otters per square mile of feeding habitat may be supported]

Area	Square miles of habitat	Projected total number of sea otters	Present population estimate
Near Islands.....	326	3,300- 5,000	27
Rat Islands.....	293	3,000- 4,400	4,200
Andreanof Islands.....	766	7,700-11,500	7,800
Delarof Islands.....	89	900- 1,300	930
Islands of the Four Mountains.....	88	900- 1,300	0
Fox Islands.....	570	5,700- 8,500	25
Krenitzen.....	200	2,000- 3,000	55
Unimak-Amak Islands.....	1,000	10,000-15,000	4,000
Sanak Island and Sandman Reefs.....	900	9,000-13,500	1,600
Shumagin Islands.....	700	7,000-10,500	2,700
Total.....	4,932	49,500-74,000	21,337

The 30 miles of deep open water between Amchitka and Semisopochnoi Islands was apparently a less effective barrier. No otters had reached Semisopochnoi in 1943 (when the Amchitka population was near maximum size) but by 1959 the population at Semisopochnoi was relatively dense (16 otters per square mile). Movement to Semisopochnoi of a substantial number of otters, rather than the slow increase of a small breeding nucleus, during this period is indicated.

The behavioral barrier

Considerable data show that the reoccupation of vacant habitat is dependent to an important degree on the inherent behavioral characteristics of the sea otter.

The sea otter does not undertake seasonal migrations. Recovery of marked sea otters at Amchitka revealed that the home range of an individual otter includes only a few miles of coast. Marakov (1965, p. 212) also found that otters in the Komandorski Islands become attached to a particular area.

Elsewhere (see Amchitka Island) it is shown that otters move into areas of nearby but unoccupied habitat only in response to "population pressure" after a large local population has developed (table 23). The Amchitka data indicate that the remanent colony which repopulated the island was probably on the Pacific coast and that significant numbers of sea otters did not move to the Bering Sea coast until 1940 or soon thereafter (fig. 73).

Substantial population movement from densely populated Kanaga to nearby unpopulated Adak and later from Adak to nearby islands east of it did not occur until dense local populations built up. In 1959 the Adak population had reached a density of 31 otters per square mile of habitat (table 28) but only one otter was observed at nearby Kagalaska (table 29). It thus appears that otters tend to maintain an established home range until the effects of a dense population force movement.

Wandering individuals

Many observations of individual otters at great distances from large local populations are available. That such wanderers eventually settle permanently in a locality that offers ideal habitat conditions is indicated by the existence of small colonies at great distances from large population centers. The small colonies found in the Near Islands, Buldir, Atka, Amlia, Seguam, and in the Umnak-Samalga and Tigalda Islands areas in the 1950-65 period, are examples.

It thus appears that vacant sea otter habitat is repopulated by two means: (1) Movement of large numbers of otters from a densely populated area to adjacent unpopulated habitat, and (2) wandering individuals that accumulate to form colonies where habitat conditions are ideal many miles distant from dense populations.

Because of the indicated 4 percent per year rate of growth of the Andreanof sea otter population, the repopulation of vacant habitat at the periphery of a densely populated area, is, today, the most important means by which the sea otter is reoccupying the places from which it was exterminated during the 18th and 19th centuries.

Dispersal of sea otters and population density

Most animals included in tagging studies at Amchitka were adults when marked and the recoveries indicated that they remained permanently along a limited area of coast (see Home Range). By analogy with other species it would seem probable that wanderers, contributing to range extension, might be composed mostly of subadult animals. That this may be true also of sea otters is indicated by our failure to observe as many mothers accompanied by small young in newly populated areas as in other areas. In 1959, we saw no otters in Kagalaska Strait, but in 1962 we observed 348 there. Aerial photographs of a group of 157 animals and another of 59 revealed not one small pup among them. In mid-November of 1965, when this area was well behind the vanguard of population expansion, I spent 2 days in Kagalaska Strait and saw a number of mothers accompanied by young.

Two possible conclusions concerning the otters which first appeared in Kagalaska Strait are indicated: (1) All were males, and (2) they were mostly subadults of both sexes and had not born young.

Estimates of population density, or the number of sea otters per square mile of available habitat, were obtained in several Aleutian areas. Among these were locations where substantial populations have existed for many years, and also recently repopulated areas.

On the basis of geographical barriers and population density, sea otter populations in Alaska may be classified according to four general categories (two densities of isolated populations and two densities of populations adjacent to available habitat).

1. Dense isolated populations

This category includes populations of sea otters that have

reached a size which heavily utilizes food resources in the available habitat. Significant population dispersal to new habitat is hindered by broad expanses of deep water which prevent feeding.

The Rat Islands (except Buldir Island) population is an example. Significant emigration of sea otters from this island group appears to be slowed by passes hundreds of fathoms deep and about 50 miles wide on the eastern and western extremities of the group. The average population density was about 14 otters per square mile of available habitat (table 21). When such populations increase and exceed the carrying capacity of the habitat, heavy mortality occurs because substantial emigration does not occur.

2. *Sparse isolated populations*

The recently established Buldir Island colony and the Samalga and Tigalda Islands populations are examples. Many years may elapse before these populations approach maximum size. The Samalga-Umnak population is separated from the nearest Andreanof population at Seguam by Amukta Pass, 35 miles wide, and by the Islands of Four Mountains, a total distance of 120 miles, where no otters are found. The Tigalda Island colony is about 140 miles east of Samalga. Such small colonies grow slowly because they are rarely augmented by immigrants.

3. *Dense local populations adjacent to areas of vacant habitat*

The Andreanof, Sanak, Unimak, and Shumagin Islands, and the Alaska Peninsula areas furnish examples of populations which today are large but may expand into adjacent vacant habitat. During aerial surveys, comparable observations of expanding distribution and increasing abundance of sea otters were obtained in these areas. Such populations expand rapidly because movement of part of the population increment to new areas is possible and minimum mortality probably occurs except at densely populated islands after they are left far behind the spearhead of population growth.

4. *Sparse local populations adjacent to areas of vacant habitat*

In the Aleutian Islands three local populations of sea otters—at Atka, Amlia, and Seguam Islands—are placed in this category. These populations occupy a tiny part of the habitat available to them. They are separated from other populations by many miles but not by geographical barriers. They may be augmented by an influx of otters from the western Andreanofs. Narrow passes between islands of this group are easily crossed.

The rate of increase of these three colonies is related inversely to their distances from the large western Andreanof population:

Colony	Distance from large population (miles)	Annual rate of increase	
		1959-62 (percent)	1962-65 (percent)
Seguam.....	130	10	10
Amlia.....	100	12	13
Atka.....	60	30	85

Possibly the annual rate of increase of the Seguam colony represents the rate of increase that may be attributed to local reproduction in an uncrowded population.

Summary

1. In 1741 when unregulated exploitation of the sea otter began, the species ranged from central Lower California, Mexico, north along the coast of the North Pacific Ocean, through the Aleutian and Kuril Islands to the northern islands of Japan.

2. The northern limit of the sea otters' range overlaps but slightly the usual southern limit of winter drift or pack ice in the Bering Sea. The farthest north colony in Alaska is in Prince William Sound (60°30' N. lat.) where the sea does not freeze.

3. The total population of sea otters in 1740 was probably between 100,000 and 150,000 animals.

4. The number of sea otters taken during 170 years of unregulated exploitation is not recorded but probably did not much exceed one-half million animals.

5. The total world population in 1911, when exploitation of the sea otter was halted, probably numbered between 1,000 and 2,000 animals.

6. Small sea otter populations apparently remained in 1911 at the following 11 areas: Kuril Islands, Kamchatka Peninsula, Commander Islands, Rat Islands, Andreanof Islands, the Unimak, Sanak Islands-Sandman Reefs area, Shumagin Islands, Kodiak Island and Prince William Sound area, in the Queen Charlotte Islands, British Columbia, on the coast of California near Monterey, and in the San Benito Islands, Baja California.

7. The first modern data on the recovery of sea otter populations were obtained in the Aleutian Islands in the mid-1930's and considerable miscellaneous data were subsequently gathered during the 1940's. Detailed field studies of population and distribution were begun by the Fish and Wildlife Service in 1954 and continued through 1965.

8. The sea otter is limited to a relatively narrow band of water around islands and along mainland shores where water depths do not exceed 30 fathoms. Under the prevailing weather conditions when aerial surveys were made, sea otters were easily observed. We concluded that in most areas about 75 percent of the sea otters present were recorded. Comparative surface and aerial surveys indicated that about 60 percent of the otters seen on an aerial survey may be missed on a surface survey.

9. Data obtained on aerial surveys in the Andreanof Islands in 1959, 1962, and 1965 indicated that in this area, having much available and unpopulated habitat, the population is growing at an exponential rate of between 4 and 5 percent per year.

10. Aerial surveys and other studies conducted between 1954 and 1965 in Alaska reveal that large areas of sea otter habitat are not yet repopulated. In certain areas repopulation of vacant habitat is proceeding rapidly (the Andreanof Islands). In isolated areas the habitat may be heavily utilized by a dense population (the Rat Islands).

11. In all observed areas where estimated sea otter populations reached 20 to 40 otters per square mile of habitat, the populations decreased to about 8 to 15 otters per square mile of habitat. The decrease occurred through mortality (e. g., Amchitka Island) or emigration (e. g., Kanaga and Adak). In years following a population "crash" the populations at islands may fluctuate between about 10 and 20 otters per square mile of habitat.

12. Reoccupation of available sea otter habitat is hindered by wide, deep passes between islands. Sea otters readily cross passes about 10 miles wide. Significant numbers may cross 30 miles of open water (e. g., Amchitka to Semisopochnoi). Passes 50 miles or more in width may be crossed by a few individual otters that wander great distances from densely populated areas (e. g., from Kiska to Buldir and from there to the Near Islands). These individuals may eventually concentrate in locations having unusually desirable habitat.

13. The most significant factor that limits the spread of sea otter populations is the tendency of individual otters to occupy a limited home range. Feeding habitat on one side of an island, or at an island near another having vacant habitat, may become densely populated (to about 40 otters per square mile of habitat) before a significant number of otters move into adjacent vacant habitat even at the home island. Where repopulation was observed, the south sides of islands were repopulated prior to the north exposures (e. g., Amchitka, Atka, and Amlia).

14. In addition to the many areas in western Alaska offering sea otter habitat which today is unpopulated, approximately 2,000 miles of coastline, including much sea otter habitat, separates the colony at Kayak Island, Alaska, from the small central California colony.

15. Several aerial surveys were made in 1958 and 1964 to 1966 along the California coast. The highest counts in 1958 and 1966 yielded 638 and 618 sea otters, respectively. Further surface and aerial surveys, begun in August 1968, yielded a high count of 1,014 otters (Peterson and Odemar, 1969), indicating a population increase since 1958 of about 5 percent per year.

16. The number of otters recorded during aerial and limited surface surveys in Alaska was 17,964 and the total population in Alaska waters in 1965 is estimated to be about 25,000.

17. The most recently published Soviet total estimate of sea otters in Soviet waters is 5,300.

18. On the basis of all data available, the world population of sea otters in 1965 was computed to be 32,909. A general estimate of the world population, presuming that some populated areas have not been observed, is about 32,000 to 35,000 animals.

19. Measurements of available sea otter habitat, much of which was not occupied in 1965, and the observed population density of relatively stable populations (10 to 15 otters per square mile of habitat) indicate that the Aleutian Islands and closely related areas of the Alaska Peninsula may eventually support a population of about 50,000 to 74,000 sea otters.

Home Range

The purpose of permanently marking sea otters is to obtain from field observations and recovery of tags, over a period of time, the following information on the life history of individual animals: (1) Maturation, (2) aging, (3) longevity, (4) reproduction, and (5) movements and home range.

Sea otters were captured on shore with a sport fisherman's landing net (fig. 82). While the netted otter struggled to free itself, using forepaws and teeth on the net, one rear flipper was grasped and a cattle or sheep ear tag of monel metal (table 39) was clamped to the web of the hind flipper with a special pliers. Two men were required, one to hold the net and the other to affix the tag. Colored plastic strips were attached experimentally to some tags, so that individual animals might be recognized in the wild.



FIGURE 82.—John Nevzoroff holds an adult female sea otter which he captured while it slept on an Amchitka beach. After capture, at least two men are required either to tag an otter or to place it in a carrying cage. (KWK 62-15-20)

All animals that could be captured were tagged, but when a choice was possible juveniles were captured in preference to adults. When studies were begun, an effort was made to capture mothers having with them very young pups. This practice, however, was soon discontinued.

Tags were recovered (1) when marked animals were recaptured, (2) from animals found dead on beaches, and (3) during harvesting operations.

Tags were placed on the hind flippers of 224 sea otters (table 39), 107 adults and 117 juveniles or pups. Among them were 88 males, 135 females, and 1 of unknown sex.

In 1956, 1959, 1961, 1962, and 1963, a total of 28 recoveries were recorded (table 40). The intervals between tagging and recovery ranged from 10 minutes to 35 months. Thirteen tagged animals were recovered dead on beaches, eight were captured and released, five were shot, a colored plastic marking device from

TABLE 39.—*Sea otters tagged at Amchitka Island, Alaska*

Year	Tag numbers	Juvenile			Adult		Total
		♂	♀	?	♂	♀	
1956.....	EL 401-409 ¹	1	1	—	4	3	9
1957.....	EL 12908 and 12910 ²	1	—	—	1	—	2
1959.....	12901-12903; 12926- 13000; ³ EL 426, 427, 429-431, 433, 440-442, and 444.	25	21	—	9	31	86
1962.....	EL 446-565	27	34	—	16	43	120
1963.....	EL 566-572	4	2	1	—	—	7
Total.....		58	58	1	30	77	224

¹ This series sheep-ear size.

² This series cattle-ear size. The high numbers (12,000 to 13,000) are the result of using tag remainders from Pribilof fur seal series. The prefix EL was hand stamped on only a few. The tags were obtained from the National Band and Tag Company, Newport, Ky.

³ Except two ruined.

one animal was recovered at a hauling-out place, and one color-marked individual was observed repeatedly.

Two hundred and eight of the animals were captured and tagged at nine traditional hauling-out areas; the remaining 16 were marked at scattered locations on Amchitka Island. Three hauling-out areas are on the Bering Sea coast, five are on the Pacific coast, and one is at East Cape where the Bering Sea and Pacific coasts meet. The minimum distance between the hauling grounds used as tagging locations is 1 mile and the maximum distance is 9 miles. Eight animals tagged at one hauling-out place were subsequently recaptured at the next nearest one.

Three females, tagged as adults and recovered nearly 3 years later, were found 2.5, 2.5, and 5 miles, respectively, from the locations of tagging. One female recovered 2 years after tagging was ½ mile from the location of tagging. Two females recovered about 1 year after tagging were 2.5 and 2 miles from the location of tagging and two others were recovered at the location of tagging.

One young adult male, whose tag bore a colored plastic flag, was observed repeatedly. This animal visited the location where we discarded fish remains in Constantine Harbor, near Kirilof Dock. He was present daily for a period of about a month and a half. He became tame and was captured by hand when he came ashore to accept food. Because of the artificial food source, the sedentary behavior of this animal may not represent the normal behavior of the adult male. One juvenile male, tagged at East Cape, was found dead 24 days later in Constantine Harbor, 9 miles from the location of marking. Among five juvenile males, recovered within a month of tagging, however, only one was as far as 3 miles from the tagging location.

TABLE 40.—Recoveries of tagged sea otters at Amchitka Island

Tag number	Date 1		Period free 2	Location 3		Sex	Age 5		How observed 6
	Tagged	Recovered		Tagged	Recovered		Tagged	Recovered	
EL 401	21-5-56	23-5-56	3 da	CH	CH	♀	J	J	BD
EL 402	26-5-56	31-5-56	6 da	SMP	RRP	♀	A	A	PS
EL12910	28-11-57	11-12-57	1 mo+	CH	CH	♂	A	A	O 7
EL12951	2-3-59	26-3-59	24 da	EC	CH	♂	J	J	BD
EL12903	1-4-59	2-4-59	24 hr	RRP	RRP	♀	A	A	O
EL12902	2-4-59	21-4-59	19 da	SMB	SMB	♀	J	J	CR
EL12972	2-4-59	4-4-59	2 da	SMB	SMB	♀	J	J	BD
EL12975	2-4-59	14-4-59	12 da	RRP	RRP	♀	J	J	CR
EL12941	5-4-59	13-2-62	34 mo	CP	KB	♀	A	A	S
EL12945	7-4-59	15-4-59	8 da	RRP	RRP	♀	J	J	BD
EL12948	8-4-59	18-3-62	35 mo	SMP	AB	♀	A	A	BD
EL12993	15-4-59	10-2-62	34 mo	RRP	RRP	♀	A	A	S
EL12995	16-4-59	18-5-61	25 mo	RRP	RRP	♀	A	A	BD
EL13000	18-4-59	8-5-59	20 da	SMP	SMP	♀	P	P	C
EL 456	15-2-62	18-2-62	3 da	RRP	SMB	♀	A	A	CR
EL 455	15-2-62	19-3-62	1 mo	B	B	♀	A	A	BD
EL 457	15-2-62	16-2-62	1 da	RRP	RRP	♀	J	J	CR
EL 457	15-2-62	26-2-62	11 da	RRP	RRP	♀	J	J	BD
EL 464	16-2-62	27-3-62	39 da	RRP	RRP	♀	J	J	BD
EL 490	26-2-62	19-3-62	21 da	RRP	RRP	♀	J	J	BD
EL 497	27-2-62	31-3-63	13 mo	SMP	AB	♀	A	A	S
EL 499	27-2-62	5-3-62	6 da	RRP	SMB	♀	J	J	BD
EL 502	1-3-62	20-3-63	13 mo	AB	AB	♀	A	A	BD
EL 513	3-3-62	27-3-63	13 mo	AB	AB	♀	A	A	S
EL 525	7-3-62	7-3-62	10 mi	SMP	SMP	♀	A	A	CR
EL 529	7-3-62	8-3-62	1 da	SMP	SMP	♀	J	J	BD
EL 526	7-3-62	8-3-62	1 da	SMP	SMP	♀	A	A	CR
EL 556	22-3-62	18-3-63	12 mo	RRP	SMP	♀	J	J	S
EL 570	25-3-63	29-3-63	4 da	CRP	CRP	♀	J	J	BD

1 Day, month, and year.

2 Period free, mi = minutes, hr = hours, da = days, mo = months.

3 Location abbreviations: AB = Aleut Beach (not to be confused with Aleut Point), B = beach, not named, CH = Constantine Harbor, CP = Constantine Point, CRP = Crown Reeper Point, EC = East Cape, RRP = Rifle Range Point, SMB = St. Makarius Bay, SMP = St. Makarius Point.

4 Distance moved: O = same location, me = meters, mi = miles.

5 Age at tagging and at recovery, P = pup, J = juvenile, SA = subadult, A = adult.

6 How observed: BD = beach dead, O = observed, PS = plastic strip found on hauling ground, S = shot, CR = captured and released.

7 From about mid-October this animal remained near Kirilof Dock. It was given fish heads and became tame. It was easily captured when it came ashore for fish heads on 28 November and was tagged. It was last seen when we left on 11 December.

The tagging of newborn or very young pups was discontinued because the frightened mother, upon release, usually made several long dives. It seemed probable that at least some of these young pups may have died as a result of unusually long periods of immersion. Also, several mothers refused to accept their helpless pups when they were released and later failed to return for them.

DISCUSSION

To date the information from tagging is meager. Many of the animals which were captured on land were there because they were ill or in weakened condition. For this reason, the rate of survival of tagged animals is probably lower than for the population as a whole. There is as yet no reason to believe, however, that the act of tagging increased the mortality within the tagged segment of the population as compared to the untagged segment (except when mothers with small pups were captured). Disturbance of the animals during tagging was brief and care was taken not to injure them. The tag placed in the web of the hind flipper had no noticeable effect on swimming. Marked animals, in the wild and in captivity, ignored their tags, except that certain individuals chewed the colored plastic flags attached to the metal tag.

The data and general field observations lead to the following tentative conclusions: (1) The home range of the female sea otter during at least a 3-year period may include about 5 to 10 miles of coastline. Soviet biologists found that the range from the "basic station is 15 to 17 km. [9.3 to 10.5 miles]" (Nikolaev and Skalkin, 1963). (2) Animals tagged on one side of Amchitka did not move around to the other side of the island (see Distribution and Numbers). (3) Males may have a larger home range than females. (4) Individual otters may use more than one of the traditional hauling-out places.

Additional information from tagged animals is found in sections on "Age at Sexual Maturity," "Age Specific Mortality," and "Juvenile Sex Ratio."

Territoriality

It is difficult to say whether territorialism exists in the sea otter in the same sense that it does in other mammals. Many sea otters, both male and female, share much of the same home range within which the two sexes mingle to some degree. Also they may segregate to haul out in traditionally established locations (see Segregation of Sexes).

I repeatedly saw lone adult male otters in the same locations near the shore of Kirilof Point, a female area. During a period of 3 weeks, one of these slept daily on the same rock. Another habitually rested in a kelp bed or on rocks on the shore of a sheltered cove. Although I saw transient males in the same general vicinity, I did not observe any behavior that might be interpreted as territorial defense.

When a female, searching for food or moving along the coast, passed the area occupied by a sedentary male he swam to her and attempted courtship. If the female was not receptive and passed on, the male returned to a favorite feeding or resting place. If the female was receptive, she chose a rock in the vicinity where the pair slept and groomed during the mated period (see Breeding Behavior) of up to several days.

Thus, males seeking an estrous female may be sedentary and wait for one in some favorite "territory," from which other males are not driven, or may actively search for estrous females. The maximum time that a male may remain in a limited location or remain away from one of the male haul-out areas was not ascertained. It is my conclusion that territoriality is but weakly expressed in the sea otter.

REPRODUCTION

Sex Ratio

Because sea otters segregate themselves according to sex, the raw data from samples killed, captured, or found dead on beaches at Amchitka Island must be carefully evaluated before drawing any conclusions concerning the sex ratio among different age classes.

PRENATAL SEX RATIO

Three samples of fetal sea otters are available from females killed in 1962 and 1963. The data are summarized in table 41. The smallest fetus in which sex was positively determined weighed 8.80 g. Among the 58 fetuses in which sex was determined, the ratio was 45 percent males: 55 percent females. The fact that the two 1963 samples show a nearly 50:50 ratio indicates that until a larger sample is available the prenatal sex ratio may, for practical purposes, be considered to be about 1:1.

JUVENILE SEX RATIO

Data on the sex ratio of juvenile otters were gathered during tagging studies when sea otters were netted, tagged, and released. This work was done mostly before the period in which high mortality occurred. The young otters were in the areas frequented primarily by females with young. Many of the young that were captured for marking were still in company of their mothers or recently separated from them. Mortality among young in company with their mothers is not known but apparently is low or moderate.

TABLE 41.—*Prenatal sex ratio at Amchitka Island*

Date taken	Number			Ratio (percent)	
	Males	Females	Total	Males	Females
22 Jan.-9 Mar. 1962.....	4	9	13	31	69
17-31 Mar. 1963.....	18	19	37	49	51
31 July-3 Aug. 1963.....	4	4	8	50	50
Total.....	26	32	58	45	55

Little geographical segregation of deserted juveniles had apparently occurred at the time tagging was done. Therefore, this class of animals contributes the best indication of sex ratio among sea otters up to approximately 1 year of age. Among 117 juveniles that were captured and marked, 58 males, 58 females, and 1 of unknown sex were recorded (table 39, section on Home Range). This evidence suggests that the sex ratio is approximately 1:1 during the juvenile period.

ADULT SEX RATIO

The areas in which females predominated were the most accessible to hunters. Also, these areas are more extensive than the locations frequented by males (see Segregation of Sexes). Primarily for these reasons the sex ratio of animals taken during cropping operations in 1962 and 1963 were biased in favor of females. The take consisted of 67 percent females and 33 percent males (table 42). In the section on mortality it was shown that the sex ratio among juveniles found dead on beaches during the late-winter to early-spring period of stress was 58 percent males: 42 percent females. These data suggest that among surviving adults, females outnumber males. The percent by which females predominate among adults, however, cannot be derived from the available data. The difference between the number of males and females taken during killing operations is a result of sexual segregation and is too great to be explained by the apparent difference in male and female mortality among juveniles.

Until further studies are conducted, it may be concluded that a nearly equal number of males and females are conceived and that the sex ratio remains approximately 1:1 until juveniles are deserted by their mothers. At this time, more males than females die of natural causes. Thus, among adults, females probably predominate over males. Harvesting operations tend to confirm this but more data are needed.

TABLE 42.—*Sex ratio of sea otters killed at Amchitka Island during experimental harvests*

[Ratio, males to females, 1:2]

Date	Males		Females		Total number
	Number	Percent	Number	Percent	
Jan.-Mar. 1962.....	43	28	111	72	154
Oct. 1962.....	6	25	18	75	24
Mar.-Apr. 1963.....	109	36	194	64	303
Total.....	158	33	323	67	481

Segregation of Sexes

Male and female sea otters at Amchitka habitually segregate themselves and, almost always occupy distinct geographical areas at all seasons. This condition first became apparent during observations when otters in various areas were counted and the numbers of each sex recorded. Additional information was obtained when otters were captured on beaches and when those dying of natural causes were recovered. During harvesting operations in 1962 and 1963, more quantitative data on the degree of segregation became available (tables 43 and 44). The terms "male area" and "female area" refer to the geographical locations used predominantly (but not exclusively) by each sex. Marakov (1965, p. 213) noted sexual segregation among otters at Medny Island, Commander Islands, U.S.S.R.

FEMALE AREAS

These are more numerous and less discrete than male areas (fig. 83, map). Seven female areas are listed in table 43. At these places the adult females usually haul out in favored sheltered places near the extremities of points. In general, they appear less bound to a limited hauling out location than the males. Certain locations, however, such as St. Makarius Point W., Rifle Range Point, and Constantine Point, are more favored than others. Tag recoveries reveal that females may use more than one of the favorite hauling grounds (see Home Range). The kill of adult females reveals that they are generally distributed along the coast when feeding. Many were taken a kilometer or more from favored haul-out locations. Observations as well as data from the kill indicate that females not only avoid the male haul-out locations but also avoid the feeding habitat adjacent to them. Among 242 adult otters killed in female areas, 93 percent were females. When 20 animals, not accompanied by a pup but in female areas, were killed selectively (31 July to 3 August 1963) in an effort to take males, only one male was obtained. This sample may indicate that males constitute only 5 percent of the animals in female areas.

MALE AREAS

Three locations on the eastern half of Amchitka (fig. 83, map) are used almost exclusively by males; the southeast tip of St. Makarius Point (SMPE) about 800 m. of beach, the north beach and tip of East Cape (ECN) about 500 m. of beach, and Crown Reefer Point (CRP) about 600 m. of beach. Along each of these

TABLE 43.—*Sex and age of sea otters taken in seven areas frequented mostly by females at Amchitka Island*

[All otters were shot during harvesting operations in 1962 and 1963. The only selection of animals shot was that adults were taken in preference to juveniles when both were present]

Location ¹	Adults						Juveniles						Adults and juveniles							
	Males			Females			Males			Females			Males			Females			Total	
	Number	Percent	Total number	Number	Percent	Total number	Number	Percent	Total number	Number	Percent	Total number	Number	Percent	Total number	Number	Percent	Total number	Number	Percent
RRP.....	0	0	20	100	20	4	50	4	50	8	4	14	4	14	24	86	28	24	86	28
SMB.....	1	9	10	91	11	2	18	9	82	11	3	4	19	4	19	96	22	19	96	22
SMPW.....	7	12	51	88	58	8	62	5	38	13	15	21	56	7	56	79	71	31	93	87
CP-IP.....	1	1	70	99	71	5	31	11	69	16	6	21	69	7	81	93	87	72	79	91
CH-KB.....	7	12	49	88	56	12	34	23	66	35	19	21	72	8	11	92	12	14	93	15
AMB.....	1	9	10	91	11	0	0	1	100	1	0	0	1	8	11	92	12	14	93	15
ECS.....	1	7	14	93	15	0	0	0	0	0	0	7	1	7	14	93	15	15	93	15
Total.....	18	7	224	93	242	31	37	53	63	84	49	15	277	85	2	326				

¹ RRP = Rifle Range Pt.; SMB = St. Makarius Bay; SMPW = St. Makarius Pt. West; CP-IP = Constantine Pt. to Ivakin Pt.; CH-KB = Constantine Harbor to Kirilof Bay; AMB = Aleut Midden Beach; ECS = East Cape South.

² Of the 326 animals taken, 84 (25.8 percent) were juveniles.

TABLE 44.—*Sex and age of sea otters taken in three areas frequented mostly by males at Amchitka Island*

[With the exception of the otters taken at CRP, otters were shot in 1962 and 1963 during harvesting operations. There was no selection of animals shot except that adults were taken in preference to juveniles. Because of its remoteness, otters were not harvested at CRP. The animals listed from there were found dead on beaches in 1956, 1959, 1962, and 1963. Remains showing no positive evidence of sex are omitted.]

Location ¹	Adults						Juveniles						Adults and juveniles								
	Males			Females			Males			Females			Males			Females			Total		
	Number	Percent	Total number	Number	Percent	Total number	Number	Percent	Total number	Number	Percent	Total number	Number	Percent	Total number	Number	Percent	Total number	Number	Percent	Total number
SMPE.....	37	97	1	2	38	14	78	4	22	18	51	91	5	9	56						
ECN.....	46	98	1	2	47	7	78	2	22	9	53	95	3	5	56						
CRP.....	17	100	0	0	17	7	88	1	12	8	24	96	1	4	25						
Total.....	100	98	2	2	102	28	80	7	20	35	128	93	9	7	137						

¹ SMPE = St. Makarius Pt. East; ECN = East Cape North; CRP = Crown Reefer Pt.

² Of the 137 animals taken, 85 (25.5 percent) were juveniles.

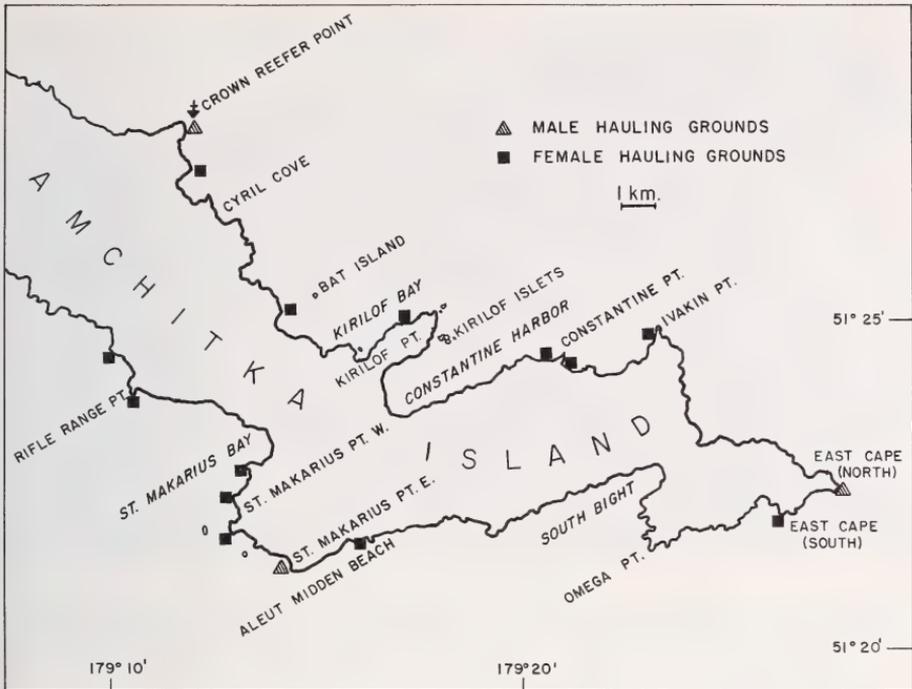


FIGURE 83.—The southeastern end of Amchitka Island showing the most favored male and female hauling grounds. Individual animals may haul out at almost any location along the shore. At the locations indicated on the map, however, aggregations of sea otters are habitually formed when numbers of animals come ashore to rest at all seasons.

beaches the majority of animals habitually haul out on 40 to 50 m. of beach. A few individuals may haul out indiscriminately at various distances from the most favored location. When a number of otters are hauled out, they usually congregate in groups, often sleeping in contact with one another (fig. 84). Among 102 adult otters killed in these areas, only 2 were females (table 44).

It appears that the males, except those actively seeking to mate, limit feeding activities to a radius of several hundred meters from the haul-out location. If they did not do this, more than 7 percent males (table 43) would have been shot in the female areas during killing operations. When mating activity was observed (see Breeding Behavior), males actively sought estrus females and mating was observed only in female areas. Thus, it is reasonable that a higher proportion of males was found in the female areas than females in male areas.



FIGURE 84.—A group of 39 otters sleeping at St. Makarius Point East, Amchitka Island, a favorite hauling ground for males. The many sleeping positions are demonstrated. Some lie on their backs, others on the belly or side, or curled nose-to-tail. (KWK 65-27-34)

JUVENILES

The foregoing paragraphs dealt primarily with adults. Segregation of sexes is more pronounced among adults and subadults than among independent or newly weaned juveniles. Among 35 juveniles taken in male areas, 80 percent were males (table 44). In female areas, among 84 juveniles examined 63 percent were females (table 43).

Since juveniles are or were recently associated with their mothers, it might be expected that a larger number would be found in the female areas than in the male areas. The percent of juveniles taken in both male and female areas was, however, the same, about 26 percent (see footnotes, tables 43 and 44). This may indicate that independent juveniles wander to all areas and mingle with any group of adults. It also appeared, however, that juveniles were more attracted to areas occupied predominantly by adults of their own sex (20 percent female juveniles on the male areas and 37 percent male juveniles on female areas). Perhaps because of the recent mother-young relationship the proportion of young males on the female area was greater than the proportion of young females in the male areas.

Discussion

The largest aggregations (animals hauled out in close proximity on the same rocks) were seen on male hauling grounds at Amchitka. I saw from 70 to over 100 on several occasions at East Cape. I seldom saw more than 10 to 15 females in close proximity on the same rock at any hauling ground (fig. 85). During aerial surveys, certain large aggregations contained few, if any, mothers with small young as far as we could ascertain.

Large aggregations were photographed at sea off Unimak Island (fig. 81) and mothers carrying small pups were not detected on the photograph. In the same general area but away from the aggregations, however, I saw many mothers carrying young on their chests. These mothers with young were usually alone but occasionally two were near each other. It thus appears that males and females habitually segregate themselves, both when on the hauling grounds and in offshore locations.

More observations of this aspect of social behavior are needed



FIGURE 85.—Rifle Range Point, a female hauling ground. Three of the females have entered the water; eleven adults and large juveniles remain on the rocks. (KWK 62-17-31)

in other island populations. Knowledge of the degree of segregation of sexes and the locations of areas where males concentrate may prove useful in management operations.

As mentioned elsewhere (Breeding Behavior), males often patrolled female feeding areas and attempted courtship with all females present. In the course of 3 or 4 hours, two to four males might pass separately through such an area.

Breeding Behavior

Observations at Amchitka are often hindered by dense fog. This fact and the tendency of mated pairs of otters to occupy offshore rocks, have prevented me from following any one pair of otters through all phases of the breeding cycle. I have, however, recorded observations of 41 mated pairs in the wild. Among these, copulation was initiated by 13 males which were not successful in completing it. Copulation was completed, apparently successfully, in eight cases. The remaining 20 observations were of paired animals in close company which, as explained later, exhibited the behavior typical of mated pairs. Excluded from the records are observations of unsuccessful attempts at courtship by males toward unreceptive females. The data on various aspects of the breeding cycle were obtained from many pairs observed briefly and from the observation of one pair which remained for about 3½ days in a sheltered cove (table 45). These observations indicate that the cycle of breeding behavior is rather uniform. A description of behavior during the different phases of the breeding cycle follows:

COURTSHIP OR PRECOPULATORY PERIOD

As mentioned elsewhere, adult males and adult females segregate themselves to a considerable degree. When a male seeks a

TABLE 45.—*Activities of a mated pair of sea otters during observations on 19, 20, and 21 August 1955*

19 August, 1634-1810. The male and female remained in close company at all times.

Activity	Number of periods	Elapsed time (minutes)		Total minutes	Percent of time
		On land	In water		
Copulation.....	2	—	35	35	37
Grooming.....	2	39	2	41	43
Sleeping.....	1	19	—	19	20
Total.....	5	58	37	95	100

TABLE 45.—Activities of a mated pair of sea otters during observations on 19, 20, and 21 August 1955—Continued

20 August, 1542-1910. The male left the female resting on the rock when he continued food diving, but he remained close to her while she was in the water.

Activity	Number of periods	Elapsed time (minutes)		Total minutes	Percent of time
		On land	In water		
Male:					
Feeding.....	4	—	79	79	38
Groom and wash.....	4	1	23	24	12
Sleep and rest.....	2	52	40	92	44
Sexual behavior (play).....	5	4	8	12	6
Investigate strange female.....	1	—	1	1	>1
Total.....	16	57	151	208	100
Female:					
Feeding.....	2	—	58	58	28
Groom and wash.....	1	21	—	21	10
Sleep and rest.....	3	108	9	117	56
Sexual behavior (play).....	2	4	8	12	6
Total.....	8	133	75	208	100

21 August, 1052-1820. The male left the female resting on the rock when he continued food diving, but he remained close to her while she was in the water.

Activity	Number of periods	Elapsed time (minutes)		Total minutes	Percent of time
		On land	In water		
Male:					
Feeding.....	10	—	310	310	70
Groom and wash.....	5	—	40	40	9
Sleep and rest.....	2	—	72	72	16
Sexual behavior (play).....	5	5	20	25	5
Sniff rock.....	1	1	—	1	>1
Total.....	23	6	442	448	100
Female:					
Feeding.....	7	—	247	247	55
Groom and wash.....	6	9	41	50	11
Sleep and rest.....	8	61	65	126	28
Sexual behavior (play).....	5	5	20	25	6
Total.....	26	75	373	448	100

On 22 August a dense fog prevented detailed observations.

Summary of activities of mated pair of otters on 19, 20, and 21 August 1955, during three observation periods totaling 749 minutes (12 hours, 29 minutes).

Activity	Total elapsed time			
	Male		Female	
	Minutes	Percent	Minutes	Percent
Feeding.....	389	52	305	41
Groom and wash.....	103	14	110	14
Sleep and rest.....	183	24	262	35
Sexual play.....	72	10	72	10
Sniff rock.....	1	>1	—	—
Investigate strange female.....	1	>1	—	—

female in estrus, he usually swims belly down and rapidly on the surface (fig. 86) and seldom dives for food. He closely skirts favorite hauling-out rocks, and he may rise high in the water to look onto the rocks, or leave the water to walk quickly about, sniffing the rocks. If he sees a feeding female floating on her back he swims directly to her. He may come up beneath her and attempt to put his forelegs around her chest from behind, his forepaws resting in or near her axillae. Or he may rise up beside her. He may rub and pat her chest, belly, and genital area with his forepaws, or he may nuzzle and appear to sniff them with his nose. If the female is unreceptive, she rolls away from him and pushes him away with her flippers and paws, or snaps at him. Before departing he may snatch whatever food items she has on her chest.

If she is receptive, the two may roll and frolic together. During



FIGURE 86.—Adult males actively searching for estrous females in areas habitually frequented by feeding females often swim belly down rather than in the more usual inverted position. (KWK 1026)

this period, the male may grasp the female about the chest from behind with his forepaws and attempt to grasp the side or back of her head or her nose in his jaws. At this rather rough stage of courtship, the female may disengage herself, snap at the male, and push him away with her flippers and paws. The two may now separate, but if the female is not determined in her resistance the male may follow her; or, occasionally, the female may follow the departing male and rough courtship behavior will continue. If the female is in estrus, she becomes increasingly submissive as courtship continues.

After the male has found an estrous female, the two continue actively to roll and splash about on the surface together. They nuzzle each other and fondle each other with the forepaws. Similar behavior was noted in the polecat by McCann (1955). Such behavior apparently lasts for a variable period, perhaps up to an hour. In the course of their activities the animals usually make their way, with the female leading, toward a suitable hauling-out rock which the female selects. This spot becomes the center of their activities during the mating period.

COPULATORY PERIOD

Copulation takes place in the water near the hauling-out rock. When the female is ready for coitus, her body becomes rigid and she lies belly up on the surface, her back somewhat bowed (i.e., concave) and her forelegs rigid and protruding vertically in front of her. The male grasps the female's upper jaw usually, including her nose, in his jaws, or he may grasp the side of her head. If the mated pair are on land during precoital play, the male leads the female into the water after grasping the side of her head in his jaws. He clasps her tightly from the back ("more canum"), his paws resting against her chest in or near her axillae. At the same time the already extruded penis is inserted as the male rests against the female's back, slightly on one side of the mid-dorsal area. The rear feet of the male are in motion, so that the two animals move about in a wide circle and roll from side to side. Periodically they lift their noses above the surface. For the most part, the male is beneath the surface and the belly and chest of the female are above it. The female frequently emits loud shrieks and gurgling gasps which indicate that she experiences difficulty in breathing.

In one case (19 August 1955), after copulation had continued for 14 minutes, the female struggled and wrenched her body, disengaging the male's penis. The male, however, retained his grip

on the female's head with his jaws, and the two animals, linked together by their heads, spun rapidly over and over in the longitudinal axis on the surface. The spinning continued for only a few seconds. Then the female became limp, the male again aligned his body with her back and grasped her with his forelegs, and copulation continued for an additional 9.5 minutes. When the male released his grip after an elapsed time of 23.5 minutes, the female's nose was gashed and bleeding. The two animals immediately began to groom and scrub their fur. Then, the female leading, the pair swam to and hauled out on the rock where they had previously engaged in courtship. Here they continued to groom and dry their fur for 10 minutes. The female was particularly vigorous in this activity. During this period and subsequent periods of association with the male on the chosen rock, the female almost constantly uttered a soft chuckling sound. After drying their fur, the pair went to sleep curled up close beside each other. The time was late afternoon and presumably, as was observed on other occasions, they slept in this location until after sunrise the next day.

While most observations indicated that the male initiated mating activities, estrous females were observed to tease or stimulate a reluctant male. In one instance (7 May 1956 at 1715 local time) I saw a male and female sleeping close beside each other in a kelp patch. They appeared to be a mated pair, and I presumed that copulation had occurred. While I watched, the female awoke and began to nuzzle the male about the head and abdomen. The male was slowly aroused from sleep and at first appeared indifferent to the attention of the female. Within about 30 seconds, however, he clasped her with his forepaws, then grasped the side of her head in his jaws. The female then became rigid (as described elsewhere) and copulation was accomplished. Unfortunately, after copulation had continued for 11 minutes, their motions carried them behind rocks, and it was not possible to obtain further observations of the pair.

In one case, a second copulation occurred about one-half hour after the first. Various observations of behavior indicate that more than one copulation may be usual.

Copulation usually occurs in the afternoon. I have 21 observations of copulation and attempted copulation during the afternoon, but only 1 recorded for morning (1030).

Barabash-Nikiforov (1947) says that during coitus the pair "cling to each other, intertwining belly to belly, and revolve around the longitudinal axis." Murie (1940) also said "position

apparently being with the ventral surfaces opposed, although of this I could not be positive." In all nine cases of completed copulation that I observed, the male clasped the female from behind and remained dorsal to her but slightly to one side of her median dorsal line during copulation. Because of the position of the female, lying rigidly on her back with forepaws extended, immediately before coitus, it would seem unusual that the position of the male would be other than dorsal to her body during copulation.

POSTCOPULATORY PERIOD

In one case this period was observed to last for 3 days (19 through 22 August 1955, table 45). The pair fed, groomed, and rested in close company (fig. 87). Occasionally they engaged in short periods of play, and the male sometimes attempted copulation. The female, however, appeared to be unreceptive during this period. The pair rested periodically on the chosen hauling-out site and slept beside each other during the night.



FIGURE 87.—A pair of sea otters (female on left) rest and groom beside each other shortly after mating. The light colored head is more typical of males than females. As shown here, females tend to be more alert and watchful than males. Males tend to be phlegmatic and take alarm less easily than females. The nose of the female was grasped in the teeth of the male during mating and is swollen. The broader and heavier head and neck of the male is evident. (KWK 975)

The male followed the female closely, often being in contact with her while the two consumed food, side-by-side on the surface. When the female dived for food the male quickly followed, often discarding a food item that he had not finished eating. When the female surfaced, the male emerged a fraction of a second behind her.

During this period the male left the female's side only after the two had emerged and groomed following a feeding period. While the female remained on the chosen rock to groom and sleep, the male dived for food nearby. While eating he swam back near the chosen hauling-out rock to eat, and often glanced at the female before diving.

On the third day of the mating period the male exhibited less interest than previously toward his mate, and several times stole food from her. Also, he followed her in food dives less promptly. The pair had left the cove by shortly after daylight on the morning of 23 August.

THE SEPARATION PERIOD

The breaking of the pair bond was observed on several occasions. The female, in each case, deserted the male. Probably because the male is larger than the female he requires more food, and as a general rule he returns to the water to continue feeding while the female rests on land. In one instance, the food dives of the male gradually carried him about 50 m. from the female's resting place. She watched him intently and, suddenly, while the male was beneath the surface gathering food, she slipped quietly into the water and swam rapidly away beneath the surface. Apparently the visual acuity of the male was inadequate to detect immediately from his feeding station the absence of the female. When the male returned for one of his periodic visits to his mate on the chosen rock and found her gone, he left the water and walked rapidly about, sniffed the spot where the female had rested, and looked quickly at possible hiding places nearby. Apparently satisfied that the female was gone, he entered the water and swam hurriedly to several nearby hauling-out places, rising high in the water to look onto them. He also rose high in the water to look across the surface in different directions. Although I observed several such episodes, I never saw a male relocate the female after her departure.

In general, it would appear that during the postcopulatory period the female exhibits less interest in retaining the pair-bond than does the male. The female may, however, exhibit sexual

interest, or even protective behavior, toward the male. What might be interpreted as protective behavior was exhibited by an adult female of an apparently mated pair that slept close beside each other on tidal rocks at 1630 on 2 March 1962. The more alert female started to leave the rock when she saw me approaching. When the sleeping male failed to awaken and follow her, she returned to him and, after pressing her paws against his face, neck, and chest and crawling on top of him, she finally aroused him. She then pressed her body against him from behind, inducing him to enter the water and follow her out of the area (figs. 88 and 89).

BREEDING BEHAVIOR VS. SOCIAL BEHAVIOR

Barabash-Nikiforov (1947) stated that "A grown cub often remains with the mother even after a new one is born, so that the mother is seen together with the newborn and yearling." This statement implies that a mother accompanied by a pup may participate in breeding activity. Murie (1940) describes a situation he observed in the Aleutians in which it appeared that the mother of a young pup engaged in coitus while the "little one . . . was crying at the far edge of the kelp."

I have observed a mother with a pup engage in rough play with a courting male during which the male attempted coitus. I have not, however, seen a female accompanied by a pup complete coitus or participate with the male in the breeding behavior cycle. In all instances that I have observed, the mother, after a period of play with the male, eventually retrieved her pup and attempted to disengage herself from the aggressive male. If the pup was large, the mother appeared to be considerably mauled as the crying, clinging pup clasped her about the head and neck from the front and the male clung to her from the rear, or tried to intrude between the mother and pup. My observations lead me to believe that it would be difficult for a mother with a pup to engage in the mating cycle of several days duration.

That a mother accompanied by a pup might become impregnated is a possibility. Further data on the physiology of reproduction in the female must be obtained before a conclusion could be indicated with some certainty. Available observations indicate to me that it is usual for females to enter estrus only when they are not accompanied by a pup.

Certain habits of the sea otter could lead to confusion during field observations. First, rough play might be mistaken for copulation. It appears that Fisher (1939) may have made this mistake. Second, sea otters, especially juveniles which are separated from



FIGURE 88.—A—An adult male and female slept beside each other on a tidal rock (male right, female left). The more alert female was aroused by the click of the camera and started to leave the rock. The male continued to sleep soundly. (KWK 62-19-6) B—The female returned and prodded the male with her forepaws and then climbed on top of him, pressing his head and chest with her paws. The male raised his paws to push her away. (KWK 62-19-5) C—The male, finally aroused, looked about sleepily while the female stared in alarm at the camera. The female nudged the male toward the water. (KWK 62-19-3)

their mothers, may attach themselves temporarily to an adult, either male or female, or to another juvenile. The two animals may play together, and when frightened may cling loosely together with their forepaws.

Figure 90 shows a juvenile which took refuge behind an adult male, beside which it slept. After being disturbed by my presence,



FIGURE 89.—A—Finally aroused, the male moved ahead of the female while she prodded him toward the water from behind. (KWK 62-19-1) B—As the pair slid into the water the female grasped the still drowsy male and gazed over him at the camera. (KWK 62-19-43) C—Finally completely aroused, the male stared in mild alarm while the female clasped his back in her forepaws. Shortly after the last photograph was taken the pair dived and made their way through a narrow channel to open water beyond the tidal rocks. (KWK 62-19-40)

the two swam off together. Since an impregnated female separates from the male shortly after copulation, and family groups include only the mother and her young, it appears improbable that such an association as illustrated would involve family ties.

As a general rule, lone females and females with young are observed apart from adult males. But a courting male, after a period of attempted courtship with a female and her young, may



FIGURE 90.—This adult male was tolerant of a deserted juvenile which slept beside him and sought shelter behind him when frightened. When the adult finally became alarmed, entered the water, and swam off, the juvenile remained in close company with him. (KWK 62-25-24)

sleep near them in a kelp bed, or the three may haul out on a rock to groom, rest, and sleep in close association. It would appear that such an association is an expression of gregariousness. On one occasion I watched an adult male and female play roughly together for about 15 minutes. The female was accompanied by a large pup, which during the play period attempted to participate, or swam about nearby and occasionally cried. Although the male tentatively attempted copulation, the female was not receptive. After the three had hauled out and the male had groomed and rested beside the mother and pup for about 20 minutes, he entered the water and left the vicinity. In this case it was apparent that, although the male was sexually motivated, the association of the male and female was casual, and they were not a mated pair. The association described above might lead an observer to form erroneous opinions concerning breeding habits.

Reproduction in the Female

In this section, data from female reproductive tracts, the conceptuses they contained, and field counts of dependent young and

independent animals are combined to present an analysis of reproduction in the female sea otter. The fundamental histological study on which much of the present analysis of reproductive tracts is based was done by Dr. A. A. Sinha under the direction of Dr. C. H. Conaway (Sinha, Conaway, and Kenyon, 1966). In that study, 136 mature tracts taken from 1954 through 1962 were used. Some material from that collection, which was not published in Sinha et al (1966), is included in the present study. It was kindly given to me by Dr. Sinha. A study of the histology of the sea otter ovary was recently completed (Sinha and Conaway, 1968).

The 1963 collections (table 46) added data from different seasons which revealed what the earlier material did not: that there is apparently a peak in frequency of births in summer.

Samples representing certain seasons are small. More specimens from summer, fall, and winter are needed before all phases of the reproductive cycle may be based on an adequately large sample. A long-continued field study of marked animals and a captive breeding colony would contribute valuable information on some phases of the reproductive cycle.

My discussion of various aspects of the reproductive material available is followed by a statistical analysis of this material by Dr. Douglas G. Chapman.

REPRODUCTIVE TRACTS

From 1954 to 1963, reproductive tracts were obtained from animals found dead on beaches, from animals captured (netted) on beaches, and from animals shot during experimental cropping studies. The adult female tracts that were collected are listed in table 46. The four larger collections from 1962 and 1963 (table 46) contribute the most useful material. The smaller collections and individual specimens taken in other years are included where useful in the following analyses. In tables 47 through 51, different

TABLE 46.—*Adult female sea otter reproductive tracts from Amchitka Island*

[Except those taken in 1960. These were taken in other areas of Alaska]

Period	Number	Remarks
1954-57	14	Taken at various seasons. Some from animals found dead. Studied by C. H. Conaway and A. A. Sinha.
Feb.-Apr. 1959	14	Most were netted on beaches, several found dead. Studied by Conaway and Sinha.
Jan.-July 1960	4	Shot (FWS). Studied by Conaway and Sinha.
Jan.-Feb. 1962	88	Shot (ADFG). Studied by Conaway and Sinha.
Oct. 1962	14	Shot (ADFG). Studied by Conaway and Sinha.
Mar.-Apr. 1963	125	Shot (ADFG). Studied by Kenyon.
July-Aug. 1963	19	Shot (ADFG). Studied by Kenyon.
Total	278	

TABLE 47.—*Phases of reproduction in the female sea otter as shown by status of ovaries and size of conceptus*

[Information from genital tracts collected from 1954 through 1963 is combined]

	Season of sample collection								Total number
	Jan.—Feb.		Mar.—Apr.		May—Aug. ¹		Sept.—Dec.		
	Number	Per cent	Number	Per cent	Number	Per cent	Number	Per cent	
Unimplanted blastocyst.....	35	57	49	50	4	31	6	100	94
Conceptuses:									
Class 1.....	8	13	9	9	0	0	0	0	17
Class 2.....	4	7	6	6	0	0	0	0	10
Class 3.....	4	7	11	11	2	15	0	0	17
Class 4.....	10	16	17	17	3	23	0	0	30
Class 5.....	0	0	6	6	4	31	0	0	10
Total conceptuses.....	26	43	49	50	9	69	0	0	84
Total pregnant.....	61	70	98	70	13	52	6	27	178
Not pregnant ²	27	30	42	30	12	48	16	73	97
Total tracts.....	88	—	140	—	25	—	22	—	275

¹ The 19 adult female sea otters taken between 31 July and 3 August 1963 were killed selectively, mothers accompanied by pups were spared. Thus, the percentage of postpartum non-pregnant specimens in this sample is less than it would have been if the kill had been non-selective.

² See table 51 for more details.

TABLE 48.—*Frequency of primiparous and multiparous sea otters*

Period sampled	Total examined	Primiparous		Multiparous	
		Number	Percent	Number	Percent
<i>1963</i>					
15 Mar.—2 Apr.....	125	21	17	104	83
31 July—3 Aug.....	12	2	17	10	83
Total.....	137	23	114

TABLE 49.—*Uterine horn of pregnancy*

Period sampled	Specimens examined	Uterine horn pregnant			
		Right		Left	
		Number	Percent	Number	Percent
Mar.—Apr.....	90	46	51	44	49
May—Aug.....	7	3	43	4	57
Total.....	97	49	51	48	49

TABLE 50.—Weight distribution of embryonic and fetal sea otters

Weight class	Collected in period 1—														
	22 Jan. to 13 Feb. 1962 ²				15 Mar. to 2 Apr. 1963				31 July to 3 Aug. 1963						
	Num-ber	Per-cent	Maxi-mum	Mini-mum	Mean	Num-ber	Per-cent	Maxi-mum	Mini-mum	Mean	Num-ber	Per-cent	Maxi-mum	Mini-mum	Mean
No. 1, <1 gram.....	8	31	0.9	0.5	0.6	8	16	0.9	0.2	0.2	0	0	—	—	—
No. 2, 1-10 grams.....	4	15	9.0	7.0	8.0	6	12	8.8	1.1	4.1	0	0	—	—	—
No. 3, 10-100 grams.....	4	15	80.0	15.0	46.0	11	23	93.0	10.9	39.9	2	25	61.9	36.1	49.0
No. 4, 100-1,000 grams.....	10	39	720.0	140.0	350.0	18	37	882.0	100.5	344.1	2	25	478.0	366.0	417.0
No. 5, 1,000-2,000 grams.....	0	—	—	—	—	6	12	1,869.0	1,067.0	1,511.2	4	50	1,810.0	1,118.0	1,497.0
Total.....	26	100	—	—	—	49	100	—	—	—	8	100	—	—	—

¹ No implanted pregnancies were found in the 1962 fall sample.

² Weights from A. A. Sinha (personal communication).

³ Three of the visibly implanted embryos included here were very small and were not weighed. These are included in the total above but only five that were weighed are represented in the maximum, minimum, and mean weights.

TABLE 51.—*Reproductive status of adult nonpregnant sea otters*

[Nine animals, adult in body size but being nulliparous and showing no follicular activity, are excluded]

Nonpregnant tracts	Samples collected in—						Total
	Spring 1963, Mar.—Apr.		Summer 1963, ¹ July—Aug.		Fall, 1957 and 1962, Oct.—Nov.		
	Num- ber	Per- cent	Num- ber	Per- cent	Num- ber	Per- cent	
Postpartum, inactive ovaries:							
Pup present.....	13	35			8	61	21
Pup absent.....	16	43	3	60	1	8	20
Inactive ovaries ²	4	11	2	40	3	23	9
Active ovaries ³	4	11			1	8	5
Total.....	37	100	5	100	13	100	55
Total tracts examined and percent not pregnant.....	125	30	14	36	17	76	156

¹ Animals were killed selectively to exclude all mothers accompanied by young. The objective was to take as many male skins as possible in a female area. Among 19 independent animals, only 1 male was taken.

² Multiparous but not showing positive evidence of being recently postpartum.

³ Estrus and proestrus.

total numbers of specimens are shown because not all specimens could be used for every aspect of this study. I did not examine all collections and samples. Those that I did examine presented adequate information for certain aspects of this study.

The reproductive tracts were removed from the animals from a few minutes to several hours after death, depending on field conditions. They were then fixed entire for 24 hours in AFA solution (95 percent alcohol, 30 percent; commercial formalin, 10 percent; glacial acetic acid, 10 percent; water, 50 percent). After fixing, the tracts were stored for later study in 70 percent isopropyl alcohol.

Sinha et al. (1966) explain how certain aspects of reproductive tract studies were conducted. I examined ovaries with a 10X Loupe after slicing them into sections about 1 mm. in width.

FIELD COUNTS OF SEA OTTERS

Field counts of sea otters were recorded whenever possible. The primary objectives were to obtain information on (1) the season of birth, and (2) the annual rate of reproduction.

Observations were limited by: (1) Environmental conditions such as wind, precipitation, and rough water; (2) a variable degree of sexual segregation among independent animals, including mothers with young; (3) the often indistinguishability of sexes and age classes; and (4) the constant movement of animals to and from local areas. In spite of these factors, useful field observations were obtained.

Counts of otters were made primarily at Amchitka Island, from beaches and cliff tops and during dory trips through inshore waters. Binoculars (7X50) and a telescope (50 power) were used for observation.

DEFINITION OF TERMS

Implanted pregnancy observations are based on visible swellings of the uterine horn, presence of a corpus luteum, and recovery of the conceptus. *Unimplanted pregnancy* observations are based on the presence of a corpus luteum not accompanied by swelling of the uterine horn. Sinha et al. (1966) demonstrated that when a corpus luteum is present and no uterine swelling is visible a blastocyst may be recovered from the uterine horn. *Multiparous* animals were separated from *nulliparous* and *primiparous* animals by the thickened appearance of the uterine horns which, after having held a conceptus, do not regain the smooth, firm texture of the nulliparous uterine horn.

Tracts were classified as *nonpregnant* when no corpus luteum was present. A female was considered to be *post partum* if one or more of the following conditions was observed: (1) lactation, (2) presence of a pup, (3) presence of a corpus albicans, (4) presence of a placental (uterine) scar. Because it appears that the young sea otter remains with its mother for about a year, certain evidence of a post partum condition may be obscure by the time the pup and mother part. The placental scar may virtually disappear and the corpus albicans may be reduced in a female accompanied by a large pup. One lactating female, whose pup was either recently lost or was not seen by the hunters, showed no placental scar and the corpus albicans was very small.

Classification of ovaries as *estrous*, *proestrous*, and *anestrous*, based on macroscopic examination of sectioned ovaries, are considered briefly in the following discussion. The objective of this study is to present a review of the natural history of reproduction.

AGE AT SEXUAL MATURITY

Sufficient data are not available to fix with certainty the age at sexual maturity. Some information was obtained from a juvenile female (approximately 1 year old), weighing about 24 lb. (10.9 kg.), that was tagged (EL 556, table 39) on 22 March 1962. On 18 March 1963, when this animal was shot 2.5 miles from the place of marking it weighed 33 lb. The dentition was that of a young adult, but the reproductive tract was decidedly immature.

It can thus be said that the female sea otter does not mature sexually until after 2 years of age.

The mean weight of 39 pregnant females was 50 lb. (22.7 kg.) (extremes 36 and 70 lb.). Among 21 primiparous females, the mean weight was 43 lb. (19.5 kg.) (extremes 35 and 52 lb.). If the marked 33-lb., 2-year-old had continued to grow during her third year at the rate she did in her second, her weight would have approximated the mean weight of the primiparous females. This suggests that the female may become sexually mature at 3 years of age.

Among northern fur seals on the Pribilof Islands, the pregnancy rate in 4-year-olds is about 3 percent and in 5-year-olds about 40 percent (Fiscus and Kajimura, 1967). If we assume a somewhat similar condition in the sea otter, it is indicated that a small percentage of females may become pregnant after attaining 3 years of age, i.e., in the fourth year, and that animals 5 or more years of age constitute the important reproducing segment of the population (see also "Implication of Other Observations," p. 245-246).

PREGNANT FEMALES

Table 47 and figure 91 summarize data from 178 females showing evidence of pregnancy. Among pregnant animals, unimplanted pregnancy reached maximum frequency (100 percent) in the fall sample. Implanted pregnancy increased in spring and reached maximum frequency (69 percent) in summer. The high frequency of large (weight class 5) fetuses in summer (50 percent, table 50) and concurrent low frequency of unimplanted pregnancies (31 percent, table 47) indicate, as do the field counts of dependent young, that parturition reaches a peak in summer. Although the fall sample of tracts is small, it demonstrates that parturition in the fall and winter accounts for a minority of births.

Among 137 pregnant females from two samples for which data are available (table 48), it is indicated that annually 17 percent of the pregnant animals became pregnant for the first time and that 83 percent are multiparous.

