U.S. Fish and Wildlife Service

Migration of Birds

Circular 16

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by Frederick C. Lincoln, 1935

revised by Steven R. Peterson, 1979

revised by John L. Zimmerman, 1998
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PREFACE TO THE 1998 EDITION

Frederick C. Lincoln's "Migration of Birds" was published in 1935. Lincoln's writing style effectively communicated the wonders of bird migration to a wide audience, both young and old, experienced observers of birds as well as the simply curious. Indeed the demand for this little book was so great that it was revised in 1950 and soon was out of print again. In 1979, Steven R. Peterson developed a second revision, adding additional examples and presenting an understanding of bird migration that reflected current research. The style, figures, and most of the content of the original publication were retained, but new illustrations were added where appropriate.

In this present revision large sections of the text have remained unchanged from the previous revision or only slightly modified to make the discussion compatible with current understanding. The geographic emphasis of Lincoln and the wealth of pertinent examples added by Peterson have been maintained. I have made substantial changes, however, in sections dealing with the evolution of migration, stimulus for migration, orientation and navigation, and the influence of weather. I have also changed the emphasis of the final section to reflect current concerns. While some investigators are mentioned by name, specific studies are not cited in the text. An extensive bibliography has been included for those interested in pursuing the subject further. I have relied heavily upon the bibliographies on migration research prepared by Stanley H. Anderson and Loren W. Ayers, University of Wyoming Fish and Wildlife Coop Unit and Thomas S. Litwin, as well as the bibliography in Peterson's revision. Additional citations have been suggested by Daniel R. Petit and Stephanie L. Jones, U.S. Fish and Wildlife Service. This edition was due to the support of the Fish and Wildlife Service Regional Nongame Migratory Bird Coordinators: Tara Zimmerman, Kent Wohl, Steve Lewis, Daniel Petit, Diane Pence, Stephanie Jones, Bill Howe, and Richard Coon. I am indebted to all these investigators and most grateful for their assistance.

John Zimmerman, 1998

INTRODUCTION

The changing picture of bird populations throughout the year intrigues those who are observant and who wish to know the source and destination of these birds. While many species of fish, mammals, and even insects undertake amazing migratory journeys, birds as a group are the most mobile creatures on Earth. Even humans with their many vehicles of locomotion do not equal some birds in mobility. No human population moves each year as far as from the Arctic to the Antarctic with subsequent return, yet Arctic Terns do.

Birds are adapted in their body structure and physiology to life in the air. Their feathered wings and tails, bones, lungs and air sacs, and their metabolic abilities all contribute to this amazing faculty. These adaptations make it possible for birds to seek out environments most favorable to their needs at different times of the year. This results in the marvelous phenomenon we know as migration—the regular, recurrent, seasonal movement of populations from one geographic location to another and back again.

Throughout human experience, migratory birds have been important as a source of food after a lean winter and as the harbinger of a change in seasons. The arrival of certain species has been heralded with appropriate ceremonies in many lands. Among the eskimos and other tribes this phenomenon is the accepted sign of the imminence of spring, of warmer weather, and a reprieve from winter food shortages. The European fur traders in Alaska and Canada offered rewards to the Native American who saw the first flight of geese in the spring, and all joined in jubilant welcome to the newcomers.

As North America became more thickly settled, the large flocks of ducks and geese, as well as migratory rails, doves, and woodcock that had been hunted for food became objects of the enthusiastic attention of an increasing army of sportsmen. Most of the nongame species were also found to be valuable as allies of the farmer in his never-ending confrontation against insect pests and weed seeds. And in more recent years, all species have been of ever-increasing recreational and esthetic value for untold numbers of people who enjoy watching birds. We soon realized that our migratory bird resource was an international legacy that could not be managed alone by one state or country and that all nations were responsible for its well-being. The need for laws protecting game and nongame birds, as well as the necessity to regulate the hunting of diminishing game species, followed as a natural consequence. In the management of this wildlife resource, it has become obvious that studies must be made of the species' habits, environmental needs, and travels. In the United States, the Department of the Interior recognized the value of this resource and is devoted to programs that will ensure sustainability for these populations as they are faced with the impacts of alteration in land use, loss of habitat, and contaminants from our technological society. Hence bird investigations are made by the U.S. Fish and Wildlife Service, the arm of the Department of Interior charged by Congress under the Migratory Bird Treaty Act with the duty of protecting those avian species that in their yearly journeys pass back and forth between the United States and other countries. In addition, the federal government through the activities of the Biological Resources Division of the U.S. Geological Survey also promotes basic research on migration. Federal agencies cooperate with their counterparts in other countries as well as with state agencies, academic institutions, and non-governmental groups to gain understanding and for the protection of migratory species through such endeavors as *Partners in Flight*, a broadly-based international cooperative effort in the Western Hemisphere.

For almost a century the Fish and Wildlife Service and its predecessor, the Biological Survey, have been collecting data on the important details of bird migration. Scientists have gathered information concerning the distribution and seasonal movements of many species throughout the Western Hemisphere, from the Arctic archipelago south to Tierra del Fuego. Supplementing these investigations is the work of hundreds of U.S., Latin American, and Canadian university personnel and volunteer birdwatchers, who report on the migrations and status of birds observed in their respective localities. These data, stored in field notes, computer files, and scientific journals constitute an enormous reservoir of information pertaining to the distribution and movements of North American birds. The purpose of this publication is to summarize these data and additional information from other parts of the world to present the more important facts about our current understanding of the fascinating subject of bird migration. The U.S. Fish and Wildlife Service is grateful to the many people who have contributed their knowledge so that others, whether in biology or ornithology classes, members of conservation organizations, or just individuals interested in the welfare of the birds, may understand and enjoy this precious resource as well as preserve it for generations to come.

EARLY IDEAS ABOUT MIGRATION

The migrations of birds probably attracted the attention and aroused the imagination of humans since our African genesis. Recorded observations on the subject date back nearly 3,000 years to the times of Hesiod, Homer, Herodotus, and Aristotle. In the Bible there are several references to the periodic movements of birds, as in the Book of Job (39:26), where the inquiry is made: "Doth the hawk fly by Thy wisdom and stretch her wings toward the south?" The author of Jeremiah (8:7) wrote: "The stork in the heavens knoweth her appointed time; and the turtledove, and the crane, and the swallow, observe the time of their coming." The flight of Migratory Quail that saved the Israelites from starvation in their wanderings through the Sinai wilderness is now recognized as a vast migration between their breeding grounds in eastern Europe and western Asia and their winter home in Africa.

Aristotle, naturalist and philosopher of ancient Greece, was one of the first observers whose writings are known to discuss the subject of bird migration. He noted cranes traveled from the steppes of Scythia to the marshes at the headwaters of the Nile, and pelicans, geese, swans, rails, doves, and many other birds likewise passed to warmer regions to spend the winter. Pliny the Elder, a Roman naturalist, in his "*Historia Naturalis,*" repeated much of what Aristotle had written on migration and added comments of his own concerning the movements of European species of starlings, thrushes, and blackbirds.

Aristotle also must be credited with the origin of some superstitious beliefs that persisted for several centuries. One of these, that birds hibernated, became so firmly rooted that the eminent nineteenth century American ornithologist, Dr. Elliott Coues, listed in 1878 the titles of no less than 182 papers dealing with the hibernation of swallows. The students of Aristotle believed the disappearance of many species of birds in the fall was accounted for by their passing into a torpid state where they remained during the cold season, hidden in hollow trees, eaves, or in the mud of marshes. Aristotle ascribed hibernation not only to swallows, but also to storks, kites, and doves. Some early naturalists wrote fantastic accounts of flocks of swallows allegedly seen congregating in marshes until their accumulated weight bent the reeds into the water, submerging the birds, which apparently then settled down for a long winter's nap. It was even recorded that when fishermen in northern waters drew up their nets they sometimes had a mixed catch of fish and hibernating swallows. Olaus Magnus, Archbishop of Upsala, published a work in 1555 entitled "Historia de Gentibus Septentrionalis et Natura" observing that if swallows so caught were taken into a warm room they would soon begin to fly about but would live only a short time.

The idea of hibernation as a regular method of spending the winter is no longer broadly accepted for birds, although the Common Poorwill is a possible exception. Many species, however, such as chickadees, swallows, hummingbirds, swifts, and nightjars regularly go into torpor under cold stress on winter nights but also even during the breeding season.

Aristotle also was the originator of the theory of transmutation, the seasonal change of one species into another. Frequently one species would arrive from the north just as another species departed for more southerly latitudes. From this he reasoned the two different species were actually one and assumed different plumages to correspond to the summer and winter seasons.

Probably the most remarkable theory advanced to account for migration is contained in a pamphlet titled, "An Essay toward the Probable Solution of this Question: Whence come the Stork and the Turtledove, the Crane, and the Swallow, when they Know and Observe the Appointed Time of their Coming," published in 1703. It is written "By a Person of Learning and Piety," whose "probable solution" stated migratory birds flew to the moon and there spent the winter.

Some people who easily accepted the migratory travels of larger birds were unable to understand how smaller species, some of them notoriously poor flyers, could make similar journeys. They accordingly conceived the idea that larger species (e.g., storks and cranes) carried their smaller companions as living freight. In some southern European countries, it is still believed these broad-pinioned birds serve as aerial transports for hosts of small birds that congregate upon the Mediterranean shore awaiting the opportunity for passage to winter homes in Africa. Similar beliefs, such as hummingbirds riding on the backs of geese, have been found among some tribes of Native Americans in the Western Hemisphere. Such fantasies, however, are not without some empirical basis, such as the observation of an Eastern Kingbird harassing a Great Horned Owl that actually perched on the shoulder of the owl's outstretched wing as the owl glided toward wooded cover.

Today we realize that birds do not migrate by "hitching" rides with other birds and that the scope of the migration phenomenon is worldwide, not simply limited to the Northern Hemisphere or the world's land masses. The migration heritage is developed just as extensively in Old World warblers migrating to and from Europe and Africa as in our wood warblers traveling from Canada and the United States to South America and back. Although South Temperate Zone species migrate northward to the tropics during the austral winter, no land species nesting in the South Temperate Zone migrates into the North Temperate Zone. Some seabirds like the Sooty Shearwater and Wilson's Storm-petrel, however, migrate to North Temperate seas after nesting on shores south of the equator.

TECHNIQUES FOR STUDYING MIGRATION

Since this publication first appeared in 1935, traditional methods as well as new procedures have been used in the study of bird migration. On occasion a method developed for a quite different but related purpose has become an invaluable innovative technique in our continuing exploration of the migration phenomenon.

Direct Observation

The oldest, simplest, and most frequently used method of studying migration is by direct observation. Size, color, song, and flight of different species all aid the amateur as well as the professional in determining when birds are migrating. Studies by Wells W. Cooke and his collaborators from 1888 to 1915 and continued by his successors in the U.S. Bureau of Biological Survey (later U.S. Fish and Wildlife Service) were of particular importance in the earlier years of these investigations in North America. Some of the largest and most interesting routes and patterns were sorted out by tediously compiling and comparing literally thousands of observations of species in a given locality at a particular time of the year.

More recently, the National Audubon Society and many state Audubon and ornithological societies publish information in their bulletins and newsletters on direct observation of migration. In the aggregate, direct observation has contributed much to our knowledge of migration, but this method is limited by its being largely restricted to daytime, ground-based data on birds either before or after a period of actual migratory flight.

The "moon watch" is a modification of the direct observation method. Many species of birds migrate at night. Until mid-century, it was not apparent just how prevalent nocturnal migration really was. Significant information has been derived from watching the passage of migrating birds across the face of a full moon through telescopes, noting both the numbers and directions of flight. Since the actual percent of the sky observed by looking through a telescope at the moon is extremely small (approximately one-hundred thousandth of the observable sky), the volume of birds recorded is small. On a night of heavy migration, about 30 birds per hour can be seen. The fact that any birds are observed at all is testimony to the tremendous numbers passing overhead. A large-scale, cooperative moon-watching study was organized and interpreted by George H. Lowery, Jr. of Louisiana State University in the 1960's.

Aural

Another nocturnal observation method which has potential for species identification during the study of migration is the use of a parabolic reflector with attached microphone to amplify call (chip) notes. This device, when equipped with a tape recorder, can record night migrants up to 11,000 feet on nights with or without a full moon. A primary disadvantage is that one cannot tell the direction a bird is traveling. Furthermore, there may be some difficulty in identifying the chip notes made by night migrants, since these calls are often different from the notes heard during the daytime. Unfortunately, the bird may not call when it is directly over the reflector and consequently it would not be recorded.

Preserved Specimens

Reference material consisting of preserved bird skins with data on time and place of collection exists in many natural history museums. The essential ingredient in studying migration by this method is to have an adequate series of specimens taken during the breeding season so differences in appearance between geographically separated breeding populations of the same species can be discerned. Such properly identified breeding specimens may be used for comparison with individuals collected during migration to associate them with their breeding areas. This provides a convenient way of recognizing and referring to individuals representative of known populations wherever they may be encountered.

Marking

If birds can be captured, marked, and released unharmed, a great deal of information can be learned about their movements. Many different marking methods have been developed to identify particular individuals when they are observed or recaptured at a later date. Since 1920, the marking of birds with numbered leg bands in North America has been under the direction of the U.S. Fish and Wildlife Service (and more recently the Biological Resources Division of the U.S. Geological Survey) in cooperation with the Canadian Wildlife Service. Every year professional biologists and volunteers, working under permit, place bands on thousands of birds, both game and nongame, large and small, migratory and nonmigratory. Each band carries a serial number on the outside and an address where recovered bands can be sent on the inside. When a banded bird is reported from a second locality, a definite fact relative to its movements becomes known. The study of many such cases leads to a more complete knowledge of the details of migration.

The records of banded birds have also yielded other important information relative to migrations, such as arrival and departure dates, the length of time different birds pause on their migratory journeys to feed and rest, the relation between weather conditions and starting times for migration, the rates of travel for individual birds, and the degree of regularity with which individual birds return to the summer or winter quarters used in former years. Many banding stations are operated systematically throughout the year and supply much information concerning the movements of migratory birds that heretofore could only be surmised. The most informative banding studies are those that focus on particular populations of birds. Examples of such planned banding programs are the extensive marking of specific populations of ducks and geese on their breeding grounds by the U.S. Fish and Wildlife Service and the Canadian Wildlife Service, as well as "Operation Recovery," the cooperative program of banding small land birds along the Atlantic Coast. When these banded birds are recovered, information concerning movements and survival rates of specific populations or the vulnerability to hunting is gained. Colored leg bands, neck collars, or streamers can be used to identify populations or specific individuals, and birds marked with easily observed tags can be studied without having to kill or recapture individuals, thus making it a particularly useful technique.

We have learned about the migratory habits of some species through banding, but the method does have shortcomings. To study the migration of a particular species through banding, the banded bird must be encountered again at some later date. If the species is hunted, such as ducks or geese, the number of returns per 100 birds banded is considerably greater than if one must rely on a bird being retrapped or found dead. For example, in Mallards banded throughout North America the average number of bands returned the first year is about 12 percent. In most species that are not hunted, less than 1 percent of the bands are ever seen again.

In 1935, Lincoln commented that with enough banding some of the winter ranges and migration routes of more poorly understood species would become better known. A case in point is the Chimney Swift, a common bird in the eastern United States. This species winters in South America. Over 500,000 Chimney Swifts have been banded, but only 21 have been recovered outside the United States (13 from Peru, 1 from Haiti, and the rest from Mexico). The conclusion is simply this: whereas banding is very useful for securing certain information, the volume of birds that need to be banded to obtain a meaningful number of recoveries for determining migratory pathways or breeding or wintering areas may be prohibitive. One problem in interpretation of many banding results is the fact that recoveries may often reflect the distribution of people rather than the distribution of birds.

Radio Tracking

Radio tracking, or telemetry, is accomplished by attaching a small radio transmitter that gives off periodic signals or "beeps" from a migrating bird. With a radio receiving set mounted on a vehicle or airplane, it is possible to follow these radio signals and trace the progress of the migrating bird. One of the most dramatic examples of this technique was reported by Richard Graber in 1965. He captured a Gray-cheeked Thrush on the University of Illinois campus and attached a 2.5-gram transmitter (a penny weighs 3 grams). The bird was followed successfully for over 8 hours on a course straight north from Urbana, across Chicago, and up Lake Michigan on a continuous flight of nearly 400 miles at an average speed of 50 mph (there was a 27 mph tail wind aiding the bird). It is interesting to note that while the little thrush flew up the middle of Lake Michigan, the pursuing aircraft skirted the edge of the lake and terminated tracking at the northern end after running low on fuel while the bird continued to fly on. The limitations of radio telemetry, of course, are the size of the transmitter that can be placed on birds without interfering with flight and the ability of the receiving vehicle to keep close enough to the flying bird to detect the signals. Despite this difficulty, there has been considerable development in the technology, and encouraging results to date give promise for the future, particularly when birds can be tracked by orbiting satellites. Yet this technique should be used cautiously, since several studies have demonstrated that transmitter-equipped birds have significantly lower survival.