Location of pregnancy

A record of the uterine horn of pregnancy is available for 97 animals. Although the sample is small, it was gathered unselectively and demonstrates that pregnancy occurs with equal frequency in the right and left uterine horns (table 49). The location of implantation of the conceptus is usually within the center one-third of the uterine horn.

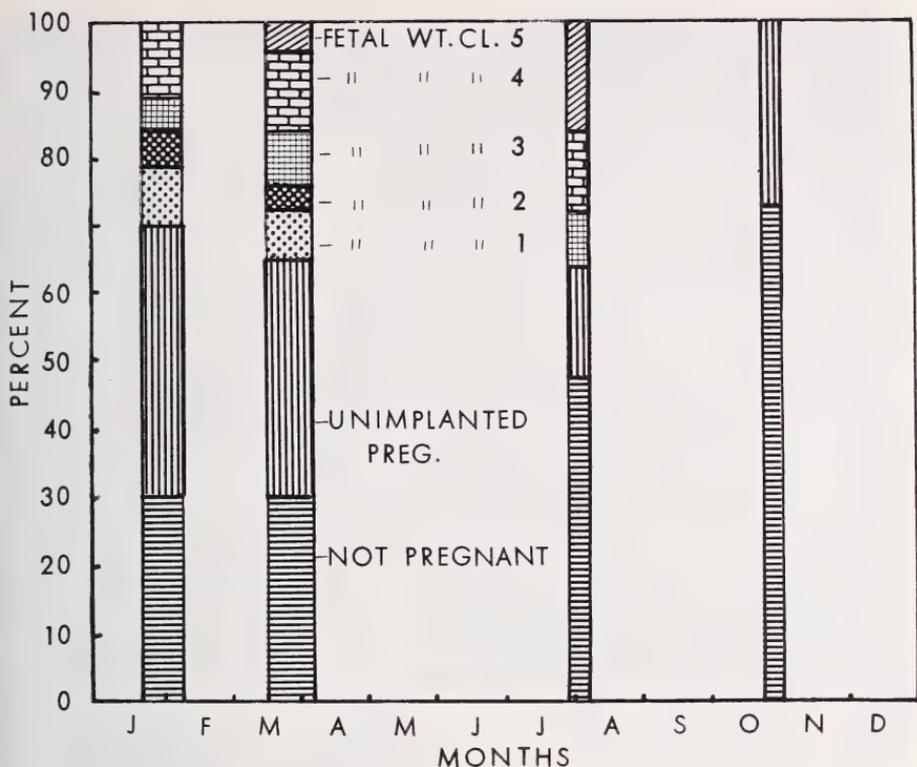


FIGURE 91.—Phases in the reproductive cycle of the female sea otter as revealed by ovary and fetal examinations of four samples of reproductive tracts. Although some of the samples are small, they illustrate that large fetuses and implanted pregnancies predominate in summer and that pregnancy is at a maximum in late winter and spring.

Conceptus size and development

To compare the conceptuses that were recovered from reproductive tract samples, the embryos and fetuses were classified according to five arbitrarily chosen weight classes following a logarithmic scale (table 50). The conceptuses ranged in weight from a fraction of a gram to 1,869 g. (4 lb.). When the weights of fetuses taken in different seasons are compared, it is shown that in winter conceptuses of small size predominate and in summer large fetuses predominate. The series of photographs (figs. 92 and 93) illustrate stages of development. The comparative sizes of the conceptuses in the samples from different seasons were useful in indicating the timing of certain phases of the reproductive cycle (see Chapman's analysis that follows).

The morphology of the female reproductive tract was studied

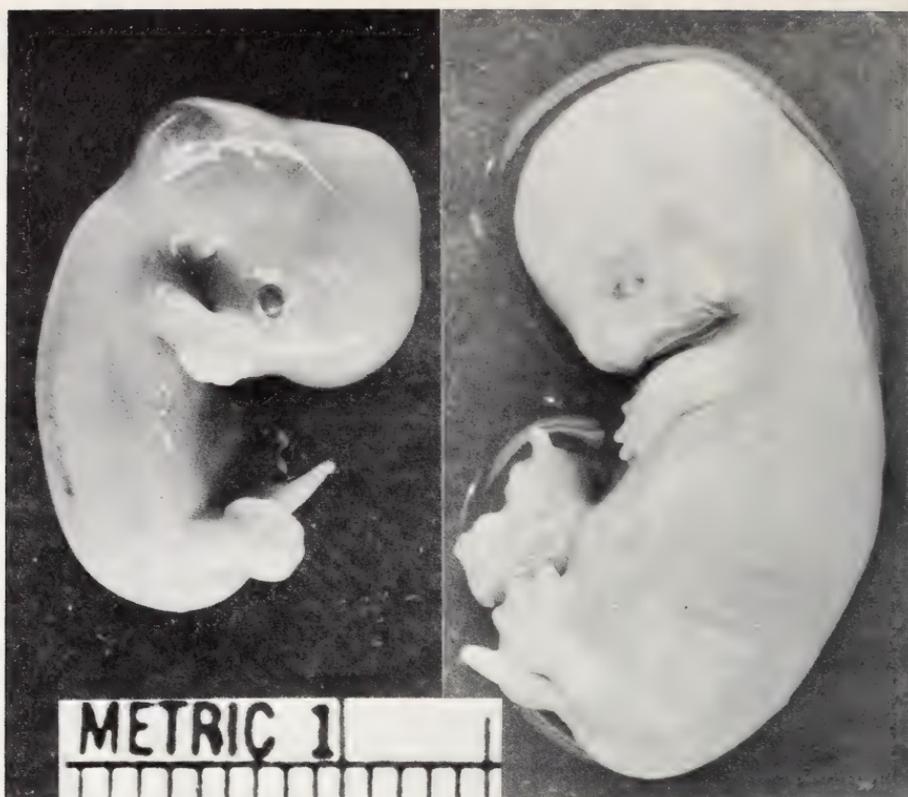


FIGURE 92.—Early fetal stages of the sea otter. Sex could not be determined in either specimen by gross examination, and the age of the fetuses is not known. Differentiation of the front and hind limb buds has barely begun in the larger fetus. Specimens from Amchitka Island, 18 and 19 March 1963: Left—Specimen JEB 63-52, weight 0.692 g., crown-rump length 17 mm. (KWK 65-18-15) Right—Specimen JEB 63-67, weight 1.12 g., crown-rump length 24 mm. (KWK 65-18-9).

and described in detail by Sinha (1965). The development of the fetal membranes, their structures, and evolutionary relationships were studied and described by Sinha and Mossman (1966). The general appearance of the gravid reproductive tract is shown in figure 93.

NONPREGNANT ADULT FEMALES

Spring sample

Although two spring samples (1962 and 1963, table 46) of female sea otters from Amchitka were taken, I studied only the 1963 specimens.

Between 15 March and 2 April 1963, 125 adult female sea otters

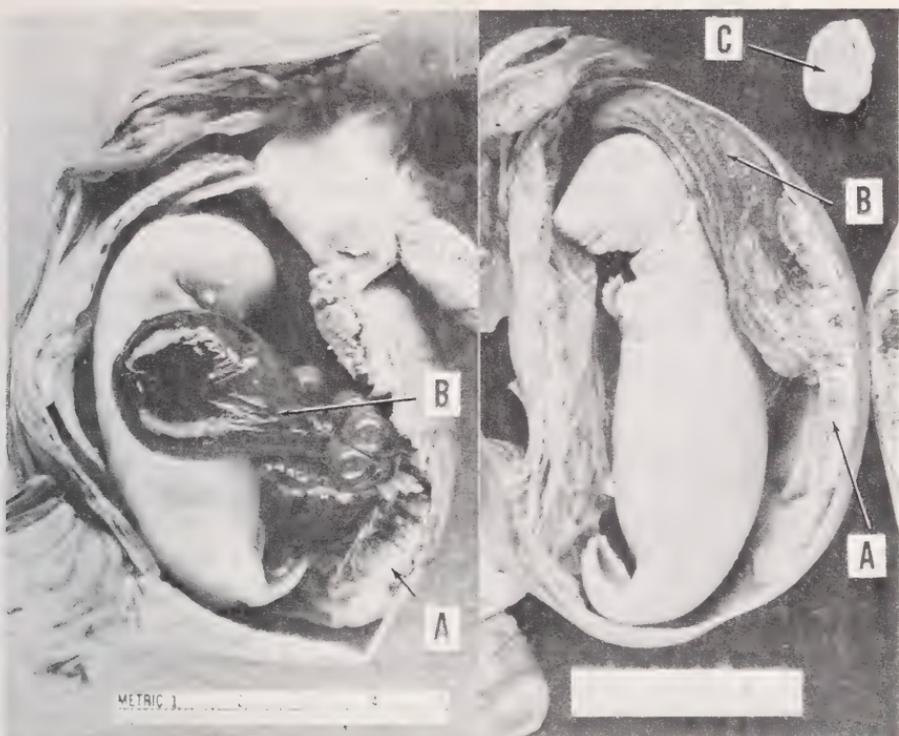


FIGURE 93.—Intermediate fetal development. One side of the uterine wall was removed to show the chorioallantoic placenta (A) and the large antimesometrial, pedunculated saclike hematoma (B). The specimen on the left shows also smaller hematoma pouches surrounding the hemotomic peduncle. The relative size of the ovary is shown. It was sectioned to reveal the large corpus luteum (C). Specimens from Amchitka Island: Left—specimen JEB 63-40, weight 11.82 g., crown-rump length 53 mm., sex ♀; taken 17 March 1963. (KWK 65-18-33) Right—specimen ADFG 520, weight 61.95 g., crown-rump length 105 mm., sex ♀; taken 2 August 1963. (KWK 65-13-11) Sinha and Mossman (1966) give a detailed description of placentation in the sea otter.

were taken and their reproductive tracts were examined (table 51). Thirty-seven (30 percent) showed no evidence of pregnancy (no corpus luteum or visible conceptus). Of these, 29 exhibited evidence of being post partum from a few days to perhaps a year. Among these 29 females that were judged to be post partum, 13 (45 percent) were accompanied by a pup. The remaining 16 (55 percent) were not, or the pup was not seen, but the female showed anatomical evidence of having borne a pup. Although it might be inferred that the loss of young is as high as 55 percent, this is not necessarily true. Large young, although still dependent on their

mothers, may be some distance (± 50 m.) from them and thus not associated with the mother by the hunter's observations. Also, large young may have recently become independent.

Among the eight remaining nonpregnant females, four showed no follicular activity or positive evidence of being post partum. One of these was diseased. It possessed a large ovarian cyst (31×15 mm.) The remaining four were multiparous (enlarged uterine horns) but did not show evidence of being post partum and appeared to be approaching estrus (follicles enlarged) or to have recently ovulated.

Summer sample

Among 14 sexually mature sea otters taken between 31 July and 3 August 1963 at Amchitka, 5 (36 percent) were not pregnant. Three of these were post partum. None was accompanied by a pup. (As explained elsewhere, this collection was selectively taken to exclude mothers accompanied by pups.) Two were multiparous inactive but their reproductive tracts revealed no evidence of being recently post partum (table 51).

Fall sample

Among 17 sexually mature females taken between 12 October and 3 November, 13 (76 percent) were not pregnant. Among these, eight (61 percent) were accompanied by young and one was lactating, indicating that a pup had recently been lost. Of the five remaining, three showed no follicular activity or indication of having recently lost a pup. One showed follicular activity indicating a proestrus condition (table 51).

FIELD COUNTS

An effort was made to record newly born young separately from older dependent young. Because of variable field conditions, the results were inconsistent and not useful to this study. Therefore, all young with mothers were grouped as dependent animals.

Counts were made in many areas but only in a consistent way during all field seasons in the Constantine Harbor, Kirilof Point to Kirilof Bay areas. After all of the data from several other areas were studied, it became apparent that because of different conditions in each area the results of counts in one area were not comparable with those made in another. Also, counts made from a cliff top cannot be compared with counts made from a dory. Females with young among coastal rocks may be missed during an

offshore dory count. Also, the number of males, i.e., the degree of sexual segregation, varies in different areas (see table 43, Segregation of Sexes).

I made the field counts from Kirilof Point and vicinity from the same observation stations at all seasons (table 52). Because they were made in different years, they cannot be considered strictly comparable but they do constitute the best material available and general conclusions are based on them.

In the summer of 1955, Kirilof Point (on the Bering Sea shore of Amchitka), bounded on the east by Constantine Harbor and on the west by Kirilof Bay and having a shoreline of about 5.5 km. (3 nautical miles), was chosen as a study area. I soon found that it was frequented primarily by females, and especially mothers with young (see Segregation of Sexes). Counts in this area were thus not representative of the ratio of dependent young to independent animals in the Amchitka population, but were biased in favor of a high ratio of dependent young to independent (includes both sexes and all ages other than dependent young) animals.

PHASES OF REPRODUCTION

Breeding season

Mating behavior (mated pairs, attempted copulation, or copulation) was observed in all months except October and December. Harsh winter weather reduces visibility and I have spent less time in the field in the fall and winter seasons. Barabash-Nikiforov

TABLE 52.—*Sea otters counted along 5.5 km. of shoreline Kirilof area, at Amchitka Island, Alaska*

[This area included parts of Constantine Harbor, all of Kirilof Point, and part of Kirilof Bay. This locality is frequented primarily by females and young. Complete counts of Kirilof Point, as well as counts from parts of the area, are included in this table]

Month and year	Number of counts	Independent animals	Dependent young	Total	Percent dependent young	Season mean percent young
January 1959.....	6	37	7	44	16	} 15
February 1959.....	7	104	17	121	14	
March, 1959 and 1962.....	2	34	5	39	13	} 15
April 1959.....	5	197	39	236	17	
May 1956.....	4	164	42	206	20	} 17
May 1959.....	1	62	11	73	15	
June 1956.....	3	126	23	149	15	
July 1956.....	6	258	85	343	25	} 22
August 1955.....	9	278	59	337	18	
September 1955.....	12	407	83	490	17	} 24
October 1957.....	3	132	49	181	27	
November 1957.....	11	315	117	432	27	
Total.....	69	2,114	537	2,651		

(1947) did not observe copulation during October and December.

Data from field observations of breeding behavior and from reproductive tracts give conflicting indications of the period of maximum mating activity. Field observations appear to indicate that most breeding activity occurs in June. By months, observations of breeding behavior were as follows:

January	1	May	9	September	2
February	2	June	17	October	0
March	3	July	1	November	1
April	1	August	4	December	0

Field observations of behavior are hampered in fall and winter by stormy weather conditions. Because comparative field observation time was not available in all seasons, I consider that field observations of mating activity are not quantitatively useful. They are qualitatively useful, however, in demonstrating that breeding activity does occur in all seasons.

Because the frequency of pregnancy in our samples increased from 27 percent in early fall (October) to 70 percent in the January-February sample (table 47), the available data indicate that maximum breeding activity occurs in the late fall to winter period. Further studies, particularly of reproductive tracts taken in fall and winter months, are needed to reveal with certainty the period of maximum breeding activity.

Gestation period

Sinha et al. (1966) demonstrated that after fertilization in the sea otter the blastocyst enters a period of rest, i.e., undergoes "delayed implantation." Thus, presence of a corpus luteum indicates pregnancy whether or not a conceptus is visible on gross examination of the tract. When the "resting stage" is completed, the blastocyst becomes implanted in the mucosa of the uterine horn and proceeds through embryonic and fetal stages of growth.

To gain some knowledge of the length of the gestation period and the duration of its unimplanted and implanted stages, data were obtained from the ovaries and conceptuses of 275 reproductive tracts (table 47 and fig. 91).

One method of estimating the gestation period of the sea otter is to assume that during the period of implanted pregnancy the rate of fetal growth may be comparable to that of the European river otter (*Lutra lutra*) and American river otter (*L. canadensis*). (A more sophisticated method, given below, is employed by Chapman.) The European animal differs from the American river otter and sea otter in that the blastocyst does not undergo a delay in

implantation and the gestation period has been determined to be about 63 days (Cocks, 1881).

The data of Hamilton and Eadie (1964) show conclusively that the gestation period of the American river otter includes a period of delayed implantation. The data of Liers (1951) appear to indicate that this period may be variable. He recorded extremes of 9 months 18 days to 12 months 15 days in the total gestation period of captive otters.

Huggett and Widdas (1951) showed that during certain phases of prenatal growth the cube roots of fetal weights fall along a straight line. They indicate that an adjustment can be made for the period before the cube root of fetal weights begins to follow a straight line. This adjustment, however, is minor and, in estimating the period of implanted gestation in the sea otter, is ignored on the graph (fig. 94).

The weights of two young European otters that were presumably

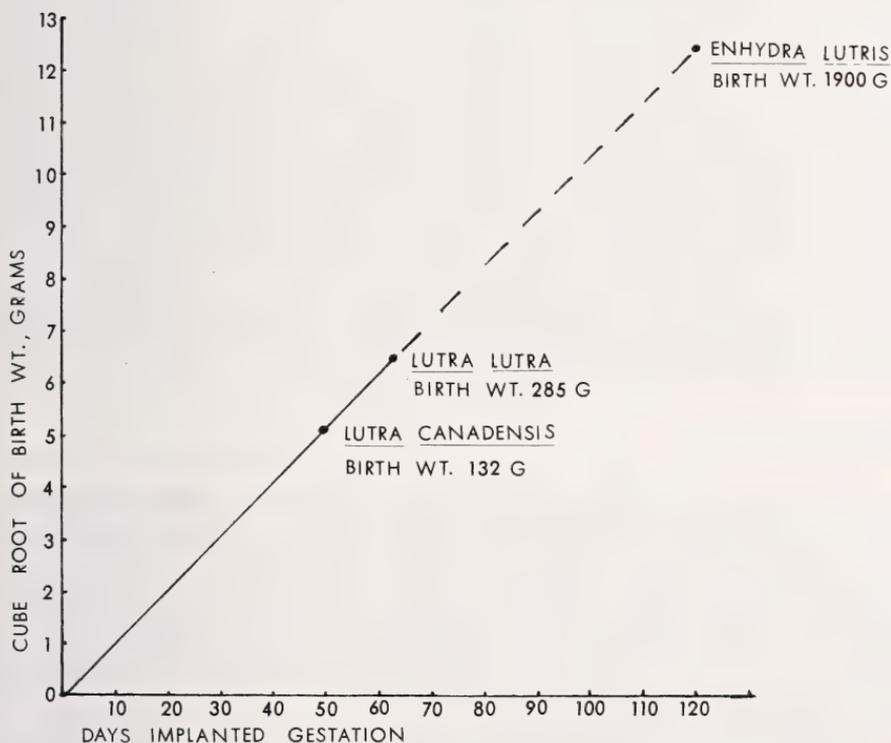


FIGURE 94.—Estimated period of implanted pregnancy. The periods are estimated for the American river otter and sea otter on the assumption that their fetal growth velocities are similar to that of the closely related European river otter (see Huggett and Widdas, 1951).

less than a week old were 285 and 290 g. (Jensen, 1964). If the smaller of the two is presumed to approximate the birth weight and its cube root is plotted according to the method of Huggett and Widdas (1951) for a gestation period of about 62 days, a fetal growth rate line is established (fig. 94). If the full-term fetus weighing 132 g., that was recovered by Hamilton and Eadie (1964), is plotted on the same growth scale as the European otter, it is indicated that the period of implanted pregnancy in the American river otter may be less than 2 months. Liers (1951) states that "The eyes open when the young are about thirty-five days old." This indicates that at birth the river otter is in an early stage of development compared to the sea otter which is born with the eyes open.

To obtain an approximation of the period of implanted pregnancy in the sea otter, it appears reasonable to compare its fetal growth rate with that of its closest relatives. If the cube root of the sea otter weight at birth (generally at least 1,900 g., see Body Measurements) is plotted on the same line of growth, then the indicated period of implanted gestation is at least 4 months. Data from reproductive tracts indicate that maximum breeding activity probably occurs in the fall to winter period and that the maximum number of births occur in the summer to early fall period. The samples indicate that the period of unimplanted gestation in the majority of animals (table 47) extends into the January to April period, i.e., to last for about 6 to 8 months. This would indicate that the total gestation period may be about 10 to 12 months. Because mating and parturition occur during all months, this method of estimating the gestation period from the available data do not permit a more precise definition.

Pupping season

Birth may take place at any season. This was stated by many early sea otter hunters, and confirmed by modern observers (Barabash-Nikiforov, 1947; Fisher, 1940a; Murie, 1940; etc.). I have handled and examined newly born young in all months. Many of these newborn were captured with their mothers during tagging operations and were returned to the mother when she was released after tagging.

Scheffer (1951) raised the question whether there was a season of birth: "The evidence of five specimens...is that the young are born in April and May, rather than the year around." Data from our samples indicate that there is a season of maximum birth frequency. The data in table 52 demonstrate that the per-

centage of dependent young in the population is relatively low in the winter and spring. After the late-winter to early-spring season of storms, which is accompanied by much mortality among juvenile otters (see Limiting Factors), an increasing number of births is demonstrated in the field counts. A summer peak in the frequency of births is confirmed by high frequency of large fetuses recovered in that season from reproductive tracts (table 47).

The frequency of nearly full-term fetuses in the samples increased from none in the January-February sample to 6 percent in the March-April sample and to 31 percent in the May-August sample (table 47). The number of dependent young with mothers also increased throughout the spring and summer (see table 52, Field Counts).

In the small midsummer sample (August) the fetuses were large, in weight classes 3, 4, and 5, none were in weight classes 1 and 2 (table 50).

These data strongly suggest that birth frequency increases in early spring and reaches a peak in summer. Our samples from the September through February period were too small to confirm the field observations of newly born young in every month.

Although the Steller's sea cow (*Hydrodamalis gigas*) is a very different animal from the sea otter, it was also a resident inshore marine mammal. It is interesting that Steller noted (*in* Stejneger, 1936, p. 355) that the sea-cow "brings forth their young at all seasons, generally however in autumn, judging from the many new-born seen at that time." The fact of bearing young at all seasons, while having a season of maximum birth frequency, may be a case of convergent evolution related to the habitat in which these animals were sympatric.

Place of birth and fetal orientation

There is no record that the birth of a sea otter has ever been observed. Fisher (1940a, p. 132) presumed that "The births of the young otters take place on the kelp beds." This infers that the young are born in water. Barabash-Nikiforov (1947, p. 97, English translation), however, saw a mother with a newly born young on shore and recovered the still warm afterbirth.

The place of birth in marine mammals may be related to fetal orientation at birth. For example, in cetaceans birth always occurs in water. Slijper (1956) summarized data on the position of the cetacean fetus at birth. In 22 observed births, all young were born tail foremost. Presumably caudal presentation is a survival factor

in an air breathing mammal born under water (Essapian, 1953). Slijper (1956), however, does not subscribe to this theory.

If caudal presentation is a survival factor in aquatic birth and it were the rule in the sea otter, it might be supposed that birth would occur in the water. Among 43 fetuses for which fetal orientation were recorded, delivery would have been cephalic in 22 (51 percent) and caudal in 21 (49 percent). These data indicate that selective evolution for caudal presentation at birth, and by inference for birth in water, has not taken place in the sea otter. By comparison, the fur seal is more specialized for life in the marine environment than is the sea otter but emerges from the water before parturition. Peterson (1965, p. 136) recorded that in 61 percent of 112 observed births the young emerged head foremost. It is thus indicated that birth in the sea otter, as in the fur seal normally occurs on land.

Period between births

Figure 91 and table 47 demonstrate that during the winter and spring when the maximum number of sea otters are pregnant, one-third of the tracts in our sample were nonpregnant. I strongly suspect that all reproductive tract samples are biased toward a low frequency of nonpregnant animals. This assumption is based on three observations: (1) that no female known definitely to be accompanied by a pup was found to be pregnant, (2) that females with young are more wary and secretive than females without young and are thus less available to hunters, and (3) that during hunting operations I noted a degree of reluctance in hunters to shoot a female accompanied by a pup if animals without pups were present. Thus, an unknown degree of bias in favor of single animals, i.e., a high percentage of pregnant animals, is included in all samples. The July to August 1963 sample is particularly biased, since single animals only were selectively killed. At this season the number of mothers accompanied by pups is approaching the annual maximum (see table 52). Thus, the percentage of nonpregnant animals in the adult female population would also approach maximum numbers at this season. This is shown by the sample (fig. 91), but it would be much more apparent had the sample been unselective.

Because the summer sample of reproductive tracts was taken selectively to exclude mothers accompanied by pups it is, in some respects, not comparable with the spring and fall samples. Nevertheless, the following conclusions concerning nonpregnant female sea otters in our samples are indicated. (1) Females accompanied

by young do not enter estrus. (2) Even if the pup is lost, estrus may be delayed until after evidence of parturition (lactation, placental scar, or corpora albicantia) has disappeared or nearly disappeared. (3) In fall there is a maximum number of nonpregnant animals in the population, since many females are accompanied by young born in spring and summer. (4) Because the percentage of proestrous and estrous animals in the nonpregnant population is small, it is indicated that impregnation takes place soon after the onset of follicular activity.

With the probability of a sampling bias toward a high frequency of pregnant animals in mind, it may be considered that more than one-third and probably at least half of the sexually mature female population is always nonpregnant (fig. 91). This coincides with general observations that the mother sea otter cares for her pup for about a year. When she separates from her young, she may become pregnant and give birth again about 2 years after the prior parturition (see analysis by Chapman that follows).

The period between normal separation of the mother from the young and the onset of estrus is unknown. If this period is long, the period between births may be longer than 2 years. That the period between separation from the young and the onset of estrus may be extended is indicated by the observation that ovaries were inactive in females which were multiparous but not lactating or accompanied by a pup and showed questionable evidence (indistinct recent corpus albicantia tissue and slight uterine discoloration) of having been post partum for a long time.

Rate of reproduction

The counts recorded in table 52 were made in an area favored by females (see Segregation of Sexes). Data obtained from animals killed in the Constantine Harbor to the Kirilof Bay areas reveal that among 91 animals 19 (21 percent) were males (Segregation of Sexes, table 43).

It was shown that for general purposes the sea otter sex ratio may be considered 50:50 (see Sex Ratio). If 21 percent of the animals in the field counts were males (from table 52: $2,114 \times 0.21 = 444$ males, $2,114 - 444 = 1,670$ females; males and females in total population = $1,670 \times 2 = 3,340$ independent male and female;

$3,340 + 537$ young = 3,877; $\frac{537 \times 100}{3,877} = 14$ percent, i.e., young to independent animals 14 percent dependent young) then the mean annual percent of young in the entire population is 14

percent. Since the young sea otter remains with its mother for about a year, the annual rate of reproduction is 14 percent, or about 16 young born per 100 independent animals per year.

From Chapman's analysis (see later section) it is shown that each 100 adult females in the breeding population produce 50 young per year. Thus, in the adult population (male and female) there are theoretically 25 dependent young per 100 adults of both sexes. It was calculated that 31 percent of the independent animals observed during field counts are juveniles. Thus, 69 percent of those observed are adults. It follows that, with a group of 69 adults there are 17 (i.e., 25 percent) dependent young, or—

	<i>Number</i>	<i>Percent</i>
Dependent young	17	14.5
Independent animals:		
Juveniles	31	26.5
Adults	69	59.0
Total	117	100

Information from reproductive tracts, from field counts of dependent and independent animals, and the ratio of males to females in the kill are used in two ways to demonstrate that the annual rate of reproduction of the Amchitka population is about 14 to 15 percent.

Twinning

Barabash-Nikiforov (1947, p. 98) and Snow (1910) report observations of mothers with two young, and reproductive tracts containing two fetuses. Our observations indicate that twinning is unusual. In 278 reproductive tracts taken in 1954-63, 178 of which showed an indication of pregnancy, no twin fetuses were found. One specimen (No. JEB 63-166) taken at Amchitka on 25 March 1963, had well-defined corpora albicantia in both ovaries and darkened scar tissue (placental scars) in both uterine horns. This female was not, however, accompanied by young.

That activity in both ovaries is not necessarily an indication of twinning was shown by one specimen (ADFG 515). Both ovaries contained well-defined corpora lutea but only the left uterine horn contained a conceptus.

In early April 1955, a female and two large young (each about 18-20 lb.) with her were captured on shore at Amchitka. They were held in captivity and liberated at the Pribilof Islands. During the days that the three animals remained in captivity, the adult allowed both young to nurse. She appeared equally permissive to both. She groomed only one of the pups, however, and when the

three were liberated together, she ignored one and took on her chest the one she habitually groomed. It was our conclusion that the deserted pup was an orphan toward which this mother exhibited tolerance.

Large young, still dependent on their mothers, will frequently play together for long periods while their mothers are diving for food. If one mother should desert her young at such a time, it is possible that an association such as we observed could occur. Although it is possible that a mother may bear twins, I believe it is doubtful that a mother could feed and groom and successfully bring two young to the stage of independence.

In the northern fur seal (*Callorhinus ursinus*) which, like the sea otter, normally bears one young at parturition and is highly specialized to marine existence, twinning is rare. Peterson and Reeder (1966) summarize data derived from Fiscus, Baines, and Wilke (1964) demonstrating the incidence of twin implantation in the fur seal at 0.14 percent among 4,223 pregnant females examined. In spite of the observation that the young fur seal appears less burdensome to its mother than the young sea otter, no evidence exists to date that a fur seal can successfully raise twins to weaning age (Peterson and Reeder, 1966).

Length of Stages of the Reproductive Cycle

Dr. D. G. Chapman, Chairman, Biomathematics Group, Laboratory of Statistical Research, Department of Mathematics, University of Washington, studied the data obtained from female reproductive tracts and prepared the following analysis:

Analysis of fetal weight data; The procedure of Huggett and Widdas (1951) is used to estimate the fetal growth velocity and hence the length of the growth period. Table 53 shows the data of table 50: fetuses classified by weight classes according to time of collection reduced to a percentage basis.

The last row in the table is obtained by (1) calculating an unweighted mean of the mean weights in the three periods; (2) finding the cube root of this mean.

The use of percentages in the table and the unweighted means in the

TABLE 53.—*Percent of fetuses in each weight class*

[This table is derived from data in table 50]

Time of collection after July	Class 1	Class 2	Class 3	Class 4	Class 5
1 month.....	31	15	15	38	0
3 months.....	18	12	22	35	12
7 months.....	0	0	22	33	44
Mean time in months after July.....	1.7	1.9	4.0	3.5	6.1
Mean of cube root of weight.....	0.74	2.21	3.27	7.18	11.45

calculation are necessary to give equal representation to all times of the year. A regression line fitted to the cube root of the weights against the mean time in months give a regression coefficient of

$$a=2.292 \text{ per month}$$

or on a daily basis

$$a=0.076$$

This is an estimate of the specific growth velocity of Huggett and Widdas (1951). In view of the very small samples obtained over all parts of the year except the January to April period, it is subject to considerable sampling error and it seems reasonable to round the estimate to 0.08. While this growth velocity is somewhat below the value calculated for the European river otter, it is quite close to values calculated for the northern fur seal (0.085 has been calculated by Chapman, unpublished manuscript).

If 1850 g. is used as an average fetal size at birth, the estimated period of fetal development after establishment of the fetus is,

$$\frac{\sqrt[3]{1850}}{.08} = \frac{12.3}{.08} = 154 \text{ days}$$

or approximately 5 months.

It is also necessary to estimate the length of the gestation period during which the blastocyst is unimplanted. From table 54 we have the numbers and percentage of pregnant animals with an unimplanted blastocyst and a conceptus during the four seasons.

It might be argued that lesser weight should be given to the two shorter periods, January to February and March to April. If the results of these two periods are averaged, and this average is incorporated into an overall unweighted average, the result is essentially the same. (The average so computed would be 61 percent versus the 60 shown in table 54.)

It thus appears that the period during which the blastocyst is unimplanted is half as long again as the implanted period, or about 7½ months. The full gestation period will also include the period required for establishment of the embryo, i.e., the period before linear growth is established. Huggett and Widdas (1951) indicate a rough procedure to estimate this but it is not known whether their values apply to animals that exhibit delayed implantation. If about ½ month is allowed for this period, it follows that the estimated total length of the period of gestation is about 13 months.

The period during which the female sea otter is not pregnant (lactating and resting period) can be estimated similarly from the data from table 47. This table shows that the percent nonpregnant in the four periods noted is 30, 30, 48, and 73, respectively. In this case the weight to be given to the two first periods does make a difference. The average of the four percentages is

TABLE 54.—*Frequency of unimplanted and implanted pregnancy, by season*

[Data from table 47]

Sample period	Number animals with unimplanted blastocyst	Number animals with conceptus	Percent unimplanted
January, February.....	35	26	53
March, April.....	49	49	50
May-August.....	4	9	31
September-December.....	6	0	100
Unweighted average.....			60

45, while the average of the three seasons, if January, February, March, and April are pooled into one value, is 50.

If the length of the gestation period is about 13 months, the first average above, i.e., 45 percent, would imply an 11-month period for lactation and resting and a 2-year total cycle. The other average, 50 percent, would imply a 13-month lactation and resting period or a total 26-month cycle. This seems less probable, though it could be the average of a breeding group in which some proportion of the animals miss being impregnated at the first opportunity after the end of lactation and thus lengthen the average cycle. It is also possible that the estimates of the length of the gestation period are high due to sampling errors and that both gestation and lactation plus resting periods are 12 months in length.

It thus seems that the best estimates available at present are as follows:

Lactation plus resting	11-12 months.
Unimplanted period	7-8 months.
Implanted fetus	4½ to 5½ months.
Gestation period	12-13 months.
Total length of reproductive cycle	2 years.
Average birth rate mature female	0.50.

IMPLICATION OF OTHER OBSERVATIONS

Recruitment and mortality rate: The observations on the proportion of primiparous animals among pregnant animals (17 percent, table 48) taken together with the 2-year cycle indicates that the recruitment rate among mature females is 0.085 per year. If the mature female herd is nearly stable in size, this will also be the mortality rate of this component of the population. This is relatively low but only slightly lower than the corresponding rate among fur seals.

Proportion of juveniles and length of juvenile stage: If 50 percent of the mature females give birth each year and nurse the young animal for nearly a year (say 10 months), this implies the ratio of dependent young to mature females is $\frac{1}{2} \times \frac{10}{12}$ or 0.42. Extensive field observations (table 52, cf. also discussion) show the ratio of dependent young to independent females is $\frac{537}{1670} = 0.32$.

The independent females include both mature and juvenile animals. If it is assumed that the survival rates of both of these groups is 1-0.085 (=0.915) *after the initial transition from dependence to independence*, then a comparison of the two ratios given above shed light on both the proportion of juveniles in the herd and the length of the juvenile stage.

For denote by

Y=dependent young (of both sexes)

J=juveniles (females)

A=adults (females)

then the above two ratios are:

$$\frac{Y}{A} = 0.42$$

$$\frac{Y}{A+J} = 0.32$$

so that

$$\frac{A+J}{A} = \frac{0.42}{0.32} = 1.31 \text{ whence } 1 + \frac{J}{A} = 1.31$$

or

$$\frac{J}{A} = 0.31 \tag{1}$$

Now let J_0 = number of juveniles in their first year after dependency let n = number of years in juvenile stage

$$J = J_0 + J_0(.915) + \dots + J_0(.915)^{n-1}$$

$$= \frac{J_0}{1-.915} (1-(.915)^n)$$

Also $A = J_0(.915)^n + J_0(.915)^{n+1} + \dots$

$$= \frac{J_0(.915)^n}{1-.915} \tag{2}$$

so that

$$\frac{J}{A} = \frac{1-(.915)^n}{(.915)^n} \quad \text{or from (2)}$$

$$0.31 = \frac{1}{(.915)^n} - 1$$

$$1.31 = \frac{1}{(.915)^n}$$

or

$$(.915)^n = \frac{1}{1.31} = .763$$

Whence $n = 3$ years approximately. This is the estimated length of the period between the end of dependence and maturity for females.

SUMMARY AND CONCLUSIONS

1. It is indicated that breeding activity reaches a peak in fall, but breeding activity was observed in all seasons.
2. Unimplanted gestation is estimated to last for 7 to 8 months.
3. Implanted gestation is estimated to last for $4\frac{1}{2}$ to $5\frac{1}{2}$ months.
4. The total gestation period is estimated to last 12 to 13 months.
5. The period between births, i.e., total length of the reproductive cycle, is about 2 years.
6. The average annual birth rate among mature females is 50 percent.
7. Parturition occurs in all months, but a minority of births occur in fall and winter months. Parturition reaches a peak in summer, and large fetuses occur with greatest frequency in summer.
8. Dependent young occur with greatest frequency in fall and with least frequency in late winter and early spring. In fall, unimplanted pregnancy reaches greatest frequency.
9. Birth normally occurs on land.

10. Caudal and cephalic presentation of the fetus occurs with about equal frequency.
11. Twinning is possible but rare, and if twins are born there is no evidence to show that both survive.
12. Females accompanied by young or showing positive evidence of parturition do not normally enter estrus.
13. Low frequency of estrous and proestrous females among nonpregnant females at all seasons indicate that impregnation occurs soon after the onset of follicular activity.
14. Annually 17 percent of the pregnant animals are pregnant for the first time and 83 percent are multiparous.
15. Pregnancy occurs with equal frequency in each uterine horn.
16. The annual rate of reproduction in the total population is estimated to be about 14 to 15 percent (i.e., about 16 young born per 100 independent animals of both sexes and all ages).
17. It is estimated that the female sea otter reaches sexual maturity at age 4 years (3 years after becoming independent).

Reproduction in the Male

Observations of courtship behavior in all seasons and the occurrence of newborn young in all months indicate that male sea otters may be sexually active at any season.

A preliminary histological study of testes was made of 40 sea otters taken in the January to April period in 1958, 1959, and 1962. These specimens indicate that spermatozoa are produced when the testes attain a weight of about 13 to 14 g. Spermatozoa are probably not produced by animals having a body weight of less than 50 lb., but most of those weighing 55 lb. and all of those weighing 60 lb. or over may produce spermatozoa.

Dr. Edward C. Roosen-Runge, Department of Biological Structure, University of Washington Medical School, Seattle, kindly examined the histological specimens of sea otter testes and contributed the following information concerning the adult:

No quantitative evaluation was attempted. Spermatogenesis was evaluated by the stages of germ cells present. The last stage of spermatogenesis is that in which the late spermatids (with dense and elongate heads) are lining the lumen of the tubule. If an appreciable number of tubular sections were found containing this stage or stages immediately preceding it, it was assumed that many spermatozoa were liberated at this time from this testis. If many stages of spermatogenesis were found, but few of the very late ones, it was assumed that there was a slowing down or a standstill somewhere in the development of germ cells or that some periodicity occurred in the liberation of sperm.

The material examined appeared to indicate quite strongly that there was such a periodicity. All adult animals showed a germinal epithelium in a state of active production of germ cells, but not all showed an appreciable number of late stages of spermatogenesis. No animal indicated as "old," [animals having well-worn teeth were arbitrarily classified in the field as old] showed any signs of diminished sperm output; in fact, all of these animals (3) showed *many* late stages of spermatogenesis.

Two cases (62-92 and 62-228) were probably hypotrophic. Both were poorly preserved (hypotrophic testicles are commonly more difficult to preserve well). It appeared to me that these two cases are possibly significant. They may indicate either a fairly high percentage of males with degenerative testicles and consequently low fertility, or they may indicate a periodicity in the spermatogenic activity which would appear more pronounced when specimens taken throughout the year are investigated. Both hypotrophic testicles showed hypotrophic Leydig cells.

The Leydig cells of the normal, adult sea otter testis appear to be aggregated in huge masses around the rete channels and almost form an "endocrine organ" in this location. From there, long strands of these cells penetrate into the septa, usually in very close apposition to thin-walled veins. The rete itself is fortified very strongly with a coarse network of collagenous fibers. The general structure of the seminiferous tubules is entirely typical for mammals.

One conclusion that appears justified on the basis of the testes examined is that the production of spermatozoa in the sea otter exhibits a mild or modified periodicity. There is no indication that a distinct seasonal periodicity in sperm production exists, as in many distinctly seasonal breeders, or that there is continuous production of sperm as in the rat. A comprehensive study of reproduction in the male sea otter remains to be done.

LIMITING FACTORS

The sea otter is highly specialized to occupy a limited aquatic environment. The feeding habitat lies between the beach and the 30-fathom curve. Its specialized characteristics which confine it to this inshore area offer both advantages and disadvantages to its survival. The advantages are that it may usually find shelter from violent storms and that its prey species, unlike the wandering populations of the pelagic prey organisms of other marine mammals, are localized. A disadvantage, though, is that population growth and expansion of range may be hindered and a local population, isolated by broad expanses of deep water, may overutilize food resources. In times of stress, a large isolated population may suffer heavy mortality caused primarily by starvation.

The sea otter's natural enemies are few. Depredation by man and natural attrition resulting from overutilization of food resources are the mortality factors that limit population size.

Mortality among sea otters was studied during the winter-spring period of environmental stress only at Amchitka Island. In other seasons, different areas were visited and an effort was made to find beach remains that would give an indication of the magnitude of winter-spring mortality.

Amchitka differs from most areas inhabited today by sea otters. It and the other densely populated Rat Islands are isolated from other areas of sea otter habitat by broad, deep passes and the whole island group is densely populated. Emigration of otters from Amchitka appears to be insignificant. Emigration from a crowded population at Kanaga Island was observed (see Distribution and Numbers). Unfortunately, this island is difficult for biologists to reach and no observations of mortality there are available.

The Shumagin and Sanak Islands groups, which I visited, have relatively small otter populations in proportion to available feeding habitat when compared to Amchitka. The observations obtained from these three areas are presented.

Natural Mortality

Data are not available to indicate exactly when the regular annual occurrence of considerable late-winter, early-spring mortality among sea otters on Amchitka Island began. Natives who trapped foxes there in 1938-39 reported that "many" dead sea otters were found on beaches in that winter. Between 10 July 1939 and 15 January 1940, however, a careful search revealed only six skeletons on beaches (Loy, 1940). Sea otter wardens J. B. Mangan and G. Ritter, who were on Amchitka from 1 February to 5 September 1940, reported salvaging only "two sea otter skins and skeletons" (Amchitka Island Report, September 5, 1940, U.S. Fish and Wildlife Service files, unpublished).

During the years that Amchitka was occupied by military forces, 1941-47, no reports of unusual sea otter mortality were made. V. B. Scheffer and I visited Amchitka on 12 November 1947 and recorded (field notes) that in walking about 4 miles of beach we found the remains of six sea otters. At the time we attributed these deaths to military personnel occupying the island, two of whom we saw target practicing along the beach. Only a fraction of the beaches where dead sea otters were found in subsequent years was examined.

In the light of later experience on Amchitka, I am inclined to believe, on the basis of what I saw on that one day in 1947, that considerable natural mortality occurred in the winter-spring period of 1946-47. In the late-winter, early-spring period of 1948, Elmer Hanson, a civilian employed by the Army on Amchitka, estimated that more than 100 otters died on Amchitka beaches. Jones and Hanson recorded 124 dead otters on the beaches in the late-winter, early-spring period of 1949 (Jones, R. D., narrative reports of 1 January to 30 April and 1 July to 30 August 1949, unpublished). Both Jones and Hanson spent much time on Amchitka during or after World War II. Neither remembers observing a significant number of dead otters on beaches before 1948. Thus, it appears that an annual late-winter, early-spring "die-off" began in the late 1940's. All available counts and estimates are shown in figure 95. An analysis of observed mortality from 1955 to 1963 at Amchitka is presented in the following pages.

Studies conducted 1955-63

During the 1955-63 study period, I repeatedly surveyed the same beaches that were searched for dead otters by previous observers. The majority of moribund otters haul out above the high

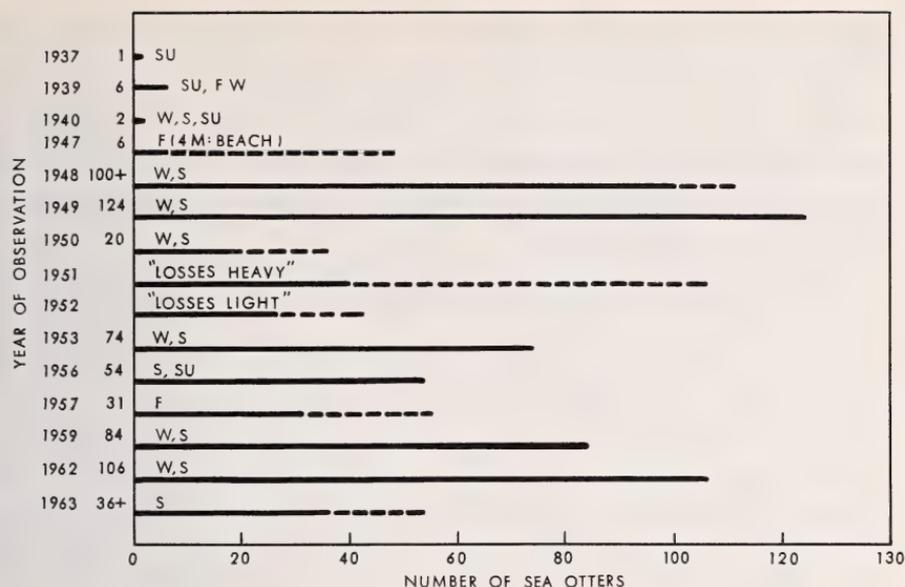


FIGURE 95.—The counts (solid line) and estimates (broken line) of dead sea otters on Amchitka beaches indicate the order of magnitude of annual mortality. Except for the counts of 1949, 1959, and 1962, the figures are only roughly comparable. The information was obtained from unpublished reports in Fish and Wildlife Service files: 1937, C. L. Loy and O. A. Friden; 1939, C. L. Loy; 1940, J. B. Mangan and G. Ritter; 1947, V. B. Scheffer and K. W. Kenyon; 1948, E. C. Hanson; 1949, 1950, 1953, R. D. Jones; 1956, 1957, 1959, 1962, K. W. Kenyon; 1963, J. E. Burdick; and from Rausch (1953). The season of observation is indicated as follows: W=winter; S=spring; SU=summer; and F=fall. In no case were all beaches searched regularly. Counts were obtained mainly on the southeastern half of the island. This data is useful only in illustrating the relative magnitude of mortality in different years.

tideline and die on shore. Dead sea otters float and if they die in the water they usually wash ashore. Thus a high percentage of those that die in study areas may be found if beaches are searched systematically and frequently.

To study annual mortality as a factor in population dynamics, and to ascertain its magnitude and understand its causes, I made an effort to gather comparable mortality data during five trips to Amchitka.

Methods of study

Certain beaches on the eastern half of Amchitka were searched systematically. Observations are available for each month of the year. Most dead otters were on or near favorite hauling-out

beaches. Other accessible beaches in the study area were searched periodically but less intensively than the favored hauling-out areas.

Each dead animal was autopsied. Specimens—including skins, skulls, bacula, reproductive tracts, stomachs, and organs appearing pathological—were preserved when practicable. The extent of decomposition determined the amount of information and specimen material that was obtained.

Because it was important to determine the period of greatest mortality, it was necessary to ascertain the usual progress of decomposition, and to estimate the approximate time of death of animals that had been dead for varying periods. Up to a point, this procedure was useful. The time of death for skeletal remains found in midsummer, however, could be placed only to the previous winter-spring season. During periods of high mortality the beaches were searched weekly. Thus, the week of death was known for many animals and the month of death for others. Data for otters that had been dead for more than $\frac{1}{2}$ to 2 months were recorded, but because of uncertainty most of these records were excluded from those aspects of the study which required more exact data. Each carcass was removed from the beach after needed data were recorded and specimens taken from it.

Average daily air temperatures in winter infrequently exceed 36° F., and spring and fall average daily air temperatures above 49° F. are unusual. For this reason, otter carcasses decompose slowly on Amchitka beaches. The study was complicated when scavengers (Bald Eagles and rats (*Rattus norvegicus*)) mutilated carcasses, sometimes preventing the gathering of certain data.

Results

Between July 1955 and April 1963, approximately 15 months were spent on Amchitka. During six study periods, a total of 331 dead otters found on the beaches were examined. Because data from certain individuals were incomplete, these are eliminated, where appropriate, from the following discussions of different aspects of mortality.

THE TIME OF MORTALITY

It would be ideal, in a study of sea otter mortality, if data could be gathered during some period of consecutive months for several years. This could not be done, so the data from various seasons in different years were used to present a composite picture of the annual cycle of mortality. The mortality study included parts

of different seasons during the six field study periods. Two seasons, 1959 and 1962, included the entire period of greatest mortality.

Data gathered in midsummer presented fragmentary evidence of the magnitude of mortality that occurred in the preceding winter-spring period. Natural decomposition of dead otters, storm waves that sweep high onto beaches, and scavengers scatter, bury, and break up skeletal remains. By midsummer of 1955, little skeletal material remained on beaches to indicate the extent of mortality that I observed briefly in late March and early April of that year.

Available data indicate that maximum mortality among sea otters at Amchitka occurs annually during the winter and early spring (fig. 96). At this time of year the Aleutians are subject to frequent and often violent atmospheric storms, and also prolonged periods of high seas. In 1962, moderate weather conditions prevailed from mid-January to mid-February and mortality up to that time was insignificant. From this time on, weather conditions were stormy. Mortality increased rapidly after 20 February and remained high until 25 March. A search of all study areas during the last week of March revealed only three freshly dead otters (fig. 97).

In 1959, late winter and early spring were less stormy than in 1962. Appreciable mortality did not occur until early March, but it continued at a high rate until mid-May. During the intensely stormy 1962 season, 106 dead otters were found in only 2 months on the same beaches where 84 dead otters were found during the comparatively mild 1959 season (fig. 96). Thus, it appeared that the magnitude and the time of greatest mortality varied in accordance with the stresses exerted on the animals by the environment.

AGE-SPECIFIC MORTALITY

No technique is known by which the chronological age of a sea otter may be determined. On the basis of body size, suture closure, and dentition, however, certain age classifications are roughly indicated. In this discussion I will distinguish only between immature and adult animals. Table 55 summarizes available data, and indicates that immature otters (fig. 98) constitute about 70 percent of the average annual mortality. Among adults, most of those found dead or dying show signs of aging (fig. 99), such as grizzled pelage and severe dental attrition.

The juveniles weigh from about 10 to 30 lb. and are still in the company of their mothers when the winter period of storms begins. Large juveniles, although capable of obtaining food by

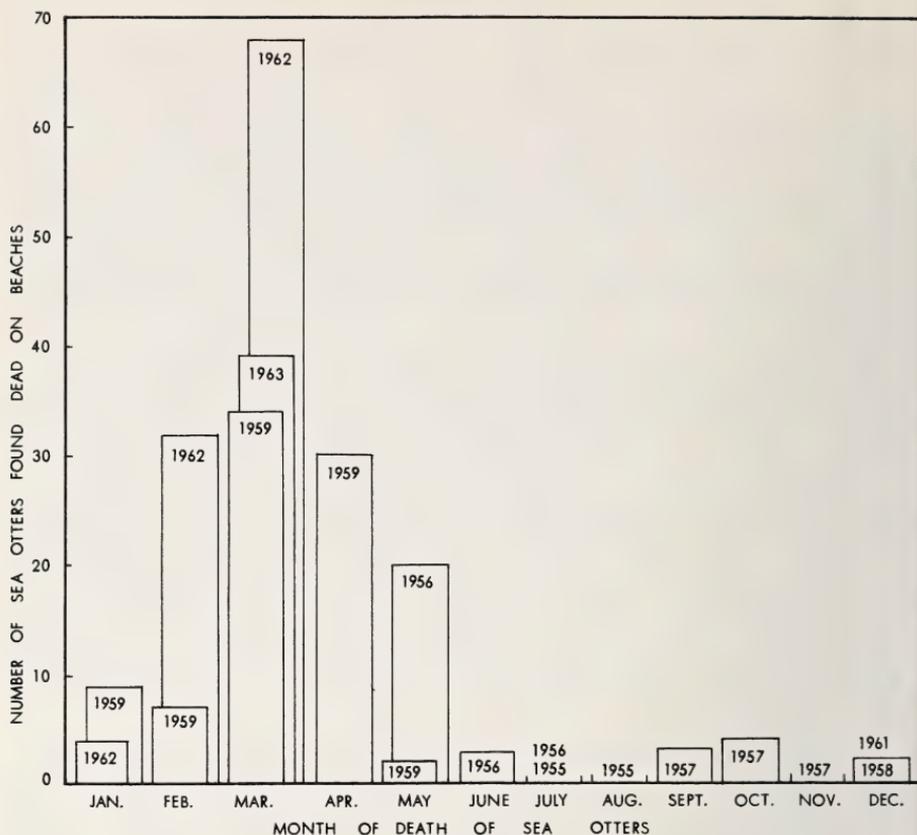


FIGURE 96.—Observed mortality of sea otters at Amchitka Island, 1955–63. Each bar represents the number of otters that were found dead and were estimated to have died in the indicated month and year. Otters dead so long that the month of death could not reasonably be estimated are excluded. Data from 259 dead otters were used in this graph. No freshly dead otters were found in June, July, or August of 1955, in July of 1956, or in November of 1957.

diving, habitually beg for and receive food from the mother. The result of this behavior is that mothers are unable to obtain sufficient food for themselves and their large offspring during periods when heavy seas render food gathering difficult. For this reason, many mothers desert their large young at this season of stress. Deserted juveniles were seen searching and screaming for their mothers in the late-winter, early-spring period.

For example, a mother and a pup, weighing about 12 lb. (5.4 kg.), were captured together and tagged on 15 February 1962. When released they swam off together. Both appeared thin but in normal health. On 18 February, the juvenile was found wander-

TABLE 55.—Mortality of sea otters, by age and sex, at Amchitka Island, Alaska, 1956-63

[Certain specimen records are eliminated from this table because inadequate data or specimen material were available]

Observation period	Juvenile						Adult										
	Males		Females		Sex?		Total		Males		Females		Sex?		Total		
	Num-ber	Per-cent	Num-ber	Per-cent	Num-ber	Per-cent	Num-ber	Per-cent	Num-ber	Per-cent	Num-ber	Per-cent	Num-ber	Per-cent	Num-ber	Per-cent	
5 May-26 July 1956	21	39	7	13	10	18	38	70	7	13	3	6	6	11	16	30	54
10 October-11 December 1957	3	10	2	6	10	30	15	48	9	29	—	—	7	23	16	52	31
21 January-20 May 1959	26	31	16	19	10	12	52	62	21	25	9	11	2	2	32	38	84
19 January-4 April 1962	51	48	23	22	7	7	81	76	10	9	15	14	—	—	25	24	106
10 March-12 April 1963	13	36	12	33	9	17	34	94	1	3	1	3	—	—	2	6	36
Total	114	36	60	19	46	15	220	70	48	16	28	9	15	5	91	30	311

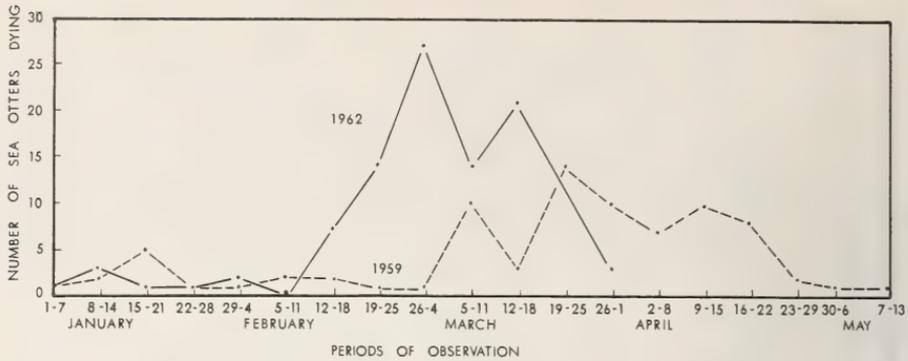


FIGURE 97.—Mortality of sea otters at Amchitka Island during weekly intervals through periods of high mortality in 1959 and 1962.

ing about alone, crying, very weak, and near death from starvation. The mother was found dead on 19 March. It might be concluded that even after deserting her pup, she was unable to regain the strength she sacrificed during storms while attempting to meet the food demands of both herself and her pup. Another pup (weighing about 17 lb., 7.7 kg.) was captured, tagged, and released together with its mother on 27 February 1962. The pup was found dead and emaciated on 5 March.



FIGURE 98.—A moribund juvenile sea otter. During the late winter and early spring season of stormy weather starving juveniles haul out on shore and die. Enteritis is usually a terminal symptom. This animal illustrates the final comatose stage that occurs shortly before death. Amchitka Island, 26 February 1962. (KWK 62-17-22)



FIGURE 99.—This aged male sea otter sought escape from a high wind in a sheltered cove. It was in a final stage of starvation, appeared to be blind or nearly blind, and showed severe dental attrition. Most adults found dead exhibited similar symptoms of aging. Amchitka Island, 26 February 1962. (KWK 62-17-3)

Small helpless pups are present in the Amchitka population at all seasons. They were, however, seldom found dead on beaches. Two were found in 1959 and two in 1962. Three reasons are suggested to explain why few are found dead. (1) Mothers habitually give more care and attention to small pups than to large juveniles. (2) Small pups require comparatively little food and mothers are able to supply their food needs without undue strain on themselves. (3) If a small pup dies it is retained by the mother until it becomes saturated with water. When she finally deserts the body it may sink and not be found on the beach.

Among captive otters we observed that when a mother otter is given a reduced ration of food she steals food from her pup. This behavior suggests that when stormy weather and reduced prey populations make it difficult to obtain sufficient food for herself and her pup, she deserts her large juvenile at an earlier age than she would during moderate summer weather when food gathering is less difficult.

Among animals found dead, the percentage of juveniles in the different study periods varied from 48 to 94 percent. Mortality

data obtained in summer, fall, and early winter are not directly comparable with data obtained in late winter and early spring. Between 1 October and 11 December 1957, 48 percent of the remains found were juveniles. The remains of most dead animals were judged to have lain on beaches since the previous winter-spring period. Only seven were judged to have died in September or later. There is a greater probability of finding remains of adults because they are more durable than remains of immature animals. The skeletons of juveniles, unless in sheltered locations well above tide line, suffer environmental attrition more rapidly than the harder bones of adults. Six months or more after the mortality period, remains of many juveniles had disintegrated and were not among the bones still on beaches. This probably explains why juveniles did not predominate.

In 1963, when juveniles composed 94 percent of the dead animals, the study period was 10 March to 12 April. The data from 1962 indicate that mortality among adults may increase as the period of high mortality advances (fig. 100). In January and February 1962, before the height of the mortality period, adults constituted 16 percent of the animals that died. During and after the period when the mortality reached its peak in March, 39 percent of animals that died were adults. This might indicate that adults are better able to withstand environmental stresses than immature animals recently separated from mothers. In 1963 the period of greatest adult mortality may not have been included in the study period, and a disproportionately high mortality of juveniles was indicated by the available data. The 1959 data show, however, that the mortality among adults may, in some years, be high throughout the period of increased mortality (fig. 101).

The 1959 and 1962 study periods are the only two which spanned entire periods of greatest annual mortality (fig. 97). Therefore, the proportion of juveniles (60 and 75 percent, respectively) to adults is probably more representative of the usual mortality pattern.

SEX-SPECIFIC MORTALITY

More males than females were found dead on beaches. Among juveniles, the disparity was greater than among adults. Rausch (1953) noted in his 1951 and 1952 investigations that "the heaviest mortality occurred . . . in subadult males." The raw data from the remains I examined, however, tend to exaggerate this difference. The accurate determination of sex by the examination of juvenile skulls or other bones is perhaps impossible. If a carcass was

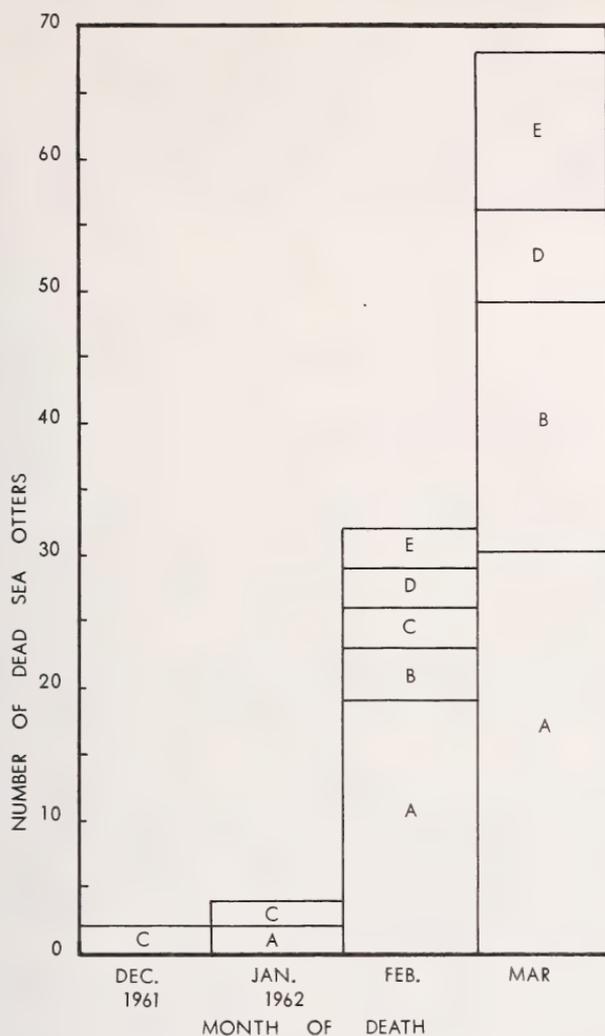


FIGURE 100.—Age and sex of sea otters dying in the winter-spring period of 1961-62. *A*—juvenile male; *B*—juvenile female; *C*—juvenile, sex unknown; *D*—adult male; *E*—adult female.

mutilated by scavengers and the reproductive organs removed, the sex of the animal was in question. On partially mutilated carcasses, the likelihood that a male might be identified was greater. Eagles, for example, usually remove the viscera first. The genitalia of the females are easily taken, but the baculum of the male is attached to the ischium by a strong ligament composed of the ischio- and bulbo-cavernosus muscles. These parts may remain attached to the skeleton, identifying it as a male for weeks longer

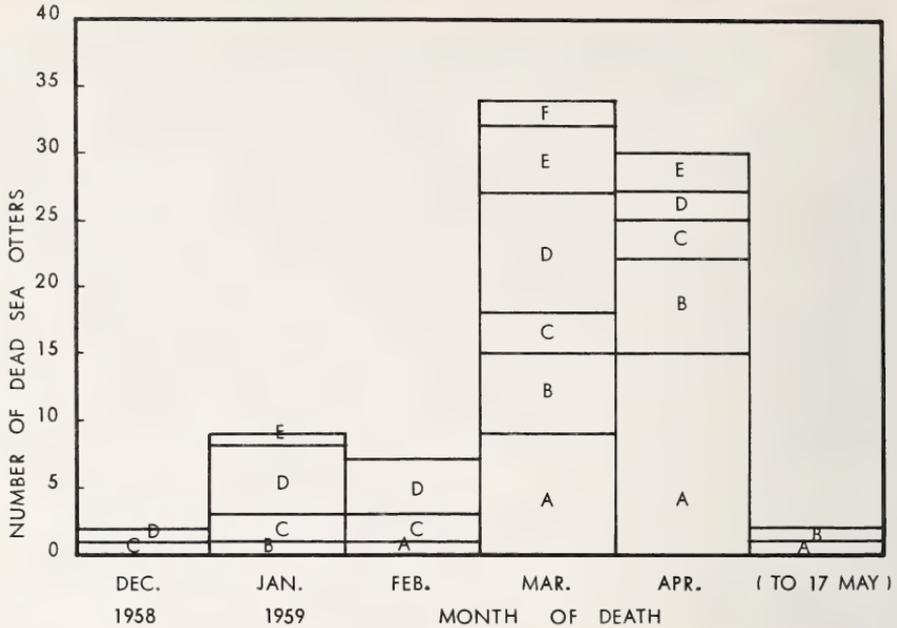


FIGURE 101.—Age and sex of sea otters dying in the winter-spring period of 1958-59. A—juvenile male; B—juvenile female; C—juvenile, sex unknown; D—adult male; E—adult female; F—adult, sex unknown.

than a female may be identified. Because of this situation and to avoid a bias in favor of males, only the freshly dead beach specimens found in 1959, 1962, and 1963 are listed to give the best available indication of the sex ratio of otters dying during the period of environmental stress (table 56).