Radar Observation

Radar was developed to identify and track aircraft electronically and was an innovation that was critical to England's success in the Battle of Britain during the early years of the Second World War. Early radar observers noted, however, that they received moving returns that could not be associated with aircraft. These radar echos, whimsically termed “angels” by observers in England, were soon discovered to be birds. That bird flight could be monitored by radar was seized upon by students of migration after the end of the war as an opportunity to obtain information on the movements of birds during both day and night and over extensive geographic areas.

Three types of radar have been used for studying birds: 1) general surveillance radar, similar to ones located at airports, that scans a large area and indicates the general time and direction of broad movements of birds; 2) tracking radar that records the path of an airplane (or bird) across the sky by “locking on” to a designated “target” and continuously following only that object; and 3) Doppler radar similar to those operated by law enforcement agencies for measuring the speed of a passing automobile or by meteorologists for detecting tornadic winds. The data collected by radar can be electronically stored in the absence of a human observer and can be correlated with weather data sets.

The use of radar in migration studies has been invaluable in determining direction and speed of mass bird movements, dates and times of departure, height of travel, and general volume, especially at night. One interesting fact to come out of current radar work is the discovery of relatively large movements of warblers and other small land birds migrating over oceans rather than along coastlines and in directions about which ground-based observers were completely unaware.

EVOLUTION OF MIGRATION

The rigors of the annual migratory journey are balanced by benefits derived from species being able to inhabit two different areas during seasons when each region provides favorable conditions. Upland Sandpipers breeding in the grasslands of North America and wintering on the pampas of Argentina never experience winter. If it were not advantageous to make the trip twice a year, the behavior would not have evolved or if once typical under one set of conditions, natural selection would have eliminated the tendency once the environment changed. An example of the latter case is the European Starling which is migratory on the continent, but the population isolated in the British Isles by the rise in sea level after the end of Pleistocene glaciation and now living in a moderate maritime climate has secondarily evolved nonmigratory behavior.

By departing in the spring from their wintering ranges to breeding areas, migrant species are probably assured of reduced interspecific competition for adequate space and resources such as ample food for themselves and their offspring. Permanent residents in temperate zones, whose wintering and breeding areas are in the same region, also gain a net benefit by being nonmigratory. Although not suffering the metabolic demands and hazards of migration, the energetic demands for survival and reproduction in an environment with a greater annual range of climactic variation, and the need to adapt to the seasonal changes in the availability and kinds of foods, are comparable. Even for permanent residents in the tropics where climatic variation is relatively low, these benefits are offset by lower reproductive success resulting from higher nest predation.

While the various kinds of wood warblers and flycatchers are wholly migratory, other species like most woodpeckers are permanent residents. Some populations of species have individuals that are migratory while other individuals breeding in the same area are not. These partial migrant species, like Blue Jays, exemplify the difficulty in suggesting simple, singular explanations for the origin of migration.

Birds require specific environmental resources for reproduction. Among both migratory and nonmigratory species alike, adequate food for the young appears to be primary in determining where, as well as when, a species will breed. American Goldfinches and Pine Siskins are closely related and winter together in gregarious flocks. With the emergence of abundant insect food in the spring, siskins disperse and begin nesting while goldfinches postpone their reproduction until late summer when thistle seeds become available for feeding young. For other species, like waterfowl, the availability of suitable nest sites rather than food for the young appears to determine the timing of breeding.

The evolution of migration also involves adaptations that affect the timing of this behavior so that the species is in the breeding or wintering habitat under the most propitious conditions. For most migrants, especially long-distance migrants, the evolution of migratory behavior demands a physiological response to environmental cues in preparation for migration that are different from the environmental factors that ultimately determine their reproductive success on the breeding range or survival on the wintering range. Thus, in the fall swallows and other insectivorous species depart southward long before food resources or weather become critical for their survival. Factors other than a decrease in food availability or cold stress, for example, must prompt their migratory departure.

The verdant flush of regrowth in the spring is clearly associated with migratory movements of many species to higher latitudes where longer daylengths provide ample time for feeding young, permitting their rapid growth and shorter exposure in the nest to predation. But the higher the latitude the shorter the breeding season, so that while summer days may be long, the summer season is short and migrants in more northerly climes may have only one chance to breed before they must again travel southward. At lower latitudes, breeding seasons are longer, allowing multiple attempts to produce young. This longer breeding season, however, is related to a higher probability that nests will suffer losses to predators.

Fall departure from higher latitudes removes individuals from climatic conditions that will eventually exceed their physiological tolerance limits. The Dickcissel is a Neotropical migrant that breeds as far north as Winnipeg, but cannot survive environmental temperatures below freezing during the short days of winter at mid-temperate latitudes. The arrival of migrants on the winter range, however, increases the chances for greater interspecific competition with resident species in years when resource availability might be reduced. This cost, plus the hazards associated with the migratory journey, decreases adult survivorship. The evolution of migratory behavior must, on average, offer a favorable balance between these various costs and benefits.

Birds appear in the fossil record distinct from their reptilian ancestors about 150 million years ago. For the next 50 million years or so a relative uniform and benign maritime climate pervaded the Earth. Sometime around 65 million years ago, however, global climate abruptly changed, perhaps from impact by a large asteroid, and the biota of the planet suffered a major episode of extinction. But a remnant lineage of birds survived and gave rise to the modern groups of birds we see today. Yet with the slow, continuing drift of the continents into higher latitudes that began soon after the first appearance of birds, and the development of mountain ranges as a result of the collision between tectonic plates, climates became more latitudinally and often longitudinally differentiated. The resulting diversity in habitats provided the selective pressures that led to the evolution of migration again and again in different species.

The general model for the evolution of migratory behavior considers a permanent resident that expands its range due to intraspecific competition into an area that is seasonally variable, providing greater resources for reproduction but harsher climactic stress and reduced food availability in the non-breeding season. Individuals breeding in these new regions at the fringe of the species' distribution are more productive, but in order to increase non-breeding survival they return to the ancestral range. This results, however, in even greater intraspecific competition because of their higher productivity, so that survival is enhanced for individuals that winter in areas not inhabited by the resident population. The Common Yellow-throat of the Atlantic coast is a good example. Birds occupying the most southern part of the species' range in Florida are largely nonmigratory, whereas populations that breed as far north as Newfoundland migrate to the West Indies in the winter, well removed from the resident population in Florida. Because a migrant population gains an advantage on both its breeding and wintering range, it becomes more abundant, while the resident, non-migratory population becomes proportionately smaller and smaller in numbers. If changing environmental conditions become increasingly disadvantageous for the resident population or interspecific competition becomes more severe, the resident population could eventually disappear, leaving the migrant population as characteristic of the species. These stages in the evolution of migration are represented today by permanent resident populations, partial migrants, and fully migratory species. As for all adaptations, natural selection continues to mold and and modify the migratory behavior of birds as environmental conditions perpetually change and species expand or retract their geographic ranges. Hence, the migratory patterns that we observe today will not be the migratory patterns of the future.

Migration involves not just the evolution of a specific behavioral pattern, but often morphological changes as well. The shape of the wing is a structural correlate with migratory behavior. Migratory species typically have proportionally longer wings, with a higher aspect ratio, than related nonmigratory species. This adaptation reduces the relative impact of wing-tip (induced) drag, resulting in greater effective lift as well as an often more efficient ratio between wing area and body weight. Furthermore, the outer primary feathers, which together with the inner primaries provide forward thrust in flapping flight, are often longer in migrants, giving the wing a pointed rather than a rounded shape. In Asia, the sedentary Black-headed Oriole has a rounded wing, whereas the closely related Black-naped Oriole with pointed wings is migratory between Siberia and India. Albatrosses, falcons, swifts, various shorebirds, and terns, many of which make long-distance journeys, have long, more pointed wings. Even among closely related migrants there is a difference. Thus the pointed wings of the Semipalmated Sandpiper, which migrates from the arctic to only northern South America has noticeably shorter wings than the Baird's and White-rumped sandpipers that fly from the arctic all the way to the southern tip of South America.

STIMULUS FOR MIGRATION

The environmental factors that have resulted in the evolution of migratory behavior are not the environmental factors that stimulate development of the migratory condition or actually cause birds to embark on migratory flights. If a bird would wait until food on its breeding range became abundant to begin its vernal migratory preparation, it would have insufficient time to migrate, establish a territory, mate, incubate eggs, and raise young to take advantage of this abundance. The timing of its entire annual cycle must result in young in the nest coincident with an optimal abundance of food or other environmental factor that has a critical effect on productivity. Similarly, if birds waited until the climate became no longer tolerable to begin preparations for fall departure from breeding areas, it would be too late to gain the necessary energy surplus above the demands of thermoregulation to allow the required physiological changes associated with migration. The stimulus for development of the migratory state must be related to the eventual advent of suitable environmental conditions for reproduction or winter survival.

In the spring, the premigratory state is characterized by a change in neural centers in the lower part of the brain (the hypothalamus) controlling hunger and satiety so that the bird gains weight by overeating. This increased energy income, a food intake that is as much as 40% greater than during other times of the year, is stored as large fat deposits under the skin, in flight musculature, and in the abdominal cavity. Small perching birds like sparrows and warblers gain about 1 to 1.5 g per day, and this increased appetite continues over a period of about two weeks prior to migration. Furthermore, these birds retain the ability to rapidly gain weight during stopover periods in the course of their migratory journey. While during nonmigratory periods fat comprises about 3-5% of a bird's body weight, short and middle distance migrants increase their fat load to about 15% of their weight, while in long-distance migrants fat is 30-50% of their weight. They are literally obese. These fat stores fuel the aerobic contraction of flight muscles, permitting flights of long duration with minimal fatigue.

Experiments have demonstrated that day length is the environmental stimulus that results in vernal premigratory weight gain. Light not only directly affects the hypothalamic feeding centers but stimulates adjacent centers in the brain to affect a shift in the bird’s endocrine secretions, specifically increasing prolactin from the pituitary, corticosterone from the adrenal gland, and the sex steroids (e.g., testosterone) from the gonads. These hormonal changes facilitate the development of fat deposits resulting from the greater food intake caused by increased appetite.

The premigratory state is also characterized by increased activity during the night, which is when most birds migrate. They become restless, perhaps in anticipation of the migratory flight. This behavior is seldom observed in the wild, but has been carefully evaluated in captive migrants. It has been shown, for example, that the intensity and duration of migratory restlessness in captives are correlated with the distance and period of migration in the wild population. Like premigratory weight gain, migratory restlessness is stimulated by long days through the effect of light on the hypothalamus, causing increased secretions of prolactin, corticosterone, and the sex steroids. Additionally, light stimulates the release of melatonin, a hormone produced in the pineal body on the top of the brain, which has also been shown to be necessary for the expression of this behavior.

It is important to emphasize that the light stimulus is a function of length of the light period rather than because of the change in daylengths. It is also clear that the absolute length of the daylight period that is considered "long" varies with species, not only in terms of the daylength characteristics of their environments but in the daily period when a species' brain is receptive to the effects of light. Both the external and internal aspects of light stimulation reflect their geographic distributions. Thus, birds wintering in the tropics have evolved a response to that photoperiod which results in premigratory changes similar to that of birds wintering in the North Temperate zone under increasing daylength. Even birds wintering in South America initiate premigratory preparation in March and April under the decreasing daylengths of the austral fall.

The adaptation of migrants to the temporal control daylength is amazing. Consider the transequatorial migrant Bobolink. This species initiates premigratory preparation under decreasing daylengths in the South Temperate Zone, migrates northward toward the equator, experiencing lengthening daylengths but decreasing daily variation in daylength, then crosses the equator and experiences rapidly increasing daylength until it finally arrives on its previous year's territory somewhere north of the fortieth parallel. That birds, many plants, and other animals depend upon daylength to regulate their annual cycles is not surprising. Of all the variables in the environment, only seasonal daylength variation has remained constant since the formation of the planet because of Earth's rotation on an axis inclined to the plane of its revolution around the Sun.

Yet the development of the migratory state is not completely driven by daylength. Birds have evolved closer control of this process by responding to other environmental stimuli, either accelerating or inhibiting the rate of response to the primary daylength stimulus. Temperature is one of the environmental factors involved. Thus, when spring is late birds do not arrive too early; similarly, when spring is advanced the birds arrive early to take advantage of the precocious environmental resources. There is also evidence that development of vegetative cover can influence light-caused reproductive development. When songbirds normally nesting on Jan Mayen Island in the Arctic Ocean arrived during a late spring to find their breeding grounds still snowbound, gonadal development was immediately truncated and the birds left, even though daylength was stimulatory.

The stimulus for autumnal premigratory preparation is not well understood. The current working hypothesis suggests that the spring photoperiod sets an internal timer that allows the expression of fall premigratory preparation after the cessation of a reproductive period which has evolved to be commensurate with species-specific environmental resources. Perhaps hormonal changes following breeding release the expression of these preset events. In many species, the postnuptual (or pre-basic) molt may inhibit the development of the premigratory state. In other species, however, migration precedes the fall molt. And some species, like Barn Swallows, molt while migrating.

WHEN BIRDS MIGRATE

Individual birds are relatively sedentary during two periods each year, at nesting time and in winter. When the entire avifauna of a continent is considered, however, during almost all periods there are some latitudinal movements of birds. Each species, or group of species, migrates at a particular time of the year and some at a particular time of the day. Other species are more irregular in their migratory behavior. Red Crossbills, for example, are erratic wanderers and will settle down and breed any month of the year when and where an adequate supply of conifer seeds is available.

Time of Year

Some species begin their fall migrations early in July, and in other species distinct southward movements cannot be detected until winter. For example, many shorebirds start south in the early part of July, while Northern Goshawks, Snowy Owls, Common Redpolls, and Bohemian Waxwings do not leave the north until forced to do so by the advent of severe winter weather or a lack of customary food. Thus, an observer in the northern part of the United States may record an almost unbroken southward procession of birds from midsummer to winter and note some of the returning migrants as early as the middle of February. While on their way north, Purple Martins have been known to arrive in Florida late in January; and, among late migrants, like some wood warblers, the northern movement may continue well into June. In some species with a broad latitudinal range, the migration is so prolonged that the first arrivals in the southern part of the breeding range will have performed their parental duties and may complete nesting while others of the species are still on their way north. As you should expect, northern and southern populations of the same species can have quite different migration schedules.

In fall, migratory populations that nest farthest south migrate first to the winter range because they finish nesting first. For example, the breeding range of the Black-and-white Warbler covers much of the eastern United States and southern Canada northwest through the prairies to Great Bear Lake in Canada (Figure 1). It spends the winter in southern Florida, the West Indies, southern and eastern Mexico, Central America, and northwestern South America. In the southern part of its breeding range, it nests in April, but those summering in New Brunswick do not reach their nesting grounds before the middle of May (Figure 2). Therefore, if 50 days are required to cross the breeding range, and if 60 days are allowed for reproductive activities and molting, they would not be ready to start southward before the middle of July. Then with an assumed return 50-day trip south, the earliest migrants from the northern areas would not reach the

Gulf Coast until September. Since adults and young have been observed on the northern coast of South America by August 21, it is very likely that they must have come from the southern part of the nesting area.