Among 117 juveniles examined on beaches in the three seasons, 58 percent were males. In 1963, the sex ratio was 50:50, but in this year the field study was abandoned while the high mortality period was probably still in progress and the results may not be representative.

That males are not as hardy as females was repeatedly demon-

TABLE 56.—Age and sex of otters found freshly dead on Amchitka beaches

Year	Juvenile				Total number	Adult				Total number	Grand total
	Males		Females			Males		Females			
	Number	Percent	Number	Percent		Number	Percent	Number	Percent		
1959.....	21	57	16	43	37	13	68	6	32	19	56
1962.....	36	62	22	38	58	8	38	13	62	21	79
1963.....	11	50	11	50	22	1	50	1	50	2	24
Total.....	68	58	49	42	117	22	52	20	48	42	159

strated when both sexes were held captive under the same conditions. A similar situation was suggested in the northern fur seal. Chapman (*in* Abegglen, Roppel, and Wilke, 1960) estimated that in the first 3 years of life females outsurvived males by a ratio of 2 to 1. Studies since then indicate that the ratio may be only 1.25 to 1 in favor of females (Chapman, unpublished manuscript).

MORTALITY FACTORS

Physical characteristics and food supply

The terminal conditions observed in a high percentage of otters found dead on Amchitka beaches are emaciation and hemorrhagic enteritis. Enteritis may, however, occur in the final hours before death after other conditions have doomed the animal.

Sea otters found dead on beaches during the late-winter and early-spring period of high mortality may be divided into two primary groups: (1) Those whose death was apparently caused by an injury in rough seas, or disease, and (2) those which showed evidence of starvation and finally exhibited symptoms of enteritis. Many dead animals cannot be placed positively into one group or the other. An emaciated and weakened animal is more subject to injury by large breakers than a strong one. An animal obviously killed by an injury might have died soon of starvation.

The actual cause of death of many animals cannot be determined because of decomposition. Table 57 lists observed conditions which may have caused death of otters that might be considered to be in group (1) above. The section "Parasites and Miscellaneous Diseases" gives additional data on mortality recorded by Dr. Robert L. Rausch in 1952 and more detailed information on several specimens that were examined in the laboratory.

The dead animals which fall into the second group are of the greatest interest from the point of view of population studies. Most of these may be separated into two age groups: (1) Juveniles, many of which approach subadulthood and, (2) old animals having worn teeth and often showing other indications of advanced age, such as gray pelage about the head, chest, and abdomen, and impaired vision caused by injuries or senile cataracts. In the 1959 study period a particular effort was made to record pertinent data from 83 individual otters found dead on beaches. The information is summarized in table 58.

Juveniles and old adults had two characteristics in common at death. Both lacked body fat and both showed a high incidence of defective teeth. In the case of the young animals, 50 percent ex-

TABLE 57.—*Abnormal conditions found in sea otters that died on beaches of Amchitka Island, Alaska*

Collection number	Age	Sex	Date	Condition
59-68	juv.	♂	15 Mar. 1959	Fractured skull.
59-92	ad.	?	29 Mar. 1959	Bruised head.
36-56	juv.	♂	31 May 1956	Bruises, blood clots around head and neck.
B20-57	juv. (pup)	♂	30 Oct. 1957	Broken neck.
59-3	juv.	♀	26 Jan. 1959	Nondraining abscess dorsally in neck and head.
47-56	juv.	♀	17 June 1956	2 broken ribs.
59-73	juv.	♀	14 Mar. 1959	Extensive body bruises and swellings.
59-49	ad.	♂	5 Mar. 1959	Body bruises perforated intestine.
59-100	ad.	♂	31 Mar. 1959	Internal hemorrhage—quantity of blood in abdominal cavity.
59-155	juv.	♀	6 May 1959	Perforated intestine and intussusception of small intestine.
44-56	ad.	♂	11 June 1956	Bruises in genital area.
59-34	ad.	♂	20 Feb. 1959	Bruised penis.
62-241	ad.	♂	12 Mar. 1962	Penis swollen and extruded.
59-130	ad.	♀	17 Apr. 1959	Uterine cyst 180 × 50 mm.
D7-57	ad.	♀	6 Dec. 1957	Abscess in jaw, liver discolored and with abnormal adhesions. ¹
59-85	ad.	♀	25 Mar. 1959	Liver with abnormal adhesions and discoloration. ¹
59-79	juv.	♀	21 Mar. 1959	Hemorrhagic nasal passages.
59-90	ad.	♂	29 Mar. 1959	Cutaneous emphysema.
59-82	juv. (pup)	♀	25 Mar. 1959	Lungs black, pneumonia?
B12-57	s.ad. ?	♀	22 Oct. 1957	Malignant neoplasm of the intestine. ¹
59-48	ad.	♀	4 Mar. 1959	Congenital cystic kidney and edema. ¹

¹ See section on Parasites and Miscellaneous Diseases for a more detailed analysis.

TABLE 58.—*Summary of observations from 83 sea otters found dead at Amchitka Island, Alaska, 1959*

Observation	Number of juveniles	Number of adults
Total animals examined.....	48	35
Skeletal remains only found ¹	18	14
Field necropsy performed.....	27	18
Dental malocclusion indicated ²	24	14
Bone damage to jaw ³	0	13
Tooth damage (dental attrition): ⁴		
None to moderate.....	44	6
Moderate to severe.....	0	29
Lesions: ⁵		
Hemorrhagic enteritis present.....	23	11
Stomach parasite (<i>T. decipiens</i>) present.....	2	6
Possible physical injury indicated.....	12	9
Food in stomach ⁶	0	0

¹ Skulls only examined.

² In juveniles, malocclusion occurs while the permanent teeth are growing, particularly when deciduous teeth are pushed out of line. In old adults, postcanine teeth may be worn to the gum-line or to the bone.

³ When teeth of old animals are severely worn, infection of the bone and osteolysis may occur.

⁴ See Dental Attrition.

⁵ See Parasites and Miscellaneous Diseases.

⁶ All carcasses showed signs of emaciation. Body weights (particularly for adults) were abnormally low (see Body Measurements).

hibited a degree of malocclusion caused by the growth of the permanent postcanine teeth. In the early stages of eruption of the permanent teeth, the deciduous teeth are pushed upward, so that occlusion is impaired. When the deciduous teeth are finally lost, the permanent teeth are still below the level of adjacent teeth (see Dentition). Adults having poor teeth comprised 78 percent of the total found dead. The attrition of teeth appears to be another result of the reduction of soft-bodied invertebrates. Hard-shelled organisms are probably eaten to a greater degree by this crowded Amchitka population than in less densely populated areas. Animals having good teeth not only compose a minority (17 percent) of the dead adults on beaches but healthy adults spend less time on shore (as indicated by animals captured there) during periods of storm surf than do emaciated juveniles and old adults.

Weather and sea conditions

In the fall of 1959, the U.S. Weather Bureau began to record weather conditions in the outer Aleutian Islands. Before this time, no such records were available. Thus, during the 21 January to 20 May 1959 study period I kept a daily record of weather conditions. These data demonstrated that the increased mortality coincided with the period of greatest storm activity.

Complete weather records are now available for the years after 1960. These data were recorded at Shemya Island, which is 200 miles west of Amchitka, but radio reports of weather at Shemya received while I was on Amchitka indicated that a few hours after weather conditions were reported at Shemya similar weather reached Amchitka. The annual cycle of weather conditions in the outer Aleutians is quite uniform.

The average seasonal mortality observed on Amchitka from 1955 through 1963 and the mean monthly wind velocities recorded 1960 through 1963 are shown in figure 102. This graph demonstrates that the period of greatest mortality, when 75 percent of the annual mortality occurs, coincide annually with the period of maximum wind velocities in the late-winter, early-spring period. It also shows that the period of least mortality occurs during the summer period of minimum wind velocities. In the fall, when the season of storms begins, a slight increase in mortality occurs. Most animals, however, emerge from the summer, early-fall period in good physical condition and the mortality remains low until after a period of sustained stormy weather reaches a peak in March.

The general coincidence of high mortality and stormy weather

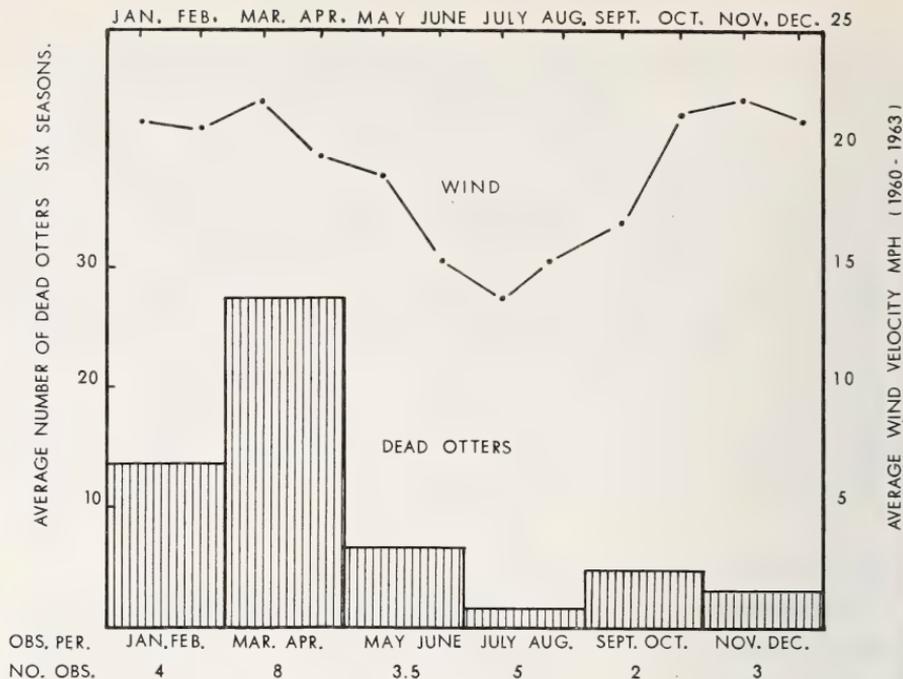


FIGURE 102.—Average seasonal mortality of 311 sea otters found dead on Amchitka beaches 1955–63, and average monthly wind velocities in the outer Aleutian Islands measured by the U. S. Weather Bureau, 1960 through 1963.

or high velocity winds was quite evident. It was also evident, however, that the wind, as such, was only indirectly responsible for precipitating mortality and that more detailed information concerning environmental stresses was needed. Therefore in 1962, between 19 January and 31 March (70 days), I kept a daily record of surf conditions and sea otter mortality for both the Bering Sea and Pacific Ocean coasts of Amchitka. Five surf conditions were recorded: calm (no surf), light surf, moderate surf, heavy surf, and violent surf.

The vast extent and great depth of the Pacific Ocean as compared to the relatively small and shallow Bering Sea creates conditions responsible for differing surf conditions on the coasts exposed respectively to these two bodies of water.

Under the force of storm winds, heavy seas may build up in the Bering Sea, but within a few hours after the passing of a storm the surf may subside and relatively calm or moderate waves may prevail.

In contrast, ground swells in the Pacific Ocean may travel to

Amchitka's shores well ahead of an atmospheric storm. Then they may continue to break violently along the exposed coast for many hours after the storm has passed. In addition, waves created by storms that fail to reach Amchitka, may break on the Pacific coast of the island. Heavy or violent wave action along the Pacific coast was recorded on 43 days during the study period, but similar conditions prevailed on only 12 days along the Bering Sea coast (figs. 103 and 104).

The data indicate that the amount of mortality that occurred in 1962 at Amchitka was related primarily to population size and available habitat. Even though the storm wave action along the Pacific coast was more intense than along the Bering Sea coast, the threshold of stresses sufficient to precipitate mortality was

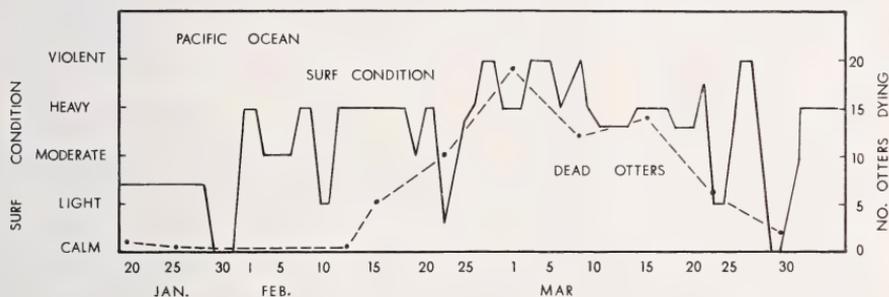


FIGURE 103.—Daily record of surf conditions and of otters found dead on the Pacific Ocean coast of Amchitka from 14 January through 30 April 1962. Partly because ground swells travel long distances in the deep Pacific Ocean, wave activity on that coast is more intense than on the Bering Sea coast (see fig. 104).

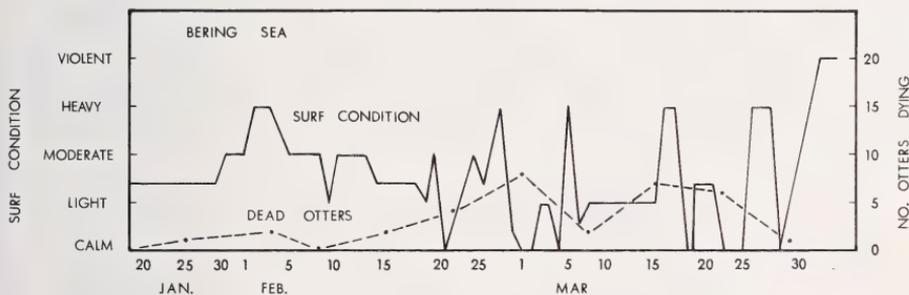


FIGURE 104.—Daily record of observed surf condition and otters found dead on the Bering Sea coast of Amchitka Island from 19 January through 30 March 1962. Surf conditions are more moderate on the Bering Sea coast than on the Pacific coast because in this relatively shallow sea ground swells do not travel ahead of storms and wave action attenuates soon after the passing of wind storms (see also fig. 103).

exceeded on both coasts. Thus, mortality occurred in proportion to the available habitat and population size rather than in proportion to the intensity of storm wave activity. About two-thirds of the available habitat, population, and mortality were found on the Pacific coast (table 59).

Although the period of heavy surf began in late January, the increasing rate of sea otter mortality did not reach a peak until the end of February (figs. 103 and 104). This is explained by the fact that the otters enter the winter with reserves of body fat and in good general physical condition. During weeks of stormy weather, those animals least able to supply their nutritional needs exhaust their physical reserve. After becoming emaciated and being subjected to continuing environmental stress, they die. Autopsies reveal that almost all animals found dead on beaches show signs of starvation in spite of the fact that their intestinal tract often contained the remains of sea urchins (see Food and Feeding Behavior).

Annual mortality at Amchitka estimated from animals found dead on beaches

Since many of the hauling-out areas on the eastern half of Amchitka were searched carefully and frequently during the period of high mortality, probably most of the dead otters in these limited areas were found. The habitually used hauling grounds constitute less than 10 percent of the shoreline on the eastern half of Amchitka. Other areas could not be searched as carefully as the areas of concentration. On several occasions, dead otters that had been buried in kelp by storm waves or carried from the beach area by eagles were found after having been missed on a previous search. A few dead otters were found well up on off-shore rocks that we rarely visited. On the basis of these and other field observations, I have estimated that at least 30 percent of the

TABLE 59.—*Sea otter mortality in relation to population counts and available habitat, eastern half of Amchitka*

	Pacific coast		Bering Sea coast	
	Number	Percent	Number	Percent
Dead otters ¹	70	66	36	34
Otter population ²	766	71	310	29
Available habitat ³	45	67	22	33

¹ Count, 19 January to 4 April 1962.

² Aerial count, 19 May 1959.

³ Square miles of water 30 fathoms or less in depth, eastern half of Amchitka. Measured from U.S. Coast and Geodetic Survey Chart 8864.

otters dying along the shores of the eastern half of Amchitka in the period of high mortality were not found. A rough estimate of the annual mortality in 1959 and 1962 on Amchitka is presented below:

	Number of dead otters	
	1959	1962
Carcasses found in winter-spring period	84	106
Estimate of carcasses not found (30%)	25	32
Estimated total mortality this period	109	138
Estimated mortality in remainder of the year (25%)	27	35
Estimated annual mortality on eastern half of Amchitka	136	173
Estimated annual mortality on western half of Amchitka (otter population 30% of eastern half, data from aerial surveys)	41	52
Total estimated annual mortality	177	225

The estimated Amchitka otter population in 1959 was about 2,080 (see Distribution and Numbers). Thus, the annual mortality there in at least two seasons was about 9 to 11 percent of the total estimated population. If, instead, the direct counts of living and dead otters are used for the eastern half of Amchitka, then the mortality in 1959 was about 8 percent ($\frac{84}{1076}$) 100 and in 1962 about 10 percent ($\frac{106}{1076}$) 100 of the population as observed in 1959.

Mortality estimates derived from reproductive tracts

The data available from other studies (see Length of stages of reproductive cycle of female sea otter, by D. G. Chapman, and Field counts of sea otters) makes possible an estimate of the mortality that occurred in the transition from the dependent stage to the juvenile stage. Since there are 50 young/100 adult females per year and since the sex ratio among young is 50:50, this implies 25 female young per 100 adult females.

Let the mortality that occurs at the end of the dependent stage be T; then

$$(1-T) \frac{Y}{2} = J_0 \text{ if females alone are considered}$$

Also

$$A = \frac{J_0 (.915)^n}{.085} \text{ from equation (2) (see "Length of stages of reproductive cycles of female sea otter," by D. G. Chapman, p. 243)}$$

so that

$$J_0 = \frac{.085A}{.766} = .111A$$

$$\therefore (1-T) \frac{Y}{2} = J_0 = .111A$$

or

$$(1-T = 2(.111) \frac{A}{Y} = .222 / \frac{Y}{A} = \frac{.222}{.42}$$

from (1) (see Chapman, as above)

whence

$$1-T = .53$$

and

$$T = .47$$

Another way of considering the same problem is as follows: Each 25 female young must survive to replace the 8.5 mortality occurring among the mature females

$$\therefore (25) (1-T) .766 = 8.5$$

$$\text{or } (1-T) (19.2) = 8.5$$

$$\text{or } 1-T = .44 \text{ and } T = .56$$

Although these are slightly different, they suggest that the transitional mortality from dependent to juvenile stage is about 50 percent. Some of this may occur during the dependent period.

Also, if the mortality among juveniles is higher than 8.5 percent this would mean the transitional mortality is slightly lower. This could also mean that the estimated length of the independent juvenile period is somewhat less than 3 years.

It should be noted that these estimates of 8.5 percent as an annual mortality, 50 percent mortality at the end of the dependent young stage, and a juvenile period of 3 years apply to females. The data do not provide comparable estimates for males.

MORTALITY ON THE SHUMAGIN ISLANDS

The outer Shumagin Islands provide interesting material for comparison with observations from Amchitka. The outer Shumagins, including Nagai and all islands lying east and west of it, are chosen because (1) A population of about 3,000 sea otters is found there, (2) it appears to offer ideal sea otter habitat, and (3) it was accessible for aerial and surface observations.

The outer Shumagins are surrounded by nearly 700 square miles of water less than 30 fathoms deep. The islands are near enough to each other to allow sea otters to move easily from one to another and near enough to other areas along the southeast coast of the Alaska Peninsula to allow population dispersion.

Between 4 and 14 June 1960, the late Tom O'Brien and I camped on Simeonof and Little Koniuji Islands. We circumnavigated Simeonof and made other dory trips to several beaches on Little Koniuji and Herendeen Islands. Also, we walked more than 15 miles on beaches. At least 80 percent of the beachline that we searched was adjacent to favorite sea otter feeding and resting areas.

We searched beaches carefully but were able to find remains of only one adult male sea otter on Simeonof and fragments of one juvenile skeleton on Little Koniuji. Both animals had been dead for several months. Considering that during aerial surveys of these same areas on 10 April 1962 we counted 549 otters, the observed mortality there was low.

Mortality observations in the Shumagin Islands and data presented in the sections on Body Measurements, Food and Feeding Behavior, and Distribution and Numbers, when compared with similar data from Amchitka, indicate that the Shumagin population (4 otters per square mile of habitat) was not overutilizing food resources as was demonstrated for the Amchitka population (19 otters per square mile of habitat) and that winter-spring starvation and accompanying mortality did not occur.

MORTALITY ON THE SANAK ISLANDS

The Sanak Islands include Sanak, Caton, and a number of small islets and rocks. The population density of this area was estimated to be about two otters per square mile of habitat (see Distribution and Numbers).

In 1960, O'Brien and I spent from 20 to 23 June exploring this area. We landed via dory on Caton Island and seven smaller islets (Leda, Wanda, Elma, Telemitz, Peterson, and Mary Islets, and Princess Rock). We searched more than 10 miles of beach and found the skeletal remains of only one adult female otter, indicating that little winter-spring mortality had occurred.

Discussion

The analysis of data obtained from two classes of populated sea otter habitat were presented. The criterion of population density was the number of otters per square mile of water less than 30 fathoms deep. It was shown that at Amchitka the population was crowded during the study period, having about 19 otters per square mile. The outer Shumagin Islands and Sanak Islands were not crowded, having respectively about four and two otters per square mile. The estimated annual winter-spring mortality at

Amchitka was 8 to 11 percent of the population (perhaps higher in certain seasons). In the areas of uncrowded population, the annual mortality was much lower. It was not calculated because too few dead otters were found.

The natural forces which control the magnitude of the sea otter population at Amchitka were a limited food supply and climate. From his observations on Amchitka, Rausch (1953) suspected that much of the annual mortality was the result of "A population that exceeded the carrying capacity of the habitat." The applicable generalization was aptly stated by Lack (1954) :

climatic factors can exert an important modifying influence in the control of animal numbers. Thus, although one may speak loosely of mortality due to climate, the actual cause of death is often starvation, which can be density-dependent.

The data presented here and in the sections on Food and Feeding Behavior and Distribution and Numbers, I believe, support Lack's statement.

The following points are the evidence that lead to the conclusion stated above:

1. The food habits studies of otters at Amchitka indicated that healthy adults, having ample body fat in the late-winter, early-spring period, fed to a large extent on fish and octopus. Sea otters at Amchitka were limited in their search for food to a relatively narrow belt of water surrounding the island where water depths do not exceed 30 fathoms (see Diving). Observations at Amchitka indicated that populations of bottom-inhabiting food species were reduced (see Food and Feeding Behavior).

2. Observations indicated that large juveniles when deserted by mothers were unable to obtain a sufficient quantity of high-calorie food species. Apparently they lacked both the skill and strength to capture and hold most fish and octopus. This may be true also of aging adults.

3. Both of these age groups were forced to obtain what nourishment they could from depleted populations of sedentary and often hard-shelled and low-calorie invertebrates. Because of the hard shells of these organisms the teeth of adult otters in the Amchitka population showed greater attrition than did those of animals from less crowded populations. The teeth of old adults were often worn to the gumline. Evidence of bone infection, which often resulted when tooth attrition was severe, was found in 72 percent of a sample of dead adults. Juveniles in the process of replacing deciduous teeth were unable to eat a sufficient quantity of the available hard-shelled organisms.

4. Both the aging animals and juveniles, forced to utilize poor quality foods, were further hindered in feeding activities by sustained periods of rough seas. Aging adults, and juveniles deserted by mothers, after exhausting accumulated summer and fall reserves of body fat, developed enteritis which is typical of that found in other species of animals under conditions of starvation and stress (see Parasites and Miscellaneous Diseases).

5. Adult otters at Amchitka weighed less than otters from less crowded populations (see Body Measurements).

6. When weakened animals exhibiting symptoms of enteritis (black feces) were captured and placed in a pool of clean water where they were furnished adequate food, some of them regained health. After they were introduced to a diet of fish, all of these captives refused to eat sea urchins and most hard-shelled mollusks. The gastrointestinal tract of similar animals that died on beaches either were empty, or contained only hard-shelled organisms.

PARASITES AND MISCELLANEOUS DISEASES

Both in the wild and in captivity sea otters are afflicted by a variety of pathological conditions. Systematic, long-term studies of pathology were not undertaken, but animals found dead or dying on beaches were examined (Rausch and Locker, 1951; Rausch, 1953) and observations of captives were recorded (Kirkpatrick, et al., 1955; Kenyon, Yunker, and Newell, 1965). Jellison and Neiland (1965, p. 8-9) list the parasites of sea otters. In the following sections these studies are reviewed briefly and additional observations are presented.

Most sea otters found dead on Amchitka Island displayed terminal symptoms of enteritis. Other pathological conditions, such as neoplastic and degenerative changes in the liver, ulceration of the jaws and alveoli of the teeth, and infections of the paws also occurred.

Internal (helminth) parasites

More than 30 sea otters found dead or in moribund condition on Amchitka beaches in 1949, 1951, and 1952 were studied by Rausch (Rausch and Locker, 1951; Rausch, 1953). The helminths recorded from these were: (Cestoda) *Pyramicocephalus phocarum* (Fabricius, 1780); (Trematoda) *Orthosplanchnus fraterculus* Odhner, 1905, *Phocitrema fusiforme* Goto and Ozaki, 1930, *Pricitrema zalophi* (Price, 1932), *Microphallus pirum* (Afanas'ev, 1941); (Nematoda) *Terranova (Porrocaecum) decipiens* (Krabbe, 1873); (Acanthocephala) *Corynosoma strumosum* (Rudolphi, 1802).

R. L. Rausch (letter, 15 Sept. 1967) states:

More recently, *Corynosoma macrosomum* Neiland, 1962, has been described from a sea otter from Prince William Sound, and a single specimen evidently representing this species had been collected earlier from the same host from Simeonof Island (see Neiland, 1962). Cestodes collected by K. W. Kenyon from sea otters from Amchitka Island have been identified provisionally as *Diplogonoporus tetrapterus* (von Siebold, 1848) (Rausch, 1964); this species also was recorded from a sea otter from Prince William Sound.

In general, these helminths probably affect the host little, if at all (Rausch, 1953). However, two species, *Microphallus pirum* and *Terranova decipiens*, were considered to be pathogenic. The cuticular spines of the former evidently cause mechanical injury to the intestinal mucosa, and, when the trematodes are abundant, severe enteritis may result. Immature specimens of *T. decipiens* frequently penetrate the intestinal wall and enter the body cavity, where other organs may be invaded. Peritonitis following such perforations may result in the death of the host.

During the 1955-63 study period, I made gross examinations of about 50 otters believed to have been in good health when killed at Amchitka. Although both *T. decipiens* and *M. pirum* were found, there were no gross lesions in the infested animals. In November of 1957, Dr. Kenneth L. Binkley examined seven adult otters at Amchitka, only one of which appeared to be in "poor" condition when captured. Only the ill animal was infested with an appreciable number of *T. decipiens* (65 worms) and *M. pirum* (many worms), but there was no sure indication that this animal's poor condition was a result of parasite infestation. Problems encountered with *T. decipiens* are discussed under "In Captivity."

In 1959 the stomachs of otters found dead on beaches were examined when possible. Among 27 juveniles, 2 contained *T. decipiens* and among 14 adults, 5 were infested. In none of the animals examined were helminths found in the coelom and no instance of perforation caused by helminths was noted. The animals, in most cases, had been dead for several days before they were examined. Peritonitis caused by perforation of the gastrointestinal tract would probably have been detected. Examination of sample areas of the small intestine revealed moderate to light infestation in some animals, but for *M. pirum* diagnosis was considered unsatisfactory because of decomposition. In addition, this parasite inhabits crypts in the wall of the small intestine and is not easily detected in gross examination.

K. A. Neiland (letter, 9 July 1962) examined the intestinal tracts of 8 adult sea otters chosen at random from 150 animals that were shot in the spring of 1962 at Amchitka. In these he found a total

of 271 *Corynosoma* sp. Infestation ranged from 1 to 98 individuals. *T. decipiens*, totaling 40 individuals, occurred in 5 of the tracts and infestation ranged from 1 to 18.

A subadult female sea otter was found dead at Patten Bay, Montague Island, by Theron Smith on 23 April 1962. The animal was estimated to have been dead for 2 or 3 days when it was received for study by Dr. Francis H. Fay. Because death apparently resulted from helminth infestation, his study of this animal (No. 27830) is quoted from his letter of 7 August 1962.

Trematoda: *Orthosplanchnus fraterculus*. Abundant in gall bladder bile ducts. Extreme fibrosis and near-occlusion of bile ducts was noted in several areas of the liver.

Microphallus pirum. Abundant in small intestine.

Cestoda: *Diplogonoporus tetraapterus*. Several large pseudophyllidean cestodes with double genital pores were present in the small intestine. A few smaller cestodes, closely associated with these, were also present and are believed to be aberrant individuals of the same species.

Nematoda: *Terranova decipiens*. Massive infection, mainly of larval worms. These had perforated the stomach in one locality and the duodenum in two. Many were free in the abdominal cavity, together with *M. pirum* and two species of *Corynosoma*. In the abdominal cavity there was about 1,000 ml. of bloody fluid with some remnants of food that evidently had oozed out of the intestine by way of the perforations. A group of nematodes was attached to the greater omentum, and several other groups had penetrated the spleen and liver. Extreme inflammation was evident in these sites even in the then decomposed tissues. All mesenteries in both the abdominal and pleural cavities were granular and inflamed. Adhesions were abundant.

Acanthocephala: *Corynosoma* sp. At least two species of *Corynosoma* were abundant in the small intestine." (These were later identified by K. Neiland as *C. strumosum* and *C. macrosomum*.)

It was apparent from the gross pathology that this animal had died as a result of its dense, infiltrating parasite population, but it was not possible to decide on which of the two most pathogenic organisms (*M. pirum* and *T. decipiens*) was primarily responsible for causing death.

External parasites

Snow (1910, p. 278) examined many sea otters and said of them "Sea-otters are particularly cleanly animals; I have never found a parasite of any description on them."

F. H. Fay (letter, 6 April 1964) said:

We have no records of Anoplura on sea otters, but on the other hand, the number of specimens examined is not great. Both Bob [Rausch] and I feel that Barabash-Nikiforov's record of two specimens of *Proechinophthirus fluctus* (= *Echinophthirus fluctus*) on sea otters probably was fortuitous. Apparently this is a common ectoparasite of *Callorhinus* and *Eumetopias* living in the same area with the otters, and it is not inconceivable that a few would occasionally be picked up by the otters. If it were a common or even uncom-

mon parasite of sea otters, you surely would have noticed it, especially in captive animals.

I have examined many sea otters and found no external parasites other than nasal mites (*Halarachnidae*). Although these are technically ectoparasites, they are found within the nasal passages. As pointed out previously (Kenyon, Yunker, and Newell, 1965), infestation of the sea otter with *Halarachne miroungae* is probably fortuitous. The only massively infected animal (over 3,000 mites) was a captive that was held under abnormal conditions in a fresh-water pool. Infestation in the wild appears to be insignificant.

Enteritis

The following discussion presents observations obtained at Amchitka Island and information contributed by M. C. Keyes, D.V.M., Bureau of Commercial Fisheries.

Enteritis is frequently observed as the terminal symptom at death in sea otters at Amchitka. It is similar to the entero toxemia found in the fur seal, harbor seal, and certain domestic animals. A *Clostridium* organism has been isolated and identified from a fur seal. Keyes (1963) uses the name necrohemorrhagic enteritis. The symptoms observed in the sea otter are quite similar to those observed in lambs and other mammals.

Symptoms exhibited by sea otters found on Amchitka beaches are listed:

1. The animal may be unable to stand or walk.
2. It may appear semicomatose or very lethargic and fearless.
3. It often exhibits hiccup-like convulsions.
4. The vibrissae may be extended rigidly forward.
5. The necropsy reveals intestinal lesions of variable extent.

Young animals may die while lesions are small, affecting 3 to 4 inches of the small intestine. The intestine is inflamed, muscle tone is lost, and affected areas become blackish or greenish black in color. In adult animals, long sections of the small intestine show this condition at death. The colon has not been specifically observed to show the extensive lesions found in the small intestine.

The small intestine and colon often contain the remains of about a dozen small sea urchins. Black tarry feces may or may not be voided before death. In young animals particularly, the progress of enteritis to death may be rapid.

6. Death may occur before the typical black fecal matter is voided. The black condition of the feces is called melena (a combination of the iron found in hemoglobin and hydrogen sulfide to-

gether produce iron sulfide, the putrefactive changes in the intestine produce the H_2S).

7. I have examined the stomachs of more than 200 otters that showed symptoms of enteritis at death. None has contained food. The stomach may contain from 10 to 50 ml. of liquid which may be pinkish, reddish brown, or yellowish. The mucosa may show inflammation.

8. Weight loss, probably caused by dehydration and starvation, characteristically accompanies enteritis. A captive juvenile male (59-159), that died showing symptoms of enteritis, lost 26 percent of its body weight in 3 days.

It appears probable that a *Clostridium* organism is present in all animals and that it becomes active when the animal is subjected to stress, such as starvation or nervous tension. Unsatisfactory conditions in captivity, such as lack of water, may cause such nervous tension. In captivity, I have observed that animals given access to an abundant supply of clear water and abundant food have not been subjected to sufficient stress to develop enteritis. As pointed out elsewhere, animals which show symptoms of enteritis when captured may recover in captivity when given abundant food and water. Stress may be caused in captivity if the fur becomes dirty and the animal is chilled. Extreme anxiety accompanies chilling, a large intake of food may occur but unless the fur condition can be improved the animal experiences stress; enteritis usually develops, and is followed in a few hours by death. In the wild, lack of nourishing food and accompanying rough, stormy seas appear to cause stress that results in enteritis and terminates in death.

Additional laboratory examination of specimen material taken from sick or dying sea otters is needed before we can attain a proper understanding of the relationship between enteritis and the trematode *Microphallus pyrum*, and the bacterium, *Clostridium*, in the sea otter.

Infection and liver degeneration

Dr. Dean Jensen, College of Veterinary Medicine, Colorado State University, kindly made a study of pathological tissues obtained from animals found dead or dying at Amchitka.

An adult female (D7-57), having well-worn teeth, weighed 56 lb. (25.4 kg.) when captured alive on 1 December 1957. Her weight at death, 6 December 1957, was 47 lb. (19 kg.). This animal lacked energy and ate sparingly during the period of captivity.

Fur preening was also inadequate. The animal, in general, appeared to be in poor condition.

Necropsy.—The liver appeared fibrous and spotted with various shades of brown and reddish inflammation. In three places the omentum adhered abnormally to the liver and there were numerous abnormal adhesions between the lobes of the liver. Yellowish scar tissue surrounded the areas of adhesion. The spleen appeared abnormal, exhibiting a somewhat opaque whitish scum over one side. Linear indentations crisscrossed this surface. Specimens were preserved in AFA solution, then transferred to 70 percent alcohol. A large abscess surrounded the root of the lower right canine tooth. Considerable osteolysis of the jaw had occurred around the root of the tooth forming a hole in the bone which measured $10 \times 8 \times 7$ mm. Other organs appeared normal to gross examination.

Dr. Jensen's analysis:

Hemopoietic system: Histopathology: Spleen: Parenchyma is diminished while capsule and trabeculae are abundant. These changes indicate atrophy from unknown cause. The periphery of some central arterioles contain a homogenous acidiphilic substance which may be amyloid [starch-like].

Liver: Many lobules show fatty metamorphosis in central zones. This change is not uniform.

Although Dr. Jensen gave no diagnosis in this case, it was apparent that this animal was moribund. It would appear that toxins from the infected jaw may have caused the fatty degeneration and sclerosis of the liver.

The results of a necropsy of another otter was similar but no localized infection was found: KWK 59-85, adult female, weight $37\frac{1}{2}$ lb. (17 kg.), collected 27 March 1959, found dead well above high-tide line in sleeping position. The liver appeared swollen and fibrous with considerable yellowish discoloration, scar tissue, and abnormal adhesions to the diaphragm and intestines. Peripheral blood vessels of the liver and intestines were turgid. The otter had bled from the rectum before death.

Malignancy

On 22 October 1957, a young adult female sea otter (B-12-57), weighing 42 lb. (19 kg.), was found dead on a rock well above high-tide line at Amchitka. A necropsy revealed abnormal tissue growth in the viscera and a quantity of dark, apparently bloody fluid in the coelom. Externally in other respects the animal appeared normal.

Dr. D. V. Brown, then Associate Professor of Pathology, Uni-

versity of Washington and Chief, Laboratory Service, Veterans Administration Hospital, Seattle, examined the specimen material and gave the following information:

Gross examination: Specimen as received, fixed in formalin, consists of a spleen, stomach, duodenum and what appears to be the greater portion of the small intestine with its mesentery. Tissue preservation appears to be good.

The spleen is firm and rubbery with a roughened, granular capsule which is gray-blue in color. It weighs approximately 60 g. and measures $14.0 \times 6.5 \times 2.0$ cm. in its greatest dimensions. On section it is homogeneous throughout with no focal areas of gross change.

The stomach appears to have a wall of normal thickness. Within the lumen there is a little green pulpy material but no suggestion of old or recent bleeding. The mucosa seems well preserved. The pylorus and duodenum appear normal.

Throughout the small intestine the bowel wall and the adjacent mesentery are irregularly thickened with firm, gray tissue which appears neoplastic [new and abnormal growth]. The bulk of this is in the distal end of the bowel apparently near the cecum. The gray tumorlike tissue infiltrates and thickens the bowel wall in some areas and extends out into the mesentery which is also thickened and gray. Toward the distal end, the mesentery contains a large coarsely nodular mass ($8.0 \times 6.0 \times 4.0$ cm.) which on section is solid and gray.

Small solid gray masses scattered through the mesentery are apparently other involved lymph nodes.

Sections for microscopic study are taken as follows: Spleen, stomach, bowel wall, lymph nodes and mesenteric mass.

Microscopic: Sections of spleen are quite well preserved. No abnormalities are recognized.

A portion of pancreas is included and it too does not seem remarkable.

Sections of enlarged lymph nodes show focal areas of apparent neoplastic invasion. The tumor here is partially replacing the nodal substance and is similar to that described below.

M. C. Keyes, D.V.M., who examined Dr. Brown's histological preparations, considers that the condition described may be diagnosed as leiomyoma or a leiomyosarcoma.

Paw infections

Several otters with infected forepaws were captured on Amchitka beaches. It appeared that puncture wounds, perhaps made by sea urchin spines, caused the infections. In captivity, infections developed in all extremities. In at least three cases infections occurred in puncture wounds or cuts originating on sharp ends of hardware cloth, used on the enclosure. Repeated doses of antibiotics successfully cured these infections in some animals.

Blindness

Otherwise healthy sea otters blind in one eye were occasionally seen at Amchitka. No wild otter blind in both eyes was observed. The cornea of the left eye of a yearling otter (Susie) was punctured near the center by a tiny "pinhole" when she was captured at Amchitka in 1955. Within weeks the eye became cloudy and eventually completely blind. About 2 years before her death in 1961 the right eye also became cloudy (presumably affected by the other blind eye) and total blindness resulted. Because she had learned the topography of her enclosure well before losing her sight, she appeared to experience no difficulty in finding her food and her way about her quarters.

Intussusception

Blocking of the small intestine by the intestine "swallowing" itself occurred in three captive otters. These animals were held in unsatisfactory cages without sufficient water for immersion. The animals appeared to experience emotional stress, as evidenced by frequent vocalization for one or more days before death occurred.

Predation

No information exists to indicate that predation by animals (other than man) on the sea otter is an important factor in its population dynamics. Available information on predation is presented below:

SHARKS

It is beyond question that some sea otters are killed by sharks. Snow (1910, p. 278) states:

Wounded otters I have taken on a few occasions, but they had been bitten by sharks, as I know from finding several of the sharks' teeth broken off in wounds.

Orr (1959) discovered the broken tooth of a great white shark (*Carcharodon carcharias*) in the lacerated body of a sea otter found dead at Pebble Beach, Calif. He considered that one other otter he examined definitely died from shark wounds and that several others found dead and bearing lacerations may have died as a result of shark attacks. That skin divers may have inflicted fatal wounds with spears, although a possibility, must be considered an opinion to be carefully weighed, since no proof that this

occurred is available. Limbaugh (*in* Gilbert, 1963) says that "white sharks may be threatening" the small sea otter population on the central California coast. The degree to which man or sharks kill sea otters along the California coast still appears to be an unresolved question. In Alaska no deaths attributable to sharks are recorded.

KILLER WHALE *Orcinus orca*

Presumably the killer whale may eat sea otters. I have watched killer whales and otters in the same area and have not seen a whale attack an otter. Nikolaev (1965b, p. 231), however, saw a killer whale catch one sea otter.

On 1 March 1959, near South Bight on the Pacific shore of Amchitka, I watched from the cliff top as five killer whales cruised about outlying reefs. As the whales approached the reefs a harbor seal left the water and climbed onto the rocks. The whales cruised close to the reefs, then proceeded eastward parallel to the shore and into an area where four sea otters were feeding. One otter was eating on the surface when the whales approached and passed only a few feet beneath it. This otter appeared to sense the presence of the whales. It stopped eating and remained motionless while they passed. Otherwise, the otters seemed undisturbed by the whales and the whales exhibited no discernible interest in the otters.

On 9 April 1959, R. D. Jones and I observed killer whales and otters in the same general area off Kirilof Point on the Bering Sea shore of Amchitka. On several occasions between 1345 and 1645 we spent nearly an hour watching two groups of killer whales, one of 9 and the other of 18. They moved parallel to the shore and remained from a quarter to one-half mile from land. Several individuals raised the head and anterior quarter of the body above the surface as if to search the surface visually. Sea otters that were food diving in their vicinity ceased this activity and lay still on the surface or moved slowly toward shore on the surface. We did not see any behavior by the whales which indicated to us that a sea otter was attacked.

A further observation by Jones (letter, 9 July 1961) is similar. At Rat Island he saw six killer whales which remained for some time "from 25 to 100 yards off" shore and in the vicinity of "a large pod (over 200) sea otters." The sea otters exhibited "no alarm" and the whales did not attack them.

Although Barabash-Nikiforov (1947) gives no observation of

a killer whale attack on a sea otter, he lists them as an enemy and presumed "that killer whales terrorize sea otters."

BALD EAGLE *Haliaeetus leucocephalus*

The sea otter population at Amchitka progressed from near extinction at the turn of the century to maximum size in about 40 years. At the same time a large population of eagles occupied Amchitka.

From many months of field observations by a number of observers there is only one authentic observation of an eagle attacking a living sea otter. This occurred on 3 June 1961 at Barr House Cove on Amchitka Island. In a letter of 17 October 1961, R. D. Jones reported what he and Vernon D. Berns observed:

We were on the beach of the cove watching the eagles with binoculars . . . [an eagle] launched and flew . . . to sea losing altitude rapidly and disappearing behind the island. The eagle quickly returned directly to the island . . . carrying a large bulky object . . . [which it] carried . . . to the nest and upon our approach took wing. It was not necessary for us to climb the pinnacle to know there was a sea otter pup in [the nest] for the screaming of the pup was all too clear. We did climb it, however, and observed three eagle nestlings and the still living pup.

Sea otter remains frequently occur in eagle nests (Krog, 1953; Kenyon, 1961, 1964) where the two species occur together. That certain individual eagles may develop a taste for sea otters, while others do not, is indicated by the failure of Murie (1959) and D. C. Hopper (*in* Jones, R. D., unpublished report of 1 January to 31 August 1953) to find sea otter remains in eagle nests they investigated on islands where sea otters were numerous. I obtained many observations at Amchitka of eagles feeding on carcasses of sea otters that died of natural causes and saw them carry parts of these carcasses away in their claws. The otter remains frequently seen in eagle nests undoubtedly include many that were obtained by scavenging rather than predation.

One observation quoted from my field notes is typical of many:

St. Makarius Bay, Amchitka Island, 2 April 1959, 0900. At water's edge an adult eagle was finishing the remains of a large fish (ca. 30 in. (0.75 m.) long, washed ashore dead) while four other eagles (all in subadult plumage) rested on the beach and bluff. In the midst of this group, a young male sea otter—just awakened from the night's sleep—squirmed about on the dry grass (est. wt.=25 lb. (11.3 kg.)). Obviously the eagles were paying no attention to the sea otter and the otter was certainly not alarmed at the eagles' presence.

In places where one or more eagles were near, I frequently saw helpless young sea otters left floating on the surface while the

mothers dived for food. Although the young otters would have been easy prey, I never saw an eagle attempt to take one.

My observations indicate that predation by the Bald Eagle on the sea otter is unimportant.

Environmental Pollution

Fur cleanliness is essential to the sea otter's survival. If the fur becomes soiled by foreign matter it loses its water-repellent characteristics, the insulating blanket of air among the dense fur fibers is lost, the animal is chilled, and soon dies.

Pollution of waters by oil and other by-products of industrial development preclude the possibility that the sea otter can today reoccupy all of its former habitat. San Francisco Bay, in early years, "abounded in otters" (Ogden, 1941). Pollution by oil and other wastes today would certainly preclude their survival there or in the vicinity of the Golden Gate. Periodically the outer coast of Washington State, which once supported a thriving sea otter population, is polluted by oil from the many ships which navigate the Strait of Juan de Fuca. That a permanent population of sea otters could today survive in this otherwise ideal coastal habitat is questionable.

Not only is the sea otter affected directly by habitat pollution but where pollution is acute, as in San Francisco Bay, food organisms are also affected and reduced or eliminated.

Poaching

Poaching or illegal killing of sea otters in Alaska is not known to be a serious problem. Holger Larsen of the U.S. Fish and Wildlife Service said "it has been known that illegal furs have moved through Valdez since 1938" (Seattle Times, 2 February 1956). The only arrests in recent years, however, were of a Fairbanks fur dealer in 1944 for the possession of a sea otter and of two men in an Anchorage hotel on 1 February 1956 who had in their possession eight sea otter pelts. Ray Woolford of the U.S. Fish and Wildlife Service said (letter of 18 March 1964):

Probably more sea otters are accidentally shot by inexperienced seal hunters than are deliberately killed with the intent to commercialize on fur. I think the accidental kills by seal hunters and others traveling coastal waters have a potential for increasing so long as seals remain unprotected and a bounty is paid on them.

Various reports of poaching by foreign nationals in the outer Aleutian Islands are not confirmed.

The problem of illegal killing of sea otters may be of more importance in California. Captain Howard Shelby of the California Department of Fish and Game reported that in one period (late 1957 and early 1958) in the Monterey area alone 18 dead otters were found. "Some had a hole clear through them, either spear or bullet wound." He said further that "it's my opinion that there are people and there are groups of people who do definitely shoot this animal. Then there are quite a group that target practice at anything." (California Senate, 1963)

Summary

1. Few sea otters were found dead on Amchitka beaches in the period 1938-40. The first report of significant natural mortality was made in the spring of 1948 when "more than 100" otters were found dead on beaches. Since the late 1940's significant late-winter, early-spring mortality was observed when biologists visited Amchitka. During five study periods from 1956 to 1963, data were obtained from 311 otters found dead or dying on beaches of the eastern half of Amchitka Island.

2. The greatest number of otters usually died in the month of March but considerable mortality also occurred in February, April, and May. In this late-winter, early-spring period about three-quarters of all annual mortality occurred.

3. Approximately 70 percent of the late-winter, early-spring mortality occurred among juveniles deserted by mothers. The other 30 percent of dead animals were predominantly adults showing signs of age.

4. During the period of stress caused by storms, mothers deserted their large juveniles at an earlier age than they did at other seasons. They appeared to do this because it was difficult for a mother to obtain sufficient food to satisfy both herself and the large juvenile. Few very small pups were found dead even though they were present in the population at all seasons.

5. Mortality was usually greater among males than among females. Among juveniles this disparity was greater than among adults. Males in captivity were found to be less hardy than females.

6. Vigorous adults were able to obtain adequate nourishment from high-calorie foods, such as fish and octopus. These organisms were seldom obtained by juveniles and aged animals.

7. A high percentage of juveniles and aged animals found

dead on beaches exhibited malocclusion of the postcanine teeth. In juveniles this condition resulted when deciduous teeth were being replaced by permanent teeth. In adults malocclusion resulted from severe tooth attrition which may have been caused by chewing hard-shelled invertebrates.

8. Prolonged storm conditions precipitated mortality but the amount of mortality was found, in 1962, to be related to the available feeding habitat and population density.

9. The relative intensity of storm wave action was greater on the Pacific Ocean coast than on the Bering Sea coast, but the mortality on each coast was proportional to population density and not to relative intensity of storm conditions, indicating that the threshold of conditions causing mortality was passed on both coasts.

10. The annual mortality of the Amchitka population was estimated in 1959 and 1962 to be about 8 to 11 percent. Two methods of estimating mortality gave similar results.

11. In the Shumagin and Sanak Islands areas, where the sea otter population was about four and two otters per square mile of water less than 30 fathoms deep, respectively, no evidence was found to indicate unusual mortality in the late-winter and early-spring storm periods.

12. The Amchitka population was about 19 otters per square mile of water less than 30 fathoms deep and had overexploited certain food resources. Because of this fact, the population was restricted by relatively high mortality which resulted primarily from malnutrition and was precipitated by environmental stresses during late-winter, early-spring storms.

13. Sea otters are infested by a variety of internal parasites but these rarely appear to be the direct cause of significant mortality. External parasites are limited to fortuitous infestations of nasal mites. Such infestation is unusual in wild otters.

14. The most frequently observed condition at death was emaciation accompanied by hemorrhagic enteritis. Chronic disease conditions and bodily injuries were observed.

15. Sharks, the Bald Eagle, and killer whale are known to kill sea otters. Predation, however, is probably an insignificant source of mortality.

16. Environmental pollution in areas now heavily utilized by man will probably prevent the sea otter from reoccupying all of its former range.

17. No evidence is available to indicate significant illegal killing by man of sea otters in Alaska. In California, however, illegal killing by man may, today, hinder the increase of the sea otter population.

IN CAPTIVITY

The sea otter is highly adaptable to life in captivity. When its environmental and food needs are met, it is hardy and appears contented in air temperatures from about 15° to 85° F. By nature it is placid and tames quickly. Some individuals accept food from the hand within a few minutes of capture.

Certain features of the captive environment are, however, extremely critical. The sea otter in captivity must have free access to an abundant supply of clean water. It also requires access to clean, dry areas but, in warm weather, it may spend entire days without leaving the water. Free air circulation is also a requirement. Cleanliness of the fur is essential; if the fur becomes soiled, the air blanket trapped among its fibers is destroyed, the skin then becomes wet, and death from chilling soon follows.

Its food requirement of about 20 to 25 percent of its body weight per day must be fulfilled. It readily eats a variety of fish, mollusks, and crustaceans but will remain in good health on a monotonous diet.

If clean water is withdrawn for even a short period, as during travel on ship or aircraft, death may occur soon after the animals are allowed to enter cold water. When water is not available, captives are emotionally upset and extremely sensitive to air temperatures. In dry cages, air temperature near 50° F. has caused distress, and animals exposed for a few hours to temperatures near 70° F. died.

The information gained from holding many captive otters is reviewed below.

Capture

Most sea otters taken alive are captured in nets. The historical record indicates that in early times, also, nets were employed. Steller (*in* Jordan, 1898-1899, Vol. 3, p. 214) states that anchored nets were spread on the water's surface and that carved wooden otters were used to attract otters into them. Of the captives he says:

When they are caught in the nets they are so frantic that in their despair

they bite off their front feet; but if a male and a female are caught together they both lacerate their skins terribly and knock out their eyes.

After capturing more than 200 sea otters in dip nets, I have concluded that Steller's description is an exaggeration. That a netted otter is frantic is true. One particularly nervous female did chew off the first joint of one hind toe and tore at the skin of her belly with her teeth, but such behavior is unusual. Usually the netted otter bit the netting and with the help of its forepaws attempted to break the strands or attempted to push the strands away from its face and body with the forepaws.

On several occasions a mother and young were taken in the same net. A large juvenile bit its mother repeatedly on the head and body in its frantic efforts to escape. These two animals were quickly separated, tagged, and when released the juvenile joined its mother and the two swam away together. After being placed in a small carrying cage, otters usually rested quietly.

Soviet biologists working in the Kuril and Komandorskie Islands used landing nets and "boundary nets" to capture otters (Barabash-Nikiforov, 1947; Voronov, 1960).

Officials of the Alaska Department of Game successfully captured otters in Prince William Sound in a nylon salmon gillnet set from a boat (J. Vania, personal communication).

At Amchitka, otters haul out at certain times to sleep on beaches. With practice and care we caught these animals in a salmon landing net (fig. 82).

We captured otters most easily during late winter and spring. In this period, prolonged storms caused juveniles and older animals to weaken and come ashore. Healthy young adults were also taken, but less often. In summer, fall, and early winter, when storm periods were of shorter duration, few otters came ashore. In summer months, when calm weather prevailed, otters were particularly difficult to net on beaches. In summer, however, numbers did haul out at night to sleep on kelp-covered rocks close to the water. At this season, we found the best opportunities for netting otters when low tide coincided with dawn.

The reasons that otters may be netted on shore with relative ease are: (1) They often sleep soundly, (2) their sight and hearing are such that unless a moving figure appears above the horizon or unnecessary noises are made, the animals are often unaware of the hunter's presence, (3) they may be easily outrun by a man unless at the water's edge, and (4) they are placid and do not become alarmed easily.

In general, we found that otters may be classified in order of

the ease with which they may be captured on shore as (most difficult first): (1) mothers with young, (2) adult females, (3) juveniles, and (4) adult males. Mothers with young were difficult to net because (1) they were alert, slept lightly, and retreated to the water at any hint of danger, and (2) they came ashore in places that were least accessible to enemies.

Because the sea otter has an acute sense of smell, animals of all age and sex classes must be approached upwind. Among rocks and near cliffs, eddy currents may carry enough scent in an upwind direction to alarm and stampede otters before they can be captured.

Captured otters were removed from the landing net either by placing a small carrying cage at its mouth (fig. 105), or by lifting



FIGURE 105.—After a sea otter was netted, a carrying cage was placed horizontally on the rocks and the otter was allowed to move from the net into the cage. After the animal entered, the cage was turned upright and the lid was fastened. The cage was then strapped to a packboard or suspended from a pole for transport to a truck or boat. (KWK 55-8-10)

the animal by its hind legs into a vertically placed cage. An otter held off the ground by its hind legs is unable to bend its body far enough to bite its captor. The caged otter (fig. 106) was then carried to a boat or to the nearest road.

Environmental Needs of Captives

From 1932 to 1937 Soviet biologists experimentally held captive sea otters (Barabash-Nikiforov, 1947). Animals were eventually held successfully in cages built at the edge of a bay where tidal water was used to flush and clean the enclosures (Reshetkin and Shidlovskaya, 1947). The details of this work were unknown to us until 1962. Even so, all coastal areas at Amchitka, where our work was done, were exposed to storm waves, so we could not use enclosures placed directly in sea water. After considerable experimentation, a satisfactory field holding facility was constructed on land.



FIGURE 106.—This 65-lb. male otter was carried for over a mile in this manner. After an initial frantic struggle when netted, it settled down and rode quite calmly in the cage. (KWK 56-3-40)

If sea otters are to survive in captivity, they should, within about 2 hours after capture, be placed in special quarters. The quarters, whether in the field or in a zoo, must essentially simulate the natural environment. If this procedure is not followed, death may occur within a few hours or weeks, depending on which needs are neglected and the degree of neglect. The following brief history of experimental attempts to hold otters in various kinds of enclosures illustrates the requirements for exacting care.

The first modern U.S. attempt to hold captive sea otters was made in March 1951. Refuge Manager Robert D. Jones of the Aleutian Islands National Wildlife Refuge and a crew of men went to Amchitka Island aboard the U.S. Fish and Wildlife Service vessel *Brown Bear*. A camp was established at Crown Reefer Point, and at least 35 otters were captured on tidal rocks. An attempt to hold these animals in shallow, mud-bottomed, fresh-water lakes was unsuccessful. All died within a few hours or a few days after capture.

In February 1954, Drs. Donald Stullken and Charles M. Kirkpatrick, in company with U.S. Fish and Wildlife Service employees, visited Amchitka. Information about the physiology of sea otters and their behavior in captivity was obtained (Stullken and Kirkpatrick, 1955; Kirkpatrick et al., 1955). Otters were kept experimentally in two ways: (1) In a large wooden tank of sea water and (2) in an abandoned house where dry grass was used as bedding. All animals placed in the tank soon showed symptoms of shock and exposure, and died within a few hours or a few days. Of those kept on dry bedding, three were given constant attention and survived. They were brought to Seattle in June 1954 by R. D. Jones. Subsequently, when shipped to the National Zoological Park in Washington, D.C., and placed in a small inside pool, all died within a week.

In March and April 1955, 31 otters were captured at Amchitka, held on bedding of dry straw in a building, then placed aboard ship in small cages having dry bedding (fig. 107). Forty percent (12) of the animals died before leaving Amchitka or aboard ship. The remainder are thought to have died soon after liberation at the Pribilofs (see Transplant Attempts). It became obvious that if the captive sea otters' fur became soiled, the animals could not again clean their fur and survive after liberation in cold water.

My sea otter studies began on 26 July 1955, when one Aleut laborer, Antone Bezekoff, and I went to Amchitka Island and remained until 5 October. Our primary purpose was to learn how to maintain captive sea otters in good health. We held otters ex-

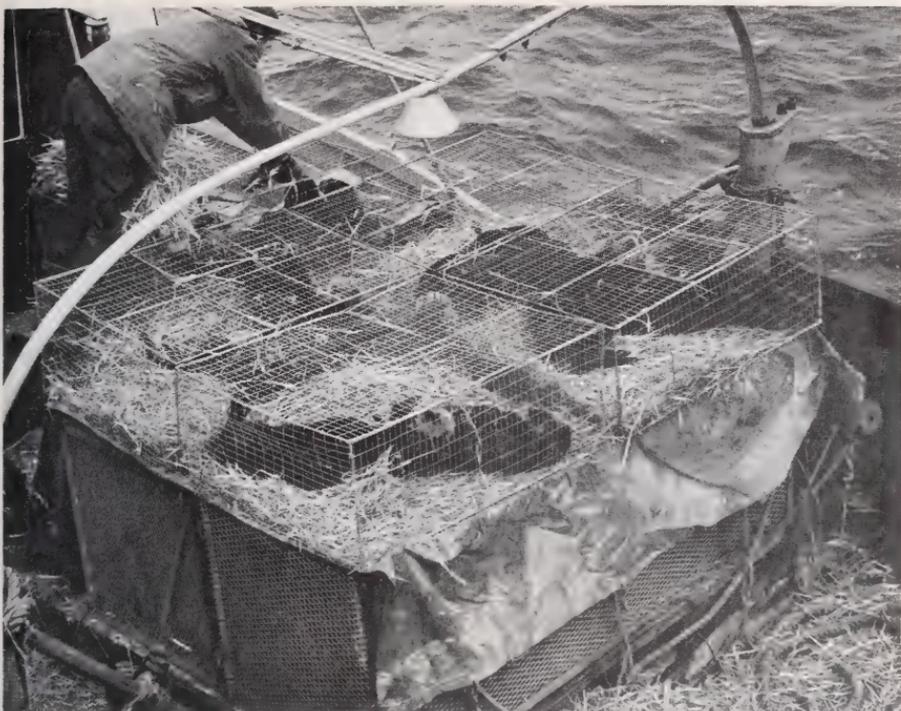


FIGURE 107.—In 1955, before it was learned that fur of the sea otter quickly lost its waterproof qualities when otters were carried in dry bedding, these animals were transported from Amchitka to the Pribilof Islands as shown. Mortality was high during the trip, and no otters are known to have survived after release. Three that were recaptured within a few minutes after release were soaked to the skin, rigid with cold and near death. (KWK 55-10-2)

perimentally in cages without water for bathing, since the 1954 studies had indicated that the otters survived best when kept dry. A female, "Susie," was given constant care and brought to Seattle where she lived in good health until shortly before her death on 27 October 1961. The pelage of animals held for more than a month in dry bedding became severely worn and matted. The fact that the otter which survived in Seattle did well in a pool demonstrated the need for access to clean water and dry areas.