Many similar cases might be mentioned, such as the Black-throated Blue Warblers still observed in the mountains of Haiti during the middle of May when others of this species are en route through North Carolina to New England breeding grounds. The more southerly breeding American

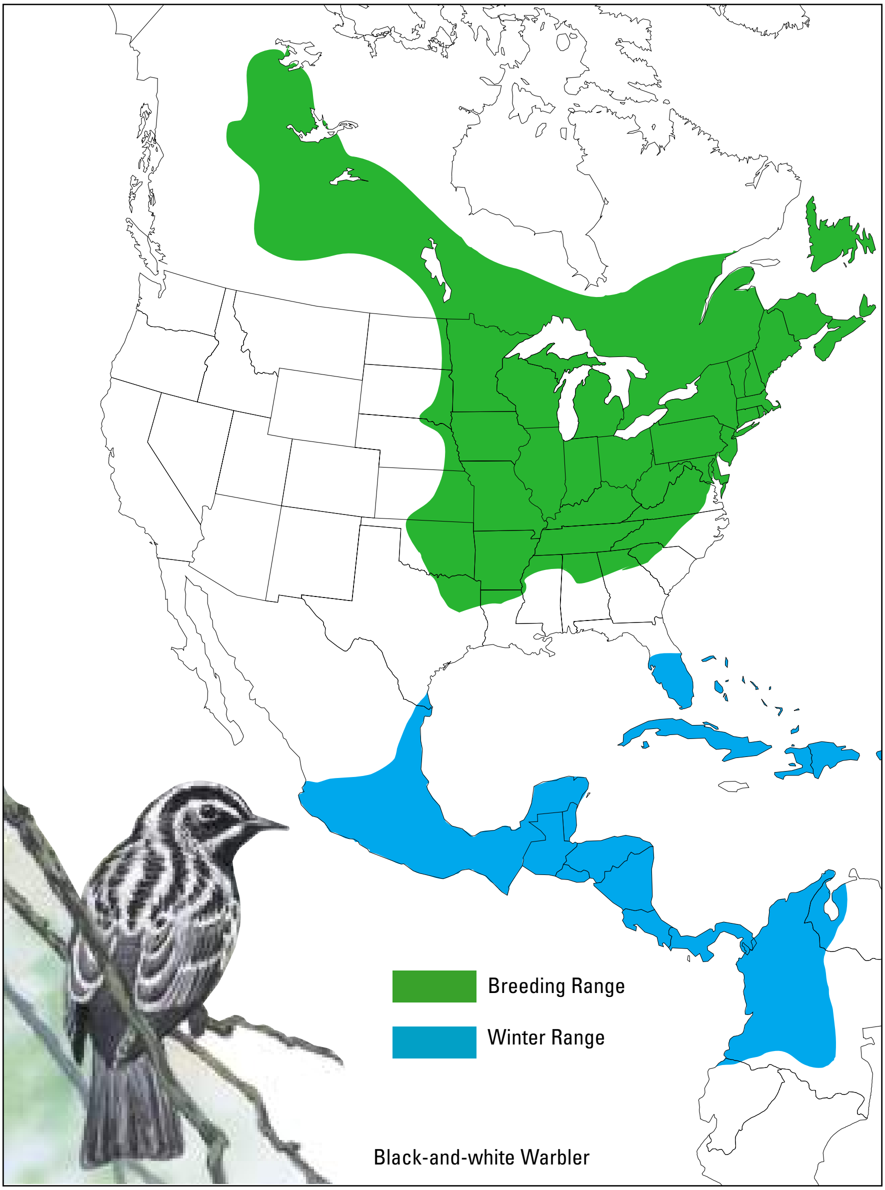

Figure 1. Summer and winter homes of the Black-and-white Warbler. A very slow migrant, warblers nesting in the northern part of the continent take 50 days to cross the breeding range. The speed of migration is shown in Fig. 2.

Redstarts and Yellow Warblers are seen returning southward on the northern coast of South America just about the time the earliest of those breeding in the north reach Florida on their way to winter quarters. Examples of the Alaska race of the Yellow Warbler have been collected in Mississippi, Florida, and the District of Columbia as late as October.

Students of migration know that birds generally travel in waves, the magnitude of which varies with populations, species, weather, and time of year.

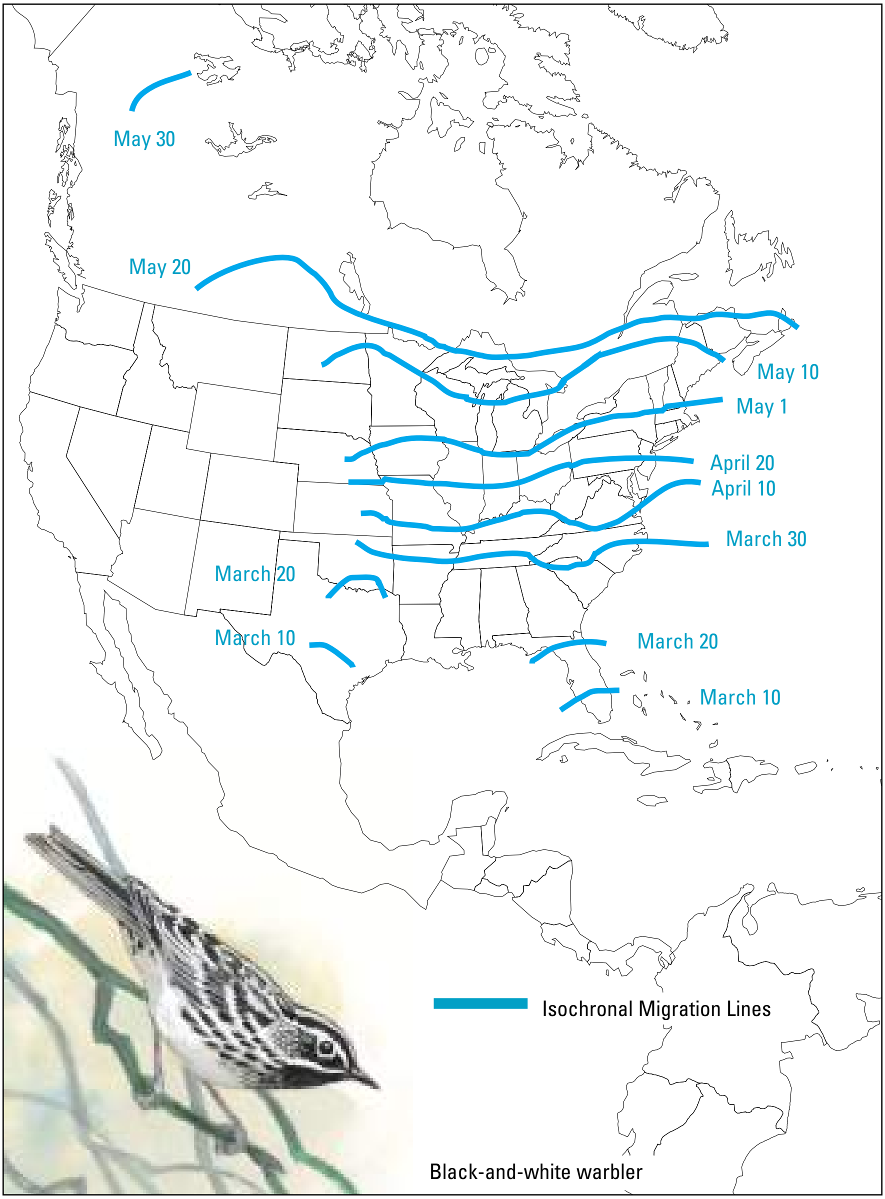

Figure 2. Isochronal migration lines of the Black-and-white warbler, showing a very slow and uniform migration. The solid lines connect places at which these birds arrive at the same time. These birds apparently advance only about 20 miles per day in crossing the United States.

Characteristically, one will observe a few early individuals come into an area followed by a much larger volume of migrants. This peak will then gradually taper off to a few lingering stragglers. If we plot numbers observed against time, the rising and receding curve is bell-shaped. In the northern part of the United States there are two general migration waves. The first one in early spring consists of "hardy" birds, including many of our common seed eaters like the finches, sparrows, and others. The second wave occurs about a month later and consists primarily of insect-eating birds such as flycatchers, vireos, and warblers. Each of these species in turn has its own frequency curve of migration within the major wave.

Time of Day

Because most birds are creatures of daylight, it seems remarkable that many should select the night for extended travel. Smaller birds such as rails, shorebirds, flycatchers, orioles, most of the sparrows, the warblers, vireos, and thrushes are typical nocturnal migrants. It is common to find woods and fields on one day almost barren of bird life and on the following morning filled with newly arrived migrants that came during the night. Waterfowl hunters sitting in their blinds frequently observe the passage of flocks of ducks and geese, but great numbers of these birds also pass through at night; the calls of Canada Geese or the conversational gabbling of flocks of ducks are common night sounds in spring and fall in many parts of the country. Observations made with telescopes focused on the full moon have shown processions of birds, and one observer estimated their passage over his area at the rate of 9,000 per hour. This gives some indication of the numbers of birds in the air at night during migratory peaks. Radar observations have shown that nocturnal migration begins about an hour after sundown, reaches a maximum shortly before midnight, and then gradually declines until daybreak. Bird echoes during peak migration periods may cover a radar screen.

It has been suggested that small birds migrate by night to avoid their enemies. To a certain extent this may be true because the group includes not only weak flyers, such as the rails, but also the small insectivorous birds, such as wrens, small woodland flycatchers, and other species that habitually live more or less in concealment. These birds are probably much safer making their flights under the protecting cloak of darkness. Nevertheless, it must be remembered that night migrants also include sandpipers and plovers. Most shorebirds are usually found in the open and are among the most powerful flyers, as some of them make annual nonstop migratory flights over 2,000 miles of open ocean.

Night travel is probably best for the majority of birds chiefly from the standpoint of feeding. Digestion is very rapid in birds, and yet the stomach of birds killed during the day almost always contains food. To replace the energy required for long flight, it is essential that either food be obtained at comparatively short intervals or stores of fat be laid on prior to migration. If the smaller migrants were to make protracted flights by day, they would arrive at their destination at nightfall almost exhausted. Since they are entirely daylight feeders, they would be unable to obtain food until the following morning. The inability to feed would delay further flights and result in great exhaustion or possibly even death should their evening arrival coincide with cold or stormy weather. By traveling at night, they can pause at sunrise and devote the entire period of daylight to alternate feeding and resting. This schedule permits complete recuperation and resumption of the journey on a subsequent evening after sufficient fat deposits have been restored. Banding studies have shown that the number of days an individual lays over during a migration stop is inversely dependent upon the amount of its fat stores upon arrival.

It has also been hypothesized that nighttime migration is advantageous because environmental temperatures are typically cooler. The effort involved in migratory flight generates considerable heat. The primary way in which flying birds loose heat in order to maintain an optimum body temperature is through the evaporation of water from air sacs that are part of its breathing system. Indeed, dehydration resulting from regulation of body temperature rather than the amount of fat stores probably limits the distance a bird can fly nonstop. Thus, by flying in cooler air, which increases heat loss by conduction and convection, less cooling by evaporation of limited body water is required and flight distances are extended.

The day migrants include, in addition to some of the ducks and geese, loons, cranes, gulls, pelicans, hawks, swallows, nighthawks, and swifts. Soaring birds, including Broad-winged Hawks, storks, and vultures, can only migrate during the day because their mode of flight makes them dependent on updrafts created either by thermal convection or the deflection of wind by topographic features like hills and mountain ridges. Swifts and swallows feed entirely on diurnal flying insects, and circling flocks of these species are frequently seen in late summer feeding as they travel gradually southward. Similarly, large flocks of Franklin's Gulls in the Great Plains feed on insects caught in thermals, using these updrafts as a source of food as well as the means permitting soaring flight that carries them on their journey with minimal expenditure of muscle power. Large flocks of Swainson's Hawks also migrate in the Plains States by thermal soaring. In the East, flights of Broad-winged, Cooper's, and Sharp-shinned hawks are regularly seen along the Appalachian ridges, soaring on the uplifted westerlies passing over the crest of the mountains.

Because many species of wading and swimming birds are able to feed at all hours, they migrate either by day or night. Some diving birds, including ducks that submerge when in danger, often travel over water by day and over land at night. Strong flyers like Snow Geese can make the entire trip from their staging area in James Bay, Canada to the wintering grounds on the Louisiana Gulf coast in one continuous flight. These birds are seldom shot by hunters enroute between these two points but are often observed migrating by aircraft pilots. Graham Cooch of the Canadian Wildlife Service tracked a flight of the blue phase of this species in 1955. The birds left James Bay on October 17 and arrived on the Gulf coast 60 hours later after a continuous flight of over 1,700-miles at an average speed of 28 miles per hour.

American Golden-Plovers, likewise, probably make the southward flight from the Maritime provinces to the South American coast in one giant leap. Other arctic shorebirds make spectacular flights. Baird's Sandpipers, for example, congregate in the Great Plains after a flight southward from above the Arctic Circle and then depart on a nonstop flight of several thousand miles. This flight takes them off the western coast of Mexico and Central America to eventual landfall in Peru. From there they continue southward at a more leisurely pace until they reach their wintering grounds in Tierra del Fuego.

An interesting comparison of the flights of day and night migrants may be made through a consideration of the spring migrations of the Blackpoll Warbler and the Cliff Swallow. Both spend the winter as neighbors in South America, but when the impulse comes to start northward toward their respective breeding grounds, the warblers strike straight across the Caribbean Sea to Florida (Figure 3), while the swallows begin their journey by a northwestward flight of several hundred miles to Panama (Figure 4). From there they move leisurely along the western shore of the Caribbean Sea to Mexico and, continuing to avoid a long trip over water, go completely around the western end of the Gulf of Mexico. This circuitous route adds more than 2,000 miles to the journey of the swallows that nest in Nova Scotia. The question may be asked: "Why should the swallow select a route so much longer and roundabout than that taken by the Blackpoll Warbler?" The explanation is simple. The swallow is a day migrant while the warbler travels at night. The migration of the warbler is made up of a series of long nocturnal flights alternated with days of rest and feeding in favorable localities. The swallow, on the other hand, starts its migration several weeks earlier and catches each day's ration of flying insects during flight.

Although most of our smaller birds make their longest flights at night, close observation shows travel is continued to some extent by day. During the latter half of a migratory season birds may show evidence of an overpowering drive to hasten to their breeding grounds. At this time flocks of birds maintain a movement in the general direction of the seasonal journey while feeding on or near the ground. Sometimes they travel hurriedly, and while their flights may be short, they can cover an appreciable distance in the course of a day.

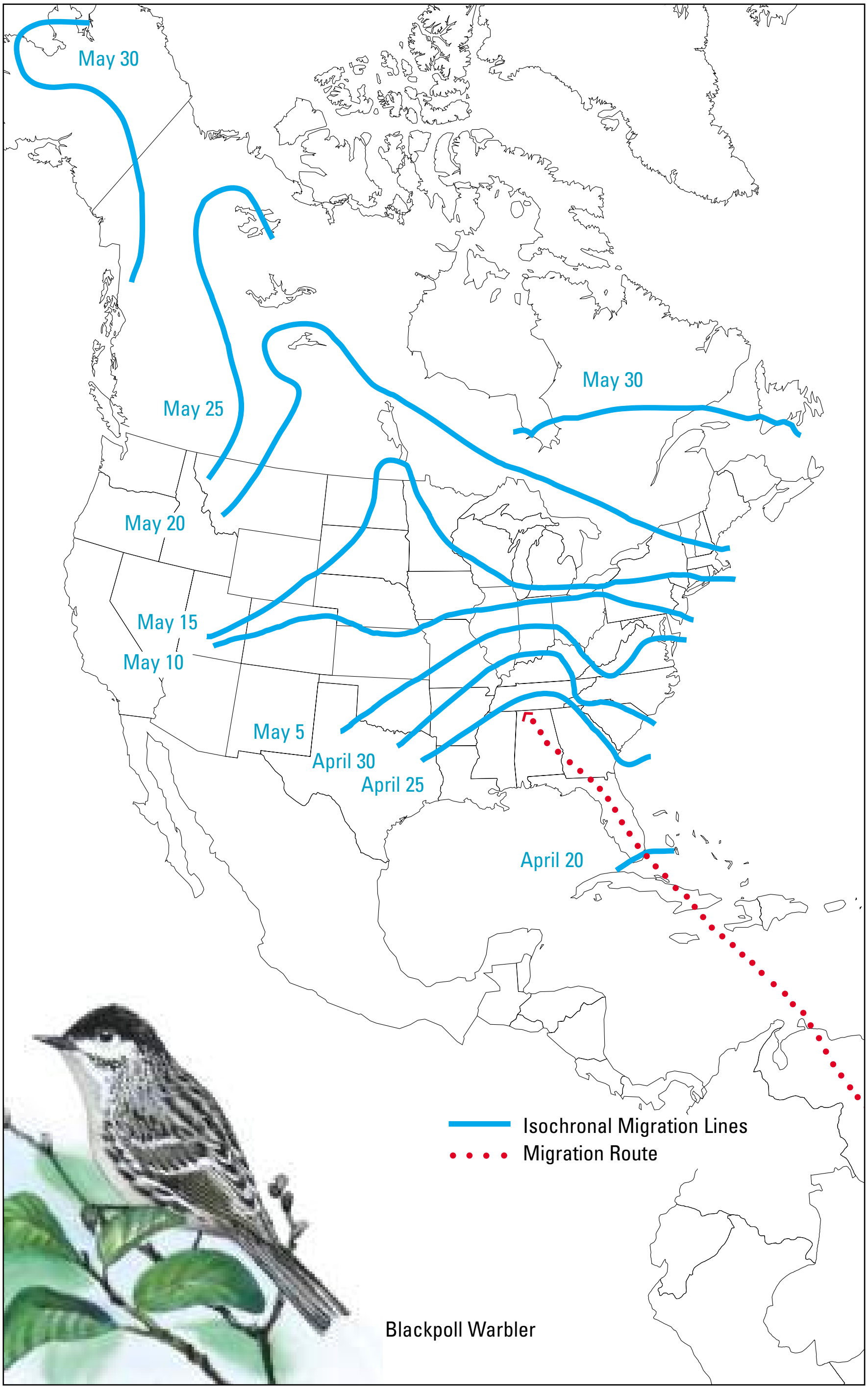

Figure 3. Migration of the Blackpoll Warbler. As the birds move northward, the isochronal lines become farther apart, which indicates that the warblers move faster with the advance of spring. From April 30 to May 10 the average speed is about 30 miles per day, while from May 25 to May 30 it increases to more than 200 miles.