Between 5 May and 26 July 1956, two experimental enclosures, with pools intermittently filled with water, were built on Amchitka. One of these was inside an abandoned building. Considerable humidity developed, and the fur did not dry properly. All developed enteritis and died within 2 or 3 weeks. Therefore, an outdoor enclosure was built containing a bathing trough through

which sea water was pumped for 3 to 4 hours each day. When given only intermittent access to water, however, the waterproof condition of their fur eventually deteriorated. In addition, animals kept with limited access to water frequently developed infections of the paws and flippers which, in combination with eventual wetting of the underfur, contributed to the mortality. Although survival was improved in the outdoor cage, it was evident that caging methods were still inadequate.

In October 1957, an outdoor, cement pool, 15 feet (4.6 m.) long, 8 feet (2.4 m.) wide, and 4 feet (1.2 m.) deep, was built on Amchitka. Surrounding the pool was a wooden platform 7 feet (2.1 m.) wide, and the entire installation was surrounded by a board fence 7 feet (2.1 m.) high (figs. 108 and 109). The enclosure was unroofed. A continuous flow of water was furnished by a clear, fresh-water stream. All healthy animals placed in this enclosure remained healthy, and several that were afflicted with enteritis and apparently starving when captured regained health.

The basic reason for the failure of early experiments with captives became obvious. Under normal conditions in the wild, the



FIGURE 108.—This enclosure around a cement pool satisfactorily prevented escape and furnished ideal conditions where otters could be held indefinitely. Water from a stream was brought to the pool in the wooden pipe, at left. A ramp was constructed (far right) on which a dory, used to obtain fish for otter food, was beached. Storm waves often destroyed the ramp. (KWK 57-27-12)



FIGURE 109.—The cement pool in the enclosure shown in figure 108 where otters were maintained in excellent health. (KWK 57-29-4)

sea otter exists only in clean water and the fur remains water-repellent. The skin is never wet but is protected by a blanket of air trapped in the fur fibers. The waterproof quality of the delicate fur is lost when animals are improperly held.

In shallow lakes (1951), mud and detritus became entangled in fur fibers, admitting water to the skin. In the large wooden tank (1954), an insufficient flow of water allowed suspended food and fecal matter to accumulate and become imbedded in the fur. Also, there was not enough space for the otters to get out of the water to dry themselves. The same results occurred as in the lake. When otters were given intermittent access to water (1956), food scraps and slime became imbedded in the fur during periods when water was not available. The progress of wetting was less rapid under the latter conditions because a degree of cleansing was possible. In addition, humidity developed with inadequate circulation of outdoor air and hindered the drying of fur when otters were held in a building.

Even in the large outdoor pool, built in 1957, care was necessary to limit the number of otters held. If more than five were held simultaneously, the pool had to be drained and cleaned daily to prevent an accumulation of food scraps and feces that affected the water-repellent qualities of the fur. Captive otters were not

affected adversely by frigid temperatures (fig. 110) when held in proper enclosures.

No conclusive data are available to demonstrate that fresh water provides a satisfactory permanent environment for captive sea otters. Although no record exists to show that sea otters were ever found in fresh water in nature, captives held in clean fresh water at Amchitka showed no detectable ill effects. One female, Susie, lived for 6 years in a fresh-water pool in Seattle. An autopsy revealed, however, that her reproductive tract had not only failed to mature but had regressed and was less developed than in normal juvenile otters. Could this condition have been related to the fresh-water environment? In addition, severe infestation of nasal mites (*Halarachne miroungae*), a condition never found in a wild otter, contributed to her death (Kenyon, Yunker, and Newell, 1965). I conclude that fresh water may be temporarily satisfactory for captive animals but that long-term studies of captive otters should be conducted on animals kept in sea water.



FIGURE 110.—Air temperatures down to $+15^{\circ}$ F. were withstood with no apparent detrimental effects by captive otters in the outdoor pool. Ice which quickly formed during cold spells was removed to provide open water. The otter in the foreground holds up its paws in typical begging posture. (KWK 59-3-1)

When bathing water was withheld, otters were kept in clean, dry litter for periods of several months. Upon reintroduction to water, however, the fur, because it was soiled, immediately became soaked to the skin. The otters shivered and showed distress (Kirkpatrick et al., 1955). With special care, (drying the fur with towels and a warm air heater) or in warm weather, until waterproofness was restored, some captives survived this ordeal. Other harmful effects of dry caging, fur wear and matting, probably cannot be remedied.

It was demonstrated that the sea otter is a hardy animal in captivity if its basic and critical environmental needs are satisfied. It must be kept in clean flowing water that washes away food scraps and body wastes. Free air circulation that aids in drying the fur is also required. The sea otter, having no blubber layer, is dependent for heat retention entirely on the insulation afforded by air trapped within its fur. If the fur becomes soiled, allowing water to reach the skin, chilling will result and if the animal is not artificially and quickly dried, death, often accompanied by enteritis, follows soon. These findings agree with those of Soviet biologists (Reshetkin and Shidlovskaya, 1947; Marakov, 1965).

Food and Feeding of Captives

KINDS OF FOOD OFFERED

Because the sea otter requires a large quantity of food, the feeding of animals held captive in remote, isolated areas, posed problems: (1) A large frozen food supply was seldom available; (2) transportation to replenish dwindling food supplies was not available and commercial facilities from which to obtain food were hundreds of miles distant; and (3) fishing activities to obtain food in Alaskan waters were often interrupted by stormy weather.

For these reasons, experiments were conducted in the hope of developing feeding methods requiring minimum expenditure of time, money, and energy. Table 60 shows foods that were offered and the degree to which they were accepted. Since canned, salted, and dried foods were not readily accepted, the prospect of using foods that are easy to transport and store was abandoned.

Fishing with trammel nets in Constantine Harbor at Amchitka Island was practical. The species taken in greatest number was fringed greenling (*Hexagrammos decagrammus*). Other species shown in table 60 were taken in lesser quantity.

In 1955 and 1956 no refrigeration was available. Fish that were

TABLE 60.—Foods offered to captive sea otters

Food item	Acceptability	Remarks
Crustacea ¹ :		
King crab (<i>Paralithodes</i>).....	Preferred	} A limited amount (2 to 3 lb. per animal) was eaten eagerly. If, however, fish was also available it was eaten and the remaining crab was left uneaten.
Tanner crab (<i>Chionoecetes</i>).....	do.....	
Shrimp (misc. sp.).....	do.....	
Mollusca ² :		
Snails, mussels, limpets.....	Accepted.....	Eaten when hungry and nothing else available.
Clams (<i>Saxidomus</i> , <i>Chione</i>).....	Preferred.....	Eaten to capacity if sufficient available.
Octopus (<i>Octopus</i>).....	Highly preferred.....	Do.
Squid (<i>Loligo</i>).....	do.....	Do.
Echinodermata ³ :		
Starfish (<i>Leptasterias</i>).....	Refused.....	Sample bitten off then discarded.
Sea urchin (<i>Strongylocentrotus</i>).....	Accepted.....	Eaten when gravid; refused when not gravid, and other foods available.
Pisces ⁴ :		
Herring (<i>Clupea</i>).....	Accepted.....	Refused at first but eaten when nothing else available.
Salmon (<i>Oncorhynchus</i>).....	do.....	Eaten reluctantly when nothing else available.
Arctic char (<i>Salvelinus</i>).....	do.....	Do.
Lanctfish (<i>Alepisaurus</i>).....	do.....	Do.
Cod (<i>Gadus</i>).....	Preferred.....	Do.
Hake (<i>Merluccius</i>).....	do.....	Do.
Rockfish (<i>Sebastes</i>).....	Highly preferred.....	Eaten regularly and consistently—many feedings.
Greenling (<i>Hexagrammos</i>).....	do.....	Do.
Lingcod (<i>Ophiodon</i>).....	do.....	Do.
Sculpin (<i>Hemilepidotus</i>).....	do.....	Do.
Poacher (<i>Agonus</i>).....	Accepted.....	Eaten when nothing else available.
Globefish (<i>Cyclopterichthys</i>).....	do.....	Do.
Halibut (<i>Hippoglossus</i>).....	do.....	Do.
Sole (<i>Lepidopsetta</i>).....	Preferred.....	Do.
Canned fish (salmon, mackerel, sardines).....	Refused.....	Refused even when very hungry.
Cooked fresh fish (Greenling, boiled).....	do.....	Do.
Salted and brined (codfish).....	Sampled.....	Small amount eaten reluctantly. ⁵
Aves: Goose flesh (<i>Phalacte</i>).....	Taken.....	Eaten reluctantly when very hungry but passed through tract undigested (Stullken and Kirkpatrick, 1955).
Mammalia: Seal flesh (<i>Phoca</i>).....	do.....	Do.
Mink food.....	Refused.....	Dried commercial mink food was mixed with fresh fish. Not eaten even when hungry.

¹ Large pieces of shell discarded but many small pieces swallowed. J. Vania found that captive otters took live Dungeness crabs (*Cancer magister*) eagerly and were preferred to the exclusion of other foods during extended periods.

² Clam shells discarded but small shells of mussels and snails crushed and swallowed.

³ Many pieces of shell swallowed.

⁴ Viscera and hard bones of head discarded but other bones and skin usually swallowed.

⁵ Soviet biologists apparently successfully fed salted cod and haddock after soaking "8-10 days in winter, 4-5 days in summer" (Shidlovskaya, 1947). Our otters might have taken some of the food items that were refused if they had been allowed to become sufficiently hungry.

alive when removed from nets were stored until needed in cages suspended in sea water from Kirilof dock.

Most fish taken at Amchitka were heavily infested with the roundworm *Terranova decipiens*. This parasite was tolerated in small numbers by sea otters but when heavy infestations were accumulated in captive animals they became lethargic and exhibited malaise. On autopsy, intestines of juveniles were found to be perforated by the worms. After 1956, all fish given to captive

otters were held frozen (at about $+10^{\circ}$ F.) for at least 24 hours. Apparently all helminth parasites were killed by this treatment.

A Soviet biologist (Shidlovskaya, 1947) states that fresh fish "is always better than frozen fish." Our experience is not in accord with this statement. During extended periods in captivity, otters were regularly fed fish that had been frozen and health remained excellent.

FOOD QUANTITY REQUIRED

During the period March 1956 through December 1957, records of the food consumed by Susie, a captive female sea otter, were kept on 602 days. Keeper Richard D. Clark used a 25-lb. capacity, Chatillon, platform-spring scale to weigh all food to the nearest $\frac{1}{2}$ lb. (occasionally to $\frac{1}{4}$ lb.). The otter was fed three times daily (morning, noon, and late afternoon). Food in excess of the otter's daily consumption was offered. Before the morning feeding, the pool was drained and all food scraps from the previous day were removed and weighed. From these data the approximate weight of the food consumed was calculated. A screen over the pool drain minimized loss of remnant food scraps. The data from the daily feeding record are summarized in table 61.

The weight of this female (six weighings) averaged 39 lb. (17.7 kg.). She consumed about (daily average, 1 year, 1957) 8.9 lb. (4.04 kg.) or about 23 percent of her body weight per day, approximately 228 g./day/kg. of body weight. The extremes, using monthly averages were 24 percent (in February) and 20 percent (in April) of body weight consumed per day.

The actual daily consumption of food ranged from a minimum of about 2 lb. (0.9 kg.) to 16 lb. (7.2 kg.). The range in amount

TABLE 61.—*Food consumption of a 39 lb. (17.7 kg.) sea otter (Susie) at the Seattle Zoo*

Observation period	Days data kept	Total food offered	Total food consumed	Kilograms of food		Average daily intake entire period
				Extremes of average daily intake ¹		
				Maximum	Minimum	
1 March–31 December 1956 ²	261	1,587.3	930.3	4.17	2.95	3.58
1 January–15 December 1957 ³	341	2,129.6	1,374.7	4.31	3.54	4.04
Total (and mean) —	602	3,716.9	2,305.0	4.24	3.24	3.81

¹ The average daily intake during each month was computed.

² Except August when no data were kept.

³ A second otter was placed in the enclosure at the end of this period.

eaten was between 4.5 lb. (2.0 kg.) and 11.5 lb. (5.2 kg.) 94 percent of the time and between 5.5 lb. (2.5 kg.) and 10.5 lb. (4.8 kg.) 78 percent of the time (fig. 111).

Figure 112 demonstrates that in a winter month (February) more food was consumed than in a summer month (August). In February the intake in a 24-hour period ranged from 6 lb. (2.7 kg.) to 14.5 lb. (6.6 kg.) and in August from 5 lb. (2.3 kg.) to 12.5 lb. (5.7 kg.). The average daily consumption in February was 9.5 lb. (4.3 kg.) and in August 8.8 lb. (4.0 kg.). About 3,400 and

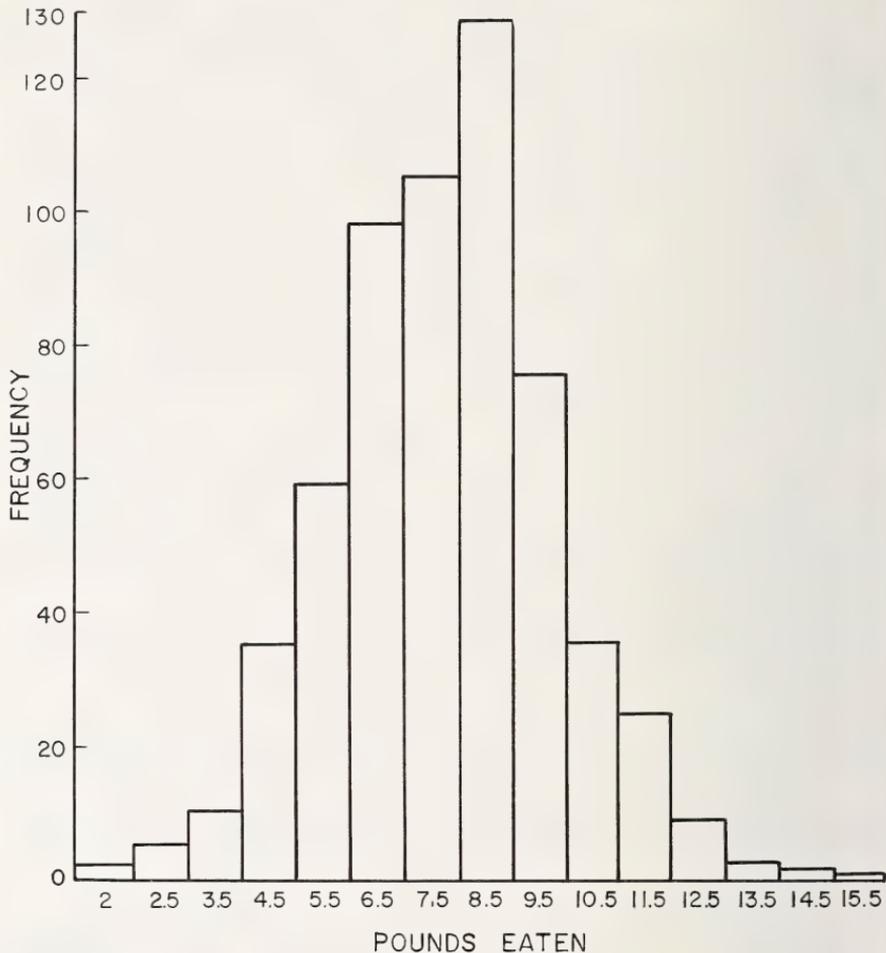


FIGURE 111.—The amount of food consumed by a captive female otter was recorded on 602 days. Food was available in excess of her daily requirement, and the amount consumed in a single day varied from about 2 lb. (1 kg.) to 16.5 lb. (7.5 kg.). Daily consumption was between 4.5 and 11.5 lb. on 567 days (94 percent of the time) and between 5.5 and 10.5 lb. on 470 days (78 percent of the time).

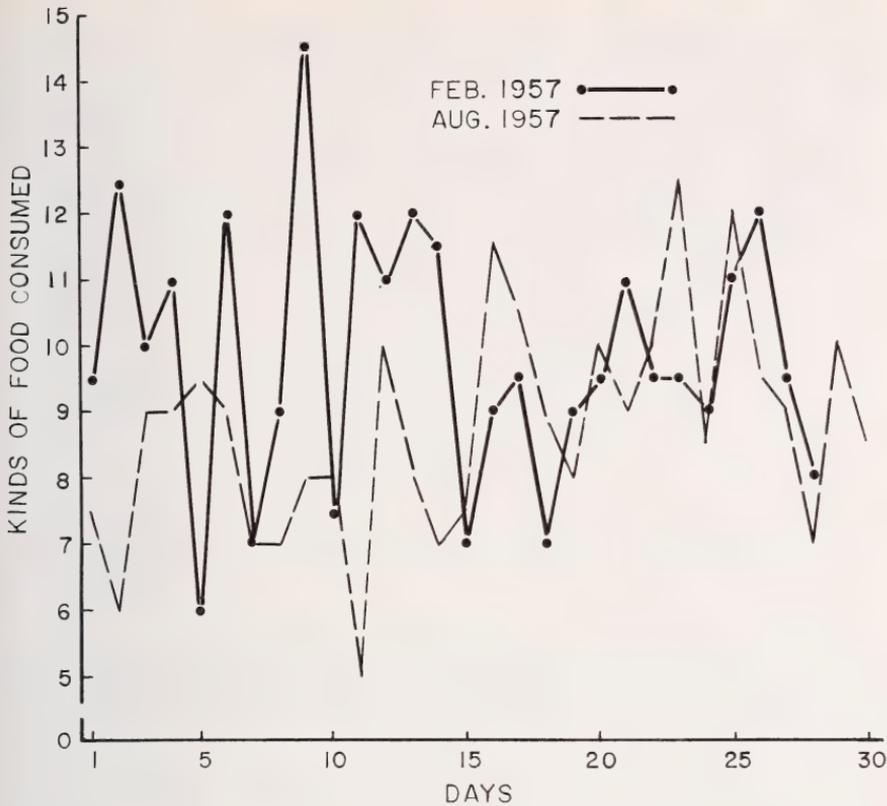


FIGURE 112.—Daily food consumption of a 39-lb. female sea otter (Susie) during a midwinter month (February) and during a midsummer month (August). More food was always available than was consumed. Average consumed in August, 8.8 lb.; average consumed in February, 9.5 lb.

3,200 calories per day were consumed in these winter and summer months, respectively, i.e., about 5 percent more in February than in August. The seasonal variation in consumption of food, however, was inconsistent (fig. 113) probably because water temperatures did not fluctuate greatly (seldom near freezing in winter to about 65° F. in summer), when compared to temperature fluctuations in other environments.

The average daily intake per month varied from 7.2 lb. (3.24 kg.) to 9.3 lb. (4.24 kg.), or from about 183 to 240 g. per kg. of body weight per day. It is interesting to note that dogs of 10 to 20 kg. daily require about 70–80 calories per kg. of body weight and the sea otter requires about 190 calories per kg. per day.

From December 1957 until September 1958, a nearly adult male, Dave, shared Susie's quarters. During the period January

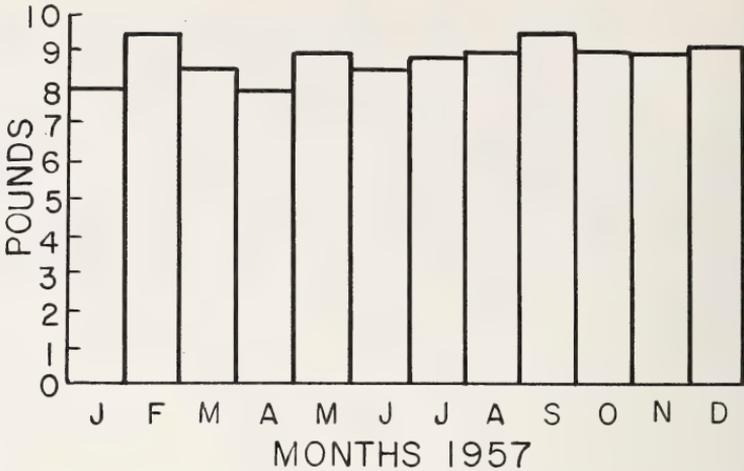


FIGURE 113.—Average daily weight of food consumed each month in 1957 by an adult female sea otter weighing about 39 lb. In this period the average daily consumption was 8.8 lb. (23 percent of the body weight).

through August, records were kept of their combined food intake. The combined weights of the two animals was about 102 lb. and they consumed (during 212 days when records were kept) an average of 25.1 lb. of food daily, or 24.6 percent of their combined body weights. Unless competition for food stimulated Susie's appetite and increased her intake, this would indicate that the rate of consumption of the male exceeded that of the female.

An adult male, Gus, now (1967) in the Tacoma Aquarium kg.), about 20 percent of his body weight, of fish and squid daily. weighs 76 lb. (34.5 kg.) and rarely fails to consume 15 lb. (6.8 His food is stored frozen in 5 lb. (2.3 kg.) blocks and three of these are offered daily (filleted rockfish morning and evening and squid at noon). From 1 September 1966 through 31 August 1967 he consumed 5,452 lb. (2,473 kg.) of food. During the year period, the otter consumed more than 99 percent of the food offered. When, on several occasions, more than 15 lb. of food was offered the otter either refused it or did not consume the entire ration at a subsequent feeding. On his uniform and regulated diet this otter appeared to remain in excellent condition.

Some captive otters were temperamental about their food. A food that was eaten enthusiastically one day was ignored or eaten reluctantly the next. This behavior was especially evident when an abundant supply of food was available. Days of high consumption might indicate that a fresh supply of particularly desirable food was available.

When the food supply was limited on Amchitka and several otters were held simultaneously in a pool, we found that large juveniles, weighing 20 lb. (9 kg.) to 30 lb. (14 kg.), maintained health and vigor when fed a minimum daily average of about 6 lb. (3 kg.) of food per animal and that adults could subsist on a minimum average of about 8 lb. (4 kg.) fed daily per animal in morning, noon, and evening feedings. Given these quantities, the animals were always hungry and tended to rob food from each other. Stullken and Kirkpatrick (1955) found that when captives held in dry bedding were given only about 12 to 15 percent of their body weight per day enteritis developed.

The northern fur seal which, unlike the sea otter, has a thick blubber layer in addition to its fur, was found to require only about 7 percent of its body weight in food per day (Scheffer, 1950b).

Conclusions

When food was offered daily in excess, the average daily consumption by a female during 602 days was about 23 percent of the body weight. The daily consumption varied greatly. Consumption per day ranged from about 5 percent to 40 percent of the body weight. This animal appeared to be in excellent health during the study period.

When a captive male was offered food that was limited to 20 percent of his body weight each day, he consistently ate the amount offered and remained vigorous and healthy.

At Amchitka when a sufficient number of fish could not be caught, otters were held temporarily in apparent good health on less than the optimum food requirement. Food representing 15 percent of the body weight per day was near the minimum temporary requirement.

COST OF FOOD

Inquiries have been received concerning the economic possibility of operating a sea otter "fur farm." Aside from the high expense of catching and transporting the animals and building suitable quarters for them, the cost of feeding would be an important consideration.

For 1 year a record was kept at the Seattle Zoo of the cost to feed an adult female sea otter (Susie). The information was given to us by Zoo Director Frank Vincenzi (letter, 8 April 1963) and is summarized below:

Clams—20 lb./week at 20 cents/lb. 52 weeks	\$ 208.00
Octopus—346 lb. at 20 cents/lb.	69.20
Fish—11,658 lb. at 10 cents/lb.	1,165.80
Total cost of food—1 year	\$1,443.00
\$27.75/week or \$3.96/day	

The cost of food for Gus in 1 year, 1 September 1966 to 1 September 1967, was more than \$1,650 (squid at 30 cents per pound and filleted fish varied from 30 cents to 35 cents per pound). Point Defiance Aquarium Director Cecil Brosseau considers that the annual food cost is close to \$1,800 or about \$5 per day.

FEEDING BEHAVIOR OF CAPTIVES

When captives were kept in ample water they ate readily. Certain individuals consumed food eagerly immediately after capture. Others, in apparent good health, refused to eat for 24 hours or slightly longer. Old and apparently ill animals sometimes refused to eat, or ate too little to survive.

Within 1 or 2 days of capture, captives learned to beg for food and even after storing a quantity under the foreleg would float on their backs, both forepaws upheld in a begging posture (fig. 114). Food was usually tossed to otters individually as they floated on their backs. Pieces of fish were sometimes caught between the forepaws but more usually the food item was allowed to strike the chest before it was grasped by the paws. Often when an attendant entered the enclosure carrying a bucket of fish the more aggressive individuals would rush from the water to take food from the hand (fig. 62). At such times they never attempted to bite and would take food lying flat on an extended hand, avoiding contact between teeth and fingers.

Large adults habitually robbed smaller adults and juveniles, even when the larger ones had all they could carry under the forelegs. The robber would approach the victim from behind or beneath and with one or both forepaws wrench the food from the smaller animal's chest (fig. 115). Certain aggressive adult females growled and snapped at a robbing male, but juveniles and subordinate adults offered no resistance other than to roll away from the robber. Frustration, or perhaps anger, was expressed by the victim at such times by slapping the chest with rapid strokes of both forepaws.

Because food reserves were often low, it was difficult to assure that all captives received sufficient food. To reduce pilferage, a bamboo pole was used to deter food-robbing animals. One adult female, however, became so adept that while diving and projecting



FIGURE 114.—Juvenile otters learned begging behavior within a day or two after capture. The paws were held up and when a piece of fish was thrown (in circle) the otters attempted to catch the food. Sometimes a food item was caught by the paws, but usually it struck the chest. (KWK 59-14-13)

no more than one foreleg above the surface, she could quickly snatch all the food from the chest of a large juvenile floating and eating on the surface. After repeated treatment with the stick, she learned not to rob her pool mates as long as an attendant stood near the pool with the stick.

Kirkpatrick et al. (1955) described how captives ate a variety of food items. During our studies at Amchitka, fishes (head and viscera removed) weighing a pound or less, were the most frequently offered food. Young animals often had difficulty in cutting the fishes' tough skin and reducing the flesh to bite-sized chunks. The fish was held between the forepaws, while the chunks, torn from the body with the canines and incisors, were crushed by the postcanines before swallowing. Bones were often discarded. When whole fish were given, the viscera were not eaten. Sometimes the tail and skin of the fish were eaten. As noted by Stullken and Kirkpatrick (1955), only bones, shells, and calcareous spines passed through undigested.



FIGURE 115.—*A*—A large and unusually light-colored adult female aggressively wrenched a food item from a juvenile otter. After grasping the food tightly to her chest with the forelegs, the adult rolled away and dived. The young otter was unable to retrieve any food after it had been stolen. *B*—The juvenile attempts to retrieve a fish which the adult female had stolen from it. The adult, after rearing back, rolled forward and dived, frustrating the attempts of the juvenile to retrieve its food. (KWK 59-13-3 and 4)

Wild sea otters habitually eat while floating on the surface (see Food and Feeding Behavior). When captives were held in enclosures without sufficient water to swim in, they ate poorly. They refused some foods that were readily eaten by captives held in a pool. They were nervous and distressed. Stullken and Kirkpatrick (1955) noted that three successfully maintained captives kept in dry bedding lost weight, frequently appeared listless, and in weakened condition during the first 10 days in captivity. Digestion was apparently disturbed when animals were kept on dry bedding without a pool. Flatus was observed frequently in otters kept on dry bedding but not in animals kept in a satisfactory pool. Similar food was given to both groups of animals.

Individual animals in apparent good health refused to eat when held on dry bedding without access to a pool. One adult male refused to eat for 4 days and was then released, weakened but still apparently healthy. An adult female kept in similar quarters refused food for 6 days before release. Juveniles, in general, were more adaptable than adults. Sea otters require an abundant supply of clean water in which they can consume food and clean their pelage while eating. Only while in transit for a brief period should they be held in cages without bathing water.

Daily Cycle of Activity

BEHAVIOR DURING THE DAY

Two days, one in midsummer (29 August 1957) and the other in midwinter (21 January 1960) were spent by V. B. Scheffer and me near the enclosure of an adult female sea otter (Susie) in the Seattle Zoo. Her activities as listed below were timed with a stop watch and recorded (table 62). Activities were classified according to four primary categories:

Grooming

Rubbing the fur with the paws, principally the forepaws. It was accomplished while sitting beside the pool or while rolling over and over in the water or lying on the surface of the pool.

Resting

When the eyes were shut the otter was presumed to be sleeping. If the eyes were open while she lay quietly, she was recorded as napping.

TABLE 62.—*Activity of a captive sea otter in daylight hours, summer (1957) and winter (1960)*

[Air temperature: 29 Aug. 1957 at 0515, 52° F. (11° C.); at 1200, 70° F. (21.5° C.); at 1900, 66° F. (19° C.)]

Activity	Minutes								Percent of total	
	In water		On land		Total					
	29 Aug.	21 Jan.	29 Aug.	21 Jan.	29 Aug.	21 Jan.	29 Aug.	21 Jan.	29 Aug.	21 Jan.
Grooming:										
Energetic.....	239	86	100	103						
Languid.....	106	11	0	17						
					445	217			48	40
Resting:										
Sleeping.....	19	0	63	13						
Napping.....	84	19	6	38						
					172	70			19	13
Feeding.....	81	63	0	0	81	63			9	12
Exercise:										
Swimming.....	190	185	0	0						
Walking.....	0	0	5	0						
Playing.....	22	5	0	0						
					217	190			24	35
Total.....	741	369	174	171	915	540			100	100
	(81%)	(68%)	(19%)	(32%)						

Feeding

Food was placed in the otter's pool at about 0900, 1230, and again in late afternoon if none remained. Food remaining overnight in the pool was eaten by the otter before her regular feeding time. Feeding activity was most intense shortly after fresh food was placed in the pool. At other times, food items were retrieved from the bottom and eaten.

Exercise (swimming)

Like many zoo animals, the sea otter developed an exercise routine during which she circled her pool. In a certain place she would dive, in another she rose to the surface and turned, swam a short distance on the surface, then dived to complete the circuit. If a number of visitors stood near the fence by her pool, the exercise routine might include a vertical rise with one forepaw on the pool edge while she glanced at the visitors. This was also done before feeding time, when she glanced in the direction from which the keeper would come. Occasionally the otter left the pool to walk briefly about her enclosure. Such short walks did not follow a set pattern similar to the swimming routine. Play was recorded when the otter picked up leaves, peanut shells, or a scrap of paper and with her teeth and forepaws bandied it about; also when small rocks were retrieved from the bottom of the pool and pounded in an apparently aimless way on the edge of the pool. This activity apparently became an exercise routine.

Because of the frequency with which it occurred, the edge of the pool eventually became damaged and zoo officials removed the rocks from the pool.

The primary purpose of these observations was to ascertain whether behavior differed in response to temperature or other environmental seasonal conditions. All conditions, except those associated with season, were similar in the two observation periods.

On 29 August the weather was clear and calm. On 21 January a high overcast persisted until 1300, after which the sky remained clear until sunset.

The summer maximum temperature was 26° F. (18.5° C.) above the winter maximum and the winter minimum was 17° F. (9.5° C.) below the summer minimum on the days of observation. This temperature difference and the difference in hours of daylight (4 hrs., 13 min. less in winter, table 63) apparently did not materially affect the otter's general pattern of daily activity. In spite of the differences in these environmental conditions, the percent of time that the otter spent in the four main activities recorded are similar (table 62).

The amount of time that the otter spent on land, however, showed seasonal differences. On the summer day the otter was in the pool both at sunrise and at sunset. On the winter day she was in her den at both these times. Also, in the winter she spent a greater percent of her time during the day on land, even though her actual time on land was nearly identical (174 and 171 minutes, table 62).

Figure 116 shows the distribution of activity by minutes throughout the summer day. (Because of its similarity, a chart for the winter day is omitted.) This shows that grooming periods were generally distributed through the day, that periods of exercise were concentrated in morning and late afternoon hours, and that periods of rest reached greatest frequency at midday and in the afternoon. There were five prolonged rest periods of relative inactivity on the summer day: from 1126 to 1222, from 1340 to 1430, from 1502 to 1542, from 1733 to 1831, and from 1907 to 1944.

Table 62 demonstrates that the amount of time spent in muscular

TABLE 63.—*Conditions during sea otter observations at the Seattle Zoo*

	29 August 1957	21 January 1960
Sunrise.....	0527	0740
Sunset.....	1853	1653
Hours of sunlight.....	13 hrs. 26 min.	9 hrs. 13 min.
Air temperature (range).....	52° to 70° F.	35° to 44° F.
Water temperature (constant).....	62° F.	38° F.

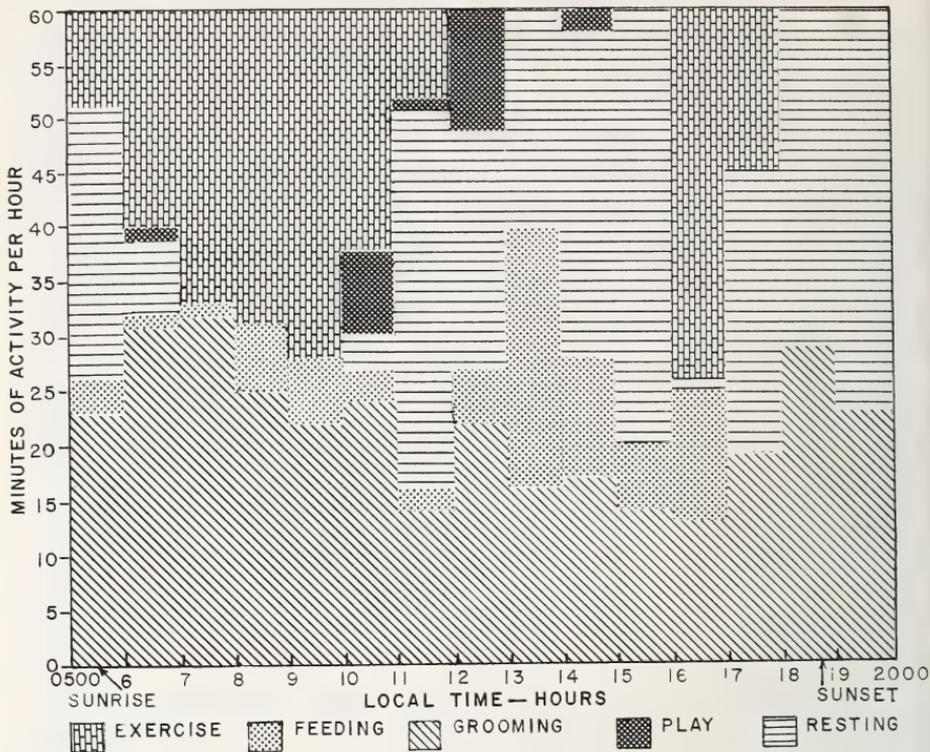


FIGURE 116.—The activities of a captive female sea otter were recorded for each minute from before sunrise to after sunset on 29 August 1957. The minutes spent in five categories of activity are summarized above for each hour of observation.

activity, grooming and exercising combined, was similar (72 percent in summer and 75 percent in winter). Grooming activity, however, consumed more time in summer than in winter.

Daily activity of wild and captive otters

The daily pattern of activity of the captive female and a wild female sea otter (further data are in the section on Breeding Behavior) would be expected to show obvious differences because a wild otter must search for food. Table 64 illustrates the differences. The data (although recorded in the same manner) are not strictly comparable because the captive otter was observed from the time of awakening in the morning until retiring at night. The wild otter was observed only from 1052 until 1820 (local time, Amchitka Island). In general, however, this comparison illustrates the fact that a wild otter must spend more than one-half of its time in feeding while the captive spent less than 10 percent of her

TABLE 64.—*Comparison of daily activities of wild and captive female sea otters in summer*

Activity	Wild otter 21 August 1955 ¹		Captive otter 29 August 1957	
	Minutes	Percent	Minutes	Percent
Feeding.....	257	55	81	9
Grooming.....	50	11	445	48
Resting.....	126	28	172	19
Exercise and play.....	25	6	217	24
Total.....	448	100	915	100

¹ See Breeding Behavior for further data.

time in this activity. The wild otter nearly satisfied her need for exercise while diving for food. The captive satisfied this need by swimming and grooming to a greater degree than the wild otter. The percent of time devoted to rest by both animals differed the least.

BEHAVIOR AT NIGHT

From 1 January to 9 September 1958, Mr. Cal Pierce, night watchman at the Seattle Zoo, recorded observations of the behavior of two captive sea otters. The objective was to obtain observations of the time each animal spent in and out of the water and in the den. For a variety of reasons, some nights were missed; substitute watchmen did not always properly record the data. Usable observations were taken on 199 of the 252 nights. Observations were usually made at hourly intervals from 1800 to 2200, and two to four times between 2200 and 0600. Usually the watchman recorded only whether each animal was in the pool, beside the pool, or in the den. Two dens were available, and both sea otters always had free access to all areas within their enclosure. Weather conditions were not recorded during the observation periods, but on several occasions the watchman noted that even during heavy rain the otters remained in the open, sleeping in or beside their pool.

Feeding, grooming, and play were not recorded systematically, but were noted on a number of occasions at various times during the hours of darkness up to about 2200. During late night and early morning hours, however, the animals usually slept quite soundly. Sometimes they awoke with a start in the light of the watchman's flashlight. If beside the pool when awakened, they immediately plunged into the water; if sleeping on the water, they would dive.

Observations made after 9 September are not used. About this time the behavior of the male became abnormal, and he spent in-

creasing amounts of time in the den. His health steadily deteriorated and he died on 22 September.

The general behavior pattern for each animal during the night is indicated in figures 117 and 118. Both animals tended to remain in the water more than out of it during the early evening hours. During late night and early morning hours, the male spent a nearly equal time in and out of the water while the female tended to spend more time out of the water than in it. Both animals preferred to remain out of doors, whether sleeping on the pool edge or in the water, but the female consistently spent more time in the den than did the male.

Even during winter months the sea otters seldom sought shelter in the den (figs. 119 and 120). The amount of time spent in the water at night, however, was greatly reduced in winter months. The male spent only 20 percent of the night in the pool during January. During the spring and summer the amount of time he

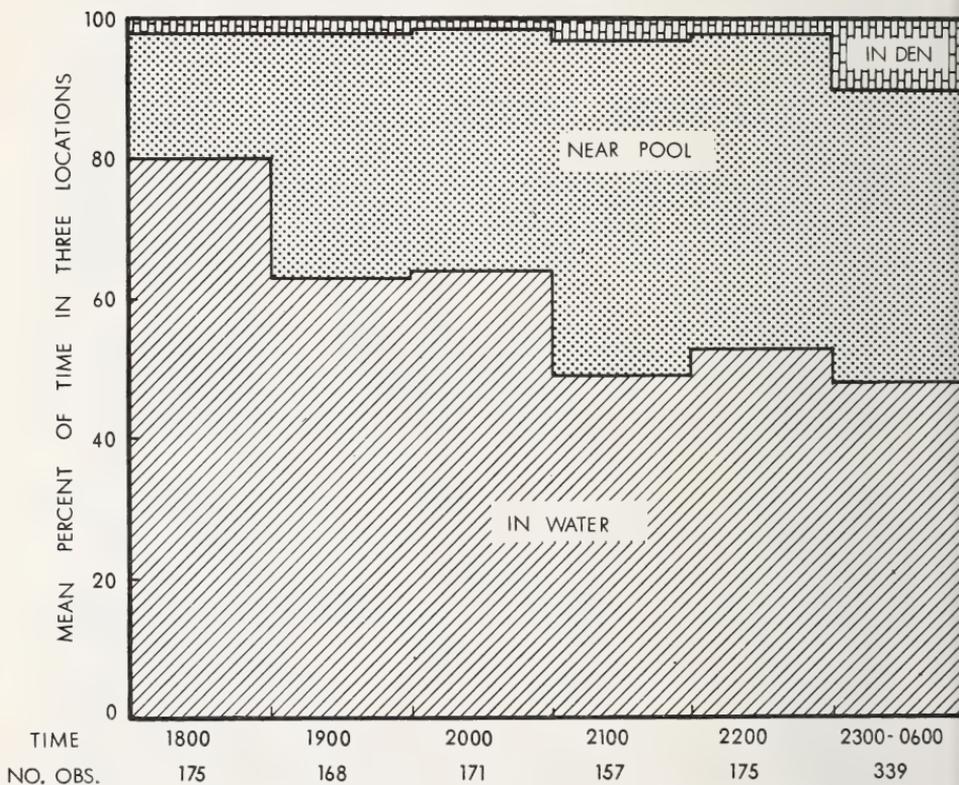


FIGURE 117.—Behavior of an adult male sea otter during a mean or average night. The mean percent of 1,185 observations of the animal in three locations during the night are shown.

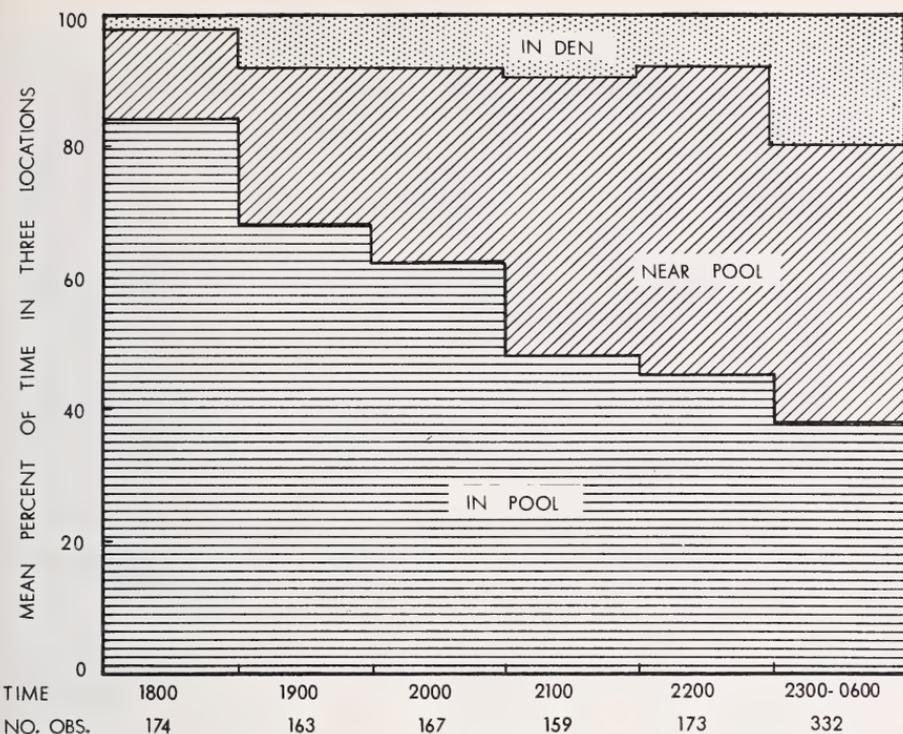


FIGURE 118.—Behavior of an adult female sea otter during a mean or average night. The mean percent of 1,168 observations of the animal in three locations during the night are shown.

spent in the water increased until in June he spent about 90 percent of his time there.

Causes of Death in Captivity

This subject was discussed in the foregoing pages in relation to environmental needs of captive otters.

The terminal symptom noted at death was often the voiding of black, tarry feces. Necropsy revealed enteritis (Stullken and Kirkpatrick, 1955).

K. L. Binkley, D.V.M., described the condition he found in three adult or near adult otters which he transported from Amchitka Island on a commercial, passenger-carrying aircraft (from a typewritten report dated 5 November 1957, in the files of the U.S. Fish and Wildlife Service):

Cause of death; acute pulmonary hemorrhage. Predisposing factors; high altitude flying in a nonpressurized plane, and promazine induced tranquility.

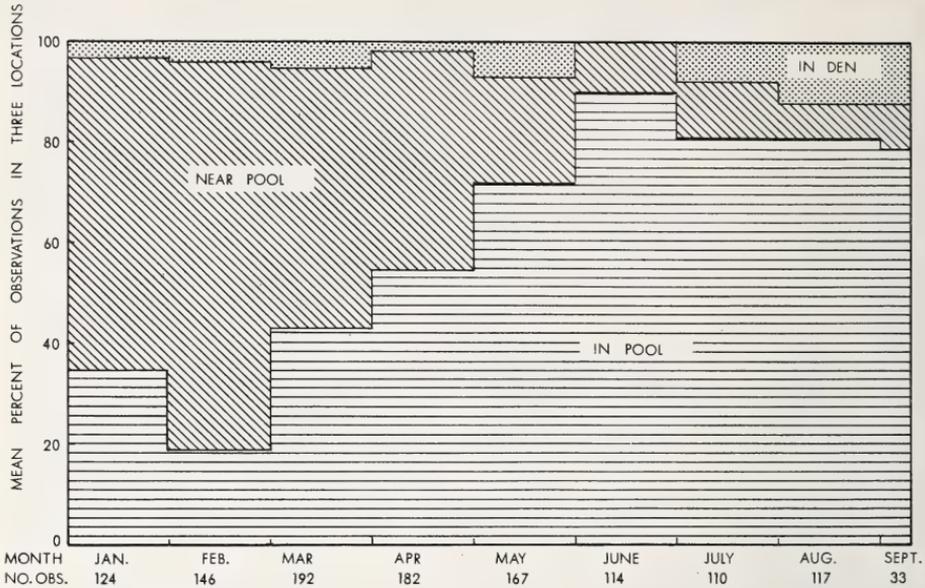


FIGURE 119.—Seasonal behavior of an adult male sea otter at night. The mean percent of 1,185 observations of the animal in three locations during 9 months is shown.

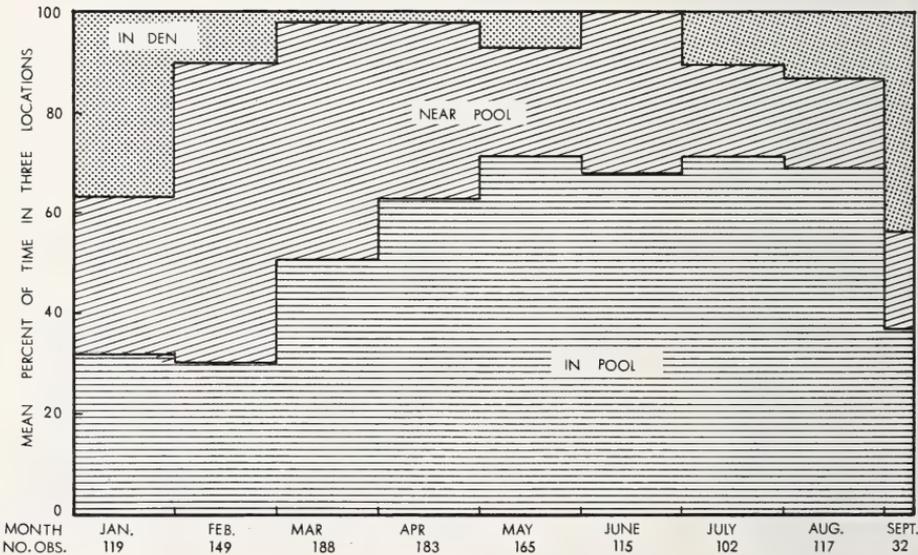


FIGURE 120.—Seasonal behavior of an adult female sea otter at night. The mean percent of 1,170 observations of the animal in three locations during 9 months is shown.

Administered 1.8 cc. Sparine. (Based on a dose of 2 mg. Sparine per lb. body weight, the weight was 43 lb. which resulted in a total dose of 90 mg. Sparine comes 50 mg./cc.) Dose administered approx. 0900 hrs 2 November, the animal died 1230 hrs 2 November. Lungs completely hemorrhagic. Trachea extremely hemorrhagic. Blood dark red, tarlike coagulations. Heart showed compensatory enlargement. Liver pale and anemic looking. Remaining organs normal with some postmortem discoloration. Stomach partially filled with food.

Overheating was probably also an important factor in the deaths of these animals. Post mortem examinations revealed that three captive otters were suffering from intussusceptions of the small intestine. This condition prevents the normal passage of intestinal contents. The reason that it occurred is not known but I suspect that stresses created by unsatisfactory holding facilities and during travel were important factors.

In review, captives died (1) as a result of chilling when the fur became soiled and its insulating air blanket was destroyed, (2) as a result of heat prostration in heated compartments when deprived of bathing water, (3) when infections occurred in the extremities, (4) when old and ill animals failed to eat after capture, (5) when parasitic roundworms (*Terranova*) ingested with fish flesh penetrated the intestine and caused peritonitis, (6) of lung hemorrhages when "tranquilized" otters were carried in small cages aboard a heated, passenger-carrying aircraft, (7) of lung congestion caused by a heavy infestation of nasal mites (*Halarachne*) (Kenyon et al., 1965), and (8) of intussusceptions of the small intestine. Enteritis was a frequent terminal condition. Causes of death are discussed further in the section on Parasites and Miscellaneous Diseases.

In conclusion, when parasite-free food requirements are met and the essential physical features of the sea otter's marine environment are duplicated, it adjusts easily to a healthy life in captivity.

Drug Use

Certain drugs were found useful in the care of captive otters. If drugs had not been used, some captives that survived probably would have died. No attempt was made to use drugs fired from a gun to capture sea otters.

Nembutal

Stullken and Kirkpatrick (1955) found that the normal anesthetic dose for dogs (40 mg. per kg. or 80 mg. per lb. of body

weight) injected intraperitoneally caused death in a sea otter in less than 30 minutes. One-half the dog dose gave good anesthesia but thermoregulation was upset. No further experiments with Nembutal were conducted.

Promazine hydrochloride "Sparine" (Wyeth)

The use of this tranquilizer was suggested by K. L. Binkley, D.V.M. It was found to be a useful agent in speeding the adjustment of nervous animals to captive conditions. The dosage of 1 mg. of Sparine per kg. (2 mg. per lb.) of body weight was satisfactory. The intramuscular injection took effect within 5 minutes. The animals so treated remained in a relaxed state for about 24 hours. This degree of sedation is, however, usually unnecessary and under certain conditions harmful, since food intake and pelage care were substantially reduced during the tranquilized period. We found that about half this dose or less, i.e., about 0.5 to 1 mg. Sparine per lb. of body weight, induced adequate tranquility and that the otters gave nearly normal attention to their bodily needs. When the effects of the drug wore off, the treated animals in all cases remained tame and well adjusted.

Sparine was particularly useful when mothers with small pups were captured. On one occasion a mother with a newborn pup was placed in the enclosure without receiving an injection. The mother grasped the pup in her mouth and swam frantically about the pool seeking escape (fig. 121), rather than swimming in the normal manner on her back with her pup on her chest. She surely would have drowned the pup if we had not recaptured her, taken the pup from her, and given her the minimum injection. Within 5 minutes we returned the pup and the mother cared for it in the normal way from then on (fig. 122).

Usually when a sea otter pup was taken from its mother it cried almost incessantly, day and night, and accepted little food voluntarily. We found that after a minimum injection of Sparine such orphans became calm and after the effects of the drug had disappeared the pup appeared to have become "imprinted" on the human foster parent. Treated pups readily accepted food and only cried when desiring attention. Unfortunately, time and facilities were not available to maintain helpless captives indefinitely.

No harmful side effects from minimum injections of Sparine were detected in otters kept in a satisfactory enclosure with a pool. Because it was important that sea otters give frequent attention to their pelage and maintain their daily intake of food, it was desirable that use of tranquilizers be kept to a minimum. The

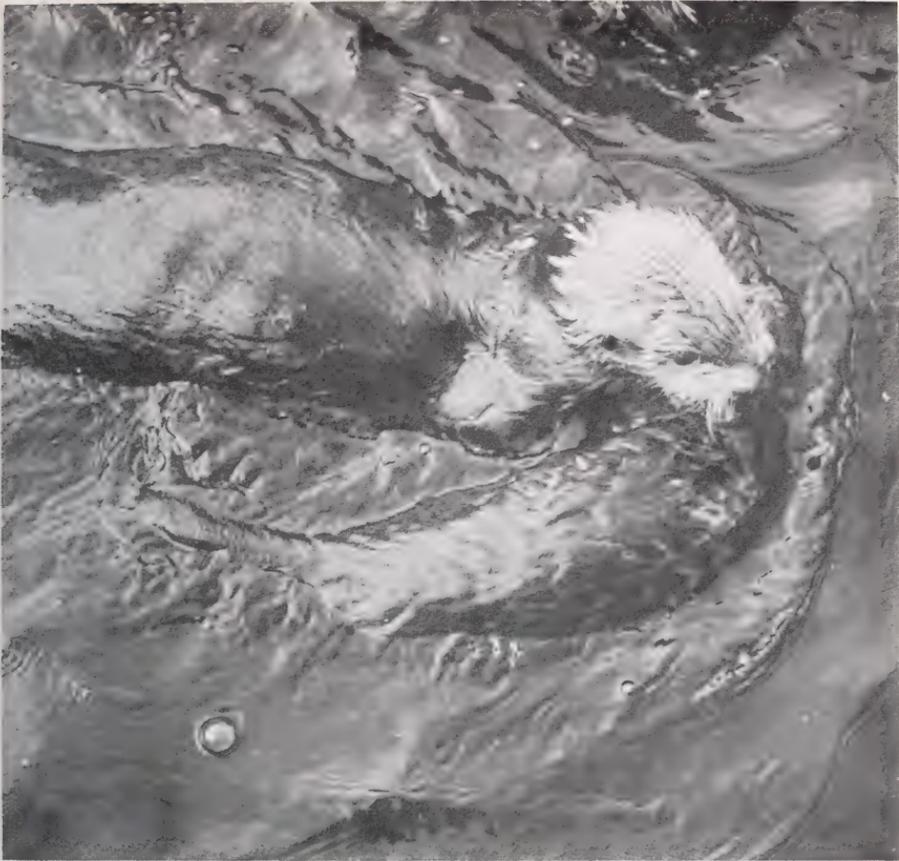


FIGURE 121.—A mother otter was placed in the pool without receiving a tranquilizer. Frantically she searched to escape while swimming about the pool, holding her pup in her mouth, the pup's head under water. Mother and pup were netted and the mother was given a small dose of Sparine (0.5 mg. per lb. of body weight). (KWK 57-29-31)

degree to which the use of Sparine on animals carried aboard an aircraft contributed to their deaths in transit is unknown (see Causes of Death in Captivity).

Propiopromazine hydrochloride "Tranvet" (Diamond)

This tranquilizer was used successfully by biologists of the Alaska Department of Game. Injections were given to captives immediately after capture (about 0.05 to 0.1 mg. per kg. or 0.1 to 0.2 mg. per lb. of estimated body weight). Before placing otters aboard aircraft during transplanting operations, a second dose of the drug, twice the amount of the first, was injected. J. Vania told me that the animals became satisfactorily relaxed and showed



FIGURE 122.—The same female and pup as shown in figure 121 about 10 minutes after the mother had received an injection of Sparine tranquilizer. Although the mother appeared drowsy, she carried the pup on her chest and groomed its fur, not as thoroughly, however, as she normally should have. She also ate, and nursed her pup. After recovering from the effects of the tranquilizer, the mother remained tame and satisfactorily cared for her pup. (KWK 57-29-28)

no harmful side effects. I have used the drug on only two sea otters. It was my general impression that the animals did not regain normal alertness as soon as those given Sparine and gave inadequate attention to feeding and pelage care.

Piperazine citrate

This vermifuge was administered as a precautionary measure to captive sea otters by injecting an aqueous solution into fish before feeding. Before fish were frozen routinely prior to feeding,

captives became heavily infested with *Terranova decipiens*. The effectiveness of the vermifuge was difficult to evaluate but it had no ill effect on the sea otters.

Vitamins

Because certain fish contain thiaminase, an enzyme that inhibits the proper utilization of vitamin B (Lee, 1948), thiamine hydrochloride was administered as a prophylactic measure. Pills containing vitamin B complex imbedded in the flesh of fish are readily eaten by otters and are administered daily to otters held permanently in captivity.

Antibiotics

Infections in paws, particularly the front paws, occurred when captive animals apparently scratched or cut these members during capture or in cages. An adult male with a badly infected front paw was given 600,000 units of Benzathine penicillin G "Bicillin" (Wyeth) and the infection disappeared after about 4 days. Two weeks later, however, the paw again began to swell and an additional dose of 600,000 units of Bicillin was administered and the infection disappeared permanently. The life of this animal, as well as those of several additional otherwise healthy animals, were probably saved through the injection of either Crystalline potassium penicillin G "Penicillin" (Wyeth) or Bicillin.

Pentobarbital sodium 3.7 gr. in each cc., isopropyl alcohol 10.5 percent, propylone glycol 10.5 percent, "Lethol" (Haver-Lockhart)

This drug administered intramuscularly was used to kill otters that were captured in nets and for various reasons were needed as specimens. The manufacturer recommended a dose of 1 cc. for every 5 lb. of body weight, but the sea otter was easily affected and we found that a dose of 10 cc. would kill large adults. The immediate effect is similar to other tranquilizers. Death followed injection in about 8 to 10 minutes.

Transportation of Captives

During transit from one location to another, the difficulty of controlling environmental temperatures and of furnishing sufficient bathing water causes severe complications. The longer the period in transit the more critical these factors become.

Sea otters have been transported in automobiles, aircraft, and

ships. After many failures, knowledge is now available to assure successful transportation, provided that control of critical conditions is possible.

AUTOMOBILE

Otters were transported only short distances by truck or automobile. They were taken from the place of capture on Amchitka to field headquarters and later between holding facilities and ships or aircraft. Because the trips were short, the animals were conveyed in small carrying cages and no complications were encountered. However, they appeared disturbed, and whined or "whistled" en route. The longest automobile ride, 40 miles, was in 1965 when an adult male, "Gus," was taken from a dock in Seattle to the Tacoma Aquarium at Point Defiance. This animal appeared quite contented throughout the trip.

AIRCRAFT

On several occasions the only air transportation available was that of commercial passenger planes. Here, because of passenger needs, it was not possible to maintain temperatures low enough for sea otters. Distressed otters whined, whistled, and sometimes screamed, and attempted to escape from their cages by tearing at the wire screen cage with their teeth and forepaws. When available, ice was placed in the cages and cold water from bottles was poured on the otters. This they drank eagerly and rubbed into their fur. This treatment did not satisfactorily solve the problem, but several otters survived trips from Seattle to Washington, D.C. in 1954 and from Amchitka to Seattle in 1955 and 1956. The only otters that survived trips on heated, passenger-carrying aircraft were given constant attention, ice, and water during the trip. Of 19 otters taken at Amchitka and carried on commercial, passenger-carrying aircraft, 6 survived to reach Seattle. Of these, only two ultimately recovered from the trip. The time en route was from 36 hours to more than 4 days, and it appeared that few animals could tolerate such prolonged periods of stress.

To avoid self-injury and reduce excitement during air transports, K. L. Binkley, D.V.M., decided to administer a tranquilizer immediately before shipment from Amchitka on 2 November 1957. He wrote:

This was done . . . and the animals shipped. Unfortunately, fatal complications developed when the tranquil animals were exposed to 11,000 feet altitude in a nonpressurized plane. Although it is not known for sure, apparently the drug causes a lowering in metabolism, and also in the animal's

ability to compensate for oxygen lack. Some action of the drug might also involve lung tissue permeability. During this attempt to ship 5 otters to the zoo in Seattle, the 4 adult otters were all administered 2 mg. Sparine per pound of body weight. A young 5-week-old pup was also included, although little hope was held for its safe arrival. In 2½ hours the pup was dead—probably from fright and altitude. In 15 more minutes the next youngest otter died, and in 5½ hours from take-off, the 3d otter (mother of the pup) succumbed. The two remaining otters died shortly after arrival in Anchorage, Alaska—or approximately 15 hours from Amchitka. Post mortem findings can be found in "Causes of Death in Captivity."

In the past, otters have been shipped in the same plane at the same altitude with no apparent [in flight] ill effects—although they did die during [delays in] shipment or shortly thereafter from other reasons. The only additional factor in this case was the tranquilizer, and until more work is done with the drug, the use of it under similar circumstances would not be indicated.

The above is from a report of 7 November 1957, by Kenneth L. Binkley, D.V.M., of the Woodland Park Zoo, Seattle, who was temporarily attached to the Sea Otter Project at Amchitka Island from 1 October to 2 November 1957.

After the unfortunate experience described by Binkley, it was decided to make one more transport of otters aboard a commercial passenger aircraft, it being the only available transportation.

In December of 1957 this attempt was made by taking eight otters via Reeve Aleutian Airways from Amchitka to St. Paul Island, Pribilof Islands reservation. No tranquilizer drugs were given. The animals were in excellent condition when they departed Amchitka on the morning of 11 December. A storm, however, caused delay, and unsatisfactory conditions inherent in an unpresurized, heated (to 75° F.), passenger-carrying aircraft caused rapid deterioration and resulted in the death of six animals on the night of 11 December. It appeared that overheating was the primary cause of death. The Pribilofs could not be reached, so two surviving males were taken to Seattle. One, an old adult, failed to recover from the trip and died on 16 December. The other, a young adult, recovered from the trip but subsequently died of unknown causes on 22 September 1958.