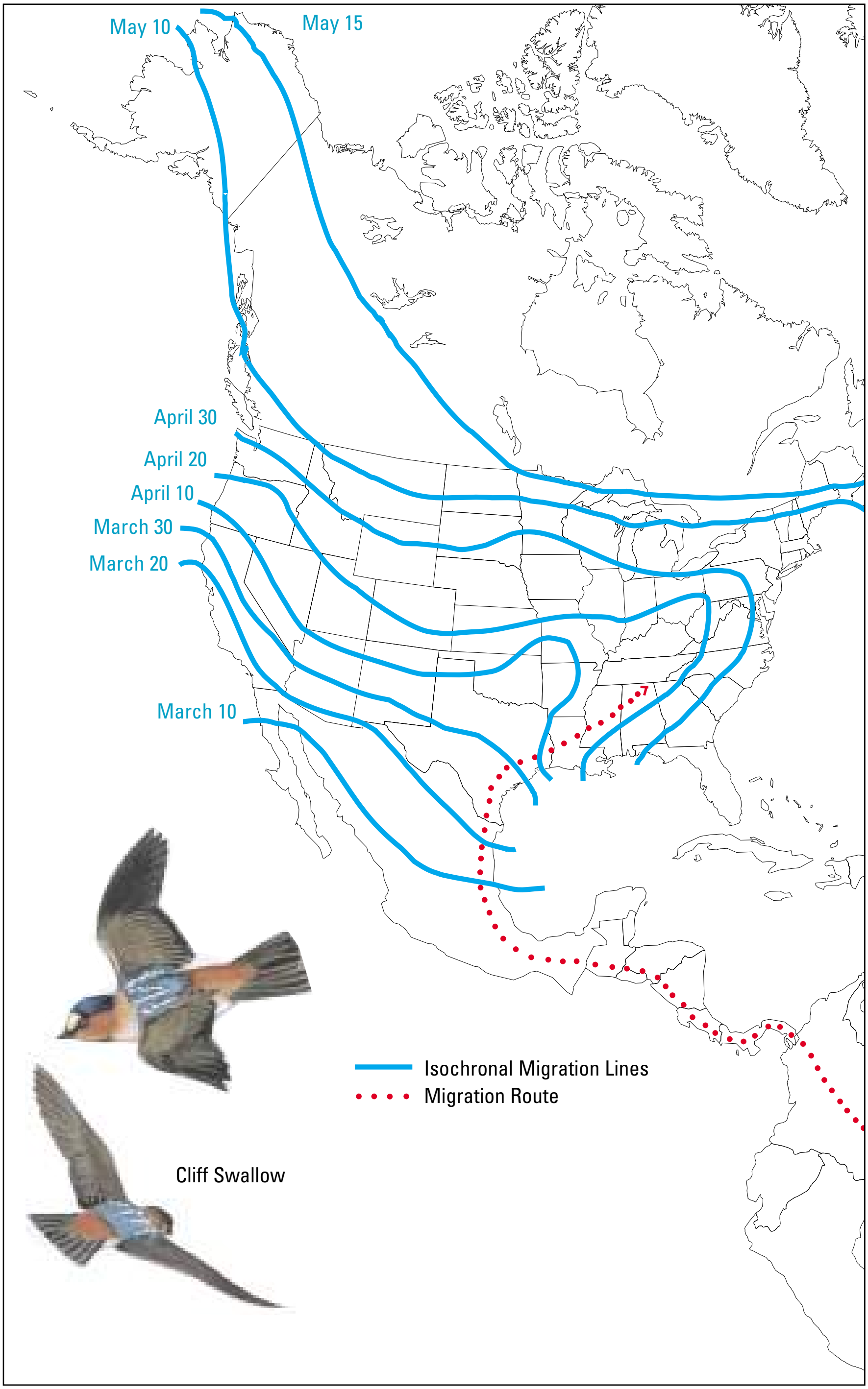

Figure 4. Migration of the Cliff Swallow. A day migrant that, instead of flying across the Caribbean Sea as does the Blackpoll Warbler (see Fig. 3), follows the coast of Central America, where food is readily obtained.

FLIGHT SPEED AND RATE OF MIGRATION

There is a widespread misconception concerning the speed at which birds can fly. One often hears stories of birds flying "a mile a minute." While undoubtedly some birds do attain this speed, such cases are exceptional; and it is safe to say that, even when pressed, few can develop an air speed of 60 miles per hour. Birds, except for the heavy-bodied, small-winged species such as auks, grebes, and other divers, generally have two different flight speeds. There is a normal rate for ordinary purposes, and an accelerated speed for escape or pursuit that may be double the normal rate.

Reliable data on the speed of birds are accumulating slowly. Accurate measurements are difficult to obtain unless the bird travels over a measured course and wind conditions at the level of flight are known. Several subtle factors, besides wind and pursuit, can influence the speed of a flying bird. For instance, species that have a courtship flight often reach their maximum speeds then. Small woodland birds often fly faster across an open area where they might be attacked by a bird of prey than under cover where there is less danger Birds in flocks generally fly faster than when flying alone.

In general, flight velocity of birds ranges from 20 to 50 miles per hour. For sustained flight, larger birds typically fly faster than smaller birds. A common flying speed of ducks and geese is between 40 and 50 miles per hour, but among the smaller birds it is much less. Herons, hawks, Horned Larks, ravens, and shrikes, timed with an automobile speedometer have been found to fly 22 to 28 miles per hour, whereas some of the flycatchers fly at only 10 to 17 miles per hour. Even such fast-flying birds as the Mourning Dove rarely exceed 35 miles per hour. A Peregrine Falcon will have difficulty catching a pigeon during a level chase at 60 miles per hour, but this predator can probably exceed 100 miles per hour during a stoop from a greater height onto its prey, although this velocity has never been accurately measured.

The rate of migration is quite different from that attained in forced flights for short distances. A sustained flight of 10 hours per day in still air would carry herons, hawks, crows, and smaller birds from 100 to 250 miles, while ducks and geese might travel as much as 400 to 500 miles in the same period. Measured as straight line distances, these journeys are impressive and indicate birds could travel from the northern United States or even from northern Canada to winter quarters in the West Indies, Central, or South America in a relatively short time, especially if they took advantage of tail winds. It is probable that individual birds do make flights this long and that Barn Swallows seen in May on Beata Island, off the southern coast of the Dominican Republic, have reached that point by a nonstop flight of 350 miles across the Caribbean Sea from the coast of Venezuela.

Radar has provided some of our best estimates of ground speeds for migrating flocks. Radar echoes identified as shorebirds migrating off the New England coast moved steadily about 45 miles per hour for several hours; songbird echoes typically traveled around 30 miles per hour. Some birds appear to reduce flight speed in proportion to the degree of assistance from a tailwind, thus conserving energy.