No further effort was made to carry sea otters on passenger-carrying commercial aircraft. In 1959, however, a U.S. Fish and Wildlife Service aircraft was available for the specific purpose of transporting sea otters. On 20 May seven otters, each about 1 year old, were placed on the R4D (DC-3) aircraft at Amchitka. On the direct flight of 3.4 hours to St. Paul Island the cabin temperature was maintained at 48° to 49° F., and the maximum altitude attained was 2,000 feet. En route the animals exhibited mild distress but when water from a bottle was poured in their

mouths and sprinkled on their fur, they became quiet. It appeared that even at the relatively low cabin temperature they suffered from heat distress when their fur was dry. All arrived at St. Paul Island in excellent condition.

Traveling cages with false wire bottoms were used during all experiments in aerial transportation to reduce fur soiling to a minimum. On the short trip from Amchitka to St. Paul the fur remained clean because the animals were not fed en route. On trips of longer duration (15 to 36 hours) fur soiling could not be avoided. Although body wastes fell through the false cage bottoms, the animals habitually lay on their backs to eat (fig. 123). Fish scraps and slime then accumulated in the fur with resultant loss of waterproof condition.



FIGURE 123.—Captive otters held on dry bedding habitually lay on their back or side. Fish scraps and slime thus fell into the fur while the animals ate. When the otters groomed and rubbed the fur with their paws, it became saturated with filth and particles of bedding material, and its waterproof quality was destroyed. When this animal was placed in water it did not float in the normal manner but sank because the air in its fur was lost. In this condition animals placed in cold water quickly chill and die. (KWK 55-5-1)

SHIP

Otters were carried aboard ship in two ways: (1) in cages with bedding and no water for bathing, and (2) in a cage which included a tank of constantly flowing sea water. Using the first method, when straw bedding could be changed frequently and conditions were such that the animals remained dry and did not chill, they remained in satisfactory condition. The three otters brought successfully from Adak to Seattle aboard a large ship in June of 1954 by R. D. Jones were well protected from the weather. The animals, however, required constant attention and when placed in a Seattle zoo pool the fur became wet to the skin, causing the animals to shiver. In another experiment (April 1955), frigid weather caused chilling and high mortality among the soiled animals resulted.

An experiment to test the second method was conducted in November-December 1965. A young adult male and an aged female were captured on 7 November at Amchitka and placed aboard the *MV Commander*. Their cage included a tank having a flow of about 50 gallons of water per minute. Between capture and arrival at Seattle on 3 December frequent storms were encountered. The female, probably near death when captured, refused to eat and died on 13 November. The male "Gus" survived the 3,000-mile trip and arrived in excellent condition.

It was demonstrated that: (1) sea otters may be transported without food and in small cages aboard unheated aircraft for several hours and arrive at their destination in excellent condition. Delays en route and overheating, however, may result in high mortality. (2) Aboard ship is a satisfactory method of transporting otters over great distances if a pool with an ample flow of clean water is available. (3) For short distances (up to 40 miles, at least) transportation by automobile is satisfactory.

Transplant Attempts

The idea of transplanting sea otters from areas of abundance to unpopulated parts of their former range, from which they were extirpated in the 19th century, has long been popular. Since 1950, six attempts to transplant otters were undertaken, the first five by the U.S. Fish and Wildlife Service and the sixth by the Alaska Department of Fish and Game. A brief resume of these attempts is presented below. Additional information concerning them is given under "Environmental Needs of Captives" and "Transportation of Captives."

A late-winter, early-spring attempt, 1951, to transplant sea otters by ship failed because of insufficient knowledge of the otters' needs in captivity. The 35 animals that were captured on Amchitka Island all died there before any were placed aboard the waiting ship.

Studies of captive otters were conducted in the winter of 1954 on Amchitka and were reported by Kirkpatrick et al. (1955) and Stullken and Kirkpatrick (1955). The knowledge gained through these studies was useful but did not assure survival of captives while awaiting transfer or while in transit to a new location.

Nevertheless, a transplant of 31 otters captured on Amchitka was attempted between 28 March and 4 April 1955. These otters were carried from Amchitka to the Pribilof Islands in cages with bedding of straw aboard the chartered fishing vessel *Paragon*. During the trip their fur became matted with filth, and when the 19 survivors were liberated each animal left a dirty brown trail in the water. Three of these were recaptured by hand within a few minutes of release. They were soaked to the skin, rigid with cold, and near death. None of the animals liberated was subsequently seen at the Pribilofs, and it is reasonably certain that none survived.

In early spring, 1956, Refuge Manager R. D. Jones, with Navy assistance, captured five otters at Amchitka and took them via ship 240 miles to Attu in the Near Islands. Jones told me that the pelage of these animals when they were released was in the usual soiled condition of animals held in dry bedding. No evidence is available to demonstrate whether or not any of these otters survived.

Because these experiences demonstrated the need for a short period of time in transit, the next experimental transplant was an attempt to take otters from Amchitka to the Pribilofs by air 11 December 1957. As described under "Transportation of Captives" none of the eight otters taken aboard a commercial, passenger-carrying airliner at Amchitka reached their destination.

The next experimental aerial transplant was undertaken in 1959 when an aircraft could be devoted exclusively to this undertaking. From 6 to 8 May, during a severe storm, 10 subadult otters were captured and placed in the pool enclosure. Three animals, in weakened condition when captured, soon died. Furthermore, the Amchitka pool was too small for 10 otters. Unless the animals were healthy when captured, their chance of survival was reduced by crowding and competition for food. Therefore, when animals died they were not replaced.

On 20 May, seven otters, including four females and three males, were taken to St. Paul Island by direct flight (see Transportation of Captives, Aircraft). They weighed 26 to 36 lb. and were estimated to be 1 to 1½ years old. They were marked with numbered monel tags on the hind flippers. The animals were liberated at Polovina Point within 20 minutes after landing. All appeared in excellent condition and, except for one, each accepted and ate a fish as it swam from shore. When liberated, the animals scattered.

On 21 May, D. L. Spencer and I watched one otter for some time from the cliffs of Reef Rookery (3 miles from the point of release). This animal was eating a large sea urchin and appeared contented and in good health. A brief aerial survey of a part of the west and south sides of St. Paul was made after takeoff on 21 May. Two additional otters were seen at this time; however, several thousand fur seals in the area made it difficult to distinguish otters.

Subsequent reports indicate that this transplant was partially successful in that the animals survived for a substantial period after liberation. Several observations of them were reported during the remainder of 1959 and in 1960. The last authentic sighting of one otter was by an experienced hunter, Maxim Buterin, in the spring of 1961. He saw it near the same place on two occasions.

Why these transplanted animals did not ultimately survive and reproduce is problematical. Two possible explanations may be considered: (1) Seven immature otters may be too small a nucleus to form a reproducing colony. Before they matured (estimated 2 to 3 years after liberation) too few survived natural attrition to form a colony. (2) The Pribilofs are at the northern limit of the species original range. Hardship caused by winter ice, as described by Nikolaev (1965) might be expected to have caused mortality.

In August 1965, John Vania and Edward Klinkhart, of the Alaska Department of Game, captured 41 and held 35 otters in a floating netted enclosure supported by a wooden frame and styrofoam floats in Constantine Harbor at Hinchinbrook Island in Prince William Sound, Alaska. Free circulation of water and a plentiful supply of food assured excellent survival in the holding facilities. The animals were transported 450 miles in a Grumman Goose Amphibian aircraft after receiving injections of a tranquilizer "Tranvet." During the 3.7-hour flight distress caused by overheating occurred. This problem of overheating was solved by constructing a container for water into the cages but 12 otters died in flight prior to the pen modification. On the last flight, after the cages had been modified, seven otters were transported. All

lived and were released in what appeared to be excellent condition. In all, 23 otters survived to be liberated on the west coast of Chichagof Island in Southeastern Alaska. Subsequent reports of sightings indicate that at least some of these animals survived the winter of 1965-66. Further transplants were conducted in 1966 and more are planned.

The knowledge and techniques are now available to hold captive otters in excellent health and to transport and liberate them in condition to survive. Large juveniles weighing about 24 to 35 lb. (11 to 16 kg.), approximately a year or somewhat older, are most adaptable to life in captivity and are hardy and more adjustable to stresses of travel than are older animals. Also, they are of a convenient size to handle. Before being transported in small carrying cages, animals should be held in a satisfactory enclosure for an adjustment period of a week or more.

It is yet to be shown that transplanted otters will form colonies and repopulate vacant habitat. Southeastern Alaska offers hundreds of miles of coastline suitable for sea otters. Will the transplanted otters behave like certain other mammals and scatter after release and therefore fail to form breeding aggregations? Might they also behave like other mammals and seek to return to the home territory where they were captured? These questions can be answered only by continued experimentation.

MANAGEMENT

Management of sea otters depends on knowledge of population size and trend. This knowledge may not become available until a cropping program has been in operation for several years. A tentative management program can, however, be set on the basis of present knowledge.

In the case of the sea otter, incomplete knowledge of population dynamics factors dictates that a flexible management program be initiated. This should be closely coordinated with a continuing program of studies of reproduction, mortality, maturation, aging, optimum population size, movements, and habitat status. Quantitatively these factors will vary in different habitats and according to population density, food availability, etc.

If a wildlife resource is to produce a maximum sustained annual yield, mortality from all causes must not exceed recruitment at an optimum population level. At the present stage of our knowledge of sea otter biology, the following recommendations for a management program appear relevant:

- (1) To attain knowledge of the population level of maximum sustainable yield, a relatively isolated study population should be chosen (Amchitka is a possible choice).
- (2) At the chosen location a sustained annual harvest should be taken without regard to economic yield.
- (3) Annual population surveys (preferably aerial) should be conducted where harvests take place.
- (4) Late winter and spring mortality should be monitored.
- (5) All female reproductive tracts, with carefully gathered field data, should be analyzed.
- (6) During harvesting operations animals of a size most desired by the fur market should be taken without regard to sex (the sex of an otter in the field is difficult to recognize) except that all females accompanied by young should be spared.
- (7) If it becomes evident that a kill predominating in males is desired, harvesting operations should be concentrated at or near known male concentration areas.

While a regular annual crop of otters is being taken from the chosen study population, otters should also be taken in other areas where they are now known to be abundant. These areas are (1) the Shumagin Islands, (2) the Bering Sea off Unimak Island and the tip of the Alaska Peninsula, (3) the Sanak Island-Sandman Reefs

area, (4) the western Andreanof Islands (including the Delarofs), and (5) the western Rat Islands.

ESTIMATED YIELD

If a harvest is taken from any population annually, the kill should probably be limited initially to about 2.5 percent of the total population (both sexes and all ages older than dependent young).

The total Alaska fur seal population is about 1,200,000 animals, including an annual production of about 350,000 young (Roppel, Johnson, Anas, and Chapman, 1966). The young constitute about 30 percent of the population. In the sea otter it was indicated (see *Reproduction in the Female*) that 2 years normally elapse between births and that the annual mean number of young in the population is about 14 percent, or approximately one-half that in the fur seal in which 1 year normally elapses between births. It has been found during many years of cropping the fur seal that, on a sustained yield basis, about 5 to 6 percent of the total population may be cropped annually. Under this management system the fur seal herd grew from a population of about 215,000 seals in 1911 to about one and a half million in the late 1940's (Kenyon, Scheffer, and Chapman, 1954) and between 1911 and 1963 yielded 2,761,170 skins (Roppel and Davey, 1965).

Thus, until further experience is gained, it may be concluded that about 2½ to 3 percent of the total sea otter population may be cropped annually on a sustained yield basis.

Further studies of reproduction and of the effect of cropping on populations may modify this preliminary estimate. In spite of the indication that a female sea otter may bear no more than one young in each 2-year interval, it is possible that because maternal care is intensive and prolonged the survival rate of young in a sea otter population might exceed that in the fur seal population.

CLOSED AREAS

Many observations indicate that before sea otters move from a populated area to adjacent vacant habitat, a large local population is formed (see *Distribution and Numbers*). They apparently move as a result of overutilization of food resources by a crowded population. It follows that if vacant habitat is to be repopulated, large local populations should be allowed to form to create the "population pressure" necessary to cause significant emigration. Thus, it is my opinion that the "spearhead" of population expan-

sion should not be disturbed if nearby but vacant habitat is to be repopulated.

HABITAT STUDIES

Studies of abundance of food species should be undertaken where sea otters are abundant and where they are sparse. It has been observed in several areas that sea otters are capable of overutilizing food resources. In a heavily utilized area, for example Amchitka, underwater exclosures large enough for a diver to enter could be established to evaluate the status of food organisms during a long period in exploited and unexploited areas. During the Amchitka study period (1955-63), it appeared that a large sea otter population was at that time overexploiting its habitat. Body weights of otters were less than those of otters from sparse populations, and the pelage of Amchitka otters appeared "poor" compared to that of otters from a sparse population. Under the condition of a depleted habitat, population manipulation may be necessary for a period of years before habitat recovery occurs and animals having optimum body size and pelage are produced.

TRANSPLANT STUDIES

Capturing, holding, and transporting sea otters is complicated and expensive. The results of experimental transplants are not yet evaluated. Why the transplant of seven healthy, subadult otters to St. Paul Island, Alaska, apparently failed ultimately to survive, in spite of survival after the animals were released, is not known (see Transplant Attempts). Repeated observations of the small Samalga-Umnak population indicate that a small isolated population grows slowly. Studies and transplant experiments undertaken by the State of Alaska and now in progress should yield valuable information. It appears probable that in certain areas and when a significant number of otters may be moved, transplanting may prove to be a valuable management device.

REFERENCES

- ABEGGLEN, C. E., A. Y. ROPPEL, and F. WILKE.
1960. Alaska fur seal investigations, Pribilof Islands, Alaska. Report of field activities June-October 1960. U.S. Fish and Wildlife Service, Marine Mammal Biological Laboratory, Seattle, Wash. Unpublished.
- ALLANSON, A.
1955. Sea otters on San Miguel. *Pacific Discovery*, vol. 8, No. 3, p. 24-25.
- ANTHONY, A. W.
1925. Expedition to Guadalupe Island, Mexico, in 1922. *Proceedings California Academy of Science*, 4th series, vol. 14, No. 13, p. 277-320.
- BAILEY, V.
1936. The mammals and life zones of Oregon. U.S. Bureau of Biological Survey, *North American Fauna* No. 55, 416 p.
- BARABASH-NIKIFOROV, I. I.
1947. Kalan. [The sea otter, pp. 1-174.] Soviet Ministrov RSFSR. Glavnoe upravlenie po zapovednikam. (In Russian.) [Translated from Russian by Dr. A. Birron and Z. S. Cole. Published for the National Science Foundation by the Israel Program for Scientific Translations, Jerusalem, 1962. 227 p., illus.]
- BAUER, RICHARD D., ANCEL M. JOHNSON, and VICTOR B. SCHEFFER.
1964. Eye lens weight and age in the fur seal. *Journal of Wildlife Management*, vol. 28, No. 2, p. 374-376, April.
- BEALS, F. L.
1943. Memorandum to Regional Director, Fish and Wildlife Service, Juneau, Alaska. Sept. 28, 1943. 3 p. 1 map.
- BEE, J. W., and E. R. HALL.
1956. Mammals of northern Alaska on the arctic slope. University of Kansas, *Miscellaneous Publication* No. 8. 309 p.
- BELKIN, A. N.
1966. On the population abundance of sea otter on the Kuril Islands. *Transactions Pacific Research Institute of Marine Fisheries and Oceanography*, vol. 58, p. 3-13.
- BENTLEY, W. W.
1959. Sea otter along the California coast. *Journal of Mammalogy*, vol. 40, No. 1, p. 147.
- BOOLOOTIAN, R. A.
1961. The distribution of the California sea otter. *California Fish and Game*, vol. 47, No. 3, p. 287-292.
- BURROUGHS, R. D.
1961. The natural history of the Lewis and Clark Expedition. Michigan State University Press, East Lansing. 340 p.

CALIFORNIA SENATE.

1963. Effect of the sea otter on the abalone resource. Senate Permanent Factfinding Committee on Natural Resources, Subcommittee on sea otters, Hearing, San Luis Obispo, Nov. 19, 1963. 148 p. (Processed.)
1965. The sea otter and its effect upon the abalone resource [Section 1, Chapter 7, pp. 129-144]. In Third Progress Report to the Legislature, 1965 Regular Session. Senate Permanent Factfinding Committee on Natural Resources (Sacramento). 144 p.

CHAPSKII, K. K.

1952. Age determination of some mammals according to bone microstructure. (In Russian.) Journal Institute Natural Sciences, Moscow, *Izvestiya Estestivnonnauchnogo Instituta imeni P.S. Lesgafta*, vol. 25, p. 47-66.

COCKS, A. H.

1881. Notes on the breeding of the otter. Proceedings, Zoological Society of London, p. 249-250.

COMMERCIAL FISHERIES REVIEW.

- 1964a. Sea otter population survey. Vol. 26, No. 4, p. 12-13.
- 1964b. Sea otter population survey continued. Vol. 26, No. 5, p. 13.
- 1964c. Sea otter population determined by census. Vol. 26, No. 8, p. 15.

COWAN, I. MCT., and C. J. GUIGUET.

1956. The mammals of British Columbia. British Columbia Provincial Museum, Handbook No. 11. 413 p.

COX, K. W.

1962. California abalones, Family Haliotidae. Resources Agency of California Department of Fish and Game, Fish Bulletin No. 118. 133 p.

DALL, W. H.

1870. Alaska and its resources. Sampson Low, Son, and Marston, London. 628 p.

DUKES, H. H.

1943. The physiology of domestic animals. Comstock Publishing Co. Ithaca, N.Y. 5th ed. revised.

EBERT, EARL E.

1968. A food habits study of the southern sea otter, *Enhydra lutris nereis*. California Fish and Game, vol. 54, No. 1, p. 33-42.

ELLIOTT, H. W.

1875. A report upon the condition of affairs in the territory of Alaska. Government Printing Office, Washington, D.C. 277 p.

ESSAPIAN, F. S.

1953. The birth and growth of a porpoise. Natural History, vol. 62, p. 392.

EVERMANN, B. W.

1923. Marine life of the Pacific. Commonwealth Club of California, Transactions, vol. 18, No. 3, p. 109.

EYERDAM, W. J.

1933. Sea otters in the Aleutian Islands. Journal of Mammalogy, vol. 14, No. 1, p. 70-71.

FAY, F. H.

1958. Pacific walrus investigations on St. Lawrence Island, Alaska. Alaska Cooperative Wildlife Research Unit. 54 p. (Processed.)

FISCUS, CLIFFORD H., and HIROSHI KAJIMURA.

1967. Pelagic fur seal investigations, 1965. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries, No. 537. 42 p.

- G. BAINES, and F. WILKE.
1964. Pelagic fur seal investigations. U. S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 475. 59 p.
- FISHER, EDNA M.
1939. Habits of the southern sea otter. *Journal of Mammalogy*, vol. 20, No. 1, p. 21–36.
1940a. Early life of a sea otter pup. *Journal of Mammalogy*, vol. 21, No. 2, p. 132–137.
1940b. The sea otter past and present. *Proceedings Sixth Pacific Science Congress*, No. 3, p. 223–236. University of California Press, Berkeley.
1941a. Prices of sea otter pelts. *California Fish and Game*, vol. 27, No. 4, p. 261–265, October.
1941b. Notes on the teeth of the sea otter. *Journal of Mammalogy*, vol. 22, No. 4, p. 428–433, November.
1942. Osteology and myology of the California river otter. Stanford University Press. 66 p.
- FISHER, H. I.
1957. Footedness in domestic pigeons. *Wilson Bulletin*, vol. 69, p. 170–177.
- FISLER, G. F.
1962. Ingestion of sea water by *Peromyscus maniculatus*. *Journal of Mammalogy*, vol. 43, No. 3, p. 416–417.
- FOX, D. L.
1953. *Animal Biochromes*. Cambridge University Press, p. 195. [Footnote by Dr. E. M. Scott concerning the purple pigment of sea otter bones, p. 195.]
- FRIEDMANN, H., and M. DAVIS.
1938. "Left-handedness" in parrots. *Auk*, vol. 55, p. 478–480.
- GENTRY, R. L., and R. S. PETERSON.
1967. Underwater vision of the sea otter. *Nature*, vol. 216, p. 435–436.
- GILBERT, P. W. (Editor).
1963. *Sharks and survival*. D.C. Heath, Boston. 578 p.
- GOLODOFF, INNOKENTY.
1966. The last days of Attu Village. [As told to Karl W. Kenyon.] *Alaska Sportsman*, vol. 32, No. 12, p. 8–9.
- GRIBKOV, P. F.
1963. O rasprostranenií morskoi vydry po poberezh'yu Kamchatskogo polostrova. [Dispersion of the sea otter along the coast of the Kamchatka peninsula.] *In Voprosy geografii Kamchatki*. [Problems on the geography of Kamchatka.] *Kamchatskaya Pravda*, Petropavlovsk-Kamchatskii, vol. 1, p. 68–71.
- GULIN, V.
1952. Neobychnyzyver'na chukotka [Unusual mammal in Chukotka]. [Torch] (Moscow), vol. 50, p. 31, illus.
- HALL, E. RAYMOND.
1945. Chase Littlejohn, 1854–1943: observations by Littlejohn on hunting sea otters. *Journal of Mammalogy*, vol. 26, No. 1, p. 89–91.
- and KEITH R. KELSON.
1959. *The mammals of North America*, vol. 2, p. 949–950. Ronald Press Co., New York.

- HALL, K. R. L.
1965. Tool-using behaviour of the California sea otter. *Medical and Biological Illustrations*, October, vol. 15, No. 4, p. 216-217.
- and G. B. SCHALLER.
1964. Tool using behavior of the California sea otter. *Journal of Mammalogy*, vol. 45, No. 2, p. 287-298.
- HAMILTON, W. J., JR., and W. R. EADIE.
1964. Reproduction in the otter, *Lutra canadensis*. *Journal of Mammalogy*, vol. 45, No. 2, p. 242-252.
- HARRIS, C. J.
1968. Otters, a study of the recent Lutrinae. Weidenfeld & Nicolson, London. 397 p.
- HILDEBRAND, M.
1954. Incisor tooth wear in the sea otter. *Journal of Mammalogy*, vol. 35, No. 4, p. 595.
- HOOPER, C. L.
1897. A report on the sea-otter banks of Alaska. U.S. Treasury Department, Document No. 1977. 35 p., 2 maps.
- HOWELL, A. BRAZIER.
1930. Aquatic mammals. Chas. C. Thomas Co., Springfield.
- HUGGETT, A. ST. G., and W. F. WIDDAS.
1951. The relationship between mammalian foetal weight and conception age. *Journal of Physiology*, No. 144, p. 306-317.
- HUTCHINSON, H. B.
1935. Sea otter in the Rat Islands—a report on the existence of. Unpublished memo written aboard the USS *Oglala*, Constantine Harbor, Amchitka Island, 21 June. 6 p.
- ICHIHARA, T.
1966. Criterion for determining age of fin whale with reference to ear plug and baleen plate. *Scientific Report of Whales Research Institute*, No. 20, p. 17-82. Whales Research Institute, Tokyo, Japan.
- JELLISON, WILLIAM L., and KENNETH A. NEILAND.
1965. Parasites of Alaskan vertebrates. University of Oklahoma Research Institute, Project 1508. 73 p. (Processed.)
- JENSEN, A.
1964. Odderen i Danmark [The otter in Denmark]. *Danske Vildtundersøgelser*, Heft 11, Kalø Ronde. 48 p. (In Danish with English summary.)
- JONES, R. D.
1949-59. Refuge narrative reports. Unpublished, in U.S. Fish and Wildlife Service files.
1951. Present status of the sea otter in Alaska. *Transactions of the 16th N. A. Wildlife Conference*, March 5, 6, and 7, p. 376-383.
1963. Buldir Islands, site of a remnant breeding population of Aleutian Canada Geese. *Wildfowl Trust 14th Annual Report 1961-62*, p. 80-84.
1965. Sea otters in the Near Islands, Alaska. *Journal of Mammalogy*, vol. 46, No. 4, p. 702.
- JORDAN, DAVID STARR.
1898-99. The fur seals and fur-seal islands of the North Pacific Ocean. U.S. Treasury Department, Document 2017, 4 parts.
- JOYNT, G. T.
1957. Sea otter observations. Unpublished letter of March 1957, U.S. Fish and Wildlife Service files.

KENYON, K. W.

1959. The sea otter. Smithsonian Report for 1958, publication 4364, p. 399-407.

1961. Birds of Amchitka Island, Alaska. Auk, vol. 78, No. 3, p. 304-326.

1964. Wildlife and historical notes on Simeonof Island, Alaska. Murrelet, vol. 45, No. 1, p. 1-8.

1965a. Food of harbor seals at Amchitka Island, Alaska. Journal of Mammalogy, vol. 46, No. 1, p. 103-104.

1965b. Aerial survey of sea otters and other marine mammals, Alaska Peninsula and Aleutian Islands, 19 April to 9 May 1965. U.S. Bureau of Sport Fisheries and Wildlife, Seattle, Wash. 52 p. (Processed.)

— and D. L. SPENCER.

1960. Sea otter population and transplant studies in Alaska, 1959. U.S. Fish and Wildlife Service, Special Scientific Report—Wildlife, No. 48. 29 p.

— and V. B. SCHEFFER.

1962. Wildlife surveys along the northwest coast of Washington. Murrelet, vol. 42, No. 3, p. 29-37.

— C. E. YUNKER, and I. M. NEWELL.

1965. Nasal mites (Halarachnidae) in the sea otter. Journal of Parasitology, vol. 51, No. 6, p. 960.

— VICTOR B. SCHEFFER, and DOUGLAS G. CHAPMAN.

1954. A population study of the Alaska fur-seal herd. U.S. Fish and Wildlife Service, Special Scientific Report—Wildlife, No. 12. vi + 77 p. (Processed.)

KEYES, MARK C.

1963. Necrotic hemorrhagic enteritis in a seal. Small Animal Clinician, vol. 3, No. 11, p. 627.

KING, JUDITH E.

1964. Seals of the world. British Museum (Natural History), London. 154 p.

KIRKPATRICK, C. M., D. E. STULLKEN, and R. D. JONES, JR.

1955. Notes on captive sea otters. Journal Arctic Institute of North America, vol. 8, No. 1, p. 46-59.

KLUMOV, S. K.

1957. [Breeding places of the fur seal (*Callorhinus ursinus*) and areas inhabited by the sea otter (*Enhydra lutris*) in the Kurils and a tentative estimation of their numbers.] Doklady Akademii Nauk SSSR, vol. 117, No. 1-6, p. 153-156. Translated and published by American Institute of Biological Sciences.

KROG, J.

1953. Notes on the birds of Amchitka Island, Alaska. Condor, vol. 55, p. 299-304.

LACK, D.

1954. The natural regulation of animal numbers. Oxford at the Clarendon Press. 343 p.

LANE, F. W.

1946. Right and left in animals. Zoo Life, vol. 1, p. 30-31.

LANG, T. G., and K. S. NORRIS.

1965. Swimming speed of a Pacific bottlenose porpoise. Science, vol. 151, p. 588-590.

LAUGHLIN, W. S.

1963. The earliest Aleuts. Anthropological papers of the University of Alaska, vol. 10, No. 2, p. 73-136.

LEE, C. F.

1948. Thiaminase in fishery products: a review. Commercial Fisheries Review, vol. 10, No. 4, p. 7-17.

LENSINK, C. J.

1958. Report on sea otter surveys 6 May to 28 September 1957. Unpublished Report, 61 p., in Fish and Wildlife Service Files.

1960. Status and distribution of sea otters in Alaska. Journal of Mammalogy, vol. 41, No. 2, p. 172-182.

1962. The history and status of sea otters in Alaska. A thesis submitted to the Faculty of Purdue University in partial fulfillment of the requirements for the degree of Doctor of Philosophy. Unpublished, copy in Fish and Wildlife Service files.

LIERS, E. E.

1951. Notes on the river otter (*Lutra canadensis*). Journal of Mammalogy, vol. 32, No. 1, p. 1-9.

LOY, C. L.

1940. Sea otter report of Amchitka Island, Alaska, July 10, 1939 to January 15, 1940. Unpublished report in Fish and Wildlife Service files.

——— and O. A. FRIDEN.

1937. Sea otter survey of Amchitka Island, Alaska, July 11 to September 1, 1937. Unpublished report in Fish and Wildlife Service files.

LUTKE, F.

1835. Voyage autour du monde . . . dans les années 1826, 1827, 1828, et 1829. Paris, Firmin Didot Freres, 3 vols. and atlas.

MANGEN, J. B., and G. RITTER.

1940. Amchitka Island Report. U.S. Fish and Wildlife Service, unpublished.

MARAKOV, S. V.

1963. Relic of nature or exploitable species?—Fate of the Komandorskii sea otter. Priroda No. 11, p. 79-83, Moscow. [Translated by U.S. Department of Commerce, Office of Technical Services, Joint Publications Research Service, Washington, D.C.]

1965. The present status of the Komandorski population of *Enhydra lutris* L. and prospects for its practical usage. In Marine Mammals, E. N. Pavlovskii, B. A. Zenkovich, et al., (Editors). [p. 212-220]. Translated by Nancy McRoy, April 1966.

MAYNARD, LT. WASHBURN.

1898 (1874). The sea otter [vol. 3, p. 300-302]. In Seal and salmon fisheries and general resources of Alaska. U.S. Treasury Department, 4 volumes, published 1898; Maynard's contribution dated 1874. (55th Congress, 1st session, House Document 92, pts. 1-4.)

MCCANN, CHARLES.

1955. Observations on the polecat (*Putorius putorius* Linn.) in New Zealand. Records of Dominion Museum, vol. 2, pt. III, p. 151-165.

MCCRACKEN, HAROLD.

1957. Hunters of the stormy sea. Doubleday, Garden City, N.Y. 312 p.

MCLAREN, I. A.

1960. Are the Pinnipedia byphyletics? Systematic Zoology, vol. 9, No. 1, March, p. 18-28.

McLAUGHLIN, PATSY A.

1963. Survey of the benthic invertebrate fauna of the eastern Bering Sea. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries, No. 401. 75 p.

MCLEAN, J. H.

1962. Sublittoral ecology of kelp beds of the open coast area near Carmel, California. *Biological Bulletin*, vol. 122, No. 1, p. 95-144.

MILLER, P., and L. G. MILLER.

1967. Lost heritage of Alaska: The adventure and art of Alaskan coastal Indians. World Publishing Co., Cleveland, Ohio. 289 p.

MILLER, G. S., and R. KELLOGG.

1955. List of North American recent mammals. U.S. National Museum, Bulletin 205. 954 p.

MITCHELL, EDWARD.

1966. Northeastern Pacific Pleistocene sea otters. *Journal Fisheries Research Board of Canada*, vol. 23, No. 12, p. 1897-1911.

MURIE, O. J.

1940. Notes on the sea otter. *Journal of Mammalogy*, vol. 21, No. 2, p. 119-131.

1959. Fauna of the Aleutian Islands and Alaska Peninsula. U.S. Fish and Wildlife Service, North American Fauna, No. 61. 406 p.

NEILAND, K. A.

1962. Alaskan species of acanthocephalan genus *Corynosoma* Luehe, 1904. *Journal of Parasitology*, vol. 48, p. 69-75.

NIKOLAEV, A. M.

1960. O dinamike chislennosti Kalanov v SSSR [Change in the number of sea otter in the USSR]. *Trudy Sakhalinsk, Kompleksn. Nauchn.-Issled. Inst. 9*, 108-121. Referat. *Zur., Biol.*, 1962 No. 141256. [Translated abstract seen.]

1961. O rasprostraneni chislennosti i biologii kalanov. [The biology and population spread of the sea otter.] *Trudy Soveshchani Ikhthiol. Kommiss. Akad. Nauk SSSR 12*, p. 214-271.

- 1965a. The status of the stock of Kurile sea otters and fur seals and measures of their reproduction. *In Marine Mammals*, E. N. Pavlovskii, B. A. Zenkovich, et al., (Editors). [P. 226-230.] Translated by Nancy McRoy, April 1966.

- 1965b. On the feeding of the Kurile sea otter and some aspects of their behavior during the period of ice. *In Marine Mammals*, E. N. Pavlovskii, B. A. Zenkovich, et al., (Editors). [P. 231-236.] Translated by Nancy McRoy, April, 1966.

— and V. A. SKALKIN.

1963. O pitanii Kuril' skikh kalanov. [The diet of the Kamchatka sea-otter in the Kurile Islands.] *Tr. Sakhalinsk. Kompleksnyi Nauchn.-Issled. Inst. 14*, p. 54-78.

NOVIKOV, G. A.

1956. Predatory mammals of USSR fauna. (In Russian.) Moscow, Academy of Sciences of USSR. 294 p.

NOZIKOV, N.

- 194?. Russian voyages around the world. Hutchinson & Co. Ltd. London. 165 p. [Translated from Russian by E. and M. Lesser.] No publication date is given.

- OGDEN, A.
1941. The California sea otter trade 1784-1848. University of California Press, Berkeley and Los Angeles. 251 p.
- ORR, R. T.
1959. Sharks as enemies of sea otters. *Journal of Mammalogy*, vol. 40, No. 4, p. 617.
— and T. C. POULTER.
1964. Northward movement of the California sea otter. *California Fish and Game*, vol. 50, No. 2, p. 122-124.
- PATCH, C. A.
1922. A biological reconnaissance on Graham Island of the Queen Charlotte Group. *Canadian Field Naturalist*, vol. 36, p. 101-105, 133-136.
- PEDERSEN, R. J., and J. STOUT.
1963. Oregon sea otter sighting. *Journal of Mammalogy*, vol. 44, No. 3, p. 415.
- PETERSON, R. S.
1965. Behavior of the northern fur seal. Doctor of Science Thesis. 214 p. [Unpublished.]
— and M. W. ODEMAR.
1969. Population growth of the sea otter in California: results of aerial censuses and behavioral studies. A paper read to the 49th Annual Meeting of the American Society of Mammalogists, June 17, 1969. New York. 7 p. + 3 figs. (Processed.)
— and W. G. REEDER.
1966. Multiple births in the northern fur seal. *Zeitschrift fur Säugetierkunde*, vol. 31, No. 1, p. 52-56.
- POLAND, H.
1892. Fur-bearing animals in nature and in commerce. Burney and Jackson, London. 392 p.
- PREBEL, E. A., and W. L. MCATEE.
1923. Birds and mammals of the Pribilof Islands, Alaska. U.S. Bureau of Biological Survey, North American Fauna, No. 46. 255 p.
- RAUSCH, R. L.
1953. Studies on the helminth fauna of Alaska. XIII. Disease in the sea otter, with special reference to helminth parasites. *Ecology*, vol. 34, No. 3, p. 584-604.
1964. Studies on the helminth fauna of Alaska. XLI. Observations on cestodes of the genus *Diplogonoporus* Lonnberg, 1892 (Diphyllobothriidae). *Canadian Journal of Zoology*, vol. 42, p. 1049-1069.
- RAUSCH, ROBERT, and BETTY LOCKER.
1951. Studies on the helminth fauna of Alaska. II. On some helminths parasitic in the sea otter, *Enhydra lutris* (L.). *Proceedings of the Helminthological Society of Washington*, vol. 18, No. 1, p. 77-81, January.
- RESHETKIN, V. V., and N. K. SHIDLOVSKAYA.
1947. [Acclimatization of sea otters, p. 175-224.] *In* Kalan, by I. I. Barabash-Nikiforov, Soviet Ministrov RSFSR. Glavnoe upravlenie po zapovednikam, (In Russian.). [Translated from Russian by Dr. A. Birron and Z. S. Cole. Published for the National Science Foundation by the Israel Program for Scientific Translations, Jerusalem, 1962. 227 p., illus.]
- ROPPEL, ALTON Y., and STUART P. DAVEY.
1965. Evolution of fur seal management on the Pribilof Islands. *Journal of Wildlife Management*, vol. 29, No. 3, p. 448-463.

- ANCEL M. JOHNSON, RAYMOND E. ANAS, and DOUGLAS G. CHAPMAN.
1966. Fur seal investigations, Pribilof Islands, Alaska, 1965. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries, No. 536. 45 p.
- SCAMMON, C. M.
1870. The sea otters. *American Naturalist*, vol. 4, No. 2, p. 65–74.
- SCAPINO, ROBERT P.
1965. The third joint of the canine jaw. *Journal of Morphology*, vol. 116, No. 1, p. 23–50.
- SCHEFFER, V. B.
1940. The sea otter on the Washington coast. *Pacific Northwest Quarterly*, vol. 3, p. 370–388.
1950a. Growth layers on the teeth of Pinnipedia as an indication of age. *Science*, September 15, vol. 112, No. 2907, p. 309–311.
1950b. The food of the Alaska fur seal. U.S. Fish and Wildlife Service, Wildlife Leaflet 329. 15 p.
1951. Measurements of sea otters from western Alaska. *Journal of Mammalogy*, vol. 32, No. 1, p. 10–14.
1955. Body size with relation to population density in mammals. *Journal of Mammalogy*, vol. 36, No. 4, p. 493–515.
1958. Long life of a river otter. *Journal of Mammalogy*, vol. 39, No. 4, November, p. 591.
1960. Weights of organs and glands in the northern fur seal. *Mammalia*, vol. 24, No. 3, p. 476–481.
1962. Pelage and surface topography of the northern fur seal. U.S. Fish and Wildlife Service, North American Fauna, No. 64. 206 p.
1963. Book review: "The natural history of the Lewis and Clark expedition," edited by Raymond Darwin Burroughs. *Pacific Northwest Quarterly*, vol. 54, No. 2, p. 80–81.
1964. Estimating abundance of pelage fibres on fur seal skin. *Proceedings Zoological Society of London*, vol. 143, part 1, p. 37–41.
- and ANCEL M. JOHNSON.
1963. Molt in the northern fur seal. U. S. Fish and Wildlife Service, Special Scientific Report—Fisheries, No. 450. 34 p.
- and BERTRAM S. KRAUS.
1964. Dentition of the northern fur seal. *Fishery Bulletin*, vol. 63, No. 2, p. 293–342.
- and FORD WILKE.
1950. Validity of the subspecies *Enhydra lutris nereis*, the southern sea otter. *Journal of the Washington Academy of Sciences*, vol. 40, No. 8, p. 269–272, August 15.
- SCHUMACHER, G. H.
1961. Funktionelle Morphologie der Kaumuskulatur. Gustav Fisher, Jena.
- SHIDLOVSKAYA, N. K.
1947. [Directions for the feeding and care of the male sea otter, p. 225–227.] *In* Kalan, by I. I. Barabash-Nikiforov, Soviet Ministrov RSFSR. Glavnoe upravlenie po zapovednikam, p. 263–266. [Translated from Russian by Dr. A. Birron and Z. S. Cole. Published for National Science Foundation by Israel Program for Scientific Translations, Jerusalem, 1962. 227 p., illus.]

SINHA, A. A.

1965. Morphology of the female reproductive organs of sea otters (*Enhydra lutris* L.). University of Missouri, Ph.D., 1965, Zoology (Unpublished).

——— C. H. CONAWAY, and K. W. KENYON.

1966. Reproduction in the female sea otter. *Journal of Wildlife Management*, vol. 30, No. 1, p. 121-130.

——— and H. W. MOSSMAN.

1966. Placentation of the sea otter. *American Journal of Anatomy*, vol. 119, No. 3, p. 521-554.

——— and C. H. CONAWAY.

1968. The ovary of the sea otter. *Anatomical Record*, vol. 160, p. 795-806.

SLIJPER, E. J.

1956. Some remarks on gestation and birth in cetacea and other aquatic mammals. *Hvalrådets Skrifter*, vol. 41, p. 1-62.

1962. Whales. Basic Books Publishing Co. 475 p. English translation of Walvissen, D. B. Centen's, Uitgeversmaatschappij, Amsterdam.

SNOW, H. J.

1910. In forbidden seas. Edward Arnold, London. 303 p.

STEJNEGER, L.

1936. Georg Wilhelm Steller. Harvard University Press. 623 p.

STELLER, G. W.

1751. De Bestiis marinis. *Novi Comm. Acad. Sci. Petropolitanae*, vol. 2, p. 289-398, 3 pls. [English translation by Walter Miller and Jennie Emerson Miller (part 3, p. 179-218). In *The fur seals and fur seal islands . . . see Jordan and Clark, 1898-1899, U. S. Treasury Department, Document 2017.*]

STILES, W. B.

1953. The sea otter (*Enhydra marina*). Unpublished manuscript, Fish and Wildlife Service files, Washington, D.C. 19 p.

STULLKEN, DONALD E., and C. M. KIRKPATRICK.

1955. Physiological investigation of captivity mortality in the sea otter (*Enhydra lutris*). *Transactions 20th North American Wildlife Conference*, p. 476-494.

SVERDRUP, H. U., M. W. JOHNSON, and R. H. FLEMING.

1942. *The oceans*. Prentice-Hall, Englewood Cliffs, N.J. 1087 p.

SWICEGOOD, Lcdr. S. P.

1936. Amchitka sea otter survey expedition. Unpublished memo from Commanding Officer, U.S. Coast Guard Cutter *Chelan*, 31 August 1936. 5 p. U.S. Fish and Wildlife Service files.

TAYLOR, WALTER P.

1914. The problem of aquatic adaptation in the Carnivora, as illustrated in the osteology and evolution of the sea-otter. University California Publication, Bulletin Department of Geology, vol. 7, p. 465-495, 15 text figures. (p. 468—drawing of skeleton in standing attitude.)

THENIUS, E., and H. HOFER.

1960. *Stammesgeschichte der Säugetiere*. Springer, Berlin. 322 p.

U. S. BOARD ON GEOGRAPHIC NAMES.

1963. Decisions on geographic names in the United States. Decision list No. 6302. 81 p.

U. S. BUREAU OF FISHERIES.

- 1906-11. The commercial fisheries of Alaska in 1905 [. . . 1910]. (Annual reports.)
- 1912-42. Alaska fisheries and fur-seal industries in 1911 [. . . 1940]. (Annual reports.)
1929. Laws and regulations for the protection of fur seals and sea otters. Department of Commerce Circular 285, 2d ed. Alaska Fisheries Service. 10 p.

VORONOV, V. G.

1960. Opyt otlova kalanov (*Enhydra lutris* L.) na Kuril skikh ostrovakh. [Experimental trapping of sea otters (*Enhydra lutris* L.) in the Kurile Islands.] Trudy Sakhalinsk. Kompleksn. Nauchn.-Issled. Inst. 9, p. 122-129. 1960; Referat. Zhur., Biol. 1962, No. 14 1222. (Abstract of translation only seen.)
1965. Present problems in the study and industrial use of the Kurile sea otter. In Marine Mammals, E. N. Pavlovskii, B. A. Zenkovich, et al. (Editors). [p. 221-225.] Translated by Nancy McRoy, April, 1966.
1967. The effect of tsunami on sea otter populations. Priroda (Nature), No. 8, p. 70-72.

WARREN, J. M.

1953. Handedness in the Rhesus monkey. Science, vol. 118, p. 622-623.

WILDMAN, A. B.

1954. The microscopy of animal textile fibres, including methods for the complete analysis of fibre blends. Wool Industries Research Association, Torridon, Headingley, Leeds. 209 p.

WILKE, F.

1957. Food of sea otters and harbor seals at Amchitka Island. Journal of Wildlife Management, vol. 21, No. 2, p. 241-242.

WILLIAMS, C. S.

1937. Notes of the distribution and food habits of the American sea otter, 1936. Unpublished manuscript, Fish and Wildlife Service files.
1938. Notes on food of the sea otter. Journal of Mammalogy, vol. 19, No. 1, p. 105-107.

Appendix 1

FIELD STUDIES OF SEA OTTERS, 1954-66

From 1949 to 1954, Refuge Manager R. D. Jones, Jr., reported sea otter observations. In the winter of 1950-51 he attempted a sea otter transplant. Dr. Robert Rausch and others of the U.S. Public Health Service studied and reported on the helminth parasites of the sea otter. These studies and the reports of other observers are reviewed elsewhere in this report. The purpose of this chronological list is to record the field activities of the U.S. Fish and Wildlife Service under the sea otter study program which actually began in 1954 but was not formally begun until 1955. Appendix 2 summarizes material gathered from 1955 through 1965.

Aleut laborers who participated in various phases of sea otter field work include the late Fred Bezezekoff (Nikolski), Anton Bezezekoff (Nikolski), John Nevzeroff (Atka), Innokenty Golodoff (Atka), and David Zaochni (Atka).

The expeditions listed below include a cumulative time of more than 2 years and 9 months of field work.

1954

10 February to 4 April. Aleutian Islands. At Amchitka Island, field studies of sea otters. (D. Hooper, R. D. Jones, C. M. Kirkpatrick, C. J. Lensink, D. E. Stullken, and F. Wilke.)

1955

15-17 March. Shumagin Islands. Observe sea otters at Simeonof, Little Koniuji, and Herendeen Islands. Transportation aboard M/V *Paragon* (Kenyon, Lensink, and Wilke).

27 March to 4 April. Aleutian Islands. At Amchitka Island capture and hold sea otters for transplant. (Jones, Kenyon, Lensink, and Wilke.)

9-10 April. Transplant attempt. Liberate sea otters at Otter Island, Pribilof Islands.

14-15 April. Shumagin Islands. Attempt to capture sea otters at Simeonof Island. (Kenyon and Wilke.)

- 26 July to 5 October. Aleutian Islands. At Amchitka Island observe sea otters; experiments with methods of holding otters in captivity and obtaining a food supply for them. (Kenyon.)
- 10 October. Seattle, Wash. Place two sea otters in Woodland Park Zoo.

1956

- 5 May to 26 July. Aleutian Islands. At Amchitka Island, field studies of sea otters and further experiments with feeding and holding in captivity. (Kenyon and Lensink.)
- 30 July. Seattle, Wash. Place two sea otters in Woodland Park Zoo.

1957

- 6 May to 28 September. Alaska survey. From Kodiak Island to Adak Island, field studies of population size and distribution of sea otters were conducted using boats and aircraft. (C. J. Lensink remained in the field during the entire period. R. D. Jones, R. Lopp, D. L. Spencer, W. Troyer, and Wilke participated with him in different areas.)
- 1 October to 11 December. Aleutian Islands. Amchitka Island, field studies of otters and further experiments in captive care and feeding of otters. (K. L. Binkley, Kenyon, and H. R. Krear.)
- 14 December. Seattle, Wash. Place two sea otters in Woodland Park Zoo.

1958

- 10-21 March. California. Search for sea otters in coastal areas and at Santa Rosa and San Miguel Islands of the Channel Islands group aboard the M/V *Trinity*. (W. J. Barmore and Kenyon.)

1959

- 14-21 January. Aleutian Islands. Adak Island. Conduct two experimental aerial surveys of sea otters using U.S. Navy UF-1 aircraft. Flight time: 5.6 hours. (Kenyon.)
- 21 January to 20 May. Aleutian Islands. At Amchitka Island, field studies of sea otters and experiments with otters in captivity were conducted. (Kenyon.)
- 19 May. Aleutian Islands. Aerial survey of sea otters from Attu to Amchitka Island using DC-3 aircraft. Flight time: 9.1 hours. (Kenyon, T. Smith, D. L. Spencer, and J. Tilford.)
- 20 May. Pribilof Islands transplant. Fly seven sea otters to St. Paul Island in a DC-3 aircraft and liberate them there. Flight time: 4.3 hours.
- 21 May. St. Paul Island. Observations of liberated otters.
- 21-28 May. Aleutian Islands. Aerial survey of sea otters from Semisopochnoi Island eastward to Herbert Island in the Islands of Four Mountains, inclusive, using a DC-3 aircraft. Flight time: 19 hours. Total flight time entire operation: 56.8 hours. (Kenyon, Smith, Spencer, and Tilford.)
- 13 July. Washington State. Aerial reconnaissance of coastal waters along outer coast of the Olympic Peninsula using a U.S. Coast Guard UF-2 aircraft. Flight time: 3 hours. (G. Eddy, Kenyon, F. Richardson, and V. B. Scheffer.)
- 14-18 July. Washington State. Boat survey of rocks and islets off the outer coast of the Olympic Peninsula. (Eddy, Kenyon, Richardson, and Scheffer.)

1960

- 2-5 March. Aleutian Islands. Aerial surveys of sea otters from the Islands of Four Mountains to the Sandman Reefs inclusive, using a DC-3 aircraft. Total flight time: 21.3 hours. (Kenyon, D. W. Rice, Smith, and Spencer.)
- 30 May to 13 July. Island surveys (surface only) in Alaska. Field studies of sea otters at Simeonof, Little Koniuji, Herendeen, and Nagai in the Shumagin Islands; at Caton and Sanak Islands; at Tigalda Island and in the waters off Unimak Island in the Aleutian Islands, and at Amak Island; transportation between islands was furnished by the M/V *Windward*. (C. H. Fiscus, Kenyon, and the late T. O'Brien.)

1961

- 3 July to 1 August. Commander Islands. Field observations of sea otters at the Soviet controlled islands of Medny and Bering; transportation aboard the USSR ships *Orel* and *Steregushti* and the U.S. FWS vessel *Penguin II*. (Kenyon, K. Niggol, A. Y. Roppel, and Wilke.)
- 21 October to 5 November. Aleutian Islands. An attempt to harvest and study sea otters in the outer Aleutians was negated when a U.S. Navy UF-2 aircraft carrying the field party crashed on 27 October at Adak Island during an aerial survey. (L. W. Croxton and Kenyon, and D. Cisney, killed in crash.)

1962

- 14 January to 4 April. Aleutian Islands. At Amchitka Island conduct field observations of sea otters and collect specimens from State of Alaska kill of 150 sea otters. (Croxton, Jones, and Kenyon.)
- 29 March and 5-10 April. Aerial surveys in Alaska. Aerial survey of sea otters in the Aleutian Islands from Kiska Island to Amak Island; the Sanak Islands; Sandman Reefs; Shumagin Islands; and areas along the south coast of the Alaska Peninsula to Kuliak Point. Total flight time: 53.6 hours. (J. J. Burns, Kenyon, J. S. Kobza, Smith, and Spencer.)
- 8-11 September. Washington State. Investigate reports of possible sea otter sightings along the outer coast of the Olympic Peninsula. (Kenyon.)
- 26-29 October. Alaska State biologists kill 24 sea otters on Amchitka. (Croxton and E. Klinkhart.)
- 27-28 October. Washington State. Investigate reports of possible sea otter sightings in the San Juan Islands of Puget Sound aboard the M/V *Trinity*. (Kenyon, Rice, and Scheffer.)

1963

- 4 March to 13 April. Aleutian Islands. At Amchitka Island collect specimens from 303 sea otters taken by State of Alaska biologists. (J. E. Burdick, E. Klinkhart, and J. Vania.)
- 1-22 July. Aleutian Islands. Field observations of sea otters at Adak Island and Buldir Island in the outer Aleutian Islands. Transportation from Adak to Buldir aboard USCGC *Clover*, return on USCGC *Klamath*. (V. D. Berns, E. L. Boeker, Jones, Kenyon, A. E. Peden, and M. Zhan.)
- 31 July to 3 August. Aleutian Islands. At Amchitka Island 20 sea otters were taken by State of Alaska biologists and specimens furnished to the Bureau of Sport Fisheries and Wildlife (E. Klinkhart and J. Vania.)

1964

In Seattle working on 1963 specimens and analyzing accumulated field data.

1965

23 January to 10 February. Field observations of coastal and island areas of Baja California, Mexico to examine sea otter habitat and search for possible surviving animals. (D. W. Rice, D. Lluch B., and Kenyon.)

18 April to 9 May. Aerial survey of sea otters in the Aleutian Islands, Cold Bay to Attu Island. (E. Klinkhart, D. L. Spencer, T. A. Smith, J. King, and Kenyon.)

23 October to 9 November. At Amchitka Island. Monitor effects of AEC-DOD Long Shot nuclear blast. Aerial surveys and surface observations. (E. Klinkhart, D. L. Spencer, T. A. Smith, R. Tremblay, and Kenyon.)

9 November to 3 December. Transport male sea otter (Gus) aboard M/V *Commander* from Amchitka to Seattle. (Kenyon, Capt. Cliff Andersen.)

1966

Work in Seattle on specimens and accumulated data.

Appendix 2

TABULAR SUMMARY OF SEA OTTERS STUDIED, 1955 THROUGH 1965

Every otter for which any record was kept is included in this table; for some of them the data were inadequate and they are not included in other sections of this report.

Place and time	Number obtained—			Number tagged and released			Number held captive		Skins taken ²		Total otters studied			
	BD ¹	Shot	Net or club ²	♂	♀	Sex?	♂	♀	ADFG	FWS	♂	♀	Sex?	All
Amchitka Island:														
Mar-Apr 1955	15	—	31	—	—	—	9	19	—	1	20	23	3	46
Aug-Sept 1955	5	—	6	—	—	—	4	2	—	—	4	2	5	11
May-July 1956	58	5	30	5	4	—	10	11	—	7	44	29	20	93
Oct-Dec 1957	31	—	23	—	—	—	10	11	—	12	24	13	17	54
Jan-May 1959	84	—	125	34	52	—	7	7	—	46	104	94	11	209
Various areas: ³														
June-July 1960	7	14	—	—	—	—	—	—	—	—	10	8	3	21
Amchitka Island:														
Feb-Apr 1962	107	154	122	43	77	—	—	—	155	6	141	234	8	383
October 1962 ⁴	3	24	—	—	—	—	—	—	24	—	6	19	2	27
Mar-Apr 1963 ⁵	42	285	13	4	2	1	—	—	303	3	126	199	15	340
Aug-Sept 1963	—	20	—	—	—	—	—	—	20	—	1	19	—	20
Nov. 7, 1965	—	—	2	—	—	—	1	1	—	—	1	1	—	2
Total	352	502	352	88	135	1	41	51	502	86	481	641	84	1,206

¹ BD = beach dead, i.e., remains of sea otters found on beaches; 41 of the remains listed were so fragmentary that no use was made of them.

² Most of these were netted on beaches; several were clubbed in 1962 and 1963 during the Alaska Department of Fish and Game cropping operations in which the U.S. Fish and Wildlife Service (FWS) cooperated.

³ Specimens were collected in the Shumagin and Sanak Islands and in the Bering Sea off the north coast of Unimak Island.

⁴ Specimens and data collected by L. W. Croxton and E. Klinkhart, Alaska Department of Fish and Game.

⁵ Specimens and data collected by J. E. Burdick.

INDEX

Many geographic locations (islands, points, passes, etc.) mentioned in the text are omitted from the index. They may be found in the text under the island groups (Andreanof Islands, Fox Islands, etc.) or adjacent geographic areas (such as Alaska Peninsula), which are included in the index. In general, scientific names of organisms are omitted from the index but are included in the text. An attempt was made to avoid repeating in the index what may be found in the table of contents.

- abalone (*Haliotis*), 108, 129, 186.
abalone fishermen, 130.
Abegglen, C. E., 261, 326.
Adak Island, Alaska, 165-166.
adaptability, 303.
AEC (Atomic Energy Commission), 340.
aerial photography, 145.
aerial survey (*see* survey).
Agattu Island, Alaska, 147.
aging, premature, teeth, 248.
aircraft transport, 316-317.
Akutan Village, Alaska, 171.
Alaria (*see also* kelp), 57.
Alaska Department of Fish and Game, iv, 39, 157.
Alaska:
 Peninsula, 177-178.
 populations of sea otters, 137-183.
 southeastern, 183.
 Statehood Act, 2.
Aleutian Islands, Alaska, 5, 133, 147-175, 337-340.
Alexander Archipelago, Alaska, 57, 183.
algae (*see also* kelp):
 coralline, 109.
 red and brown, 111.
Alizarin red S dye, 53.
Allanson, A., 186, 326.
Alles, J. J., iii.
Amak Island, Alaska, 172-175.
Amchitka Island, Alaska, 151-157, 337, 338.
Amlia Island, Alaska, 167-168.
Anacapa Island, Calif. 186.
Anas, R., 324, 334.
Andersen, C., 340.
Anderson, H., 130.
Andreanof Islands, Alaska, 160-168.
Año Nuevo Island, Calif., 187.
Anthony, A. W., 187, 326.
antibiotics, 315.
Aquarium, Tacoma, Wash. (Point Defiance), iv, 39, 105, 300, 316.
Argobuccinum, 118.
Arseniev, V. A., 187.
Ashbrook, F. G., 41.
Asia, 4.
Atigaru Point, Alaska, 133.
Atka Island, Alaska, 166-167.
Atka mackerel, 102.
Atka Village, Alaska, 166, 167.
Attu Island (Near Islands), Alaska, 147-149, 320.
auction, public, 3.
Augustine Island, Alaska, 179.
automobile transport, 316.
Bailey, V., 185, 326.
Baines, G., iii, 146, 243, 328.
Banfield, A. W. F., iii, 183.
Barabash-Nikiforov, I. I., 5, 66, 70, 109, 111, 132, 133, 135, 187, 188, 218, 221, 235, 238, 239, 242, 279, 285, 287, 326.
Barmore, W. J., 338.
Bauer, R. D., 52, 326.
Beals, F. L., 148, 152, 156, 157, 326.
bedding, dry, 303.
Bee, J. W., 133, 326.

behavior:

- adoption, 101.
 - begging, 300.
 - daytime, 303.
 - dependence of young, 87-89.
 - diving of young, 98.
 - exercise of captive, 304.
 - family ties, 223-224.
 - feeding, 300, 304.
 - food gathering by young, 98.
 - frustration, 82-85.
 - gregariousness, 224.
 - grooming, 39, 73, 74-76, 100, 303-304.
 - interspecific strife, 102.
 - juveniles vs. adults, 221-222.
 - killing fish, 108.
 - maternal:
 - mother-young bond, 91-94.
 - moving young, 95.
 - segregation of mothers, 213.
 - solicitude, 89-94.
 - nighttime, 307.
 - nursing, 96.
 - play, 101, 224.
 - pounding:
 - chest, 82-86, 300.
 - rock, 304-305.
 - technique, 109.
 - protective, 221.
 - resting, 99, 303-305.
 - running, 70.
 - seasonal, 305.
 - sleeping, 59.
 - stealing, 216, 220, 299, 300-301.
 - swimming of young, 98.
 - tameness, 300, 312.
 - walking, 70, 112.
 - washing, 112.
- Belkin, A. N., 187, 189, 326.
- Bentley, W. W., 187, 326.
- Bering Island, U.S.S.R., 1, 188.
- Bering, V., 135, 188.
- Berns, V. D., iii, 280, 339.
- Bezekoff, A., iii, 171, 288, 337.
- Bezekoff, F., iii, 171, 337.
- Binkley, K. L., iii, 272, 309, 316, 317, 338.
- Biological Structure, Department of, University of Washington, 247.
- Bixby Creek, Calif., 186.
- blindness, 106, 278.
- blood quantity, 30.
- blubber, 6, 39, 105.
- body (general description), 6.
- Boeker, E. L., iii, 339.
- Bond, R. M., 186.
- bones:
 - damage, 51.
 - fossil, 4.
 - purple, 111.
 - white, 111.
- Boootian, R. A., iii, 186, 326.
- Bristol Bay, Alaska, 173.
- British Columbia, Canada, 183-184.
- Brooks, J. W., iii.
- Brosseau, C., iii, 39, 300.
- Brown, D. V., iii, 276, 277.
- Bryan, W. F., 73.
- Buccinum*, 118.
- Buldir Island, Alaska, 150.
- Buldir Reef, Alaska, 67, 69.
- Burdick, J. E., iii, 339.
- Burns, J. J., iii, 339.
- Burroughs, R. D., 185, 326.
- Buterin, M., 321.
- caging, dry, 293.
- calculus, dental, 52.
- California Department of Fish and Game, 130.
- California, killing sea otters, 282.
- California sea otter population, 185-187.
- California Senate, 130, 186, 327.
- Canada, National Museum of, 183.
- Canadian hunters, 136.
- Canton (*see also* China), 1.
- Cape Halkett, Alaska, 133.
- Cape Sagak, Alaska, 170.
- Carlisle, J. G., iii, 186.
- Carlson, C. E., iii.
- Carmel Cove, Calif., 129.
- Carnivora, 4.
- Caton Island, Alaska (*see* Sanak Islands).
- cataracts, 261.
- Cedros Island, Mexico, 133, 187.
- cetacean, 4.
- Channel Islands, Calif., 186.
- Chapman, D. G., iii, 225, 241, 243, 261, 267, 324, 330.
- Chapskii, K. K., 52, 327.
- Chernabura Island, Alaska, 176.

- China, 41.
 Chinese, 185.
 Chirikof Island, Alaska, 182.
 Chukotsk Peninsula, U.S.S.R., 135.
 Cisney, D., 339.
 clams, 109, 118, 122, 123.
 Clark, R. D., 295.
 claws, retractile, 6, 74.
 Clupeidae, 83.
 Cocks, A. H., 237, 327.
 Commander Islands, U.S.S.R., 1, 3, 133, 187, 339.
 Commercial Fisheries Review, 186, 327.
 communication, 77-80.
 Conaway, C. H., iii, 225, 335.
 confiscated skins, 41, 179, 180.
 Cook, Captain J., 1.
 Cook Inlet, Alaska, 179.
 Coolidge, Calvin, 135.
 cormorant, 131.
 Cowan, I. McT., iii, 184, 327.
 Cox, K. W., iii, 108, 129, 130, 327.
 crab, king, 110.
 crabs, 106, 116, 123-124, 126, 127.
 Croxton, L. W., iii, 183, 339.
Cyclopterichthys (see also fish), 121.
 Dall, W. H., 183, 327.
 Davey, S. P., 324, 333.
 Davis, M., 82.
 Dawson, Y. E., iii.
 Delarof Islands, Alaska, 158-160.
 dentition, 6, 43-52, 263.
 "die-off," 2, 40-41, 88.
 diseases:
 abscesses, periapical, 51, 52.
 enteritis, 274-275, 289, 293, 299.
 infections, 276, 277, 290, 315.
 intussusception, 278.
 liver degeneration, 275-276.
 malignancy, 276-277.
 peritonitis, 272.
 distance from shore, 66.
 Ditcher, J., 183.
 diving, 64-70, 204.
 DOD (Department of Defense), 340.
 Dorofeev, S. V., iii, 188.
 drinking sea water, 28.
 Dukes, H. H., 31, 327.
 DuMont, P. A., iv.
 Eadie, W. R., 237, 238, 329.
 eagle, bald, 252, 266, 280-281.
 ear, 6.
 earthquake damage, 181.
 Ebert, E. E., 130, 327.
 echinoderms (see also sea urchin), 110.
 Eddy, G., 338.
 Edwards, M. A., iii.
 Elliott, H. W., 181, 182, 327.
Elymus, 57.
Enhydra lutris ssp., 4-5.
Enhydriodon, 4.
 Ensenada, Mexico, 187.
 Essapian, F. S., 240, 327.
 Evermann, B. W., 41, 327.
 evolution, 4.
 Eyerdam, W. J., 179, 327.
 False Pass, Alaska, 170.
 fasting, 105.
 fat, body, 105.
 fathom, iv.
 Fay, F. H., iii, 31, 273, 327.
 feeding (see also food):
 adaptations, 48.
 digestion time, 105.
 location, 105.
 method, 81-82.
 pelagic, 69.
 time of, 59.
 feet (see also flippers), 6.
 fetal orientation, 239-240.
 Fiscus, C. H., iii, 68, 133, 171, 172, 173, 230, 243, 327, 339.
 fish:
 in feces, 123.
 listed, 294.
 method of eating, 122.
 percent in diet, 64.
 Fisher, E. M., 41, 42, 43, 87, 108, 111, 136, 221, 238, 239, 328.
 Fisher, H. I., 82, 328.
 fishing, 293.
 Fisler, G. F., 29, 328.
 Flemming, R. H., 29, 335.
 flippers, 6, 70.
 food:
 calories required, 127, 297.
 costs, 299-300.
 holding, 6.
 regulated diet, 298.
 selectivity, 301.

food—Cont.

- species listed, 116–117.
- storage capacity, 112.
- Food Science Pioneer Research Laboratory, 127.
- Forziati, A. F., 53.
- fossil bones (*see* bones).
- Fox, D. L., 111, 328.
- Fox Islands, Alaska, 169–175.
- Friedman, H., 82, 328.
- Friden, O. A., 152, 156.
- fulmar, 131.
- fur (*see also* pelt):
 - color, 8, 9.
 - farm, 299.
 - insulation, 6, 293.
 - wear, 293.
 - wetting of, 291.
- gastrolith 111.
- Gentry, R. L., 55, 59, 328.
- Gilbert, P. W., 279, 328.
- Gilmore, R. M., iii.
- Glaser, F., 135.
- Golodoff, I., iii, 147, 328, 337.
- goose, Emperor, 103, 131.
- Greengo, R. E., 184–185.
- greenling, fringed, 293.
- Gribkov, P. F., 135, 328.
- grooming (*see* behavior).
- growth:
 - adolescent, 229–230.
 - prenatal, 237.
- Guadalupe Island, Mexico, 133.
- Guiguet, C. J., iii, 184, 327.
- Gulin, V., 135.
- gull, glaucous-winged, 63, 103.
- Gunther, E., iii, 184.
- Gus (captive otter), 39, 298, 300, 316, 319, 340.
- habitat, 6, 146–147.
- Halarachne*, 103, 292.
- Hall, E. R., 4, 66, 133, 326, 328.
- Hall, K. R. L., 83, 85, 108, 329.
- Hamilton, W. J., Jr., iii, 237, 238, 329.
- Hanna, G. D., iii, 122, 181.
- Hansen, H. P., 110.
- Hanson, E., 2, 250.
- Harbo, S. J., iii.
- Harris, C. J., 3, 329.
- Hartt, A. C., iii, 66, 67, 68.
- harvest, 2, 324.

- hearing, 56.
- heart, 27–28.
- helminth parasites (*see also* parasites), 271–273.
- Hertlein, L. G., iii.
- Hexagrammos*, 293.
- Hildebrand, M., 48, 329.
- Hokkaido, Japan, 133.
- Hooper, C. L., 66, 112, 329.
- Hooper, D. C., 2, 163, 164, 280, 337.
- Howell, A. B., 60, 329.
- Hubbs, C. L., iii.
- Huggett, A. St. G., 237, 238, 243, 329.
- Hutchinson, H. B., 147, 152, 329.
- ice:
 - crushes sea otters, 181.
 - influence on distribution, 133–135
 - transport, 182.
- Ichihara, T., 52, 329.
- India, 4.
- inland waters:
 - Puget Sound, 57, 184, 185, 339.
 - Southeastern Alaska, 183.
 - Strait of Juan de Fuca, 5, 281.
- Islands of the Four Mountains, Alaska, 168–169, 339.
- insulation (*see* fur).
- intestine:
 - perforated, 294.
 - length, 26.
- Izembek Bay, Alaska, 172, 173.
- Japanese, 147, 176.
- jaw-muscles and joints, 42–43.
- Jellison, W. L., 271, 329.
- Jensen, A., iii, 28, 29, 238, 329.
- Jensen, D., 275.
- Johnson, A. M., iii, 37, 52, 171, 324, 326.
- Johnson, E. J., iii.
- Johnson, M. L., iii.
- Johnson, M. W., 29.
- Jones, B. F., 66, 68, 148.
- Jones, R. D., Jr., iii, 2, 123, 128, 131, 148, 149, 150, 163, 164, 165, 166, 170, 173, 250, 279, 280, 288, 319, 320, 329, 330, 337, 338, 339.
- Jordan, D. S., 284, 329.
- Joynt, G. T., 67, 68, 152, 159, 164, 329.
- juvenile stage, 245.
- Kagalaska Island, Alaska, 166.
- Kaiekov, 181.

- Kajimura, H., 171, 230.
 Kamchatka, U.S.S.R., 41, 133, 189.
 Kanaga Island, Alaska, 164-165.
 Karrick, N. L., iii, 127.
 Kavalga Island, Alaska, 159.
 Kayak Island, Alaska, 179-181.
 Kellogg, R., 4, 332.
 kelp (*see also* algae):
 beds, 57, 67-69, 73.
 drifting, 67, 69.
 Kelson, K. R., 4, 328.
 Kenai Peninsula, Alaska, 179-181.
 Keyes, M. C., iii, 274, 277, 330.
 kidney, 27-28.
 killing, accidental, 281.
 kill of sea otters, 139, 339.
 King, J., 340.
 King, J. E., 27, 330.
 King, J. G., iii.
 Kirkpatrick, C. M., iii, 2, 19, 43, 111,
 131, 271, 288, 293, 299, 301, 303,
 309, 311, 330, 335, 337.
 Kiska Island, Alaska, 150.
 Kismaliuk Bay, Alaska, 171.
 Klein, D. R., iii.
 Klingbeil, J. A., 183.
 Klinkhart, E. G., iii, 321, 339, 340.
 Klumov, S. K., 189, 330.
 Kobza, J. S., 339.
 Kodiak Island, Alaska, 179.
 Kraus, B. S., 44, 334.
 Krear, H. R., iii, 338.
 Krenitzin Islands, Alaska, 171-172.
 Krog, J., 280, 330.
 Kudiakof Island, Alaska, 173.
 Kujulik Bay, Alaska, 178.
 Kuril Islands, U.S.S.R., 3, 133, 189.
 Laboratory of Statistical Research,
 University of Washington, 243.
 Lack, D., 270, 330.
 Ladreau, F., 186.
 Lane, F. W., 82, 330.
 Lang, T. G., 63, 330.
 Larsen, H., 281.
 Larson, C., iv.
Larus glaucescens (*see* gull).
 Laughlin, W. S., iii, 179, 331.
 Lavrentiya, U. S. S. R., 135.
 Lee, C. F., 315.
 Leedy, D. L., iii.
 Lensink, C. J., iii, 2, 135, 136, 139, 140,
 146, 156, 164, 165, 171, 173, 175,
 176, 177, 179, 180, 182, 183, 331,
 337, 338.
 Lethol, 315.
 Lewis and Clark, 185.
 lice, 76.
 Liers, E. E., 237, 331.
 Limbaugh, C., 279.
 Ling, J. K., iii, 32, 35.
 Littlejohn, C., 66, 328.
 liver, 27-28.
 Lluch B., D., 340.
 Locker, B., 271, 333.
 London, England, 40, 41.
 longevity, 53.
 Long Shot, 340.
 Lopp, R., 179, 338.
 Lower (Baja) California, Mexico, 5,
 133, 187, 340.
 Loy, C. L., 152, 156, 250, 331.
 Lukannon, 181.
 Lutke, F., 181, 331.
Lutra, 42.
Lutra canadensis (*see* otter, American
 river).
Lutra lutra (*see* otter, European
 river).
Lutra reevei, 4.
Macrocystis (*see also* kelp and algae),
 57.
 Macy, P. T., iii.
 Magee, E. G., iii.
 Mangan, J. B., 250, 331.
 Manville, R. H., iv.
 Marakov, S. V., 69, 188, 208, 293, 331.
 Margolis, L., iii.
 Marine Mammal Biological Labora-
 tory, 39.
 marking, 200-204.
 Martin-Rice, Ltd., 40.
 Martin, V. F., iii, 185.
 Massey University, 35.
 Mattison, J. A., 105.
 Maynard, W., 37, 331.
 McAtee, W. L., 135, 181, 333.
 McCann, C., 39, 331.
 McCracken, H., 175, 331.
 McLaren, I. A., 4, 331.
 McLaughlin, P. A., iii, 174, 332.
 McLean, J. H., 129, 332.
 McRoy, C. P., 173.

- measurements, iv.
 body weight, adult, 20.
 intestine length, 26.
 length (*see* Body Measurements),
 19.
 miscellaneous, 26.
 organ weights, 27.
 skin length (compared with body
 length) 26.
 weight loss at death, 25.
 weight, pregnant female, 230.
 weight (*see* Body Measurements).
 19.
- Medny Island, U.S.S.R., 188.
 Mexico, 5, 187.
 midden, 129, 179, 184, 185.
 Middle Reef, Alaska, 69.
 migration, 6.
 mile, nautical and statute, iv.
 military, at Amchitka, 250.
 Miller, G. S., 4, 332.
 Miller, P. and L. G., 1, 332.
 mink, 43.
 Mitchell, E. D., iii, 4, 332.
 mite, nasal, 103, 274, 292.
 mollusks, 110.
 molt, 37-39.
 monia, pearly (*see* oyster, rock).
 Monterey, Calif., 130.
 Morro Hermoso, Baja California,
 Mexico, 133, 187.
- mortality:
 age-specific, 253, 258.
 body fat, 261.
 body weight, 271.
 defective teeth, 50, 261, 263.
 during flight, 317.
 emaciation, 261.
 enteritis, 261, 271.
 estimated, Amchitka, 266, 268.
 factors, 261.
 food depletion, 270.
 juveniles, desertion of, 270.
 peak period, 266.
 rate, 245.
 Sanak Island, 269.
 sex-specific, 258.
 Shumagin Islands, 268.
 starvation, 261, 271.
 storm waves, 264, 266.
 studies, 1955-63, 250, 251.
 study methods, 251, 252.
- mortality—Cont.
 time of, 252, 253.
 tooth attrition, 270.
 weather related, 263.
- Mossman, H. W., iii, 232, 335.
 Murie, O. J., 1, 123, 150, 157, 159, 165,
 175, 218, 221, 238, 280, 332.
- muscle:
 masseter, 42.
 masticatory, 42.
 temporal, 42.
- musculature of jaw, 42-43.
Musculus, 118.
- mussels, blue, 52, 83, 106.
 Mustelidae, 4.
- Naknek River, Alaska, 175.
 Natividad Island, Mexico, 187.
 Nazan Bay, Alaska, 166.
 Near Islands, Alaska, 147-149, 188.
 Neiland, K. A., iii, 271, 272, 329, 332.
 Nelson, U. C., iii.
 nembutal, 311.
Nereocystis (*see also* kelp), 57.
 Nesterov, G. A., 188.
 netting, 284-286.
 Nevzoroff, J., 129, 337.
 Newell, I. M., iii, 271, 292, 330.
 Niggol, K., 339.
 Nikolaev, A. M., 65, 105, 135, 149, 189,
 204, 279, 321, 332.
 Nikolski Village, Alaska, 146, 170, 171.
 Norris, K. S., 63, 330.
 Novikov, G. A., 39, 332.
 Nozikov, N., 181, 332.
- O'Brien, T. P., iii, 339.
 octopus, 102, 118.
 Ogden, A., 1, 133, 187, 281, 333.
 Oglala Pass, Alaska, 154.
 Ogliuga Island, Alaska, 159.
 Oregon, 185.
 orphan, 243.
 Orr, R. T., iii, 187, 278, 333.
 Osmeridae (smelt), 83.
- otter:
 American river, 4, 9-13, 43, 55,
 184, 236.
 European river, 39, 236, 238.
- oyster, rock (pearly monia), 43, 109,
 118.
 oystercatcher, black, 103.

- parasites, 103, 271-274, 294, 295, 315.
 Pavlov Islands, Alaska, 182.
 Patch, C. A., 183, 333.
 Peden, A. E., 339.
 Pedersen, R. J., 185, 333.
 pelt, in commerce (*see also fur*), 40-42, 185.
 pentobarbital, 315.
 Perleshin, S. D., 187.
Peromyscus, 29.
 Peterson, R. L., iii.
 Peterson, R. S., 55, 59, 240, 243, 328, 333.
 Pierce, C., 307.
 pinnipeds, 4.
 piperazine citrate, 314.
 play (*see also behavior*), 109.
 Pleistocene, 4.
 Pliocene, 4.
 Poland, H., 40, 333.
 pollution, environmental, 281.
 pool, Amchitka, 290.
 porpoise, speed of, 63.
 Port Moller, Alaska, 173-175.
 Poulter, T. C., 187, 333.
 population:
 barrier, behavioral, 195.
 barrier, geographic, 194-195.
 dense isolated, 196-197.
 dispersal, 196.
 optimum density, 193-194.
 pressure, 324-325.
 rate of increase, 191-193.
 remnant, 189.
 sparse isolated, 197.
 sparse local, 197.
 summary, 198-200.
 world, 189.
 Prasil, R. G., iii, 186.
 Preble, E. A., 135, 181, 333.
 preservation:
 stomachs, 113-115.
 reproductive tracts, 228.
 preservatives used, 228.
 Pribilof Islands, Alaska, 2, 133, 181-182, 337.
 Prince William Sound, Alaska, 133, 179-181, 285.
 processing, pelt, 40-41.
 promazine hydrochloride, 312.
 Promyshlenniki, 1.
 protection, Federal, 1, 2.
 propiopromazine hydrochloride, 313.
 prostration, heat, 6, 311, 317, 321.
 Puget, P., 184.
 Queen Charlotte Islands, Canada, 183.
 Radovich, J., iii.
 Rankin, J., iii.
 rat, 103, 252.
 Rat Islands, Alaska, 149-158.
 Rausch, R. L., iii, 2, 270, 271, 272, 333, 337.
 recruitment rate, 245.
 Reeder, W. G., 243, 333.
 Reeve Aleutian Airways, 170, 317.
 Refuge, Aleutian, 1.
 regulations, Federal (*see protection*).
 Repenning, C. A., iii, 4.
 reproduction:
 blastocyst, 244.
 birth:
 interval, 240.
 place, 239-240.
 rate, 245.
 season, 22, 230.
 breeding season, 235, 236.
 conceptus, 231-232.
 copulation, 217-219.
 courtship, 214-217, 247.
 counts of mothers, young, 228-229, 234-235.
 females:
 nonpregnant, 232-235.
 pregnant, 230.
 fetus, 239-240, 243-245.
 gestation period, 236, 244.
 implantation, location, 230.
 lactation period, 244-245.
 length of cycle, 245.
 length of stages of, 243.
 mating of mothers having young, 221.
 pair bond, breaking, 220.
 phases of, in female, 235.
 postcopulatory period, 219-220.
 precopulatory period, 214-217.
 pregnancy:
 implanted, 229.
 location, 230.
 unimplanted, 229-230.
 pupping season, 238.
 rate of, 241-242.
 separation, 220.

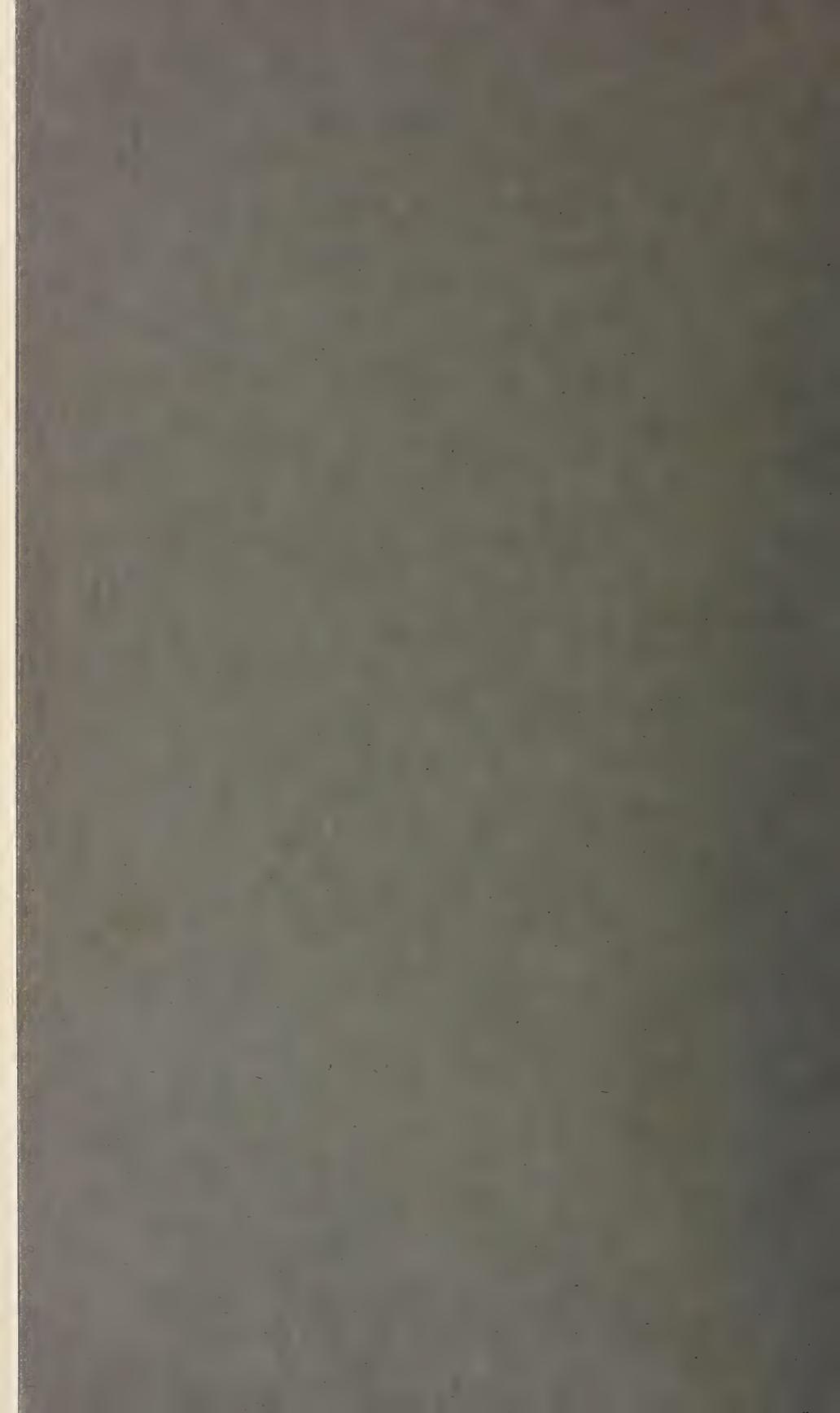
- reproduction—Cont.
 spermatogenesis, 247–248.
 sexual maturity:
 age of, 229–230.
 female, 245–246.
 male, 247.
 summary of findings, 246–247.
 terms, definition of, 229.
 tracts, female, 225–228.
 twinning, 242.
 unimplanted period, 245.
- research, biological, 3.
 Reshetkin, V. V., 287, 293, 333.
 Rice, D. W., iv, 339, 340.
 Richardson, F., iii, 338.
 Ritter, G., 250, 331.
 Roosen-Runge, E. C., iii, 247–248.
 Roppel, A. Y., iii, 261, 324, 326, 339.
 running (*see* behavior).
- Sagen, L. V., iii.
 Sakhalin, U.S.S.R., 133.
 Samalga Island, Alaska, 170–171.
 Sanak Island, Alaska, 174–176.
 San Benito Islands, Mexico, 187.
 Sandman Reefs, Alaska, 174–176.
 Sand Point, Alaska, 176.
 San Francisco Bay, Calif., 281.
 San Juan Islands, Wash., 184.
 San Luis Obispo, Calif., 130.
 San Miguel Island, Calif., 186–187.
 San Simeon, Calif., 129.
 Santa Barbara Island, Calif., 186.
Saxidomus (*see* clam).
 Scammon, C. M., 133, 187, 334.
 Scapino, R. P., iii, 42, 43, 334.
 scent glands, 4.
 Schaller, G. B., 108, 329.
 Scheffer, V. B., iii, iv, 2, 5, 21, 24, 28,
 29, 31, 35, 37, 39, 44, 52, 53, 55, 157,
 184, 238, 250, 299, 324, 326, 334, 338,
 339.
Schizothaerus (*see* clam).
 Schneider, K., iv, 3, 53.
 Schumacher, G. H., 42, 334.
 Sczuck, E., iii.
 Scott, D. B., iii, 50.
 Scott, E. M., 111.
 sea cow, Steller's, 239.
 sea cucumber, 121.
 sea lion, Steller, 103.
 sea urchin, 52, 128–129, 188.
 a starvation diet, 132.
 method of ingestion, 119, 121.
 seal, fur, 34, 37, 39, 136, 324.
 mortality, 261.
 pregnancy, 230.
 twinning, 243.
 seal, harbor, 102, 185.
 Seattle Fur Exchange, 41.
 Seguam, Island, Alaska, 168.
 Semidi Islands, Alaska, 182.
 Semisopochnoi Island, Alaska, 157–
 158.
Serripes (*see* clam).
 sex, identification of, 14–19.
 sex ratio, 241.
 Seymour, A. H., iii.
 shark predation, 278.
 shearwater, 131.
 shedding (*see* molt).
 sheep ranch, 170.
 Shelby, H., 186, 282.
 Shemya Island, Alaska, 147.
 Shidlovskaya, N. K., 119, 121, 287, 293,
 295, 334.
 Shelter Cove, Calif., 130.
 ship transport, 319.
 Shumagin Islands, Alaska, 176–177,
 337, 339.
 Siberia, 1.
 sight, 55.
 in food finding, 107.
 Simeonof Island, Alaska, 177.
 Sinha, A. A., iii, 225, 228, 229, 232,
 236, 335.
 sirenian, 4.
 Sitka, Alaska, 183.
 Skalkin, V. A., 65, 105, 204, 332.
 skin:
 preparation, 42.
 storage, 42.
 Skripnikov, E. P., 188.
 skull, study of, 42.
 Slater, D. W., iv.
 sleep (*see* behavior).
 Slijper, E. J., 29, 239, 240, 335.
 smell, 55.
 sense of, 286.
 Smith, A. G., iii.
 Smith, T. A., iii, 273, 338, 339, 340.
 smoking (of fur), 40–41.

- Snow, H. J., 66, 69, 89, 91, 110, 242, 273, 278, 335.
- Southeastern Alaska, 57.
- Soviet Union, 3.
 sea otter populations, 187-189.
- Sparine, 311-312.
- speed (*see* swimming and running).
- Spencer, D. L., iv, 68, 146, 161, 172, 178, 178, 338, 339, 340.
- spleen, 27, 29.
- squid, 119.
- Stager, K. E., 186.
- starfish, 119.
- Stejneger, L., 239, 335.
- Steller, G. W., 1, 79, 284, 285, 335.
- Stiles, W. B., 335.
- Stillwater Cove, Calif., 129.
- stones, stomach, 111.
- storage of food, 111.
- Stout, J., 185, 333.
- Stoves, J. L., 40.
- St. Paul Island, Alaska, transplant to, 317.
- stress, 30.
 causes of, 275.
- Strongylocentrotus* (*see* sea urchin).
- Stullken, D. E. 2, 19, 288, 299, 303, 309, 311, 330, 335, 337.
- subspecies 5.
- Sumner, L. 186.
- survey:
 aerial 140-145, 321, 338, 339, 340.
 surface, 146, 338, 339.
- survival factor, 239
- Susie (captive otter), 106, 109, 289, 292, 298, 299.
 age, 53.
- Sutwik Island, Alaska, 178.
- Sverdrup, H. U., 29, 335.
- Swicegood, S. P., Lcdr., 152, 156, 335.
- swimming, 60-64.
 methods of, 60-62.
 speed and agility, 62-64.
 of young, 98.
- tactile sense, in feeding, 106.
- tagging (marking), 200-204.
- Tahoma Reef, Alaska, 69.
- tail, 6.
- Tanaga Island, Alaska, 163-164.
- taste, 56.
- taxonomy, 4.
- Taylor, W. P., 4, 60, 335.
 teeth (*see* dentition).
 temperament, 285, 298.
 temperature:
 body, 29-30.
 environmental, 305.
 frigid, 292.
- Terranova decipiens* (*see* parasites).
- Thenius, E., 4, 335.
- Thomas, R., iv, 146, 172.
- three-mile limit, 66.
- Tiderip Point, Alaska, 171.
- Tigalda Island, Alaska, 172.
- Tilford, J., 338.
- Todd, E. I., iv.
- topping, of pelt, 40-41.
- touch, 56.
- tranquilizers, 312, 314.
- transplant, 2, 182, 183, 338.
- Tranvet, 313, 321.
- Treaty of 1911, 135.
- Tremblay, R., 340.
- Troyer, W., 179, 338.
- tsunami, 181.
- tunicates, 110, 121.
- Ulak Island, Alaska, 160.
- Umnak Island, Alaska, 172-175.
- Unalaska Island, Alaska, 171.
- Unga Village, Alaska, 176.
- Unimak Island, Alaska, 172-175.
- University of Illinois, 42.
- University of Washington, 185.
- United States:
 Board on Geographic Names, 158, 168, 335.
 Bureau of Fisheries, 1, 135, 136, 139, 152, 175, 179, 336.
 Coast and Geodetic Survey, iv, 167.
 Coast Guard, 1, 172.
 Department of the Interior, 152.
 Fish and Wildlife Service, 337.
 Geological Survey, 181.
 National Bureau of Standards, 53.
 National Institute of Dental Research, 50.
 National Park Service, 186.
 Navy, 165, 338.
 Navy Department Survey, 1932, 147.
 Public Health Service, 337.

- Vancouver Island, Canada, 1, 5.
 Vandersluys, C., 184.
 Vania, J. S., iv, 3, 39, 285, 313, 321, 339.
 Vasilief Bay, Alaska, 166.
 vessels:
 Chelan, 152.
 Brown Bear, 288.
 Clover, 339.
 Commander, 319, 340.
 Hakuyo Maru, 152.
 Klamath, 339.
 Orel, 339.
 Paragon, 320, 337.
 Penguin II, 339.
 San Patrick, 160.
 Steregushti, 339.
 Trinity, 187, 339.
 Windward, 173, 339.
 Veniaminov, I., 181.
 vertebrates, 110.
 vibrissae, 37, 107.
 Vincenzi, F., iv, 299.
 vitamins, 315.
Volsella, 118.
 von Bloeker, J. C., 186.
 Voronov, V. G., 181, 285, 336.
 walking (*see* behavior).
 Warren, J. M., 82, 336.
 Washington State, 184, 281, 339.
 water, fresh and sea, 292.
 Welander, A. D., iv.
 whale, killer, 279.
 whiskers (*see* vibrissae).
 Widdas, W. F., 237, 238, 243, 329.
 Wildman, A. B., 33, 336.
 Wilimovsky, N. J., iv.
 Wilke, F., iv, 2, 5, 113, 243, 261, 328, 336, 337, 338, 339.
 Williams, C. S., 123, 150, 163, 165, 175, 336.
 Williams, L., iv.
 Wilson, Woodrow, 135.
 Woolford, R., 281.
 World War II, 1, 147, 152, 176.
 worms, annelid (*see also* parasites), 110.
 Yadon, V. L., iv.
 young, newborn, 20.
 Yunker, C. E., iv, 271, 292, 330.
 Zaochni, D., 337.
 Zhan, M., iv, 339.
 Zoo, Seattle (Woodland Park), iv, 105, 299, 307, 337, 338.
 Zoological Park, National, 288.

As the Nation's principal conservation agency, the Department of the Interior has basic responsibilities for water, fish, wildlife, mineral, land, park, and recreational resources. Indian and Territorial affairs are other major concerns of America's "Department of Natural Resources."

The Department works to assure the wisest choice in managing all our resources so each will make its full contribution to a better United States—now and in the future.



DL
151
N864
NH

NATURAL HISTORY
OF THE
SWAINSON'S WARBLER



NUMBER 69

UNITED STATES
DEPARTMENT OF THE INTERIOR
BUREAU OF SPORT FISHERIES AND WILDLIFE

NORTH AMERICAN FAUNA

This publication series includes monographs and other reports of scientific investigations relating to birds, mammals, reptiles, and amphibians, for professional readers. It is a continuation by the Bureau of Sport Fisheries and Wildlife of the series begun in 1889 by the Division of Ornithology and Mammalogy (Department of Agriculture) and continued by succeeding bureaus—Biological Survey and Fish and Wildlife Service. The Bureau distributes these reports to official agencies, to libraries, and to researchers in fields related to the Bureau's work; additional copies may usually be purchased from the Division of Public Documents, U.S. Government Printing Office.

Reports in NORTH AMERICAN FAUNA since 1950 are as follows (an asterisk indicates that sale stock is exhausted):

- *60. Raccoons of North and Middle America, by Edward A. Goldman. 1950. 153 p.
- *61. Fauna of the Aleutian Islands and Alaska Peninsula, by Olaus J. Murie; Invertebrates and Fishes Collected in the Aleutians, 1936-38, by Victor B. Scheffer. 1950. 406 p.
- *62. Birds of Maryland and the District of Columbia, by Robert E. Stewart and Chandler S. Robbins. 1958. 401 p.
- *63. The Trumpeter Swan; Its history, habits, and population in the United States, by Winston E. Banko, 1960. 214 p.
- *64. Pelage and Surface Topography of the Northern Fur Seal, by Victor B. Scheffer. 1961. 206 p.
- 65. Seven New White-winged Doves From Mexico, Central America, and Southwestern United States, by George B. Saunders. 1968. 30 p.
- 66. Mammals of Maryland, by John L. Paradiso. 1969. 193 p.
- 67. Natural History of the King Rail, by Brooke Meanley. 1969. 108 p.
- 68. The Sea Otter in the Eastern Pacific Ocean, by Karl W. Kenyon. 1970. 352 p.
- 69. Natural History of the Swainson's Warbler, by Brooke Meanley. 1971. 90 p.

NATURAL HISTORY
OF THE
SWAINSON'S WARBLER

by Brooke Meanley, *Wildlife Biologist*

Patuxent Wildlife Research Center

Division of Wildlife Research

BUREAU OF SPORT FISHERIES AND WILDLIFE



NUMBER 69

UNITED STATES
DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
BUREAU OF SPORT FISHERIES AND WILDLIFE



North American Fauna, Number 69
Published by
Bureau of Sport Fisheries and Wildlife
February 1971

U.S. GOVERNMENT PRINTING OFFICE
WASHINGTON : 1971

Contents

	Page
INTRODUCTION	1
Methods	2
Acknowledgements	3
HISTORY	5
DISTRIBUTION	13
Breeding Range	13
Atlantic Coastal Plain	13
Gulf Coastal Plain	15
Southern Appalachians	17
Ozark Mountains	19
Piedmont Province	19
Extralimital records (United States)	19
Winter Range	20
Cuba	20
Jamaica	20
Swan Islands	20
Mexico	21
British Honduras	21
MIGRATION	22
Spring	22
Fall	23
ECOLOGICAL RELATIONS	25
Coastal Plain	26
Ocmulgee River floodplain forest in Georgia	30
The Great Dismal Swamp	33
Bayou Boeuf Swamp, La., and Monkey John Swamp, S.C.	35
Western Kentucky	36
Southern Appalachians	36
Allegheny Plateau in West Virginia	39
Toxaway River Gorge	41
DESCRIPTION	43
Size	43
Distinguishing characters	44
Adult plumage	44
Juvenile plumage	45
Geographic variation	45
Molting	45
BREEDING BIOLOGY	46
Territorial behavior	46
Arrival on the breeding grounds	46
Homing	46
Territories	47

	Page
Defense of territories	50
Courtship and mating	51
Vocalizations	52
Pouncing	53
Nesting behavior	54
Nesting period	54
Nest site and materials	55
Egg laying and clutch size	60
Cowbird parasitism	62
Incubation	62
Care of nestlings	63
Care of fledglings	64
VOICE	64
Song	64
Whisper song	65
Flight song	66
Incomplete song	66
Singing behavior	66
Seasonal song cycle	68
Daily pattern	69
Rate of singing	69
Cadence of delivery	71
Comparison with associates	72
Alarm or call note	72
FEEDING BEHAVIOR AND FOOD	74
Feeding behavior	74
Bill wiping	75
Food	75
MISCELLANEOUS NOTES ON BEHAVIOR	77
Ground locomotion	77
Preening	77
Head scratching	77
Tail spreading	78
FACTORS AFFECTING THE POPULATION	79
SUMMARY	81
LITERATURE CITED	84

ILLUSTRATIONS

Frontispiece, Pair of Swainson's Warblers at nest near Jacksonville, Fla.	vi
FIGURE	
1. The Reverend John Bachman	5
2. Audubon's painting of Bachman's type specimen	6
3. Type locality of the Swainson's Warbler	7
4. Edisto River near Jacksonboro, S.C.	8
5. John Abbot	9
6. Abbot's painting of the "Swamp Worm-eater"	10
7. Brier Creek, Screven County, Ga.	11

CONTENTS

v

	Page
8. Distribution of the Swainson's Warbler	14
9. Canebrake along edge of Ocmulgee River near Macon, Ga. _	27
10. Canebrake habitat in Ocmulgee River floodplain forest near Macon, Ga.	28
11. Canebrake habitat in Ocmulgee River floodplain forest near Macon, Ga.	29
12. Canebrake habitat in Ocmulgee River floodplain forest near Macon, Ga.	30
13. Typical canebrake breeding territory occupied by a male Swainson's Warbler near Macon, Ga.	31
14. Mixed swamp hardwood habitat in the Dismal Swamp in southeastern Virginia	34
15. Part of scrub palmetto territory of a male Swainson's Warbler in Monkey John Swamp, S.C.	35
16. Rhododendron-hemlock association mountain habitat of the Swainson's Warbler along Collison Creek, Nicholas County, W. Va.	37
17. Mountain breeding habitat, Collison Creek, Nicholas County, W. Va.	38
18. Mature mountain cove hardwood habitat of the Swainson's Warbler near Charleston, W. Va.	39
19. Umbrella magnolia, prominent understory tree in habitat of the Swainson's Warbler near Charleston, W. Va.	40
20. Overlapping territories in the Dismal Swamp occupied by the same male Swainson's Warbler for 3 successive years. _	47
21. Variation in size of male Swainson's Warbler territory during breeding season	49
22. Display of male Swainson's Warbler during boundary dis- pute with a neighboring male	51
23. Swainson's Warbler incubating during flood stage in Ocmulgee River floodplain forest canebrake near Macon, Ga.	56
24. Swainson's Warbler nest in greenbrier vine, 2 feet above the ground, Dismal Swamp in Virginia	57
25. Nest of the Swainson's Warbler compared with nest of the Cardinal	58
26. Nest and eggs of the Swainson's Warbler in cane	61

Photographs are by the author unless otherwise credited.



A pair of Swainson's Warblers at their nest near Jacksonville, Fla.
(Photograph by Samuel A. Grimes).

Introduction

The Swainson's Warbler (*Limnothlypis swainsonii*) is one of the least known of songbirds in the southern United States and one that is widely sought by bird enthusiasts. It is unusually appealing to the student of birds because it is hard to find, because its forbidding habitat is challenging, and because it is associated with the Audubon-Bachman period of North American ornithology.

The difficulty of becoming well acquainted with the Swainson's Warbler has been noted by a number of field ornithologists. In the Alabama River bottoms, Arthur H. Howell of the U.S. Biological Survey reported (1928, p. 284-285) it as confined to the deep swamps and riverbottom woods where canebrakes occur, and remarked that its secretive habits conceal it from all but the most persistent observers. In the big swamps above Mobile in May 1911, July 1913, and May 1914 he heard at least nine of these warblers, but because of the impenetrable vegetation was unable to collect any.

Maurice G. Brooks, Professor of Wildlife Management at West Virginia University, and his coworker W. C. Legg (Brooks and Legg, 1942, p. 81) found this elusive warbler extremely difficult to observe in the dense shadows of the "rhododendron hells" of the Alleghenies:

With their neutral brown coloration, their rapid movements, and their apparent liking for the centers of the thickets, they seemed to blend imperceptibly into their surroundings.

While the remarks of Sprunt and Chamberlain (1949, p. 435) are generally true—that "Swainson's Warbler remains today one of the few land birds really difficult to find and study"—there are times when it can be observed at closer range than almost any other songbird. It is not a very suspicious bird. It seems hard to find chiefly because of the character of its habitat.

The bird student seeking this species in a briery-viny entanglement or canebrake disrupts the peaceful atmosphere of the bird's home, naturally frightening it. Or perhaps it is the never-ending wall of nearly impenetrable vegetation between the observer and the bird that discourages one. But in some habitats, when the

birds are on breeding territories, and especially during the courtship and preincubation periods when the pair are traveling together, they can often be approached to within 5 feet and kept under observation at close range for many minutes. Several times during its preincubation period, one paired bird fed within 2 feet of my eyes as I lay prone on the ground. I found canebrakes to be the best habitat for sustained observations: the visual conditions are generally uniform, and the birds tend to stay away from the densest part of the canebrake.

Although the Swainson's Warbler is not as abundant as some of the other southern warblers, in 1968 I knew of at least two areas in which I could find 50 individuals in a single day. One of these was the Great Dismal Swamp in southeastern Virginia; the other was the Ocmulgee River floodplain forest, 3 to 5 miles southeast of Macon, Ga., where I first became acquainted with the Swainson's Warbler (Meanley, 1945, p. 395-401). When stationed at Camp Wheeler near Macon, 1944-46, I began making observations in the extensive riverbottom canebrakes, and I returned to this area for further study in 1963 and each spring thereafter through 1968. During these 24 years the habitat and number of individuals remained virtually unchanged.

When living at Alexandria, La., in 1956 and 1957, I made observations in Bayou Boeuf Swamp, at the edge of that central Louisiana city. In Arkansas in 1967 I obtained information on territorial and nesting behavior in the batture (land between the levee and the river), between the mouth of Bayou Meto and Pendleton Ferry, along the Arkansas River. Mountain habitats near the City of Charleston and in Nicholas County, W. Va., were visited during the spring of 1965 and 1966. In 1966 I began observations in the Great Dismal Swamp, a few miles south of Norfolk, Va. This continues to be my main study area.

METHODS

Habitats in breeding territories were analyzed in several ways. Plant species composition was determined by sampling $\frac{1}{4}$ -acre plots. In canebrake and scrub palmetto (*Sabal minor*) habitats, the density and number of stems were determined by sampling 10-foot-square quadrats.

The light-shading effect of the combined canopy, lower tree, and shrub strata was determined in $\frac{1}{4}$ -acre plots of several tracts. A 2-foot-diameter hoop divided into eight equal sections was held directly overhead, and 20 random readings were made, sighting upward. Readings were taken between 11:30 a.m. and

12:30 p.m. on sunny, windless days. To measure the light intensity, I placed a mirror on the ground in the exact spot where a Swainson's Warbler had been feeding less than 1 minute before, held an exposure meter 1 foot above the mirror with the photoelectric cell upward, and took a reading.

Territory-mapping and transect methods were used in making censuses. Dimensions of territories were determined by spot-mapping males on maps marked off into transects or grids. Studies of territorial behavior were facilitated by color-marking birds of both sexes with celluloid or metal leg bands. Birds were captured with mist nets for marking.

Birds taken on the breeding and wintering grounds were weighed shortly after capture; birds taken during migration were weighed after being held in a freezer for various periods of time.

Measurements are from files in the U.S. National Museum. Time is given as Eastern Standard Time unless otherwise indicated. Bird names used in the text are from the A.O.U. Check-list of North American Birds (1957); plant names are from Fernald (1950) and Radford, Ahles, and Bell (1964); and insect names are from Lutz (1935).

ACKNOWLEDGEMENTS

I am grateful to many persons for their contributions to this project. Anna Gilkeson Meanley, my wife, worked with me on several occasions in the Ocmulgee riverbottom canebrakes and in the Great Dismal Swamp. Linda Hall, Lucille F. Stickel, Nancy C. Coon, Paul A. Stewart, and Van T. Harris reviewed the manuscript. Samuel A. Grimes gave me a copy of his superb photograph of a pair of Swainson's Warblers at their nest, and Frederick C. Schmid made several excellent photographs for me. Oliver H. Hewitt of Cornell University presented me with a photograph of John Abbott, and E. Milby Burton of the Charleston Museum gave me permission to use a photograph of the Reverend John Bachman. The Fogg Art Museum of Harvard University and the Harvard College Library made available a copy of John Abbot's illustration of the Swainson's Warbler. H. L. Stoddard, Sr., and Robert A. Norris of the Tall Timbers Research Station, Tallahassee, Fla., gave me specimens that struck the TV tower at the station. Eugene P. Odum and William Dopson of the University of Georgia and James B. Cope of Earlham College gave me data from specimens in their collections. J. Fred Denton of Augusta, Ga., and M. G. Vaiden of Rosedale, Miss., provided me with important data from their studies. John W. Aldrich, Gorman M.

Bond, and Allen J. Duvall of the U.S. Fish and Wildlife Service helped with taxonomic problems and other matters. I also wish to thank Olin Sewall Pettingill, editor of the *Living Bird*, and George A. Hall, editor of the *Wilson Bulletin*, for permitting me to quote extensively from papers of mine appearing in those journals.

History

The Swainson's Warbler was described by Audubon from specimens collected by John Bachman (fig. 1) on the banks of the Edisto River in South Carolina in 1832 or 1833. Audubon named



FIGURE 1.—The Reverend John Bachman. He collected the type specimen of the Swainson's Warbler along the banks of the Edisto River in South Carolina in 1832 or 1833. Photograph courtesy Charleston (S.C.) Museum.



FIGURE 2.—Audubon's painting of the Swainson's Warbler, from Bachman's type specimen.

the new bird for his friend the English ornithologist William Swainson, giving it the scientific name *Sylvia Swainsonii*.¹ Audubon's painting of the new warbler (fig. 2) appeared in his *Birds of America* (1834a, plate 198). The description appeared in his

¹The present generic name, *Limnothlypis*, meaning marsh finch, is credited to Stone (1914, p. 26).



FIGURE 3.—The arrow-designated circle in South Carolina marks Bachman's type locality; that in Georgia marks the approximate locality where Abbot collected specimens some 25 years before Bachman.

Ornithological Biography (Audubon, 1834b, p. 564–565). The type specimen was given to the U.S. National Museum by Spencer F. Baird, one-time Secretary of the Smithsonian Institution, who acquired it from Audubon.

The discovery of this new species by Bachman, some 25 miles south of Charleston, is described as follows (in Audubon 1834b, p. 564) :

I was first attracted by the novelty of its notes, four or five in number, repeated at intervals of five or six minutes apart. These notes were loud, clear, and more like a whistle than a song. They resembled the sounds of some extraordinary ventriloquist in such a degree, that I supposed the bird much farther from me than it really was; for after some trouble caused by these fictitious notes, I perceived it near me and soon shot it.

Bachman collected five specimens in the spring of 1832 or 1833. The type locality apparently is in the vicinity of Jacksonboro and Parker's Ferry Landing, S.C. (figs. 3 and 4). Audubon reported



FIGURE 4.—The Edisto River near Jacksonboro in South Carolina, where Bachman collected the type specimen of the Swainson's Warbler.

that the type specimen was collected in 1832, the year that he was on an expedition to Labrador. However, Arthur T. Wayne (1906, p. 227), Charleston ornithologist of the late 1800's and early 1900's, pointed out that since Audubon was in Labrador in 1833 and not 1832 the type specimen must have been collected in 1833.

While John Bachman gets the credit for the discovery of the Swainson's Warbler, John Abbot (fig. 5), a Georgia naturalist, apparently collected a specimen some 25 years earlier but made no public record of the event. However, he made an identifiable portrait of the bird (fig. 6). Many of Abbot's Georgia bird paintings were deposited in the British Museum and the Boston Society of Natural History. Those, including the Swainson's Warbler, deposited in the latter place now repose in the Fogg Art Museum, Harvard University. Walter Faxon (1896, p. 207), one of the first persons to study Abbot's paintings, made the following remarks about the painting of the Swainson's Warbler:

On looking through the Abbot bird-portraits several arrest the eye from their historic interest. Plate 68 is a good representation of Swainson's War-

bler, drawn at least a quarter of a century before this species was described and named by Audubon. On the reverse of the plate is the following autograph note by Abbot: L. 6. May 8. Swamp.—Swamp Worm-eater.

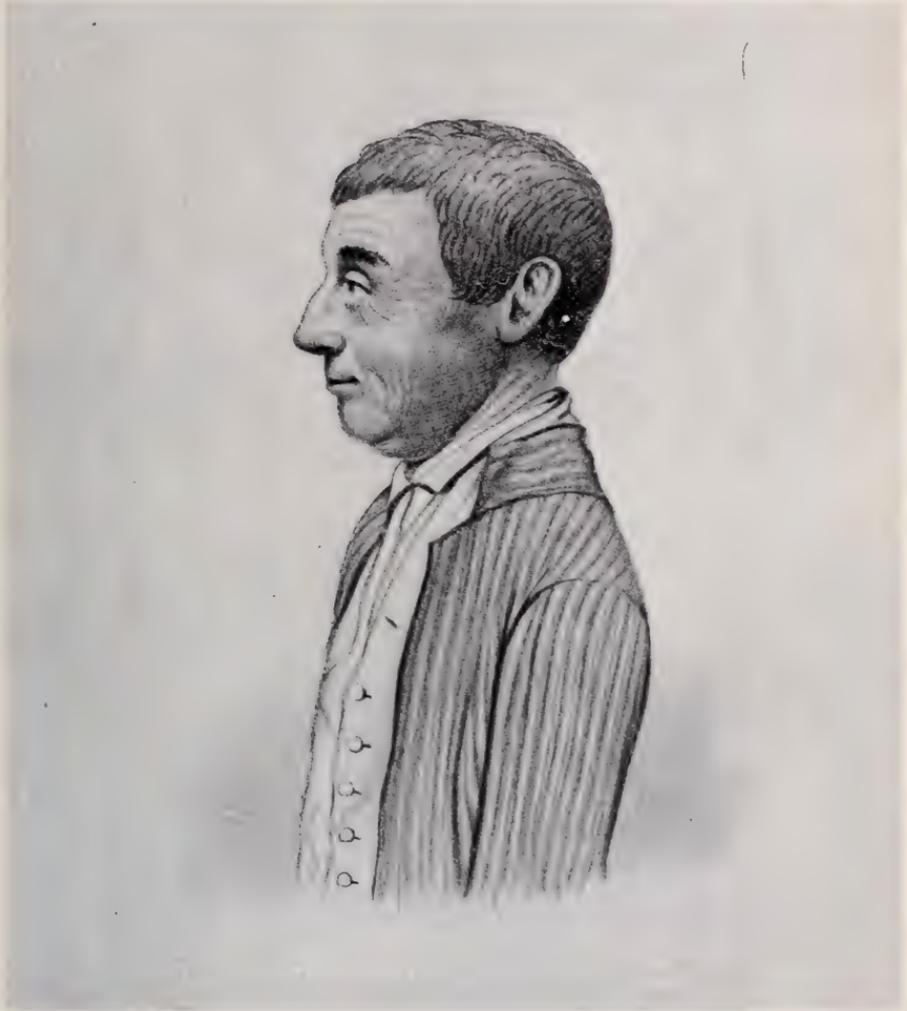


FIGURE 5.—John Abbot (self portrait), Georgia naturalist who collected a specimen of the Swainson's Warbler about 25 years earlier than Bachman, but did not report it. His painting of the bird was discovered many years later. Photograph courtesy Oliver H. Hewitt, Cornell University.

During his first years in Georgia after the Revolutionary War, Abbot lived in the town of Jacksonboro in Screven County. Jacksonboro, no longer in existence, was located in the Savannah River valley near Sylvania. Abbot did much of his collecting in a swamp along Brier Creek (fig. 7), a tributary of the Savannah.



FIGURE 6.—Photograph of John Abbot's painting of the Swainson's Warbler, which he called the "Swamp Worm-eater." Illustration courtesy Fogg Art Museum, Harvard University, and the Harvard College Library.

After Bachman collected his historic five specimens in 1832 or 1833, the Swainson's Warbler was almost a lost species for the next 50 years. According to William Brewster (1885a, p. 66). only eight or nine specimens were collected during that period. Then in 1884, Brewster and Arthur T. Wayne made significant collections and studies in the vicinity of Charleston, S.C. (Brewster, 1885a). Wayne reported the first nest and eggs known to

science (Brewster 1885b, p. 468), near Charleston on June 6, 1885. Troup D. Perry (1886, p. 188) of Savannah, Ga., found a nest 22 days earlier (May 16) but did not report his discovery as soon as did Wayne.

Since the Swainson's Warbler was thought to be restricted to the Coastal Plain, ornithologists were surprised to learn by the 1930's that this warbler was a locally common breeding bird to an elevation of about 3,000 feet in the Southern Appalachians. Before the 1930's there had been several records from the Piedmont suggesting the possibility of an up-country population. L. M. Loomis (1887, p. 347-348) found the bird at Chester, S.C., 150 miles from the coast, and W. H. LaPrade, Jr., (1922, p. 88-89) found a nest with eggs at Atlanta, Ga., 1,050 feet above sea level in the foothills of the Appalachians.



FIGURE 7.—Approximate location on Brier Creek, Screven County, Ga., where Abbot collected the "Swamp Worm-eater."

The first record of this species in the Appalachians is apparently based on a specimen collected on June 14, 1924, by P. C. Bibbee (see Brooks and Legg, 1942, p. 76) in West Virginia. The bird was taken at Buzzard's Rocks, Monongalia County, in what Brooks and Legg describe as "a rugged region of hemlock-and-rhododendron-clad mountains only a few miles from the Pennsylvania border."

Additional early records from the Appalachians are those of T. D. Burleigh, who collected three specimens near Asheville, N.C., on September 17, 1930, August 31, 1931, and September 14, 1932, (in U.S. National Museum collection) and those of E. A. Williams (1935, p. 458-459) who sighted several birds near Tryon, N.C., on May 8, 1934. The Swainson's Warbler was established as a breeding bird of the Appalachians in the summer of 1932 when F. M. Jones discovered several nests in southwestern Virginia near Bristol (Murray, 1939, p. 9).

Distribution

BREEDING RANGE

The Swainson's Warbler spends nearly 6 months of the year in the United States (fig. 8). During this period the bird is primarily associated with the river floodplain forests and swamps of the South Atlantic and Gulf Coastal Plains, and with the rich moist woods of the Mixed Mesophytic forest (see Braun, 1950, p. 39-49) of the Southern Appalachians. The mountain habitats are in the hemlock-rhododendron (*Tsuga canadensis*-*Rhododendron maximum*) association and the cove hardwoods forest. Apparently the Piedmont Province is generally unsuitable for occupation by this species. While there are scattered records of its occurrence in the Piedmont Province during the breeding season, there appear to be no breeding concentrations in this in-between area. The swamps and floodplain forests of the Coastal Plain, and sections of the Mixed Mesophytic forest where this species occurs in the mountains, are more humid than most of the forests of the Piedmont.

During the summer the climatic features of the two major physiographic regions occupied by the Swainson's Warbler are somewhat similar. Blair (1942, p. 130, 132) has classified the climate of the South Atlantic and Gulf Coastal Plains as Humid Subtropical type, and the climate of the Southern Appalachians as Humid Continental type (warm long summer subtype). The Humid Subtropical climatic type has a moderate-to-heavy rainfall at all seasons, usually with a maximum in summer; 9 to 12 months with mean temperature above 50° F.; and a growing season of 220 days or more. The Humid Continental type (warm long summer subtype) has a rainfall between 20 and 40 inches with a summer maximum; 6 to 9 months with mean temperature above 50° F.; and a growing season of 140 to 220 days.

Atlantic Coastal Plain

Along the Atlantic Coastal Plain the Swainson's Warbler occurs from extreme southern Delaware to southeastern Virginia and southward and inland as far as the fall line to about Jacksonville and the Suwannee River in Florida.

The northern limit on the Atlantic coast is the Pocomoke River Swamp in Sussex County, Del., and Worcester County, Md. The Pocomoke Swamp lies about 10 miles inland from the Atlantic



FIGURE 8.—Distribution of the Swainson's Warbler. Hatched area indicates general limits of breeding range; solid black area indicates general limits of winter range.

Ocean and extends from just above the Delaware-Maryland line southward nearly to the Virginia boundary. Only a few scattered pairs nest in this cypress-gum disjunct swamp.

The Swainson's Warbler is locally common in the Great Dismal Swamp in southeastern Virginia and northeastern North Carolina, and in certain floodplain forests just below the fall line. In many of these river floodplains its distribution coincides with that of the giant cane (*Arundinaria gigantea*). It was also reported to be common in the 1960's in the Ocmulgee River floodplain forest, 3 to 5 miles south of Macon, Bibb County, Ga.; in the Savannah River Valley, from Augusta, Richmond County, Ga., downstream about 25 miles; and in the Wateree River Swamp, northwest Sumter County, S.C. Scattered pairs and singing males have been reported from many other areas in the Carolinas and Georgia.

The distributional status of the Swainson's Warbler in the lower Coastal Plain of South Carolina and Georgia has apparently changed in the last 50 years. In the *Living Bird*, Fifth Annual, (Meanley, 1966, p. 152), I made the following comments regarding the former abundance of this species in the lower Coastal Plain of the Southeast:

At the close of the 19th century and the beginning of the 20th, Swainson's Warblers were apparently more numerous in the lower Coastal Plain than they are today. Wayne (1910:149-150) found them to be common breeding birds near Charleston, South Carolina, as did Perry (1887:142) near Savannah, Georgia. During the period of 22 April to 25 September 1884, Wayne collected 47 specimens of this species near Charleston. Considering modes of travel available to Wayne and the limited area of his operations, his collecting of so many specimens would seem to indicate a sizable population in the area. Perry (1887) reported 24 active nests near Savannah in the spring of 1887, which likewise suggests that Swainson's Warblers were more abundant in the late 19th century than at present. E. S. Dingle of Huger, South Carolina, who worked with Wayne and who bridged the gap between Wayne's time and the present, informed me in April 1958 that he had noted during his lifetime a marked downward trend of the population in the coastal area. A. Sprunt, Jr. (*in* Sprunt and Chamberlain, 1949:435), a protégé of Wayne's, has seen this warbler only four times in the lower Coastal Plain of South Carolina.

In the lower Savannah River Valley, an area extending 30 miles upriver from Savannah, E. O. Mellinger and I found only scattered individuals and occasional pairs during the early 1960's—certainly not the numbers and concentrations found farther up the valley near Augusta, as reported by Murphey (1937:42), Norris (1963:47), and J. F. Denton (*pers. commun.*).

Gulf Coastal Plain

In the Gulf Coastal Plain the Swainson's Warbler occurs from north of the Suwannee River in northern Florida, northward and

westward to southern Alabama, eastern, Mississippi, and the lower Mississippi Valley as far as southern Illinois, and westward through southern Arkansas and the southeastern corner of Oklahoma to at least Brazos County, Tex.

During the mid-20th century, areas where it was reported as locally common were mostly in the lower Mississippi Valley. However, the lower Mississippi Valley was the center of the most intensive ornithological investigations during the period. It undoubtedly was common also in many areas east of the lower Mississippi Valley.

In northwestern Florida it was formerly reported as a locally common breeding bird along the Wacissa River near Waukeenah, along the Suwannee River near Old Town (Wayne, 1893, p. 338; 1895, p. 367), and along the Aucilla River (Howell, 1932, p. 386). F. M. Weston (1965, p. 105) regarded it as an uncommon summer resident at Pensacola.

In Alabama it is rather widely distributed, with breeding concentrations in the Alabama River bottoms above Mobile and in the vicinity of Bear Swamp a few miles west of Montgomery (Howell, 1928, p. 284; Imhof, 1962, p. 439).

In the Louisiana section of the lower Mississippi Valley, G. H. Lowery (personal communication, 1962) reported it as commonly breeding in the vicinity of Baton Rouge, and I found it locally common in 1956-57 in Bayou Boeuf Swamp near Alexandria as well as in the Tensas River area a few miles south of Tallulah.

In the Mississippi River Delta, at Rosedale, Bolivar County, Miss., M. G. Vaiden (personal communication, 1968) found nests and reported the species as fairly common in the batture along the Mississippi River.

In eastern Arkansas I found it locally common in the lower White River bottoms, in the East Moon Lake and Scrubgrass Bayou areas, and along the Arkansas River between the mouth of Bayou Meto and Pendleton Ferry. Five nests were located in the latter locality between 1966 and 1968.

Apparently the Swainson's Warbler was a breeding bird in the late 1800's and early 1900's in the St. Francis River "sunken lands" of southeastern Missouri and northeastern Arkansas, where it occurred in canebrakes with the Bachman's Warbler (*Vermivora bachmanii*) (Widmann, 1895, p. 115-117). Since the time of Widmann's investigations, much of the swampland in that area has been drained and the canebrakes destroyed.

At Memphis, Tenn., B. B. Coffey, Jr., (1941, p. 30-31) reported Swainson's Warblers nesting within the city limits and in at least

10 localities in surrounding Shelby County. These warblers occur regularly in most of the Coastal Plain riverbottoms of western Tennessee and in the Reelfoot Lake area. Mengel (1965, p. 389) reported the species as "fairly common locally in lowland forests of extreme western Kentucky (Fulton, Hickman, and Ballard Counties), rare and local in swamp forests of the Pennyroyal and Western Highlands."

The Gulf Coastal Plain extends as far northward as the southern tip of Illinois, a short distance above the confluence of the Ohio and Mississippi Rivers. Records from the Coastal Plain of southern Illinois are as follows: Olive Branch, Alexander County, May 15 and 20, 1909, and Reevesville, Johnson County, June 21-22, 1909 (Howell, 1910, p. 216); Cairo, Alexander County, September 1, 1938, female collected (Ammann, 1939, p. 185-186); and DuQuoin, Perry County, a few miles north of the Coastal Plain, June 7, 1907 (Gross, 1908, p. 225).

The breeding range of the Swainson's Warbler west of the Mississippi Valley is imperfectly known. It has been found during the breeding season as far west as Brazos County, Tex. (Purrington, 1966, p. 35); and in southeastern Oklahoma (McCurtain County) just beyond the Coastal Plain (Sutton, 1967, p. 491).

Southern Appalachians

The Swainson's Warbler breeds in the mountains in south-central West Virginia, perhaps southeastern Ohio, eastern Kentucky, southwestern Virginia, eastern Tennessee, western North and South Carolina, and northern Georgia and Alabama.

In West Virginia, Swainson's Warblers occur mostly on the Allegheny Plateau, west of the main Allegheny ridges. M. G. Brooks and W. C. Legg (1942, p. 78) found the species locally common near Mt. Lookout, Nicholas County, where elevations are between 2,200 feet and 1,300 feet at the Gauley River level. The three principal streams along which Swainson's Warblers were found are Gauley River; Collison Creek, a tributary of the Gauley; and Anglins Creek, a tributary of Meadow River.

The Swainson's Warbler breeds commonly in the mountain ravines opposite Charleston, W. Va., in the Kanawha River Valley. Charleston lies at an elevation of about 600 feet, and the birds are found from the city limits upward. Fifty miles west of Charleston, in the Ohio River Valley, there are records from Huntington, W. Va., (Seeber and Edeburn, 1952) and across the river at Chesapeake, Lawrence County, Ohio (Green, 1947, p. 211). M. G. Brooks (1965, p. 281) states that Swainson's Warblers are known from 14 West Virginia counties.

In the mountains of eastern Kentucky this warbler was first noted by G. H. Brieding (1944, p. 6-7) on Black Mountain, Harlan County, on July 5 and 6, 1944. R. M. Mengel (1965, p. 391) collected a specimen on June 26, 1951, near Elkhorn City, on the line between Dickinson County, Va., and Pike County, Ky. The elevation at this point is about 2,200 feet.

Farther south along the Appalachian chain in the Holston Mountains of southwestern Virginia and northeastern Tennessee, nesting has been recorded by F. M. Jones near Bristol, Washington County, Va. (Murray, 1939, p. 9). Three miles northeast of Shady Valley, Johnson County, Tenn., W. M. Perrygo and C. Lingeback collected an adult male at an elevation of 3,000 feet on June 8, 1937, and observed two others at 2,600 feet elevation 5 miles north of Shady Valley near Beaverdam Creek (specimen in U.S. National Museum).

In western North Carolina, T. D. Burleigh collected three specimens near Asheville, in the Pisgah National Forest, one each on September 17, 1930, August 31, 1931, and September 14, 1932 (specimens in U.S. National Museum). At Tryon, near the North Carolina-South Carolina border, E. A. Williams (1935, p. 458-459) observed a Swainson's Warbler on May 8, 1934, and the following year observed a pair from May 9 to 14.

An important concentration area of this species in the Southern Appalachians is where the States of North Carolina, South Carolina, and Georgia meet. H. M. Stevenson, Jr., (1941, p. 46) reported Swainson's Warblers from Highlands, Macon County, N.C., June 20, 1937, at 3,800 feet elevation, and July 3, 1937, at 3,700 feet elevation. J. F. Parnell and T. L. Quay (1964, p. 144) reported Swainson's Warbler "as a rather common summer resident" at Toxaway River Gorge, Transylvania County, N.C. In that area at an elevation of 1,400 feet Parnell observed an adult feeding young. R. H. Peake, Jr., (1965, p. 114) reported finding a bird near Cashiers, Jackson County, N.C., April 22, 1965.

In western South Carolina an adult male was taken by W. M. Perrygo at Walhalla, Oconee County, June 25, 1940. Also in Oconee County, J. B. Shuler (1962, p. 75-76) noted a singing male in the Sumter National Forest, May 19 and 30, 1962.

The first record in the mountains of Georgia was obtained June 3, 1948, by C. Neal and J. F. Denton (Denton, 1948, p. 24-25), at an elevation of 1,700 feet on Tray Mountain near Robertstown, White County. In the same locality, Denton and Neal (1951, p. 27-28) saw three males on May 8, 1949, and four males on May 9, 1950. At Clayton, Rabun County, Ga., E. O. Mellinger (personal

communication) observed two pairs almost daily during April, May, and June 1968.

In Alabama, T. A. Imhof (1962, p. 439) recorded this species in the northeastern corner of the State (Long Island Gulf, Jackson County), at 1,150 feet, June 7, 1957.

Ozark Mountains

There are records of birds in two locations in the Arkansas Ozarks. D. A. and F. C. James and S. Hilty (1966, p. 577) recorded three territorial males 12 miles southeast of Yellville, Marion County, Ark., June 25, 1966. At Fayetteville, Washington County, in the northwestern corner of the State, the Jameses (1966, p. 518) observed a male on territory daily, May 4 to 31, 1966.

Westward beyond the Ozarks, the breeding range extends into the Prairie Plains physiographic region of northeastern Oklahoma. Nice (1931, p. 155) reported that A. J. Kirn located several nests along the Little Caney River near Copan, Washington County, in June 1914 and June 1917. This locality is only about 10 miles from the Kansas border. A more recent occurrence in the same county was reported at Bartlesville, April 23, by S. Veal (Williams, 1966, p. 524).

Piedmont province

The following are records made during the breeding season. Records from the Piedmont province before May and after July may represent either birds on their breeding grounds or migrants.

Virginia.—Charlottesville, in the upper Piedmont, in the foothills of the Blue Ridge Mountains: Summer 1913 (Ferneyhough, 1914, p. 291), and spring 1961 through 1964, by R. S. Merkel (Scott and Cutler, 1964, p. 442).

South Carolina.—Greenwood County, near the Savannah River Valley, approximately 40 miles above the fall line: July 3, 1924, nest (F. W. Hahn in Sprunt and Chamberlain, 1949, p. 436).

Georgia.—Atlanta, in the foothills at an elevation of about 1,200 feet: May 27, 1920, and May 30, 1922, nests (LaPrade, 1922, p. 88-89). Athens: May 20, 1921 (Burleigh, 1938, p. 24).

Kentucky.—Bullitt County: June 27, 1937 (Carpenter, 1937, p. 32).

Extralimital records (United States)

Records of occurrence beyond the limits of the normal breeding range are as follows: Kearney, Neb., April 9, 1905, by C. A. Black (Worthen, 1906, p. 227); Holly, Prowers County, Colo., May 12, 1913 (Lincoln, 1918, p. 236); Prospect Park, New York City,

May 5, 1950, by Carleton and Helmuth (Bull, 1964, p. 362); Mt. Carmel, Wabash County, Ill., April 1878 (Ridgway, 1878, p. 163); Lake Quivira, Johnson County, Kans., May 11, 1957 (Hardy, 1957, p. 10); and Linwood, N.J., May 23, 1968 (Savell, 1968, p. 159).

WINTER RANGE

The main wintering grounds are the Caribbean archipelago in the general area of latitude 20° N., including Jamaica and Cuba, and the Yucatan Peninsula south to British Honduras (fig. 8).²

Cuba

Oriente Province.—Guantanamo: January 18, 1914, male collected (Ramsden, 1914, p. 253).

Las Villas Province.—Cienfuegos: December 23, 1948, through January 3, 1949, several specimens collected (Eaton, 1953, p. 169).

La Habana Province.—Havana: September 25, year ?, one specimen collected, and April 14, 1922, one specimen collected, both possibly migrants (from the distribution files of the Migratory Bird Populations Station of the Bureau of Sport Fisheries and Wildlife, at Laurel, Md.).

Jamaica

St. Thomas Parish.—Kingston: December 31, 1946, and February 5 and 7, 1947, 3 females collected; December 3, 1946, through February 7, 1947, 9 birds observed (Tordoff, 1952, p. 321). Port Royal Mountain: February 18, 1879, specimen collected by E. Newton (Merriam, 1885, p. 377).

St. Andrew Parish.—Hope: February 1879, specimen collected by E. Newton (Merriam, 1885, p. 377). Hermitage: April 8, 1879, specimen collected by E. Newton (Merriam, 1885, p. 377). Mt. Elizabeth: October 1 and 7, 1879, December 21, 1881, and March 16, 1882, specimens collected by E. Newton (Merriam 1885, p. 377).

Swan Islands

A specimen was collected on March 1, 1912 (Peters, 1913, p. 378). The Swan Islands are in the Caribbean Sea, between the Yucatan Peninsula and Jamaica, near latitude 18° N. and longitude 84° W.

² There are several records for the Bahama Islands that probably represent migrants, and they are treated as such here.

Mexico

Quintana Roo.—Santa Lucia: January 24, 1912, specimen collected (Peters, 1913, p. 378). Chetumal: February 12, 1949, specimen collected (Paynter, 1955, p. 242). Cozumel, Cozumel Island: December 27, 1961, specimen collected by L. C. Binford (Louisiana State University collection).

Campeche.—Pacaytain: January 15, 1940, specimen collected (Traylor, 1941, p. 219).

Veracruz.—Veracruz: winter of 1887-88 (distribution files, Migratory Bird Populations Station).

British Honduras

February 20, 1956, specimen collected by S. M. Russell (Louisiana State University collection) in the Orange Walk District.

Migration

SPRING

Swainson's Warblers apparently follow the most direct routes in migrating from wintering to breeding grounds. From West Indian wintering grounds they apparently reach the United States by island-hopping to southern Florida. Birds moving northward from eastern Cuba and Jamaica may touch some of the Bahama islands and cays enroute: there are March and April records from Bimini, Andros Island, and Cay Lobos.

The northern coast of Yucatan is a natural departure point for trans-Gulf flight to the Gulf Coast of the United States. Studies by G. H. Lowery (1945, p. 92-121; 1946, p. 175-211) and H. M. Stevenson (1957, p. 39-77) and observations by several other ornithologists lend credence to a trans-Gulf movement of Swainson's Warblers from the northern coast of Yucatan and the shore of the Bay of Campeche. The distribution of casualties at the base of the Tall Timbers TV tower near Tallahassee, Fla., 50 miles from the Gulf, indicates that the spring flight through that region is mainly in a southwest-to-northeast direction (Stoddard and Norris, 1967, p. 11, 15). Stoddard and Norris believe that this is mainly a trans-Gulf flight, with a minor segment of the flight skirting the Gulf. The lesser migration, which they refer to as the "Florida Peninsula-West Indian Flight" comes through mainly on easterly, southeasterly, and southerly winds.

It is probable that some of the Swainson's Warblers that winter in eastern Mexico migrate around the Gulf, moving northward along the eastern coasts of Mexico and Texas. The numerous spring records from coastal Texas could represent both trans-Gulf and circum-Gulf migrants.

Exceptionally early arrivals reach Florida by the middle of or the third week of March. There are records by J. Johnson and D. R. Paulson for March 16 offshore near Eau Gallie and for March 19 at Goulds, south of Miami (Stevenson, 1960, p. 304), and Bush Key pond, Dry Tortugas, March 17, 1964 (Robertson and Mason, 1965, p. 136). The first wave of migrants reaches northern Florida during the last week in March. At Tallahassee, during the period 1956 to 1966, 14 of 83 birds striking the Tall

Timbers TV tower arrived in the last week of March (Stoddard and Norris, 1967, p. 71). The earliest arrival date at Tallahassee was March 21.

Earliest arrivals at other localities are as follows: New Orleans, La., one on March 30 and four on April 1 (Kopman, 1905, p. 292; and 1915, p. 186); Savannah, Ga., March 25 (Burleigh, 1958, p. 495); Macon, Ga., March 31 (B. Meanley, MS.); and noted by K. McCracken and E. Payne, Corpus Christi, Tex., March 28 (Webster, 1966, p. 531).

Average dates of first arrivals are: Baton Rouge, La., April 2 (Lowery, 1945, p. 107); Alexandria, La., April 3 (B. Meanley, MS.); Macon, Ga., April 3 (B. Meanley, MS.); Augusta, Ga., April 3 (J. F. Denton, Jr., personal communication); Suffolk, Va. (Dismal Swamp), April 15 (B. Meanley, MS.); Clayton, Ga. (mountains), April 17 (E. O. Mellinger, personal communication); Charleston, W. Va., April 15-17 (Sims and DeGarmo, 1948, p. 3); and Maryland-Delaware boundary (Pocomoke Swamp), April 21 (Meanley, 1950, p. 94).

The main flights at Tallahassee, Fla., for the period 1956 to 1966 were during the first and second weeks in April, when 50 of 83 birds that struck the Tall Timbers TV tower (Stoddard and Norris, 1967, p. 71) were reported to be this species. At Macon, Ga., from 1963 to 1968, the main flights were in the second week of April (B. Meanley, MS.). At Charleston, W. Va., the main flight was April 19 (Sims and DeGarmo, 1948, p. 3). At the Dismal Swamp in southeastern Virginia, the main flight was during the third week in April (B. Meanley, MS.).

FALL

During 3 years at Macon, Ga., and at Gillett, Ark., I made weekly observations from the time the local population arrived in the spring until it departed in the fall, and I found that most of the breeding population remained until about the middle of September. A. T. Wayne (1910, p. 150) reported that at Charleston, S.C., "The song period lasts from their arrival until September 15." E. Sims and W. R. DeGarmo (1948, p. 3) stated that at Charleston, W. Va., "singing males were heard briefly in early mornings as late as September 15."

Apparently the bulk of the birds migrate through the Deep South between the middle of September and the middle of October. At the Tall Timbers TV tower at Tallahassee, Fla., Stoddard and Norris (1967, p. 71) reported, 58 of 60 fall strikes of this species occurred between September 11 and October 10.

The earliest migrants reach the middle Gulf Coast by early

August and the Florida Keys by mid-August and early September. Migrants were reported at Gulfport, Miss., on August 8 and 19, and at Deer Island, Miss., on August 26 (Burleigh, 1945, p. 110); at Sombrero Key, Fla., on August 17 (Howell, 1932, p. 386); and at Dry Tortugas, Fla., by September 2-9 (Sprunt, 1951, p. 224).

Late records of departure are: Knoxville, Tenn., October 7 and 8 (Howell and Tanner, 1951, p. 62); Tybee Island, near Savannah, Ga., October 18 (distribution files, Migratory Bird Populations Station); Tallahassee, Fla., October 14 (Stoddard and Norris, 1967, p. 71); and Sombrero Key, Fla., November 8, 10, and 13 (Howell, 1932, p. 386).

The migration route to the wintering grounds is apparently the reverse of that to the breeding grounds. The distribution of casualties at the base of the Tall Timbers TV tower indicates that the heaviest flight is from northeast to southwest, the direction of trans-Gulf migration. Some birds that migrate through southern Florida also pass through the Tallahassee area in the fall (Stoddard and Norris, 1967, p. 71).

The coast of Georgia and the eastern coast of Florida are also a southward migration route, as evidenced by the following records: Tybee Island, Ga., September 23 and 24 and October 2 and 18 (Burleigh, 1958, p. 496); Jacksonville, Fla., October 5 and 7, 19 birds picked up at TV towers (Cunningham, 1965, p. 29); St. Augustine, Fla., September 14 (distribution files, Migratory Bird Populations Station); Miami, Fla., October 2 (L. A. Stimson, distribution files, Migratory Bird Populations Station); and Loxahatchee National Wildlife Refuge, Fla., October 6 (P. W. Sykes, Jr., personal communication).

Southward movement along the Gulf Coast in Texas and northern Mexico would be expected, but records are fewer for the fall than for the spring: Rockport, Tex., October 20 (C. H. Hagar, distribution files, Migratory Bird Populations Station); Kemak, Tex., September 27 (J. S. Heiser, distribution files, Migratory Bird Populations Station); and Matamoros, Tamaulipas, Mexico, just over the Texas border from Brownsville, August 29 (Phillips, 1911, p. 84).

Early arrival records in the West Indies are: Havana, Cuba, September 25 (Bent, 1953, p. 38); and Mt. Elizabeth, Jamaica, October 1 and 7 (Merriam, 1885, p. 377).

Ecological Relations

The optimum habitat of the Swainson's Warbler is a rich, damp (but not wet) woods with deep shade and moderately dense undergrowth. This combination occurs in the physiographic areas in which this species is nearly always found—namely, the floodplain and swamp forests of the Atlantic and Gulf Coastal Plains and certain plant associations of the mixed mesophytic forest of the Southern Appalachians. When in swamps, the Swainson's Warbler frequents those parts that usually are not inundated, but occasionally on the Coastal Plain it may be observed foraging along the wet margin of a swamp or in low wet spots that have been left from receding floodwaters in floodplain forests. In such situations, its foraging behavior on the ground may resemble that of the Louisiana Waterthrush (*Seiurus motacilla*). Where inundation is present in a floodplain forest, it is usually the result of late spring floods or heavy rains, after the birds have selected a breeding territory in a dry section of woods.

Whether on the Coastal Plain or in the mountains, this species is usually near some major drainage system. The river valleys provide moist conditions on the breeding grounds, as well as "highways" for migration.

In Coastal Plain forests, where most of my experience has been, it is my observation that the Swainson's Warbler, more than its closest avian associates, is restricted to the shadier part of the forest. Species such as the Carolina Wren (*Thryothorus ludovicianus*), the White-eyed Vireo (*Vireo griseus*), the Prothonotary Warbler (*Protonotaria citrea*), the Hooded Warbler (*Wilsonia citrina*), the Kentucky Warbler (*Oporornis formosus*), the Cardinal (*Richmondia cardinalis*), and the Rufous-sided Towhee (*Pipilo erythrophthalmus*) spend only a part of their time in parts of the forest as shady as those frequented most of the time by the Swainson's Warbler. The deep shade of the Swainson's Warbler environment is the result of dense upper canopy, layer of lower trees, and shrub strata. Herbaceous ground cover is absent in most of the warbler's habitats, and where it occurs it is usually of little consequence as a shade producer.

The Swainson's Warbler lives mostly in the shrub stratum and

on the ground. In many habitats, the shrub stratum, or undergrowth, is composed mainly of a single species such as giant cane in the floodplain forest, sweet pepperbush (*Clethra alnifolia*) in the swamp forest, scrub palmetto in the bottomland forest, and rhododendron (*Rhododendron maximum*) in the mixed mesophytic forest. The structure of the undergrowth may be remarkably uniform, as in some canebrakes, palmetto thickets, and sweet pepperbush stands.

COASTAL PLAIN

In the Coastal Plain Province, river floodplain forests and swamps are the principal physiographic types in which the Swainson's Warbler lives during the breeding season, or summer half of the year. Since the terms swamp, riverbottom, hardwood bottom, and floodplain forest are often used synonymously, an explanation of these terms seems appropriate. The lowland forest bordering a southern river is generally known to the forester or plant geographer as a riverbottom or bottomland. It is usually a complex of several forest communities, including swamps, floodplain forests (also known as hardwood bottoms), and riverfront hardwoods. Most swamps are permanently flooded except during droughts; they thus differ from floodplain forests which are periodically flooded, usually in late winter or spring. There are several types of swamps. Those in riverbottoms are known as river or alluvial swamps; they are found in the lowest part of the bottomland, either bordering the river or between the floodplain forest and adjacent uplands. Swamps found away from riverbottoms are known as nonalluvial or inland swamps; good examples are the Great Dismal and Okefenokee Swamps.

Recognized as subdivisions within the floodplain or bottomland forests of the lower Mississippi Valley are the first bottoms, and the ridge bottoms (or cane ridges). In low, poorly drained flats of the first bottoms, the Overcup Oak-Bitter Pecan (*Quercus lyrata-Carya aquatica*) type is predominant. The Sweetgum-Water Oak (*Liquidambar styraciflua-Quercus nigra*) type is found in the better drained parts of the first bottoms. Sweet Pecan (*Carya illinoensis*), Sweetgum, and Southern Red Oak (*Quercus falcata*) are prominent on the cane ridges. These subdivisions are not as distinct or are non-existent in the South Atlantic coastal floodplain forests.

In floodplain and swamp forests, the main plant formations selected by the warbler are usually canebrakes (figs. 9-12), scrub palmetto, and sweet pepperbush. Greenbrier (*Smilax* spp.) is



FIGURE 9.—Canebrake along the edge of the Ocmulgee River, about 3 miles south of Macon, Bibb County, Ga., 1968.

often associated with sweet pepperbush where the Swainson's Warbler is found.

The canebrake is the prime and classic habitat of the Swainson's Warbler on the Coastal Plain. This habitat has mostly disappeared, having been reclaimed for agriculture, or grazed, burned, or flooded out of existence. Canebrakes are restricted mostly to floodplain forests or hardwood bottoms. In the lower Mississippi River Valley they occur on first bottom ridges, which are well-drained areas; whereas on the South Atlantic Coastal Plain they occur along the river and stream edges in floodplain forests where there is little change in elevation from the river to the edge of the uplands. Thus, they are subject to partial inundation during periods when the bottomlands are flooded.

Scrub palmetto occurs in floodplain forests and swamps in the southern part of the Coastal Plain breeding range of the Swainson's Warbler. Sweet pepperbush is an important plant for the Swainson's Warbler in the northern part of its Atlantic Coastal Plain breeding range. This was the principal habitat in which I found it in the Great Dismal Swamp of southeastern Virginia and the Pocomoke Swamp on the Eastern Shore of Maryland. In some places, sweet pepperbush stalks have a somewhat canebrakelike aspect, the main stems growing fairly straight, with similar spacing or density and shade effect.



FIGURE 10.—Canebrake habitat in the Ocmulgee River floodplain forest near Macon, Ga. The longest poles are 30 feet in length. The diameter of the largest poles is $1\frac{1}{4}$ inches.



FIGURE 11.—Canebrake habitat in the Ocmulgee River floodplain forest near Macon, Ga. The overstory is mainly ash, hackberry, elm, and ash-leaved maple.



FIGURE 12.—Canebrake habitat in the Ocmulgee River floodplain forest near Macon, Ga. Of 91 territorial males that I observed along the Ocmulgee over a period of years, 87 had territories in canebrakes.

Ocmulgee River floodplain forest in Georgia

In this area the Swainson's Warbler is found in the extensive canebrakes some 3 to 5 miles southeast of Macon in Bibb County in central Georgia (Meanley, 1945). The largest stands I have ever seen of the fast-disappearing canebrake habitat occur in this area. In 1968, there were still some sections in the Ocmulgee



FIGURE 13.—Typical canebrake breeding territory occupied by a male Swainson's Warbler near Macon, Ga., May 1965.

floodplain forest where canebrakes, nearly uninterrupted, covered 1-square-mile areas. The cane poles in these stands averaged about 15 feet in height and three-fourths of an inch in diameter at ground level. The largest poles reached 30 feet in height and an inch and a half in diameter at base. In the *Living Bird*, Fifth Annual, (Meanley 1966, p. 155) I published notes on the density of a tract of cane in a male Swainson's Warbler territory (fig. 13) near Macon:

The number of cane poles in 10 quadrats varied from 18 to 75 per 10-foot-square quadrat. There were about 20,000 cane poles per acre in my sample area which was virtually devoid of other plants, except for a scattering of large trees.

Of 91 territorial males that I observed in seven nesting seasons near Macon, 87 had territories (averaging about 1 acre each) in patches of cane growing beneath the floodplain forest canopy. The floodplain forest in this area was composed mainly of the following trees (in descending order of abundance): hackberry (*Celtis occidentalis*), boxelder (*Acer Negundo*), red ash (*Fraxinus pennsylvanica*), American elm (*Ulmus americana*), sweetgum, water oak, swamp chestnut oak (*Quercus Michauxii*), silver maple (*Acer saccharinum*), and mulberry (*Morus* sp.). The understory was mostly cane, but in openings included blackberry (*Rubus* sp.), swamp privet (*Forestiera acuminata*), or saplings of the above-mentioned trees. The coverage of the combined strata of upper canopy, lower trees, and understory was about 85 percent. Twelve exposure meter readings, made at feeding sites of four Swainson's Warblers, ranged from 100 to 225 footcandles.

The ground in areas occupied by the warblers is dry except during periodic flooding. During three nesting seasons when I entered the floodplain forest the water was 6 feet deep in some canebrake areas where I usually conducted studies. Sometimes these floodwaters recede in less than a week, and the habitat returns to normal. Such flooding sometimes occurs during the height of the nesting season, with a devastating effect on nesting success, since the average nest height is about 4 feet, and some nests are only a foot and a half from the ground.

A 7-acre tract of cane about 3.5 miles southeast of Macon had three territorial males in 1944, five in 1945, four in 1963, and one in 1968. There was gradual reduction in the amount of cane in this tract over the 24-year period. In 1968, I counted 19 territorial males along a 2-mile transect about 5.5 miles southeast of Macon in an area known as Bond Swamp.

The following notes that I made on breeding bird associates appeared in the *Living Bird*, Fifth Annual, (Meanley 1966, p. 158-159):

In the Ocmulgee River floodplain forest near Macon, the nesting species in closest association with the Swainson's Warbler were the Cardinal (*Richmondia cardinalis*), Hooded Warbler (*Wilsonia citrina*), and the White-eyed Vireo (*Vireo griseus*). All three nested in or on the edge of canebrakes as well as in other plant associations. The Cardinal fed mainly along the edge of cane thickets and in forest openings such as logging roads. The Hooded Warbler, which fed regularly from 2 to 30 feet above the ground,

ranged through the more open growths of cane as well as the more open parts of the forest undergrowth. The White-eyed Vireo preferred mostly a less homogeneous habitat, more often the edge of viney thickets, and usually fed from 5 to 20 feet above the ground.

Other species, present in canebrakes but not so closely associated with the Swainson's Warbler, were the Carolina Wren (*Thryothorus ludovicianus*), Kentucky Warbler (*Oporornis formosus*), Rufous-sided Towhee (*Pipilo erythrophthalmus*), and Prothonotary Warbler (*Protonotaria citrea*). The Carolina Wren ranged throughout the floodplain forest, especially about old logs and brush piles. The Kentucky Warbler occurred most often where there was a denser ground cover, particularly of herbaceous plants, than in the canebrakes. The Towhee, a ground-feeder like the Swainson's and Kentucky Warblers, fed in the canebrakes but usually where the leaf litter and cover was thicker than in the areas used by the Swainson's Warbler. The Towhee also fed in other parts of the forest and in the edge of habitats. The Prothonotary Warbler preferred the banks of streams that flowed through the canebrakes and the vegetation along the banks.

During migration, Worm-eating Warblers and Ovenbirds (*Seiurus aurocapillus*) moved through the canebrakes as well as other parts of the floodplain forest.

The Great Dismal Swamp

This extensive southern swamp a few miles south of Norfolk, Va., covers an area of about 600,000 acres in Nansemond and Norfolk Counties, Va., and in Pasquotank, Gates, and Camden Counties, N.C. In 1968 the Swamp was still a great wilderness, but with no virgin timber remaining. The part of the Swamp in which the Swainson's Warbler occurs is generally devoid of surface water (but low and damp) owing to drainage in connection with logging operations during the past 200 years. Being on low flat land with a high water table, some Swainson's Warbler territories are partially inundated after heavy rainfall.

The Dismal Swamp is quite diversified floristically but in the past apparently was predominantly forested with swamp blackgum (*Nyssa silvatica* var. *biflora*) (Kearney, 1901). It is in the remnant of this forest type, now of mixed species composition, that the Swainson's Warbler is mainly found today.

I examined such a mixed forest community along the northern end of Jericho Ditch (fig. 14), about 3 miles southeast of Suffolk, Va., in June 1966 and found that it was composed of the following plants: Predominant trees of the upper canopy were swamp blackgum, red maple (*Acer rubrum*), sweetgum, willow oak (*Quercus phellos*), water oak, tulip poplar (*Liriodendron Tulipifera*); lower trees were American holy (*Ilex opaca*), paw-paw (*Asimina triloba*), swamp magnolia (*Magnolia virginiana*), and red bay (*Persea borbonia*); undergrowth was mainly sweet pepperbush and greenbrier, but netted chain-fern (*Woodwardia areolata*)



FIGURE 14.—Mixed swamp hardwood habitat in the Dismal Swamp in southeastern Virginia, 1968. Major forest species are swamp blackgum, sweetgum, and red maple. Note Swainson's Warbler nest 2 feet from the ground in sweet pepperbush, center of picture.

covered the ground where there was more light. The Swainson's Warbler foraged mostly in openings between clumps of sweet pepperbush and greenbrier and in the small pure stands of sweet pepperbush. It nested mostly in the greenbrier tangles. A community of this composition also is the major Swainson's Warbler habitat in the Pocomoke Swamp on the Eastern Shore of Maryland.

I counted eight territorial males along a 0.5-mile transect in the vicinity of the Virginia-North Carolina line on April 20, 1958. Bird associates during the breeding season in the sweet pepperbush-greenbrier undergrowth are the White-eyed Vireo, Prothonotary Warbler, Prairie Warbler (*Dendroica discolor*), Ovenbird, Hooded Warbler, and Cardinal. The presence of the Prairie Warbler in this habitat was most unexpected, since nowhere else have I encountered it breeding in closed-forest habitat. An interesting breeding bird of this same swamp forest, but at higher elevations, is Wayne's Black-throated Green Warbler (*Dendroica virens waynei*).

Bayou Boeuf Swamp, La., and Monkey John Swamp, S.C.

Observations were made in the scrub palmetto breeding ground habitat in Bayou Boeuf Swamp near Alexandria, La., in the spring of 1956 and 1957, and in Monkey John Swamp near Savannah,



FIGURE 15.—Part of scrub palmetto territory of a male Swainson's Warbler in Monkey John Swamp, Jasper County, S.C., May 1964.

Ga., (fig. 15) in the spring of 1964. The physical features of these two areas were quite similar. Red ash, American elm, water oak, sweetgum, and hackberry formed an important part of the forest in both areas.

In Monkey John Swamp the density of the combined layers of the upper canopy and lower trees was about 90 percent. The undergrowth, almost entirely scrub palmetto, averaged about 3 feet in height, with about 800 plants per acre. Most of the ground area beneath the palmettos was dry. Wet spots under the palmettos in the territory of a Swainson's Warbler were generally avoided.

In the scrub palmetto habitat of Bayou Boeuf Swamp, I found a population density of 10 territorial males per 100 acres in April 1957.

Western Kentucky

R. M. Mengel (1965, p. 69) states that the ridge bottoms—the driest habitat of the alluvial forests, contain the finest broadleaf forest and the richest small bird populations of the region. It is in such areas that Swainson's Warbler is most numerous.

These are the cane ridges so favored by the Swainson's Warbler in the lower Mississippi Valley.

SOUTHERN APPALACHIANS

In the Southern Appalachians the Swainson's Warbler is primarily associated with the moist lower slopes of mountain ravines and various drainage systems of the Mixed Mesophytic Forest Region. On these lower slopes, where the proportion of hemlock in the mesic forest increases, rhododendron is often the main understory species; and it is within this association (figs. 16–17) that the warbler is most often found. It also occurs in some cove hardwood forests (fig. 18), where the understory may be composed of a heterogeneous growth of deciduous shrubs, and in other habitats.

In areas where the Swainson's Warbler is locally common, individuals of a population may "spill over" from optimum to marginal habitats, as cited by Brooks and Legg (1942, p. 70–80), who in West Virginia found a singing bird near the top of a ridge in a thicket beneath dead chestnut (*Castanea dentata*) trees. Parnell and Quay (1964, p. 139) reported a few Swainson's Warblers in dry sites, such as an oak-hickory forest in Toxaway Gorge in western North Carolina.



FIGURE 16.—*Rhododendron*-hemlock association. Mountain breeding habitat of the Swainson's Warbler along Collison Creek, on the Allegheny Plateau, Nicholas County, W. Va., May 15, 1966.



FIGURE 17.—Mountain breeding habitat, Collison Creek, Nicholas County, W. Va.



FIGURE 18.—Mature mountain cove hardwood habitat of the Swainson's Warbler near Charleston, Kanawha County, W. Va., May 1965. Tulip poplar is the dominant plant species.

Allegheny Plateau in West Virginia

In West Virginia the Swainson's Warbler is best known from the rugged Allegheny Plateau region of the south-central and southwestern part of the State. Studies of its habitats have been concentrated mainly in the Mt. Lookout section of Nicholas County along the Gauley River drainage (Brooks and Legg, 1942), and at Charleston in the Kanawha River area (Sims and DeGarmo, 1948).

In the Mt. Lookout region Brooks and Legg (1942, p. 78-79) found Swainson's Warblers in virtually all areas containing tangles of rhododendron, mountain laurel (*Kalmia latifolia*), hemlock, and American holly. In May 1940 they recorded 10 or 11 singing males within 1.5 miles along Franzy Creek, a small branch of Collison Creek.

On the south side of the Kanawha River, in Donley Hollow, at the edge of the city of Charleston, Eleanor Sims found 18 Swainson's Warbler nests during 1945-47 (Sims and DeGarmo, 1948, p. 1). This is a rather good indication of the local abundance of the species in this section of the Allegheny Plateau.

At the foot of the mountain where Donley Hollow meets the floodplain the elevation is only 600 feet. As one travels up the



FIGURE 19.—Umbrella magnolia, prominent understory tree in habitat of the Swainson's Warbler near Charleston, W. Va.

ravine beside Donley Branch and climbs several hundred feet higher, Swainson's Warblers can be heard singing on both forested slopes, often two or three hundred feet up from Donley Branch. I counted seven singing males as I walked a mile up the hollow on May 15, 1965. There are probably fewer birds in the hollow now than at the time Sims and DeGarmo made their study, since the lower, moister slopes are now occupied by suburban residences.

The Donley Hollow habitat is like a Coastal Plain floodplain forest on the side of a hill. In these moist hollows or mountain ravines the dominant canopy species of the mature cove hardwoods forest is tulip poplar. The diameters at breast height of the four largest tulip poplars in one Swainson's Warbler breeding territory in 1965 were 25, 30, 33, and 36 inches. Other trees of the upper canopy layer were mainly beech (*Fagus grandifolia*), buckeye (*Aesculus* sp.), black oak (*Quercus velutina*), red maple, and sweetgum. Lower trees were umbrella magnolia (*Magnolia tripetala*) (fig. 19), dogwood (*Cornus florida*), and paw-paw. The undergrowth was mainly spicebush (*Lindera benzoin*), with occasional thickets of greenbrier and Japanese honeysuckle (*Lonicera japonica*). Thinly distributed herbaceous plants of the

ground flora were nettle (*Laportea canadensis*), mayapple (*Podophyllum peltatum*), violet (*Viola* sp.), baneberry (*Actaea* sp.), and Christmas fern (*Polystichum acrostichoides*). Twenty exposure meter readings at Swainson's Warbler feeding sites ranged from 50 to 245 footcandles.

The closest avian associates of the Swainson's Warbler in this habitat are the same as in most Coastal Plain breeding localities: the White-eyed Vireo, the Hooded and Kentucky Warblers, the Cardinal, and the Rufous-sided Towhee.

Toxaway River Gorge

Parnell and Quay (1964) found the Swainson's Warbler to be a common summer resident in Toxaway River Gorge, Transylvania County, N.C., in the summer of 1961. This section of southwestern North Carolina is in the part of the Southern Appalachians where North Carolina, South Carolina, and Georgia come together. There are breeding records from the mountains of all three States.

In Toxaway Gorge, Swainson's Warblers were found at altitudes of 1,200 to 2,800 feet. According to Parnell and Quay (1964, p. 144), these birds—

showed a preference for dense stands of rhododendron, mountain laurel, and dog hobble (*Leucothoe editorum*) along the narrow riverbottom Pine Flats. The Mixed Mesophytic Coves and Slopes and the Oak Forest were utilized to a lesser degree.

The Pine Flats are generally more mesic, more mature, and less disturbed than the other habitats. Canopy species are white pine (*Pinus strobus*), Virginia pine (*Pinus virginiana*), hemlock, and tulip poplar. The understory is mainly rhododendron. The Mixed Mesophytic Cove and Slope Forest canopies included such species as red maple, sweet birch (*Betula lenta*), hemlock, beech, basswood (*Tilia americana*), and tulip poplar. They have poorly developed shrub layers, but local thickets of rhododendron and laurel occur. The sparsity of Swainson's Warblers in this forest type may be due to the poorly developed shrub stratum. The Oak Forest gradually becomes differentiated from the Mixed Mesophytic type as the sites become drier. Mountain laurel is the main Oak Forest understory species.

Most of the same avian associates of the Swainson's Warbler as in the Coastal Plain and other localities of the Southern Appalachians are found in Toxaway Gorge. Parnell and Quay (1964, p. 145) list the Worm-eating Warbler (*Helminthos vermivorus*) as an associate of the Swainson's Warbler. The Worm-eating War-

bler is also a nesting associate in the Pocomoke Swamp in Maryland, in the Arkansas River bottoms near Gillett, Ark., and at Charleston, W. Va., Mountain warblers breeding in the Toxaway Gorge included the Black-throated Blue (*Dendroica caerulescens*), the Black-throated Green (*Dendroica virens*), the Chestnut-sided (*Dendroica pensylvanica*), the Canada (*Wilsonia canadensis*), and the Blackburnian (*Dendroica fusca*).

Description

SIZE

The Swainson's Warbler is a rather short and stocky bird. Its length, 5 to 5½ inches, is about average for warblers, but it is heavier than most of the *Dendroica*s and *Vermivora*s. Four males collected during the breeding season weighed 13.2, 15.4, 16.2, and 16.6 grams (Mengel, 1965; Norris and Johnston, 1958; and L. C. Binford, Louisiana State University Collection). Two females taken in winter, one in Quintana Roo, Mexico, and one in British Honduras, weighed 13.7 and 13.9 grams (L. C. Binford and S. M. Russell, Louisiana State University Collection). A live male at Andros Island, Bahamas, in March, weighed 15.6 grams (Walkinshaw and Walkinshaw, 1961).

A series of birds that struck a Tallahassee, Fla., TV tower in spring migration averaged lighter than those striking the tower in the fall. The mean weight of the spring series of 15 birds was 14.9 grams, whereas the mean weight of the fall series of 19 was 18.9 grams (table 1). The Tallahassee TV tower is less than 50 miles from the Gulf Coast, and birds coming in from a trans-Gulf or circum-Gulf migration would have used up much of their reserve fat; whereas those leaving the United States would have a large fat reserve for the long journey to the wintering ground. Norris (1963, p. 47) reported that two birds that struck a TV tower in the Savannah River Valley in South Carolina on September 24, 1957, were excessively fat: one was recorded as having 19 percent fat, and the other, 24 percent.

TABLE 1.—Weights of Swainson's Warblers killed at TV tower, Tallahassee, Fla., during migration

[In grams]

	Spring (15 specimens)	Fall (19 specimens)
Minimum	11.3	14.3
Maximum	15.7	20.4
Mean	14.9	18.9
Median	13.9	18.3
Standard deviation	±1.2	±1.7

Measurements in millimeters of 11 male specimens collected during the breeding season on the Coastal Plain are as follows: Wing,³ 67.5–72.5 (70.2); tail, 46.5–52.0 (49.1); exposed culmen, 15.0–16.5 (15.3); tarsus, 17.0–19.0 (17.8); middle toe, 12.5–14.0 (13.2). Measurements in millimeters of 10 female specimens collected during the breeding season on the Coastal Plains, are: Wing, 66.0–72.0 (69.0); tail, 46.5–52.0 (49.4); exposed culmen, 14.8–16.0 (15.3); tarsus, 17.5–19.0 (18.2); middle toe, 13.0–14.0 (13.3).

DISTINGUISHING CHARACTERS

Sexes of the Swainson's Warbler are alike. Upperparts, including wings, are brown, except the crown which is reddish brown; underparts are yellowish-white and unstreaked. There is no white in wings or tail. The bill is large, thick at the base, and sharply pointed.

Similar species.—The Worm-eating Warbler has black stripes on its crown. The Ovenbird is streaked below. Immature Connecticut Warblers (*Oporornis agilis*) and Mourning Warblers (*Oporornis philadelphia*) in fall plumage have eye rings.

ADULT PLUMAGE

The crown of the Swainson's Warbler varies from almost cinnamon to chocolate brown, with a barely distinct buffy median stripe from the base of the culmen through the forehead. There is a white or pale yellowish superciliary (eye) stripe, a dusky spot in front of the eye, and a brownish postocular streak. The sides of the head are otherwise pale buffy brownish. Back, scapulars, rump, upper tail coverts, tail, and wing coverts are olive brown or olive-grayish brown. Tertiaries are warmer brown (toward mummy or prouts brown); secondaries and primaries are dusky, edged with brown. (The closed wing appears browner than the back). Underparts are yellowish white to nearly plain white (possibly geographic variation), shaded with olive or olive-grayish on the sides. Adults in autumn are indistinguishable from breeding birds.

The bill is brownish, except the undersurface of the lower mandible, which is flesh colored. The iris is brown. Legs and feet are of a pale (pinkish) flesh color. The culmen is slightly curved, narrowed, and elevated between the nostrils. The foregoing description of plumage and soft parts is partly from R. Ridgway (1902 p. 436–437).

³ Wing measurements are for the chord, from bend of wing to tip of longest primary.

JUVENILE PLUMAGE

The juvenile wings and tail are similar to those of adults. Upperparts are brown; throat and chest are dark brown; and other underparts are mottled brown and white. There is no whitish line over the eye.

GEOGRAPHIC VARIATION

Breeding birds from the Southern Appalachians differ from Coastal Plain birds in that underparts tend to be whiter (less tinged with yellow). The underparts of 15 Coastal Plain specimens in breeding plumage were primrose yellow; whereas seven mountain specimens in breeding plumage were almost immaculate below but had a light suffusion of naphthalene yellow on breast and abdomen. There is no significant size difference between these two forms.

The mountain form was described as a new subspecies by B. Meanley and G. M. Bond (1950, p. 191-193) and is known as *Limnothlypis swainsonii alta* (Appalachian Swainson's Warbler). The type specimen, adult male, United States National Museum No. 362424, was collected at Walhalla, S.C., on June 25, 1940, by W. M. Perrygo and S. Y. Hoyt (original number 4,681).

MOLTING

Virtually nothing is known of the molt of this species. M. G. Vaiden (1940, p. 126) collected a male in partial molt on July 17, 1939, in Sunflower County, Miss.

Breeding Biology

TERRITORIAL BEHAVIOR

Arrival on the breeding grounds

The Swainson's Warbler is one of the last of the southern warblers to arrive on the breeding grounds, but it is earlier than most of the northern transient members of the family. When I visited the Dismal Swamp on April 11, 1969, all of the resident breeding warblers except the Swainson's Warbler had returned. Wayne's Black-throated Green Warbler had already begun to nest. Since the foliage was only about one-third out, and since Swainson's Warbler occupies the shadiest part of the swamp, its late appearance is probably timed with that of the foliage.

Since males sing the first day on the breeding grounds, the schedule of their arrival is better known than that of females; but females have struck the TV tower at Tall Timbers Research Station, Tallahassee, Fla., as early as the first week in April (William Dopson and James B. Cope, personal communication). At the Dismal Swamp in southeastern Virginia, earliest males have been recorded as arriving on April 15. On April 20, 1969, I observed a mated pair on their breeding territory in this swamp.

In the relatively late season of 1966, at my Macon, Ga., study area, the local male population arrived during a period of about 1 week. The first four males arrived on April 12; by the next morning there were eight males; there were nine on the 14th, and ten on the 15th, the date I departed from the area. When I returned on April 28 there were 19 males in the area. Apparently the males, and probably the females, arrive at night. I was on the breeding grounds 2 whole days preceding the arrival of the first males on the 12th, and on that morning I was there before dawn. At day-break on April 12, I heard the first Swainson's Warbler.

Homing

Individuals that establish a territory one year may return to the same place in succeeding years. John Weske banded a Swainson's Warbler on territory in the Pocomoke Swamp in Maryland in May 1960, and the bird was recovered at virtually the same place the following four seasons by mist-netters David Bridge and Vernon Kleen. In my study area in the Dismal Swamp, a marked male occupied the same general territory for 3 successive years.

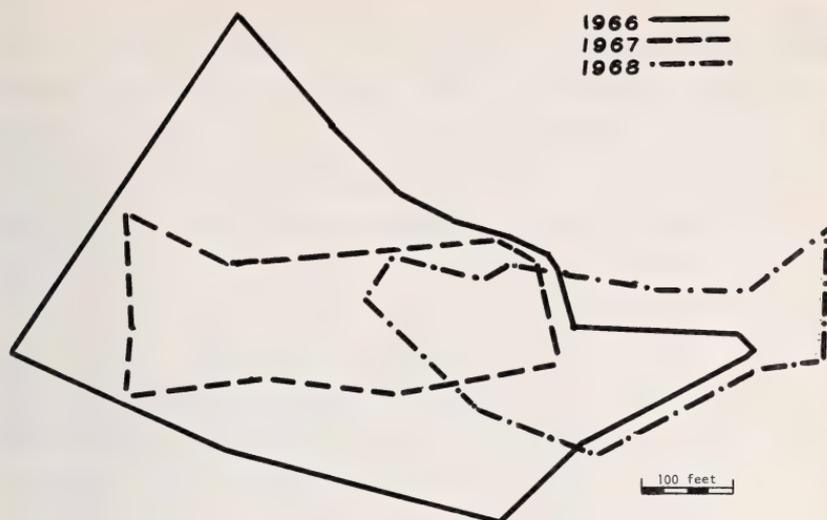


FIGURE 20.—Overlapping territories occupied by the same (marked) male Swainson's Warbler for three successive years (1966, 1967, 1968) in the Dismal Swamp in Virginia.

Territories

Males establish territories soon after arrival on their breeding grounds. The size and distribution of territories in an optimum area may depend upon the extent and arrangement of the habitat, as well as upon competition with other male Swainson's Warblers for food and space. Where prime habitat is limited in extent, it may support several territories, thus creating a group or "colony" of birds. This situation frequently occurs in southern canebrakes and is not unlike breeding "colonies" of the Kirtland's Warbler (*Dendroica kirtlandii*) in Michigan jack pine (*Pinus Banksiana*) habitat. In a 7-acre canebrake in the Ocmulgee River floodplain forest near Macon, Ga., there were four territories, and not all of the canebrake was occupied.

Sprunt and Denton (in Griscom and Sprunt, 1957 p. 51) reported that four territories in Georgia ranged in size from 0.72 to 0.91 acre (table 2). Two of the territories were adjacent and two were not. The smallest territory that I measured at Macon contained only 0.3 acre (table 2). It was in a block of woodland approximately 2 acres in size and was separated from the main forest by a cleared powerline right-of-way 50 yards wide.

In the Dismal Swamp, prime habitat is spotty; the territories are farther apart and larger than in the Ocmulgee River floodplain forest, where optimum habitat often occurs in larger blocks. The territory of one paired male in the Dismal Swamp covered

nearly 6 acres, and that of another nearly 4 acres (table 2). The overlapping territories occupied by the same Dismal Swamp male in 1966, 1967, and 1968 (fig. 20) contained 4.8, 1.7, and 1.6 acres respectively. In contrast, territories in the floodplain forest canebrakes seldom exceeded 1 acre. In two Dismal Swamp territories, only a part of each defended area was suitable for feeding and nesting; whereas in the canebrakes virtually all of the defended area was utilized for feeding. The "excess" area of the Dismal Swamp territories is used mainly for singing, but it is also defended.

Sometimes in discontinuous habitat a male may occupy a split territory or a territory composed of separate segments. One such territory in Monkey John Swamp, a few miles north of Savannah, Ga., had three segments. Two of the segments were on opposite sides of a cypress (*Taxodium distichum*) pond; the third was across a road from the pond. The occupied segments totaled 0.6 acre (table 2).

TABLE 2.—Size of Swainson's Warbler territories

Locality	Size (acres)	Reference
Ocmulgee River bottom, Bibb County, Ga.	0.3	Meanley, 1969, p. 247.
Monkey John Swamp, Jasper County, S.C.	0.6	Do.
Savannah River bottom, Richmond County, Ga.	0.72	Griscom and Sprunt, 1957, p. 51.
Do.	0.79	Do.
Ocmulgee River bottom, Bibb County, Ga.	0.83	Do.
Little River Swamp, Tift County, Ga.	0.91	Do.
Dismal Swamp, Nansemond County, Va.	1.7	Meanley, 1969, p. 247.
Do.	3.9	Do.
Do.	4.8	Do.

Males may remain in the same area for most of the summer. One marked Arkansas male occupied the same territory for at least 4 months (April 15 to August 15). Six males occupied the same territories in my Dismal Swamp study area from April 20 to at least June 30, the date of my last visit that season.

However, shifting of boundaries takes place from time to time, and the size and shape of territories change. In the Dismal Swamp where Swainson's Warblers have plenty of room to spread out because of low population densities, and where territories are seldom contiguous, a territory may retain its identity throughout the breeding cycle.

During various phases of the breeding cycle different parts of the territory may receive major use, but the original territory

established by the male shortly after arrival on the breeding grounds may be defended at any time. When the male is not paired he uses most of the territory. If the first nest is destroyed, and the male and female become separated before the start of a second nesting attempt, the whole territory may be used. The part used is smallest during the mating and nest-building periods (fig. 21), and sometimes during egg-laying. Stenger and Falls

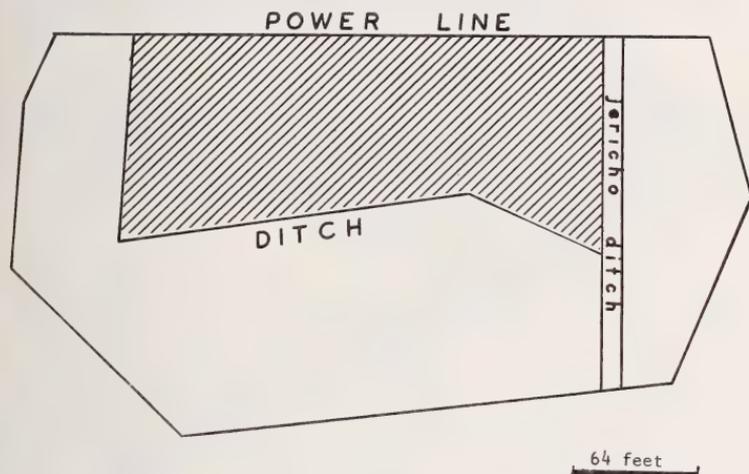


FIGURE 21.—Variation in size of the territory of a male Swainson's Warbler during breeding season. Only the hatched area (with densest cover) was occupied during the courtship and mating period. Dismal Swamp in Virginia, April 1969.

(1959, p. 136) found that the area utilized by Ovenbirds was larger during the premating, mating, incubation, and nesting periods than during nest-building and egg-laying.

Swainson's Warblers usually occupy larger territorial areas during the first few days after their arrival on the breeding grounds; and after the nesting season males that remain on their territories may extend the boundaries considerably. A male in the Dismal Swamp that occupied 4.1 acres in May and June occasionally extended his range over an 8-acre area in July.

The size and shape of a territory changes during each nesting attempt, because a different nest site is chosen each time and the sites may be several hundred feet apart. The male gives the nest site a wide berth when the female is incubating, thus giving the appearance that the nest is out of the territory when actually it is inside near the edge. The part of the territory most frequented by one Dismal Swamp male during a first nesting attempt was

avoided during the second nesting when the female built her nest there and started incubating.

Defense of territories

Territories are defended by singing, chasing, and combat. The song signals ownership, and each male's primary advertising song is usually different from his neighbor's.

Paired males appear to be more aggressive than unpaired males and usually initiate border encounters, which most often take place along territory boundaries. A paired and an unpaired male with adjacent territories at Macon, Ga., contended each time at virtually the same point along the boundary. As these males chased each other along the boundary, the paired female was close by but remained 10 to 15 feet within her territory, chipping excitedly.

A territorial male with an incubating mate at Pendleton Ferry, Ark., apparently had more time for hostile activity and thus was involved more often than the Macon paired male, which I observed during preincubation traveling with his mate. The Pendleton Ferry male would fly from any point in his territory deliberately to start a fight at the mutual boundary. He always began chipping excitedly as he moved toward his neighbor's territory, and both males chipped constantly during border clashes. In addition to chasing, the birds fluttered about on the ground after making contact and sometimes flew together a few feet up from the ground, grasping each other's bill.

Sometimes when a male invades a neighbor's territory and is chased out, he may perform a display on his side of the boundary. Such displays most often occur immediately after prolonged encounters. The wing and tail feathers are spread laterally (fig. 22), and the tail is vibrated. The bird sidesteps back and forth along a branch, frequently turning around, all the time chipping excitedly. Ficken and Ficken (1962, p. 110) observed a similar display in the Redstart (*Setophaga ruticilla*). At the end of a chase in which its adversary is evicted from the territory, a Swainson's Warbler male may fly up to a perch and sing vigorously for 10 to 15 seconds.

Following boundary encounters, males drift back into their territories and usually sing unbroken courses of songs for several minutes. Sometimes they start singing close to the boundary, in which case songs are incomplete, consisting only of the first two or three notes. Then as they move farther into their respective territories, they sing more complete songs.



FIGURE 22.—Display of a male Swainson's Warbler during or immediately following a boundary dispute with a neighboring male. The display resembles a female soliciting copulation. The wings are quivered, the tail feathers are alternately spread and closed, and the bird may step sideways back and forth along the limb.

There is usually little antagonism toward other species, and vice versa. White-eyed Vireos, Prothonotary Warblers, Hooded Warblers, Cardinals, and occasionally other species nest in territories of the Swainson's Warbler and, like the Swainson's Warbler, live close to the ground. On one occasion I saw a Hooded Warbler chase a Swainson's Warbler, after which the latter flew to a high branch within its territory and sang vigorously for about 10 seconds.

COURTSHIP AND MATING

I have never been present the minute the pair-bond was formed, nor have I witnessed male courtship displays before pair formation.

On one occasion when a female entered a male's territory for what I believe was the first time, she was chased for short dis-

tances but not driven beyond the territory boundary. The action of the two birds reminded me somewhat of the well-known sexual chase of Red-winged Blackbirds (*Agelaius phoeniceus*), when the females arrive on the breeding grounds.

During prenesting I observed a display by a paired male where he assumed a posture similar to a female ready for copulation. The posturing occurred when the male was perched about 3 feet from the ground and was approached by the female to within about 1 foot. When the female alighted near the male, he uttered a faint *twee-twee-twee* that was barely audible from where I was standing less than 8 feet away. The next day under similar circumstances, the same male extended his rump feathers only and uttered the same faint notes.

Also during prenesting, a paired male was observed to perform a "moth" or floating" flight. I could not locate the female at the time.

Vocalizations

During the courtship and mating period, a pair spends most of the day foraging on the ground, usually within 30 feet of each other and often only 2 to 3 feet apart. The male sings very little during this period and is otherwise less vociferous than the female. He may do some sustained singing early in the morning, usually before 7 a.m. I spent 3 consecutive days in the territory of one male, and after 7 a.m. on these days he sang four, none, and two primary advertising songs. During the day singing was more subdued and appeared to be for the purpose of signaling the female when she was momentarily out of contact with the male. Sometimes a song was incomplete, consisting only of the first, second, or third notes.

Vocalizations other than song are used by the pair to maintain contact. "Chipping" by the female is the most obvious and frequently used vocalization. Some females chip often enough for the investigator to follow a pair during most of the day in habitats where he can move about easily.

The chipping of the female often differs from the conventional alarm (chip) notes of both sexes. At times the chip note is more subdued, more of a squeak, and toward the end of the vocal performance the notes run together into a sort of muted chatter. At that point the chipping has the ring of excitement, and has attracted the male, who may attempt copulation.

Sometimes a very faint *chip* (that I could barely hear at 20 feet) is used by both members of the pair. This is a single chip,

well-spaced and not in a series like constant chipping when the birds seem excited. A paired female sometimes utters a faint *zeep* when a male in an adjacent territory sings.

On one occasion a pair that I had under observation was joined by a third bird, presumably a female. The visiting female fed with the pair for about 4 minutes, and at no time was chased by the male. The paired female chipped constantly while the interloper remained.

Pouncing

During the mating period males resort to pouncing on the females. The male flies to the female, who usually is foraging on the ground, and either pecks her rump feathers or pounces on her. I observed this behavior for several breeding seasons before I was sure that sometimes copulation was taking place. It was difficult to believe that copulation could occur under such circumstances. Hann (1937, p. 154) also had difficulty in observing copulation during similar behavior by Ovenbirds on the ground:

When copulation takes place on the ground, it is practically always accompanied by a struggle, which looks more like mortal combat than sexual intercourse. The fact that the female does not flee, and may even court the procedure, however, dispels any doubt as to her willingness. When they emerge from the struggle, the male usually flies to a nearby perch with an evident feeling of satisfaction, and the female, after shaking her ruffled feathers, proceeds with her eating or nest building.

Essentially the same behavior is exhibited by the Swainson's Warbler.

Pouncing may occur with or without an "invitation" from the female. Most of the time the female appears to be unaware that it is going to happen. Sometimes the female's excited chipping immediately precedes the stalking and pouncing.

After observing pouncing behavior a few times, I could always anticipate when it was going to happen. The male, feeding on the ground, usually within 20 feet of his mate, discontinued feeding and mounted a branch or log, usually 6 to 12 inches from the ground. Then he remained virtually motionless in a crouched position for 1 to 5 minutes, facing and watching the female who was foraging on the ground or perhaps preening. In his crouched position the flank feathers of the male were slightly fluffed out, and his head was drawn in close to his body. Occasionally he would slowly move his head slightly to one side. When the female moved too far out of range, the male shifted to a closer perch and continued his crouched stance. His performance reminded me of a cat getting ready to pounce on its prey. He would then fly to

the female, and the two would flutter together on the ground. Sometimes the male stopped short of the female, and sometimes when contact was made copulation did not take place. The female sometimes responded with a faint *tweet-tweet-tweet*. Following such an encounter, the male might fly off singing a song as loud as the primary advertising song but not resembling it. These flights were sometimes upward in a sort of spiral. One male I watched often sang a whisper song after pouncing. Usually, however, the pair started feeding within a few feet of each other and near the spot where pouncing occurred. Pouncing is also known in the Red Warbler (*Ergaticus ruber*) (Elliott 1969, p. 188).

Nice (1943, p. 174-175) reported Song Sparrow (*Melospiza melodia*) pouncing as a form of courtship display "confined typically to the early stages of the nesting cycle." The male flies down to his mate, collides with her, and then flies away singing. Nice states that pouncing by the Song Sparrow early in the season has no immediate connection with copulation.

Pouncing on the mate occurs during the long period while song is inhibited and also during building. It may be a technique of the male for impressing himself upon his mate during the time of silence, of making his presence keenly felt.

Howard (1929, p. 22) observed that after the sexual chase recently paired Yellow Buntings (*Emberiza citrinella citrinella*) flutter together on or near the ground or peck each other as they rise in perpendicular flight, like fighting males. Howard believed that the sexual chase and pouncing show that the male is ready to copulate and that the female is not ready to receive him.

One male that I watched for 2 days pounced about three times each hour; another that I watched for 3 days before the beginning of nest building pounced about once every 10 minutes. A third male pounced about once an hour on the day nest building began; nest building was sporadic that day and occurred mostly in the morning, for just 2 or 3 minutes following pouncing.

Copulation occasionally occurs while the female is perched on a limb of a shrub or tree. When copulating in this manner the male sometimes holds onto the female's crown feathers.

NESTING BEHAVIOR

Nesting period

The prenesting period for paired Swainson's Warblers is relatively brief, for nesting begins soon after pair formation. For example, I visited the breeding grounds in the Dismal Swamp on April 12, 1969, at which time the Swainson's Warblers had not

yet returned. When I returned on April 20, I found birds paired in at least one territory, and by April 23, nest-building had started in that territory.

The earliest nesting anywhere is reported by Wayne (1910, p. 150) who collected eggs containing small embryos on April 28, at Charleston, S.C. However, May 1 is about the average date for the beginning of nesting throughout the Swainson's Warbler range.

Nest building at Macon, Ga., and Pendleton Ferry, Ark., started about 3 weeks after the first males arrived on the breeding grounds. A completed nest ready for eggs was found at Macon on April 27, 1946, and nests with full clutches were found by May 3, 1945. A nest containing one Swainson's Warbler egg and three Brown-headed Cowbird (*Molothrus ater*) eggs was found at Pendleton Ferry on May 1, 1967. This nest was probably constructed during the third week in April.

In the Dismal Swamp the earliest record of nest building is April 23, 1969. This is about 8 days after the average arrival date of first males. In this same area I observed two nests under construction on May 1.

On the Allegheny Plateau near Charleston, W. Va., Sims and DeGarmo (1948, p. 4) state, nest building begins about 2 weeks after arrival on the breeding grounds. They found a completed nest as early as May 1.

Renestings or second nestings occur throughout June and into early July. Perhaps the latest date is a nest with slightly incubated eggs found on July 13, 1886, at Savannah, Ga. (Perry 1886, p. 188). Young from this nest would have fledged about August 1.

Nest site and materials

For three or four days before nest building, and possibly longer, another activity of the pair is the examining of nest sites. The male of a pair that I watched at this activity led the way more than his mate, and at times he examined nest sites alone. One might therefore conclude that the male selects the nest site.

The average height of 10 nests in various localities was 4 feet 0 inches, with a range of 1 foot 9 inches to 6 feet 3 inches. Nests are usually built in the predominant understory vegetation (fig. 23). In the Dismal Swamp, nests are frequently placed in green-brier vines (fig. 24), as well as in Japanese honeysuckle, sweet pepperbush, and switch cane (*Arundinaria tecta*).

Most nests in my Dismal Swamp study area were located within 30 feet of a road or path. Vegetation in these situations is denser because of better exposure to light.



FIGURE 23.—A Swainson's Warbler incubating during flood stage in Ocmulgee River floodplain forest near Macon, Ga., May 1946. Water is 3 feet deep.

In Bayou Boeuf Swamp in central Louisiana, one nest in a scrub palmetto thicket was placed in a blackberry vine in such a way that it was directly beneath the broad frond of a scrub palmetto. The nest was completely shielded from above as if it had a roof over it 4 inches from the rim.

In a canebrake the nest is rarely located in the densest part of the stand, but is usually nearer the edge where the stand is thinner and the cane poles are smaller. In a mature mountain cove



FIGURE 24.—Swainson's Warbler nest in greenbrier vine, 2 feet above the ground, Dismal Swamp in Virginia.

hardwood forest at Charleston, W. Va., Sims and DeGarmo (1948, p. 4) found that—

the bird avoids placing the nest in dense cover, yet in all instances, a patch of some type of such cover is within a distance of twenty-five to fifty feet. In many cases, this thicket is a growth of greenbrier but may be grape, honeysuckle, blackberry or bittersweet. There appears to be a definite effort to locate the nest in such a manner that it is in close proximity to a screen of protective cover.

All nests that I found in territories of known boundaries were inside the territorial borders. However, they were often near the edge, or the male spent most of his time in an area to one side of the nest. Sprunt and Denton (in Griscom and Sprunt, 1957, p. 51) had this to say about the location of the nest in the defended territory:

The territory defended by the male is used primarily for mating and feeding and not for nesting. The nest itself is usually located along the margin of the territory but may be entirely outside of it . . .

I wonder whether Sprunt and Denton's observations were not made during the incubation period when most males avoid the nest site, which is often near the edge of the territory, thus giving the impression of being outside it. When the eggs hatch, the male attends the young along with the female; then the territory no longer has a buffer zone.

The Swainson's Warbler builds a large and bulky nest (fig. 25), apparently larger than that of other warblers that nest above the ground. Of two nests, in Dismal Swamp, that I saw under construction from the beginning, one took 2 days and one 3 days to complete, and they were built entirely by the females. At one site the male was often close by but visited the nest no more than twice each day during the 3 days of construction; the male did not assist in construction and apparently visited the nest in search of the female. At the other site, during the initial stages of construction the male occasionally accompanied the female to the nest as she flew in with nesting materials; he brought along no material and left almost immediately after arriving at the nest.

At both these Dismal Swamp nests the female did virtually all of the building before noon. Building of the nest that I watched



FIGURE 25.—The large, bulky nest of a Swainson's Warbler (right) and the nest of a nesting associate, the Cardinal, a species nearly twice the size of the warbler.

more closely took parts of 3 days, mostly between 7 and 11 a.m. Building was resumed in the late afternoon of each day between 4 and 5 p.m. However, during the late afternoon building period no more than half a dozen trips were made to the nest each day. The female made between 100 and 125 trips each morning. From 9:25 to 10 a.m. one morning, she made 34 trips, an average of about one trip a minute. During any sustained period she spent an average of 24 seconds at the nest, with a range of 9 to 70 seconds. The female sometimes chipped a few times while working on the nest. During the nest-building period, her mate rarely sang after 8 a.m.

All nest materials were gathered from the ground within 30 feet of the nest. Dry leaves, used in the bulky part of the nest and the outer layer, were obtained from the drier part of the woods; the cypress needles and red maple flower pedicels used in the lining came from a wet spot near the nest site.

Nests are constructed of a rather wide assortment of materials, but there is a selection of certain plant parts. The number of species of plants represented in a nest depends somewhat on the composition of the forest in which the nest is located. There seldom were more than a dozen species of plants in the nests I examined. The number of plant pieces in a Pendleton Ferry, Ark., nest totaled 418; there were 323 in a Dismal Swamp nest. The most pieces were in the lining of the cup. Sticks are seldom used in nests, and the few that occur seem almost incidental. But the first of three nests built by a female in a single season in the Dismal Swamp contained a great many sticks, which is the reason why it weighed more than the second and third nests.

In canebrakes the foundation of a nest is often a bunch of dead leaves that have lodged in the axils of a cane stalk. The Dismal Swamp female that built three nests used the relatively large leaves of the swamp magnolia as a platform for each of them. Each was at a site where several greenbrier vines crossed a horizontal limb of a shrub, so that the half dozen magnolia leaves formed a rather level base. Deposited upon these magnolia leaves were dried leaves, sticks, vines, and tendrils that formed the rather loose outer layer of the nest. Most of the leaves were swamp magnolia, red maple, red bay, and greenbrier. Most of the sticks were greenbrier.

The next layer was more compact, consisting almost entirely of decomposed or skeletonized leaves of the swamp magnolia. This layer formed the outer shell of a cup composed of finer materials in which the eggs were deposited. In positioning the

leaf skeletons, their tips were drawn toward the rim at a gradually sloping angle to the curve of the cup. All of them were placed in a regular pattern, being drawn clockwise from near the base on one side of the cup to emerge and protrude from the rim almost at the opposite side. All of the protruding petioles thus pointed away from the circle of the rim at a narrow angle. This layer was constructed similarly in all three nests. Swamp magnolia leaves, being elongated in shape, are well suited for this part of the nest structure.

Next to the layer of magnolia leaves was a layer of cypress twigs with needles. Cypress twigs and needles were also used as a lining for the upper inside half of the cup and for the rim of the nest. The lower inside half and bottom of the cup were lined mostly with pedicels of red maple flowers. All 11 of the Dismal Swamp nests were lined with these pedicels. Apparently they are a preferred item for the lining, since I have also found them in nests at Macon, Ga. F. M. Chapman (1907, p. 53) reports that J. N. Clark found them in linings of nests of the Worm-eating Warbler in New Jersey.

The Dismal Swamp female that built three nests in one season used fewer materials in constructing each succeeding nest; thus her nests were progressively lighter; dry weights were 47.7, 39.8, and 26.3 grams. Dimensions of an Arkansas nest were as follows: Greatest outside diameter, 15.0 cm.; inside diameter of cup, 4.0 by 5.0 cm.; outside depth, 7.8 cm.; inside depth, 4.2 cm.

EGG LAYING AND CLUTCH SIZE

At a Louisiana nest, there was a lapse of 2 days between the completion of the nest and the laying of the first egg; at a Dismal Swamp nest there was a lapse of 4 days. Eggs were laid daily until the clutches were complete, and incubation began with the laying of the last egg in each. At one Dismal Swamp nest the eggs were laid in the morning before 7 a.m. By marking eggs, incubation period at a nest at Augusta, Ga., was determined to be 14 or 15 days (J. Fred Denton, personal communication). The incubation period of eggs in a nest in the Dismal Swamp in 1969 was 13 days (F. C. Burford, personal communication). The first egg of this clutch of four was laid on May 1, and an egg was deposited daily; the first egg was hatching at 6:30 a.m. on May 17.

Of six first clutches in nests in Georgia, four consisted of three eggs each and two had four eggs. Of second clutches in four nests

in Dismal Swamp, three had two eggs and one had three. The somewhat globular eggs are white (fig. 26), but slightly spotted eggs are found on rare occasions (Wayne 1910, p. 149).



FIGURE 26.—Nest and eggs of the Swainson's Warbler in cane.

Cowbird parasitism

In some parts of its breeding range the Swainson's Warbler may be rather heavily parasitized by the Brown-headed Cowbird. During the first week in May 1967 at Pendleton Ferry, Ark., I located three Swainson's Warbler nests, all of which were parasitized. At one of the nests the warbler was incubating three cowbird eggs and one of its own. Three days later it was still incubating, but one of the cowbird eggs and its own egg were missing. At another one of the nests a warbler was incubating a single cowbird egg, and at the third a warbler was incubating three cowbird eggs; evidently the warbler eggs had been removed by the cowbirds.

Kirn (1918, p. 97-98) reported several parasitized nests in Copan County, Okla.; Sims and DeGarmo (1948, p. 5), in the course of 3 years, found three of 18 nests parasitized at Charleston, W. Va. I found that none of 11 Dismal Swamp nests were parasitized. Dismal Swamp is near the northern limit of the southeastern breeding range hiatus of the cowbird (Webb and Wetherbee 1960, p. 83-87), and I found only two or three cowbirds during an entire day in the Swamp in the spring of 1968. From 1944 to 1946 at Macon, none of six nests were parasitized, since at that time the area was out of the cowbird breeding range. By 1960, however, cowbirds were commonly breeding there.

INCUBATION

Information on behavior during the incubation period was obtained from a nesting pair in the first week of May at Pendleton Ferry, Ark., and from a pair in the Dismal Swamp in the middle of June. The Pendleton Ferry pair was the one mentioned above whose nest contained three cowbird eggs and one warbler egg. The nest was located about 2 feet above the ground between two cane poles. The height of the Dismal Swamp nest was also about 2 feet, and it was placed in a greenbrier vine. At each nest, incubation was performed only by the female.

During incubation the Pendleton Ferry female spent about 78 percent of her daylight time on the nest. The average period on the nest was 70 minutes; the average period off was 19 minutes. The longest period on the nest was 110 minutes, and the shortest was 30 minutes. The longest period away from the nest was 25 minutes; the shortest was 15 minutes. The Dismal Swamp female averaged 54 minutes on and 15 minutes off the nest. Lawrence (1953, p. 138), summarizing studies of six wood warblers, found that the birds were at the nest 67 to 83 percent of the time.

The two females I observed always sat in the same positions when incubating. Each left the nest each time in the same direction and fed in the same general area. The Pendleton Ferry female fed as far as 75 yards from her nest, but usually only about 30 yards from it. She fed both alone and with her mate. On one occasion her mate, which had not sung for more than an hour, flew to within 50 feet of the nest and sang two songs. The female chipped and left the nest, and the two flew off together to feed. Sometimes on leaving the nest the female flew out to about 30 yards from the nest where she chipped several times, presumably to attract her mate.

Upon returning to the vicinity of her nest, each female invariably chipped two or three times just before settling down.

The Dismal Swamp female was often fed by her mate when she left the nest during the incubation period. She followed the male on the ground like a fledgling following its parent. The male, walking about with cocked tail, gathered food and presented it to her.

During the several days of my observations, the Pendleton Ferry male never visited the nest. He did not come closer than 40 feet and usually stayed more than 100 feet distant. The Dismal Swamp male once, while the female was off feeding, visited the nest briefly and, not finding the female there, flew off and began singing vigorously. At dusk the Pendleton Ferry male was usually seen closer to the nest (40 to 50 feet) than during the lighter part of the day. He fed and sang in all areas surrounding the nest but was seldom closer than 50 feet. He did not sing as much as an unmated male in an adjacent territory.

CARE OF NESTLINGS

Most of my information on the care of nestlings is based on observations made during a 7-hour period on July 7, 1967, in the Dismal Swamp. Between 9:45 a.m. and 4:45 p.m. the 3-day-old nestlings were fed 14 times, eight times by the male and six by the female. The intervals between feedings ranged from 9 to 59 minutes. The female was at the nest 53 percent of the time brooding the young and sometimes standing on the rim. If she was brooding when the male came to the nest, she moved to the rim while he fed the young. Only the male removed fecal sacs from this nest, although at a Macon, Ga., nest the female also removed fecal sacs, sometimes swallowing them.

The male always approached from the same direction and worked his way slowly through the undergrowth until he was 2

to 3 feet beneath the nest; then he hopped up to the rim. The female approached from various directions, and flew 20 to 30 feet directly to the rim of the nest. On three occasions the male and female departed from the nest at the same time. Each time they flew in different directions.

Sims and DeGarmo (1948, p. 5) found that at several West Virginia nests young left after 10 days of nest life. At Augusta, Ga., the young remained 12 or more days in their nests (Griscom and Sprunt 1957, p. 53). Young that I observed at Macon, Ga., fledged at 10 days.

CARE OF FLEDGLINGS

Fledglings of a Dismal Swamp brood, just 2 days out of the nest, were fed only by the female during my 2 days of observations (June 13-14, 1967). The male was usually within 100 feet of the young and sang much of the time. The three fledglings usually did not attempt to follow the parents, but stayed within a relatively small area where they waited for the female to return with food. Most of the time they were perched 6 to 12 inches from the ground in heavy cover. During one 2-hour period, two of the three fledglings remained close together (5 to 10 feet) within a 20-foot-square area; at other times they were 50 to 100 feet apart. Sometimes after being fed, a fledgling attempted to hop along after its parent, but was soon left behind as the parent flew off in quest of food.

The fledglings were fed an average of every 15 minutes. When returning with food the female would walk and hop, rather than fly, to the waiting young. The young, hearing the approaching female parent rustling through the leaf litter, would intensify their chipping as she reached a point about 20 feet from them.

On three occasions, just as the female was about to feed a fledgling, the male pounced on her. As related above, pouncing also occurs during the prenesting period after the birds have paired.

Voice

SONG

The song of the Swainson's Warbler is loud and ringing and of marked musical quality. As Dingle (in Bent, 1953, p. 36) states,

The bird student who hears the song of Swainson's warbler as he sings in his wooded retreat is fortunate, for it is one of the outstanding warbler songs and, once heard, leaves a lasting impression upon the listener. At a distance it bears much resemblance to the songs of the hooded warbler and

Louisiana waterthrush. Close up, however, the appealing quality, lacking in the other two, impresses the listener strongly.

Songs of different individuals of the species vary. I have stood in one spot and heard the songs of five Swainson's Warblers, each distinctly different.

The song consists of three or four high introductory notes, all separated, followed by a phrase of four or five syllables uttered rapidly and slurred (Brooks and Legg, 1942, p. 82).

The songs of seven birds were analyzed from tape recordings made by W. W. H. Gunn (in Griscom and Sprunt 1957, p. 26-27) at Charleston, W. Va. Gunn's rendition is as follows:

tee-o tee-o (tee) whit-sut-say bee-o, or *tee-o tee toot-sut-say bee-u*, or *whee-u whee whit-sut-say bee-o*.

. . . they have loud ringing songs closely resembling those of the Louisiana Waterthrush both in tonal quality and phraseology. However, certain characteristic differences are evident: First, songs of Swainson's Warblers are noticeably shorter in duration, being composed of fewer syllables. Then too, the slow opening notes comprising the first part of the song differ markedly in phrasing between the two species, and although there is a remarkable resemblance in the second portion of the song, the Louisiana Waterthrush then typically goes on to add a final phrase missing from songs of Swainson's Warblers.

Gunn says that the duration of the Swainson's song is $1\frac{1}{4}$ seconds and that of the Louisiana Waterthrush's $1\frac{1}{2}$ to 2 seconds.

At a distance the strongly accented slurred ending (the first note high in pitch, the second low) of the Hooded Warbler song is suggestive of the ending of the Swainson's Warbler song, and often is confusing.

Whisper song

Berger (1961, p. 169) defines the whisper song as "the soft inward rendering of the primary advertising song, with or without variations." Muted or whisper songs of the Swainson's Warbler are a continuous chatter or musical twittering that may go on for as long as 3 minutes. I have never noticed any resemblance to the primary advertising song; rather they sound more like the continuous chattering notes of Goldfinches (*Spinus tristis*) in the spring, but are more musical. I have also heard in the spring a chattering song of kinglets (*Regulus satrapa* and *R. calendula*) and Blue-gray Gnatcatchers (*Polioptila caerulea*) that sounded a bit like the Swainson's Warbler whisper song. In the floodplain forest canebrakes of the Ocmulgee River in Georgia in April, I have heard all four of these species rendering these notes at nearly the same time. There have been times when I was not sure

whether I was hearing a Swainson's Warbler whisper song or notes of the other three birds. In fact, the whisper songs of several species of warblers sound alike. I have been fooled by the Prothonotary Warbler and the Yellowthroat (*Geothlypis trichas*), thinking I was hearing a Swainson's Warbler.

The whisper song is seldom audible beyond 30 feet. It is given throughout the breeding season. Mayfield (1960, p. 127) thought that the Kirtland's Warbler sang whisper songs mainly when other males were nearby. Morse (1967, p. 497) found that in the Parula Warbler (*Parula americana*) muted and incomplete songs were associated with a high level of aggression. I have heard the Swainson's Warbler give the whisper song when in the presence of other males, following a conflict at a territorial border, when alone on an isolated territory, and after pouncing on a female just as she was about to feed fledglings. I have heard the whisper song of the Swainson's Warbler most often when there was no other male or female of the species, or any other bird, nearby.

The whisper song may be delivered when the bird is standing or moving on the ground, perched on a limb, or in flight. I heard one male give the whisper song as he flew along about 2 feet above the ground for a distance of 50 feet. The whisper and primary advertising songs may be alternated: I observed a perched Swainson's Warbler that sang both, preening in between, and then hopped to the ground, alternating the songs while foraging.

Flight song

I have heard flight songs that had no resemblance to whisper or primary advertising songs. They were as loud as the primary advertising songs but continuous and run together, and they lasted as long as the flight. One singing bird took off from the ground in a spiralling flight to a height of about 35 feet; another flew from the ground at a 60-degree angle to a perch 40 feet up.

Incomplete song

Incomplete songs—songs without endings and songs consisting of only the first, second, or third notes—may be heard at any time during the breeding season. As mentioned above, incomplete songs are sometimes given following territorial bouts with neighboring males. They are often heard when a bird is startled or frightened. For example, a Dismal Swamp male alternately sang only one and then two notes when a Common Grackle (*Quiscalus quiscula*), a nest robber, invaded his territory.

SINGING BEHAVIOR

The primary advertising song is sung only by the male, and so

are whisper songs, as far as I can ascertain. When singing the primary advertising song, the bird changes the position of its head more than that of its body. The body is only slightly angled upward from the silent perching position; the head is thrown back with the bill pointed upward at a sharp angle, although not quite perpendicular. (Bird artists who have attempted to portray a singing bird of this species have usually done so incorrectly.) The bird's head and body are not tilted upward when singing muted or whisper songs.

The Swainson's Warbler sings from the ground, and from trees, shrubs, vines, and logs, usually below 30 feet. I have heard a bird singing from a perch as high as 50 feet, but singing from such a height is very uncharacteristic.

Singing from the ground is usually sporadic, since it is done while hunting for food. The bird nearly always stops to sing when foraging along the ground, assuming virtually the same posture as when singing from a branch; sometimes it starts singing before coming to a complete halt. After a male has spent some time on the ground intermittently foraging and singing, he may fly to the limb of a tree, where he rests, preens, or continues singing.

During the first few days after they arrive on the breeding grounds, birds in the canebrakes of the Ocmulgee River floodplain forest sing much more often from the ground than from trees or shrubs. In 40 hours of observation, three of four individuals were observed to sing only from the ground during their first week, April 12-19, 1965. During April 12-15, 1966, soon after the birds had arrived on the breeding grounds, one male sang only from the ground when under observation for 10 hours. When I next observed this bird, on April 28, it sang also from trees. Another male sang 135 songs from the ground and 65 from trees when under observation for 90 minutes on April 15.

When the Swainson's Warbler sings from trees, some of the perches most often used are dead branches well out from the trunk in the lower parts of the trees. The bird sings from a stationary position when perched in a tree or shrub, as pointed out by Brewster (1885a, p. 73-74) :

While singing he takes an easier posture, but rarely moves on his perch. If desirous of changing his position he flies from branch to branch instead of hopping through the twigs in the manner of most warblers.

However, a singing bird may reverse its position on the same perch and resume singing while faced in the opposite direction.

In the course of 1 hour a Charleston, W. Va., male sang from 18 perches, once only from each of 17, and five times from one.

In the Dismal Swamp on June 3, 1966, a Swainson's Warbler shifted from perch to perch during the first half hour or more of the morning song. The bird started singing at 4:27 a.m. It sang from the first location for 11 minutes, from the second for 10 minutes, from the third for 10 minutes, from the fourth for 4 minutes, from the fifth for 1 minute, and from the sixth for 1 minute. It began feeding and singing from the ground at 5:15 a.m.

Seasonal song cycle

The song period in the breeding range lasts from 5 to 6 months, depending on locality, but the most vigorous singing occurs during April and May. Males still mated in June and July sing almost as frequently as earlier in the breeding season. Singing is fairly regular but mostly in the morning until about August; it is sporadic from mid-August to mid-September when birds begin to leave the breeding grounds.

In floodplain forests of the Ocmulgee River in Georgia and the Arkansas River in Arkansas, I heard individuals singing daily in July and August. On August 6, 1966, during a 2-hour period (11 a.m. to 1 p.m.) when I was in a canebrake near Pendleton Ferry, Ark., a male sang 93 songs. In this same area on September 7, 1968, four males sang sporadically in the morning until about noon. They sang complete, incomplete, and whisper songs. Much of their singing was instigated by Carolina Wrens, which are among the loudest songsters of the southern woods.

The male sings vigorously following arrival on the breeding ground and until the pair bond is formed. Then, while traveling with and courting his mate during the prenesting period, he sings very little. Most of the singing is during the first 2 or 3 hours after daylight. After 7:30 or 8 a.m. during this period males may sing only half a dozen songs during the rest of the day. Such songs later in the day are usually for the purpose of rallying the mate.

During nest building, singing may be sporadic, and often very little singing is done. The male may sing infrequently in the morning while the female is working on the nest, but in the afternoon when nest building is at a virtual standstill the pair remains together and the male sings hardly at all. On the first day of nest building, a Dismal Swamp male sang only one cadence, of 7 seconds, between 9 a.m. and 6 p.m. The next day he did not sing at all after 9 a.m.

During incubation the male sings more often than during the courtship, mating, and nest-building periods. One of the functions

of song during incubation appears to be to let the female know of her mate's whereabouts. I assume this, since the incubating female, upon leaving the nest, often goes to the male, with whom she feeds.

Singing during the nestling period is sporadic, since the male assists in the feeding of the young; after the young leave the nest, apparently only the female attends them, and the male increases his singing. During a 2-hour period (10:30 a.m. to 12:30 p.m.) when a Dismal Swamp female was attending her fledglings, the male sang a course about once every 10 minutes. After destruction of its mate's first nest, another male sang vigorously throughout the day and moved about the territory much more than usual; the female became very quiet and avoided the male, although she remained in the territory.

Daily pattern

The daily singing schedules of the Swainson's Warbler and other passerine woodland birds are about the same. In the Ocmulgee River forest the first singing of the Swainson's Warbler and other woodland birds was noted on a mild, cloudy morning, April 14, 1966. Sunrise was at 6:07 a.m. The first bird that sang was a Cardinal at 5:25 a.m., followed by a Rufous-sided Towhee at 5:32, a White-throated Sparrow (*Zonotrichia albicollis*) at 5:33, a Wood Thrush (*Hylocichla mustelina*) at 5:35, and then two Swainson's Warblers at 5:47. The Swainson's was the first warbler to sing, followed by a Prothonotary Warbler at 5:55 a.m. and a Hooded Warbler at 5:57 a.m. Almost all species of woodland birds were singing by 6 a.m.

In one of my study areas in the Dismal Swamp on June 3, 1966, the first Swainson's Warbler sang at 4:27 a.m., following a Cardinal, Wood Thrush, Wood Pewee (*Contopus virens*), Crested Flycatcher (*Myiarchus crinitus*), Hooded Warbler, and Tufted Titmouse (*Parus bicolor*), all of which began singing after 4:05 a.m. Sunrise was at 4:44 a.m.

On April 14, 1966, in the Ocmulgee floodplain forest, two Swainson's Warblers with adjoining territories stopped singing at 7 and 7:14 p.m. On June 2, 1966, in the Dismal Swamp, a Swainson's Warbler sang until 6:45 p.m. Only the Wood Thrush, Cardinal, and Wood Pewee sang later in that section of the woods. Sunset was at about 7:28 p.m.

Rate of singing

A song is sung in a course or series, that is, a period of steady singing for several minutes at a time. Sometimes in the early

morning the pause between courses is so brief that they seem to run for half an hour or more. Norris and Hopkins (1947, p. 8) noted that the average interval between songs of a male at Tifton, Ga., was 10.7 seconds.

The rate of singing is usually faster at the beginning of a course of songs (see table 3). During the first hour of morning song on June 2, a Dismal Swamp male sang at a fast but gradually diminishing rate of speed: nine songs per minute for the first 8 minutes, and five or six per minute thereafter.

The rate of singing is sometimes relatively constant over long periods of time. A male in the Ocmulgee floodplain forest on April 19 sang between 40 and 46 songs (40, 42, 46, 43, 42) in each 15-minute period from 8 to 9:15 a.m. Table 4 shows songs per 15-minute interval by a male in the Dismal Swamp.

TABLE 3.—*Songs per minute in courses by a territorial male Swainson's Warbler*

[4:15 p.m. to 6:43 p.m., 15 June 1966, in the Dismal Swamp in Virginia. Data from Meanley, *Wilson Bulletin*, 1968, p. 75]

Minutes in course	Time	Songs in each minute
5	4:15-4:20	8, 5, 5, 3, 2.
5	4:27-4:32	8, 6, 5, 2, 4.
6	4:40-4:46	7, 7, 7, 4, 4, 4.
13	4:50-5:03	8, 6, 4, 5, 5, 4, 5, 6, 6, 5, 5, 4, 1.
12	5:13-5:25	9, 6, 5, 4, 5, 4, 4, 4, 3, 4, 4, 2.
5	5:26-5:31	5, 5, 5, 6, 5.
3	5:48-5:51	8, 4, 1.
2	6:14-6:16	5, 5.
5	6:33-6:38	7, 5, 3, 4, 2.
3	6:40-6:43	5, 6, 4.

TABLE 4.—Number of songs per 15-minute interval of a territorial male Swainson's Warbler

[Observation made 3 June 1966, at Dismal Swamp, Nansemond County, Va. Sunrise about 4:44 a.m., sunset about 7:28 p.m.; sunny most of day; first song at 4:27 a.m.; sang until 6:45 p.m. previous evening. Data from Meanley, Wilson Bulletin, 1968, p. 76]

Hour beginning at—	Songs in 15-minute period ending at —				Total songs in hour	Temperature in woods (° F.)
	15 min.	30 min.	45 min.	60 min.		
4 a.m.	0	27	84	75	186	42
5 a.m.	61	33	50	48	192	47
6 a.m.	52	51	44	47	194	51
7 a.m.	54	53	48	43	198	52
8 a.m.	38	47	35	35	155	59
9 a.m.	24	23	29	0	76	61
10 a.m.	0	0	0	0	0	67
11 a.m.	0	0	0	0	0	67
12 noon	0	0	0	0	0	69
1 p.m.	0	0	1	0	1	68
2 p.m.	0	25	7	3	35	70
3 p.m.	8	21	12	31	72	70
4 p.m.	21	1	20	17	59	69
5 p.m.	0	0	0	0	0	62
6 p.m.	0	0	0	0	0	60
7 p.m.	0	0	0	0	0	55
Total in day					1,168	

Cadence of delivery

As pointed out by Reynard (1963, p. 139), an additional feature of bird song "unconsciously recognized but not particularly noticed is the cadence of delivery." Reynard defined the cadence of delivery of a song as—

the average length of time from the first note of a song unit to the first note of the succeeding unit throughout the whole song performance. The period timed includes that in which the song unit is heard and the silent period between song units.

I recorded cadence of delivery of three territorial males on May 2 in the Dismal Swamp between 7 and 8 a.m.: the deliveries recorded were 20, 20, and 14. The average cadence for the sample was 13.7 seconds. Reynard (1963, p. 141-142) lists the cadence

of song delivery of several other parulids as follows: Yellow Warbler (*Dendroica petechia*), 11.2 seconds; Prairie Warbler, 12.9 seconds; Ovenbird, 21.2 seconds; and Hooded Warbler, 9.8 seconds.

Some of the factors that influence the rate of singing are the stage of the reproductive cycle, time of day, and degree of excitement. During the nest-building period one male Swainson's Warbler had an extremely rapid cadence of 4 seconds early in the morning (at 6, 6:30, and 6:35 a.m.). He was signaling his mate, which at the time was building the nest. The course, or series, was short in each case, containing only four to six songs. On each of the three occasions, the female discontinued nest building and flew to her mate, a distance of about 100 feet.

Comparison with associates

On hot June days in the Dismal Swamp, I found the Swainson's Warbler to be one of the most frequent singers in the woods if it had an active nest or fledged young in its territory. The Red-eyed Vireo (*Vireo olivaceus*) sang more continuously, but its song did not stand out like that of the Swainson's Warbler. In the early afternoon when song activity is generally at a minimum for most birds, the Swainson's Warbler often was the most persistent singer. On July 8, 1967, a Swainson's Warbler was the only species that I could hear singing during a driving rainstorm.

I have to disagree generally with Brewster (1885a, p. 72) who says that the Swainson's Warbler is a "fitful and uncertain singer" and that "you may wait for hours near his retreat, even in early morning, or late afternoon, without hearing a note." I have noted such behavior in many species of birds, but it may result from particular conditions at the time of observation. If one visits a Swainson's Warbler territory daily in the early part of the breeding season before pairing, it will soon be observed that this warbler sings as frequently as most of the other woodland birds. Frequency of singing, as pointed out above, depends on the stage of the breeding cycle, the time of day, and the meteorological conditions, among other factors. Between the formation of the pair bond and nesting, they sing very little.

ALARM OR CALL NOTE

Next to the primary advertising song, the *chip* or *tchip* note, given by both sexes, is the best known vocalization of the Swainson's Warbler. The *chip* note is sharper than the similar note of the Kentucky Warbler, an associate in much of the Swainson's Warbler breeding range. To me, the Swainson's Warbler *chip* is

most like the *chip* of the first or last note of the song of the White-eyed Vireo. The two species occur together in the Coastal Plain Province, and I often have been fooled by the Vireo. However, it is not long before the Vireo reveals its identity as it follows through with the rest of the song or starts singing after giving the sharp *chip* note. Brooks and Legg (1942, p. 83) thought the Swainson's Warbler *chip* similar to that of the Mourning Warbler.

The chip call is used during intraspecific territorial strife, when alarmed by such nest robbers as snakes, Blue Jays (*Cyanocitta cristata*), and Common Grackles, and as a call-note for members of a pair.

A variation of the chip note is used by the female during the mating period (see section on Courtship and Mating). In this case the notes may be softer and more musical, and they are run together, almost forming a chatterlike song.

Another vocalization uttered by both sexes resembles the *zeep* note of various species of warblers during fall migration. I have heard Swainson's Warbler give this note in September when still on the breeding territory. On April 28 in the Dismal Swamp, 3 days before nest building, I heard a female utter a soft *zeep* each time her mate sang. The note was so weak and the male so far from her that I am sure he seldom heard it.

Feeding Behavior and Food

FEEDING BEHAVIOR

The Swainson's Warbler is primarily a ground feeder, but it sometimes searches for food a few feet above the ground in undergrowth. It also forages along the top sides of logs that are lying on the ground, and it may fly to the side of a tree trunk to pick off an insect that is a foot or so from the ground. Sometimes it reaches or hops up a few inches from the ground to take insects from the undersides of leaves of low-growing herbaceous plants, and occasionally it flies from perches in the lower parts of trees in pursuit of insects. Large insects are held in the end of the bird's bill and beaten against the ground until broken into several pieces.

The Swainson's Warbler searches for food in a manner different from that of other ground-feeding parulids that I have observed. Insects are located mainly as the bird pokes its bill under leaves or piles of leaves, pushing them upward and searching the ground beneath or examining the undersides of the leaves. A leaf may be held up momentarily and tilted at an angle as the bird inspects the underside. If part of a leaf is curled, the upper and the lower mandible of the bird are parted to uncurl it. Sometimes, as the bird moves hurriedly forward lifting and shoving leaves from side to side, its entire body disappears beneath the leaves. Most of the Swainson's Warblers that I collected in the course of their food searching in the Ocmulgee River floodplain forest had their bills caked with mud.

The bill of the Swainson's Warbler is larger and sharper pointed than the bills of the Ovenbird, the Louisiana Waterthrush, and the Kentucky Warbler, ground-feeding parulids that in the generally level terrain of the southern floodplain forest obtain their food primarily from the surface of the leaf litter. The Kentucky Warbler works across the forest floor, often under a partial cover of low herbaceous vegetation such as wood-nettle, jewelweed (*Impatiens* sp.), or poison-ivy (*Rhus Toxicodendron*). It hops along, flushing insects and picking them off stems and from beneath leaves of low-growing plants, and pokes its bill into piles of leaves or sticks. The Ovenbird (a walker) feeds similarly, but more in the open, as does the Louisiana Waterthrush (also a

walker), which feeds about wet leaf litter and shallow pools and occasionally does some leaf-flipping, in contrast to the shoving aside and "plowing" of the leaf litter by the Swainson's Warbler. The Swainson's Warbler also obtains some food from the surface of the leaf litter.

Within a breeding territory, a male usually uses several, perhaps half a dozen, foraging areas on the ground to which it consistently returns. Such areas are usually less than 50 feet square and free of obstructions at and just above ground level. In one Georgia canebrake I observed a male for 30 minutes as it searched for food in one of these special feeding sites measuring 20 by 30 feet.

When foraging in the shrub strata or undergrowth, the Swainson's Warbler probes into clusters of dead leaves and the axils of cane plants, as is typical of the Worm-eating Warbler, a species which closely resembles the Swainson's Warbler in size and plumage and often occurs in the same place.

Bill wiping

After feeding, a Swainson's Warbler mounts a limb and, before preening, spends a number of seconds wiping its bill. Bill wiping presumably is done to remove caterpillar hairs or other insect parts and pieces of dirt. The Swainson's Warbler has a good reason to spend more time wiping its bill than most other parulids because of its continuous probing beneath the leaf mantle in moist or wet silty soil.

FOOD

A total of 11 Swainson's Warbler stomachs have been examined by biologists of the U. S. Department of the Interior. All were from birds collected in Alabama and Georgia canebrakes. These examinations indicate that the Swainson's Warbler is totally insectivorous. Among favorite food items typically occurring beneath the leaf mantle are crickets (Gryllidae), ground beetles (Carabidae), ants (Formicidae), and spiders (Arachnidae).

Caterpillars (Lepidoptera) occurred in five of six stomachs collected in May and June in Alabama and were the most important by volume in four; ground beetles were the principal food item in one; and hymenopterous insects (probably ants) were most important in one. Spiders occurred in three of the stomachs.

The following items, in order of volume, occurred in stomachs of two birds taken at Macon, Ga., in May: ground beetles, caterpillars, stinkbugs, (Pentatomidae), homopterous insects (Homoptera), silken fungus beetles (Nitidulidae), and beetle larvae.

Crickets formed 43 and 40 percent by volume of the stomach contents of two birds collected near Augusta, Ga., in September; other major items in the two stomachs were Acrydiinae (grasshoppers), ichneumids, ants, and spiders. A stomach taken at Augusta in August contained the following items: 13 insect or spider eggs and the mass of silky material covering them, 16 ants, two ground beetles, three unidentified beetles, seven undetermined insect larvae, one caterpillar, one millipede (Diplopida), one stinkbug, one rove beetle (Staphylinidae), one darkling beetle (Tenebrionidae), and one beetle larva.

Near Cienfuegos in Cuba, Eaton (1953, p. 172) collected several Swainson's Warbler stomachs that contained the bones of small lizards (Iguanidae). He also found such bones in the stomachs of Worm-eating Warblers and Ovenbirds.

Miscellaneous Notes on Behavior

GROUND LOCOMOTION

The gait of the Swainson's Warbler is different from that of any other ground-feeding parulid. In searching for food, usually in dry leaf litter, its gait is described by Brewster (1885a, p. 74) as "distinctly a walk." Norris (1963, p. 47) also observed that it walked, and that its "gait was rather rapid and jerky, suggestive of that of the starling." He further stated that the Swainson's Warbler may hop "when traversing leaf litter." After 25 years of observing this species for many hours each spring, I would say that it hops some of the time, though mostly it moves in a rather rapid step that is a sort of a cross between a walk and a hop, suggesting a canter.

In searching for food on the ground it moves along hurriedly, often turning from side to side, and sometimes making a complete turnabout (180°) in a single hop or jump.

Another characteristic peculiar to this species while foraging on the ground is the quivering or tremulous movement of the posterior part of its body which sometimes occurs. This is not just a tail movement, but a part of the lower trunk of the body also is involved. I have observed this movement in both sexes.

PREENING

"This species often sits and engages in preening and scratching—apparently more so than does any other warbler of my acquaintance." So writes Norris (1963, p. 47), a Georgia ornithologist who knows this warbler well. I once observed a male preening continuously for 7 minutes. They seem to do a lot of preening in the center of the breast; this behavior must be related to the method of foraging, wherein the breast constantly is coming in contact with leaves and soil.

HEAD SCRATCHING

Ficken and Ficken (1968, p. 136) have suggested that the "head scratching method may prove a valuable addition to the set of complex characters that can be used in defining genera." In the course of a series of observations of Swainson's Warblers in the Dismal Swamp in Virginia, I observed head scratching in

three individuals: four times in one, three times in another, and once in a third. The three birds used the direct method, bringing the foot forward and under the wing. Ficken and Ficken (1968, p. 136) indicate that some *Vermivora* scratch directly and others indirectly and that all species of *Dendroica* observed in the wild scratched indirectly.

TAIL SPREADING

Tail spreading or fanning by a male may occur following territorial boundary disputes with another male. This is usually done by a male that invades another's territory and is driven out. I once saw a male on territory fanning its tail while being pursued slowly by a Redstart that had young in the territory.

Factors Affecting the Population

The Swainson's Warbler is the least abundant of southern warblers, except for Bachman's Warbler. There are several reasons why the Swainson's Warbler is not more successful. From my observations it would appear that it has a lower nesting success than most other species of warblers. In a total of 16 nests of which I am reasonably sure that my presence had nothing to do with desertion, only three were successful. Some of these were second attempts; others were initial attempts, in which case the birds may have been successful on the second try. At three of the nests, cowbirds removed all of the Swainson's Warbler eggs. A mouse expropriated another nest during the laying period, and two nests were abandoned with clutches intact.

Some of the reasons for its low nesting success may be the vulnerability of the large, bulky nest that is poorly concealed, is located close to the ground, and contains white eggs. Other species of warblers nesting in the same breeding range have better-concealed nests, most of which are much smaller, and all of which contain speckled eggs except the very rare Bachman's Warbler, which also has white eggs. Furthermore, most Swainson's Warbler nests are lined with dark material, so that the white eggs stand out against the dark background.

In the Dismal Swamp, I found that whenever a Common Grackle or a Blue Jay had a nest in or near a Swainson's Warbler nesting territory, the warbler's nest was almost always robbed. However, since the Grackle and Jay begin nesting before the Swainson's Warbler, and their nesting seasons overlap the first nesting attempt of these warblers, a second attempt can be made after the two nest plunderers have completed nesting and left the area.

Since the Swainson's Warbler places its not-too-well-hidden nest close to the ground, it is well within the "cruising" range of various snakes and mammals. C. E. Collier, Jr., (1941, p. 28) discovered a milk snake (*Lampropeltis triangulum*) in the act of robbing a Swainson's Warbler nest, near Clarksville, Tenn. The snake had one of the warbler's eggs in its mouth at the time.

Cowbird parasitism is becoming a more important limiting factor. Friedmann (1929, p. 150) and Mayfield (1965, p. 13-18) believe that the cowbird originated in the prairies and plains of the West, and only in the last 100 years or so invaded the eastern forest. As late as 1950 most of the southeastern Coastal Plain

was outside the breeding range of the cowbird, but it is gradually extending its breeding range into that area (Webb and Wetherbee 1960, p. 83-87). The cowbird is a common breeding bird throughout the lower Mississippi Valley and Appalachian mountains nesting range of the Swainson's Warbler.

Since one of the choice nesting sites of the Swainson's Warbler in the Coastal Plain is the river floodplain forest, production is markedly limited when such areas become inundated during the nesting season. In the Ocmulgee River floodplain of central Georgia, virtually all of the Swainson's Warblers nest within half a mile of the river. This is where the canebrakes are located. Some of the birds nest right up to the river bank. I have seen some Swainson's Warbler territories that were under 12 feet of water. Three out of 10 years that I worked in this area the nesting ground was flooded during May when the Swainson's Warbler was nesting.

Calhoun (1941, p. 306) found a similar situation in the Hatchie River bottoms in Hardeman County, Tenn. He made the following statement about these conditions:

If the Swainson's warbler nests in this same type of region, it would be exceedingly difficult to study its nesting habits because such areas are subject to flooding in the spring and early summer.

In the Coastal Plain part of its range the Swainson's Warbler would probably have a difficult time maintaining its present population level, not only because of low nesting success, but also because of its narrow habitat requirements. Canebrakes, prime habitat of this species, have disappeared faster than any other bottomland plant community. Habitat has disappeared faster in the lower Mississippi Valley than elsewhere in the range. Very early, rich bottomlands of the lower Mississippi Valley were stripped of their valuable hardwood timber and then cleared and drained for the agricultural use of their highly productive soils. Habitat in the Great Dismal Swamp and some other South Atlantic lowlands has contracted because the deep shade required by this species disappeared with the harvesting of the mature forest. The cut-over areas were drained and reforested with pine.

It is possible that the Swainson's Warbler can adapt to so-called marginal Coastal Plain habitat better than is suspected. Some occur there, but these usually are bachelor males. But if the Swainson's Warbler ever has to make a last stand it may well be in the Southern Appalachians, where many of them occur in national forests and national parks or in areas unsuitable for agricultural production.

Summary

The Swainson's Warbler is one of the least known of southern birds. Studies of its life history and ecology were made by the author principally in canebrakes along the Ocmulgee River a few miles south of Macon, Ga., and near Pendleton Ferry, Ark., in deciduous thickets in the Dismal Swamp, Va., in scrub palmetto in Monkey John Swamp, S.C.; and in mountain cove hardwoods near Charleston, W. Va.

The Swainson's Warbler was described by Audubon from specimens collected by John Bachman on the banks of the Edisto River in South Carolina in 1832 or 1833. John Abbot, a Georgia naturalist, collected a specimen some 25 years earlier but made no record of the event. However, he made an identifiable portrait of the bird. His illustrations of birds were discovered many years later in several museums.

The Swainson's Warbler spends nearly 6 months in the United States. During this period (summer half of year) it is primarily associated with the river floodplain forests and swamps of the South Atlantic and Gulf Coastal Plain and the rich moist woods of the Mixed Mesophytic forest of the Southern Appalachians.

The main wintering ground is the Caribbean archipelago in the general latitude of 20° N., especially the islands of Jamaica and Cuba; individuals also winter in the Yucatan Peninsula and British Honduras.

Some migrants apparently fly across the Gulf, some around it. First spring migrants reach the southern coast of the United States usually by the last half of March or the first week in April. Most birds are on the breeding grounds by April 15, but some arrive by the first week in April. In the fall most have departed from the breeding grounds by September 15.

The optimum habitat is rich damp woods with deep shade, moderately dense undergrowth, and relatively dry ground. Giant cane, scrub palmetto, and sweet pepperbush are the most important plants of Coastal Plain breeding grounds; rhododendron and cove hardwood shrubs are important in the mountains.

In April 1968, I counted 19 territorial males along a 2-mile transect through canebrakes near Macon, Ga. I found eight territorial males along a 0.5-mile transect in the Dismal Swamp in

Virginia, April 20, 1958. Brooks and Legg counted 10 or 11 singing males along 1.5 miles of Franzy Creek in Nicholas County, W. Va.

The Swainson's Warbler is 5 to 5½ inches in length, and during the breeding season weighs about 15 grams. Breeding birds of the Southern Appalachians usually have whiter underparts than Coastal Plains birds.

The Swainson's Warbler is one of the last of the southern warblers to arrive on the breeding grounds, but is earlier than most northern transient members of the family. One banded male returned to the same territory in Maryland for five consecutive breeding seasons.

Nine territories ranged in size from 0.3 to 4.8 acres. The size and shape of a territory varies during different phases of the breeding cycle.

Hostile encounters between neighboring males usually take place along territorial boundaries. Paired males usually initiate border encounters with unpaired males. A display is sometimes performed by an aggressive male after it is driven back into its territory.

During courtship and mating the male sings very little. Frequently he flies to the female, who usually is foraging on the ground, and either pecks at her rump or pounces on her. Copulation sometimes takes place during pouncing.

First nests usually are built by the first week in May. Although other investigators reported finding nests outside the defended territory, all nests that I found were within the territory. The large bulky nest of this species is usually placed 2 to 6 feet above the ground. It is built by the female from materials gathered close to the nest site; she takes 2 or 3 days to complete it.

Three and occasionally four white eggs are laid. At a Dismal Swamp nest the incubation period was 13 days. The cowbird parasitizes nests in some parts of the breeding range.

During incubation two females spent 54 and 78 percent of daylight time on the nest. Both sexes feed young and clean the nest. Young remain in the nest 10 to 12 days. Fledglings of one brood were attended only by the female.

The song of the Swainson's Warbler is loud and ringing and of marked musical quality. It consists of three or four high introductory notes, all separated, followed by a phrase of four or five syllables uttered rapidly, and slurred. Songs are delivered at a rate of about 8 or 9 per minute for the first few minutes of morning song, then decrease to 5 or 6 per minute for most of the

morning. Songs are given in courses or series. The rate of singing is usually faster at the beginning of a course. The number of songs sung by a territorial male in 1 day, June 3, in the Dismal Swamp was 1,168. It produced 186 songs the first hour and sang at a fairly constant rate from 5 to 8 a.m., 192, 194, and 198 songs per hour.

Muted or whisper songs are a continuous chatter that may go on for as long as 3 minutes. They do not resemble the primary advertising song and may be given in the presence of other Swainson's Warblers or when alone. The alarm note is a sharp *chip*. A weaker chip is used for communicating during courtship.

The primary advertising song is sung from the ground and from perches at low elevations. The whisper song is usually given from the ground.

The Swainson's Warbler is primarily a ground feeder, but sometimes searches for food a few feet above the ground in undergrowth. Insects, its main food, are located as the bird pokes its bill under leaves, pushing them upward and examining the underside, and searching the ground beneath. Foods gleaned from beneath the leaf mantle usually are ground beetles, crickets, ants, and spiders. Sometimes caterpillars are taken in the course of foraging in the shrub strata.

The usual gait of the Swainson's Warbler is a cross between a hop and a walk, suggesting a canter. The direct method is used in head scratching, that is, bringing the foot forward and under the wing. Tail spreading or fanning by a male may occur following a territorial boundary dispute with another male.

The Swainson's Warbler is one of the least abundant of southern warblers. It has a low nesting success because its large bulky nest is poorly concealed, is located close to the ground, and contains white eggs. In parts of its range it is highly parasitized by the cowbird. In some Coastal Plain floodplain forests, nests are destroyed during floods.

Literature Cited

AMERICAN ORNITHOLOGISTS' UNION.

1957. Check-list of North American birds. 5th ed. Baltimore. 691 p.

AMMANN, GEORGE ANDREW.

1939. Swainson's warbler in Illinois. Wilson Bulletin, vol. 51, No. 2, p. 185-186.

AUDUBON, JOHN JAMES.

1834a. Birds of America, vol. 2, Robert Havell, Jr., London.

1834b. Ornithological biography, vol. 2. Adam and Charles Black, Edinburg. 588 p.

BENT, ARTHUR CLEVELAND.

1953. Life histories of North American wood warblers. Smithsonian Institution, U.S. National Museum Bulletin 203. 734 p.

BERGER, ANDREW J.

1961. Bird study. John Wiley and Sons, New York. 389 p.

BLAIR, THOMAS A.

1942. Climatology. Prentice-Hall, Inc., New York 484 p.

BRAUN, E. LUCY.

1950. Deciduous forests of eastern North America. Blakiston, Philadelphia. 596 p.

BREWSTER, WILLIAM.

1885a. Swainson's warbler. Auk, vol. 2, No. 1, p. 65-80.

1885b. The nest and eggs of Swainson's warbler (*Helinaia swainsoni*). Forest and Stream, vol. 24, p. 468.

BRIEDING, GEORGE H.

1944. Swainson's warbler in Harlan County, Kentucky. Redstart, vol. 12, Nos. 1 and 2, p. 6-7.

BROOKS, MAURICE.

1965. The Appalachians. Houghton Mifflin Company, Boston. 346 p.

_____ and WILLIAM C. LEGG.

1942. Swainson's warbler in Nicholas County, West Virginia. Auk, vol. 59, No. 1, p. 76-86.

BULL, JOHN.

1964. Birds of the New York area. Harper and Row, New York. 540 p.

BURLEIGH, THOMAS DEARBORN.

1938. The birds of Athens, Clarke County, Georgia. Georgia Ornithological Society, Occasional Paper No. 1. 35 p.

1945. The bird life of the Gulf Coast region of Mississippi. Occasional Papers Museum of Zoology, Louisiana State University, Baton Rouge. 166 p.

1958. Georgia birds. University of Oklahoma Press, Norman. 746 p.

CALHOUN, JOHN B.

1941. Notes on the summer birds of Hardeman and McNairy counties. Journal of the Tennessee Academy of Science, vol. 16, No. 4, p. 293-309.

CARPENTER, FLOYD S.

1937. Swainson's warbler in Bullitt County. Kentucky Warbler, vol. 13, No. 4, p. 32.

CHAPMAN, FRANK M.

1907. The warblers of North America. D. Appleton and Company, New York. 306 p.

COFFEY, BEN.

1941. Swainson's warbler in the Memphis area. Migrant, vol. 12, No. 2, p. 30-31.

COLLIER, CLARENCE E., Jr.

1941. Snake in a Swainson's warbler nest. Migrant, vol. 12, No. 2, p. 28.

CUNNINGHAM, RICHARD L.

1965. Fall migration—Florida region. Audubon Field Notes, vol. 19, No. 1, p. 28-33.

DENTON, J. FRED.

1948. First record of Swainson's warbler in the Georgia mountains in summer. Oriole, vol. 13, Nos. 2 and 3, p. 24-25.

_____ and DOROTHY NEAL.

1951. The abundance and distribution of some summer birds of Tray Mountain, Georgia. Oriole, vol. 16, No. 3, p. 27-28.

EATON, STEPHEN W.

1953. Wood warblers wintering in Cuba. Wilson Bulletin, vol. 65, No. 3, p. 169-174.

ELLIOTT, BRUCE G.

1969. Life history of the red warbler. Wilson Bulletin, vol. 81, No. 2, p. 184-195.

FAXON, WALTER.

1896. John Abbot's drawings of the birds of Georgia. Auk, vol. 13, No. 3, p. 204-215.

FERNALD, MERRITT LYNDON.

1950. Gray's manual of botany. Eighth (centennial) Edition. American Book Company. New York. 1632 p.

FERNEYHOUGH, J. BOWIE.

1914. Bird-study at the University of Virginia Summer School. Bird-Lore, vol. 16, No. 4, p. 290-292.

FICKEN, MILLICENT, and ROBERT W. FICKEN.

1962. The comparative ethology of the wood warblers: a review. Living Bird, vol. 1, p. 103-122.

1968. Head-scratching in wood warblers. Auk, vol. 85, No. 1, p. 136.

FRIEDMANN, HERBERT.

1929. The cowbirds: a study in the biology of social parasitism. Charles C. Thomas, Springfield, Illinois. 421 p.

GREEN, N. BAYARD.

1947. Swainson's warbler in southern Ohio. Wilson Bulletin, vol. 59, No. 4, p. 211.

GRISCOM, LUDLOW, and ALEXANDER SPRUNT, Jr.

1957. The warblers of America. Devin-Adair Company, New York. 356 p.

GROSS, ALFRED O.

1908. Swainson's warbler (*Helinaia swainsoni*). Auk, vol. 25, No. 2, p. 225.

HANN, HARRY W.

1937. Life History of the oven-bird in Southern Michigan. *Wilson Bulletin*, vol. 49, No. 3, p. 145-237.

HARDY, JOHN WILLIAM.

1957. First specimen from Kansas of Swainson's warbler. *Bulletin of the Kansas Ornithological Society*, vol. 8, No. 2, p. 10.

HOWARD, H. E.

1929. An introduction to the study of bird behavior. Cambridge University Press, London. 136 p.

HOWELL, ARTHUR H.

1910. Breeding records from southern Illinois. *Auk*, vol. 27, No. 2, p. 216.

1928. Birds of Alabama. Department of Game and Fisheries of Alabama. Birmingham. 384 p.

1932. Florida bird life. Florida Department of Game and Fresh Water Fish. Coward-McCann, New York. 579 p.

HOWELL, JOSEPH C., and JAMES T. TANNER.

1951. An accident to migrating birds at the Knoxville Airport. *Migrant*, vol. 22, No. 4, p. 61-62.

IMHOF, THOMAS A.

1962. Alabama birds. State of Alabama Department of Conservation, Game and Fish Division. University of Alabama Press, University. 591 p.

JAMES, DOUGLAS A., and FRANCES C. JAMES.

1966. Spring migration—Central Southern region. *Audubon Field Notes*, vol. 20, No. 4, p. 515-519.

———, FRANCES C. JAMES, and S. HILTY.

1966. Nesting season—Central Southern region. *Audubon Field Notes*, vol. 20, No. 5, p. 575-577.

KEARNEY, THOMAS H.

1901. Report on a botanical survey of the Dismal Swamp region. Contributions from the U.S. National Herbarium, Washington, vol. 5, No. 6. 585 p.

KIRN, ALBERT J.

1918. Observations of Swainson's warbler. *Oologist*, vol. 35, No. 6, p. 97-98.

KOPMAN, H. H.

1905. List of birds seen in Jefferson Parish, Louisiana, April 1, 1904. *Auk*, vol. 22, No. 2, p. 140-145.

1915. List of the birds of Louisiana. Part VII. *Auk*, vol. 32, No. 2, p. 183-194.

LAPRADE, W. H., Jr.

1922. Nesting of Swainson's warbler in Atlanta. *Oologist*, vol. 39, No. 6, p. 88-89.

LAWRENCE, LOUISE DEKIRILINE.

1953. Notes on the nesting behavior of the Blackburnian Warbler. *Wilson Bulletin*, vol. 65, No. 3, p. 135-144.

LINCOLN, FREDERICK C.

1918. Notes on some species new to the Colorado list of birds. *Auk*, vol. 35, No. 2, p. 236-237.

LOOMIS, LEVERETT M.

1887. *Helinaia swainsonii* near Chester C.H., S.C. *Auk*, vol. 4, No. 4, p. 347-348.

LOWERY, GEORGE H., Jr.

1945. Trans-Gulf migration of birds and the coastal hiatus. *Wilson Bulletin*, vol. 57, No. 2, p. 92-121.

1946. Evidence of trans-Gulf migration. *Auk*, vol. 63, No. 2, p. 175-211.

LUTZ, FRANK E.

1935. *Field book of insects*. G. P. Putnam's Sons, New York. 510 p.

MAYFIELD, HAROLD.

1960. The Kirtland's warbler. *Bulletin 40*, Cranbrook Institute of Science, Bloomfield Hills, Michigan. 242 p.

1965. The brown-headed cowbird, with old and new hosts. *Living Bird*, vol. 4, p. 13-28.

MEANLEY, BROOKE. 1945. Notes on Swainson's warbler in central Georgia.

Auk, vol. 62, No. 3, p. 395-401.

1950. Swainson's warbler on Coastal Plain of Maryland. *Wilson Bulletin*, vol. 62, No. 2, p. 94.

1966. Some observations on habitats of the Swainson's warbler. *Living Bird*, vol. 5, p. 151-165.

1968. Singing behavior of the Swainson's warbler. *Wilson Bulletin*, vol. 80, No. 1, p. 72-77.

1969. Pre-nesting and nesting behavior of the Swainson's warbler. *Wilson Bulletin*, vol. 81, No. 3, p. 246-257.

_____ and GORMAN M. BOND.

1950. A new race of Swainson's warbler from the Appalachian Mountains. *Proceedings of the Biological Society of Washington*, vol. 63, p. 191-195.

MENDEL, ROBERT M.

1965. *The birds of Kentucky*. Ornithological Monographs No. 3, American Ornithologists' Union, Lawrence, Kansas. 581 p.

MERRIAM, C. HART.

1885. Swainson's warbler in Jamaica. *Auk*, vol. 2, No. 4, p. 377.

MORSE, DOUGLASS H.

1967. Competitive relationships between parula warblers and other species during the breeding season. *Auk*, vol. 84, No. 4, p. 490-502.

MURPHEY, EUGENE EDMUND.

1937. Observations on the bird life of the Middle Savannah Valley 1890-1937. *Contributions from the Charleston Museum IX*, Charleston, S.C. 61 p.

MURRAY, J. J.

1939. Swainson's warbler in southwest Virginia. *Raven*, vol. 10, Nos. 10 and 11, p. 9.

NICE, MARGARET MORSE.

1931. *Birds of Oklahoma—Revised Edition*. University of Oklahoma Press, Norman, Biological Survey, vol. III, No. 1. 224 p.

1943. Studies in the life history of the song sparrow. 2. The behavior of the song sparrow and other passerines. *Transactions of the Linnaean Society of New York*, vol. 6. 328 p.

NORRIS, ROBERT A.

1963. Birds of the AEC Savannah River Plant Area. *Contribution of the Charleston Museum XIV*, Charleston, S.C. 78 p.

_____ and MILTON N. HOPKINS, Jr.

1947. The breeding of Swainson's warbler near Tifton, Georgia. *Oriole*, vol. 12, No. 1, p. 7-9.

_____ and DAVID W. JOHNSTON.

1958. Weights and weight variation in summer birds from Georgia and South Carolina. *Wilson Bulletin*, vol. 70, No. 2, p. 114-129.

PARNELL, J. F., and T. L. QUAY.

1964. The summer birds of the Toxaway River Gorge of southwestern North Carolina. *Wilson Bulletin*, vol. 76, No. 2, p. 138-146.

PAYNTER, RAYMOND A., Jr.

1955. The ornithogeography of the Yucatan Peninsula. *Peabody Museum of Natural History, Yale University Bulletin* 9. 347 p.

PEAKE, RICHARD H., Jr.

1965. Swainson's warbler in Jackson County, North Carolina. *Chat*, vol. 29, No. 4, p. 114.

PERRY, T. D., Jr.

1886. Nesting of Swainson's warbler. *Ornithologist and Oologist*, vol. 11, No. 12, p. 188.

1887. Some additional notes on Swainson's warbler. *Ornithologist and Oologist*, vol. 12, No. 9, p. 141-142.

PETERS, JAMES L.

1913. List of birds collected in the territory of Quintana Roo Mexico, in the winter and spring of 1912. *Auk*, vol. 30, No. 3, p. 367-380.

PHILLIPS, JOHN C.

1911. A year's collecting in the state of Tamaulipas, Mexico, *Auk*, vol. 28, No. 1, p. 67-89.

PURRINGTON, ROBERT D.

1966. Checklist of the birds of Brazos County, Texas. Privately printed. 55 p.

RADFORD, ALBERT E., HARRY E. AHLES, and C. RITCHIE BELL.

1964. Guide to the vascular flora of the Carolinas. University of North Carolina, Chapel Hill. 383 p.

RAMSDEN, CHARLES T.

1914. Swainson's warbler (*Helinaia swainsoni*) at Guantanamo, Cuba. *Auk*, vol. 1, No. 2, p. 253.

REYNARD, GEORGE B.

1963. The cadence of bird song. *Living Bird*, vol. 2, p. 139-148.

RIDGWAY, ROBERT.

1878. Notes on birds observed at Mount Carmel southern Illinois, in the spring of 1878. *Bulletin of the Nuttall Ornithological Club*, vol. 3, No. 4, p. 162-166.

1902. Birds of North and Middle America, part IX. Smithsonian Institution, U.S. National Museum Bulletin 50. 834 p.

ROBERTSON, WILLIAM B., and C. RUSSELL MASON.

1965. Additional bird records from the Dry Tortugas. *Florida Naturalist*, vol. 38, No. 4, p. 131-138.

SAVELL, WILLIAM E.

1968. Swainson's warbler—first New Jersey record. *Ebba News*, vol. 3, No. 4, p. 159.

SCOTT, F. R., and DAVID A. CUTLER.

1964. Spring migration—Middle Atlantic Coast region. *Audubon Field Notes*, vol. 18, No. 4, p. 439-442.

SEEBER, EDMUND L., and RALPH M. EDEBURN.

1952. A preliminary report of the birds in the Ohio River Valley in West

Virginia between the Great Kanawha and Big Sandy River. Privately distributed. 37 11 (mimeo).

SHULER, JAMES B.

1962. Swainson's warbler in the South Carolina mountains. *Chat*, vol. 26, No. 3, p. 75-76.

SIMS, ELEANOR, and W. R. DEGARMO.

1948. A study of Swainson's warbler in West Virginia. *Redstart*, vol. 16, No. 1. p. 1-8.

SPRUNT, ALEXANDER, Jr.

1951. Some observations on the fall migration at Dry Tortugas, Florida. *Auk*, vol. 68, No. 2, p. 218-226.

_____ and E. BURHAM CHAMBERLAIN.

1949. South Carolina bird life. University of South Carolina Press, Columbia. 585 p.

STENGER, JUDITH, and J. BRUCE FALLS.

1959. The utilized territory of the ovenbird. *Wilson Bulletin*, vol. 71, No. 2, p. 125-140.

STEVENSON, HENRY M., Jr.

1941. Summer residents of the Highlands, North Carolina region. *Oriole*, vol. 6, No. 4, p. 41-48.

1957. The relative magnitude of the trans-Gulf and circum-Gulf spring migrations. *Wilson Bulletin*, vol. 69, No. 1, p. 39-77.

1960. Winter season and winter bird-population study—Florida region. *Audubon Field Notes*, vol. 14, No. 3, p. 304.

STODDARD, HERBERT L., Sr., and ROBERT A. NORRIS.

1967. Bird casualties at a Leon County, Florida TV tower: an eleven-year study. *Bulletin of Tall Timbers Research Station*, No. 8. 104 p.

STONE, WITMER.

1914. Types of bird genera *Limnothlypis* new genus. *Science*, n.s. vol. 40, No. 1018, p. 1-38.

SUTTON, GEORGE MIKSCH.

1967. Oklahoma birds. University of Oklahoma Press, Norman. 674 p.

TORDOFF, HARRISON B.

1952. Notes on birds of Jamaica. *Auk*, vol. 69, No. 3, p. 320-322.

TRAYLOR, M.

1941. Birds from Yucatan Peninsula. *Field Museum of Natural History*, Publication 493, Zoology Series, vol. 24, No. 19, p. 192-225.

VAIDEN, M. GORDON.

1940. Mississippi bird records. *Wilson Bulletin*, vol. 52, No. 2, p. 126.

WALKINSHAW, LAWRENCE H., and CLARA M. WALKINSHAW.

1961. Mist-netting birds on Andros Island. *Bird-Banding*, vol. 32, No. 1, p. 46-51.

WAYNE, ARTHUR TREZEVANT.

1893. Additional notes on the birds of the Suwannee River.

Auk, vol. 10, No. 4, p. 336-338.

1895. Notes on the birds of the Wacissa and Aucilla River regions of Florida. *Auk*, vol. 12, No. 4, p. 362-367.

1906. The date of discovery of Swainson's warbler (*Helinaia swainsonii*). *Auk*, vol. 23, No. 2, p. 227.

1910. Birds of South Carolina. Contribution from the Charleston Museum I, Charleston, S.C. 254 p.

WEBB, JOHN S., and DAVID KENNETH WETHERBEE.

1960. Southeastern breeding range of the brown-headed cowbird. *Bird-Banding*, vol. 31, No. 2, p. 83-87.

WEBSTER, FRED S., Jr.

1966. Spring migration—South Texas region. *Audubon Field Notes*, vol. 20, No. 4, p. 525-532.

WESTON, FRANCIS MARION.

1965. A survey of the birdlife of Northwestern Florida. *Bulletin of Tall Timbers Research Station*, No. 5, 147 p.

WIDMANN, OTTO.

1895. Swainson's warbler, an inhabitant of the swamp woods of southeastern Missouri. *Auk*, vol. 12, No. 2, p. 112-117.

WILLIAMS, ELLISON A.

1935. Swainson's warbler in the North Carolina mountains. *Auk*, vol. 52, No. 4, p. 458-459.

WILLIAMS, FRANCIS.

1966. Spring migration—Southern Great Plains region. *Audubon Field Notes*, vol. 20, No. 4, p. 522-525.

WORTHEN, CHARLES K.

1906. Swainson's warbler in Nebraska. *Auk*, vol. 23, No. 2, p. 227.

As the Nation's principal conservation agency, the Department of the Interior has basic responsibilities for water, fish, wildlife, mineral, land, park, and recreational resources. Indian and Territorial affairs are other major concerns of America's "Department of Natural Resources."

The Department works to assure the wisest choice in managing all our resources so each will make its full contribution to a better United States—now and in the future.



HECKMAN
BINDERY INC.



AUG 97

Bound -To -Please® N. MANCHESTER,
INDIANA 46962

SMITHSONIAN INSTITUTION LIBRARIES



3 9088 01316 8596