The intensity of migration depends not only upon extrinsic environmental conditions but also on intrinsic circumstances affecting the drive motivating the birds' behavior; birds travel faster when hurrying toward the breeding grounds. Radar investigations along the eastern coast of the United States and in England indicate spring migration is several miles per hour faster than in the fall. Also, directions of the migrants in the spring were less diverse than in the fall, suggesting less time lost in passage. Furthermore, fat stores in the spring are greater than in the same species during their fall migration. This would provide vernal migrants greater energy reserves for longer flights at that season. In fall, the flights are more leisurely, so that after a few hours of flying, birds often pause to feed and rest for one or several days, particularly if they find themselves in suitable surroundings. Some indication of this is found in the recoveries of banded birds, particularly waterfowl. If we consider only the shortest intervals between banding in the north and subsequent recovery in the south, it usually takes a month or more to cover a straight-line distance of a thousand miles. For example, an American Black Duck banded at Lake Seugog, Ontario, was killed 12 days later at Vicksburg, Mississippi. If the bird was taken shortly after its arrival, the record would indicate an average daily flight of 83 miles, a distance that could have been covered in about 2 hours' flying time. Among the thousands of banding records of ducks and geese, evidence of rapid migrations is decidedly scarce, for with few exceptions, all thousand-mile flights require 2 to 4 weeks or more. Among sportsmen, the Blue-winged Teal is well known as a fast-flying duck and quite a few of these banded on Canadian breeding grounds have covered 2,300 to 3,000 miles in a 30-day period. Nevertheless, the majority of those that have traveled to South America were not recovered in that region until two or three months after they were banded. Probably the fastest flight over a long distance for one of these little ducks was one made by a young male that traveled 3,800 miles from the delta of the Athabaska River, northern Alberta, Canada to Maracaibo, Venezuela in exactly one month. This flight was at an average speed of 125 miles per day. A very rapid migration speed was maintained by a Lesser Yellowlegs banded at North Eastham, Cape Cod, Massachusetts on 28 August 1935 and killed 6 days later, 1,900 miles away, at Lamentin, Martinique, French West Indies. This bird traveled an average daily distance of more than 316 miles.

It seems probable that most migratory journeys are performed at a slow rate of flight. Migrating birds passing lightships and lighthouses or crossing the face of the moon have been observed to fly without hurry or evidence of straining to attain high speed. The speed or rate of migration would therefore depend chiefly on the duration of flights and tail wind velocity.

The Canada Goose affords a typical example of regular but slow migration. Its advance northward is at the same rate as the advance of the season (Figure 5). In fact, the isotherm of 35°F (16°C) appears to be a governing factor in the speed at which the these geese move north; from an evolutionary viewpoint we might expect this. If the geese continually advanced ahead of the freezing line, they would find food and open water unavailable.

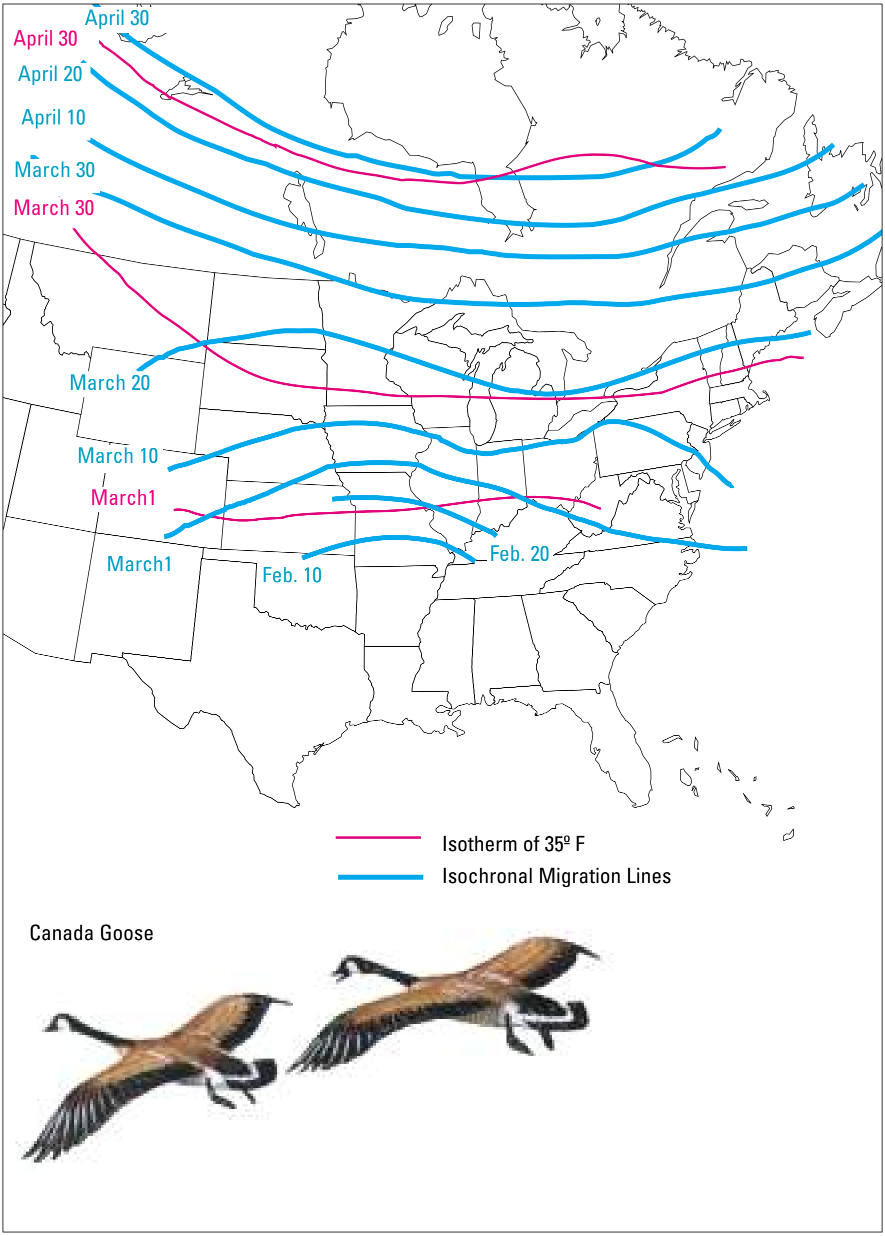

Figure 5. Migration of the Canada Goose. The northward movement keeps pace with the progress of spring, because the advance of the isotherm of 35°F agrees with that of the birds.

By migrating north just behind the advance of this isotherm, birds that breed in the far north will find food and open water available and have as long a breeding season as the climate will allow.

Few species perform such migrations that follow suitable conditions so closely. Many species wait in their winter homes until spring is well advanced, then move rapidly to their breeding grounds. Sometimes this advance is so rapid that late migrants actually catch up with species that may have been pressing slowly but steadily northward for a month or more. The following examples of well-known migrants illustrate this.

The Gray-cheeked Thrush, which winters in northern South America, does not start its northward journey until many other species are well on their way. It does not appear in the United States until the end of April: 25 April near the mouth of the Mississippi and 30 April in northern Florida (Figure 6). A month later, or by the last week in May, the bird is seen in northwestern Alaska. Therefore, the 4,000-mile trip from Louisiana was made at an average rate of about 130 miles per day.

Another example of rapid migration is furnished by the Yellow Warbler. This species winters in the tropics and reaches New Orleans about April 5, when the average temperature is 65°F (31°C). By traveling north much faster than the spring season progresses, this warbler reaches its breeding grounds in Manitoba the latter part of May, when the average temperature is only 47°F (22°C). They encounter progressively colder weather over their entire route and cross a strip of country in the 15 days from May 11 to May 25 that spring temperatures normally take 35 days to cross. This "catching up" with spring is typical in many species that winter south of the United States as well as in most northern species that winter in the Gulf States.

The Snow Goose presents a striking example of a late but very rapid spring migration. Most of these geese winter in the great coastal marshes of Louisiana, where every year over 400,000 spend the winter. Congregations of 50,000 or more may be seen grazing in pastures or flying overhead in flocks of various sizes. Their breeding grounds are chiefly on Baffin and Southampton Islands in the northern part of Hudson Bay where conditions of severe cold prevail except for a few weeks each year. Even though the season in their winter quarters is advancing rapidly, their nesting grounds are still covered with a heavy blanket of ice and snow. Thus, Snow Geese remain in the coastal marshes until the last of March or the first of April, when local birds are already busily engaged in reproduction. These data support the general hypothesis that a species' premigratory development in response to stimuli such as daylength and temperature has evolved so that the timing of its physiological preparation will lead to its arrival on the breeding range at the optimum conditions for reproduction. The flight northward is rapid, almost nonstop so far as the United States is concerned; although the birds are sometimes recorded in large numbers in the Mississippi Valley, along the Platte in Nebraska, and in eastern South Dakota and southeastern Manitoba. Normally, however, there are few records anywhere along the route of the great flocks that winter in Louisiana. When the birds arrive in the James Bay region, they apparently enjoy a prolonged period of rest because they are not seen in the vicinity of their breeding grounds until the first of June. During the first 2 weeks of that month, they pour onto the arctic tundra by the thousands, and each pair immediately sets about the business of rearing a brood.

The American Robin is a slow migrant, taking an average of 78 days to make the 3,000-mile trip from Iowa to Alaska. The same stretch of country

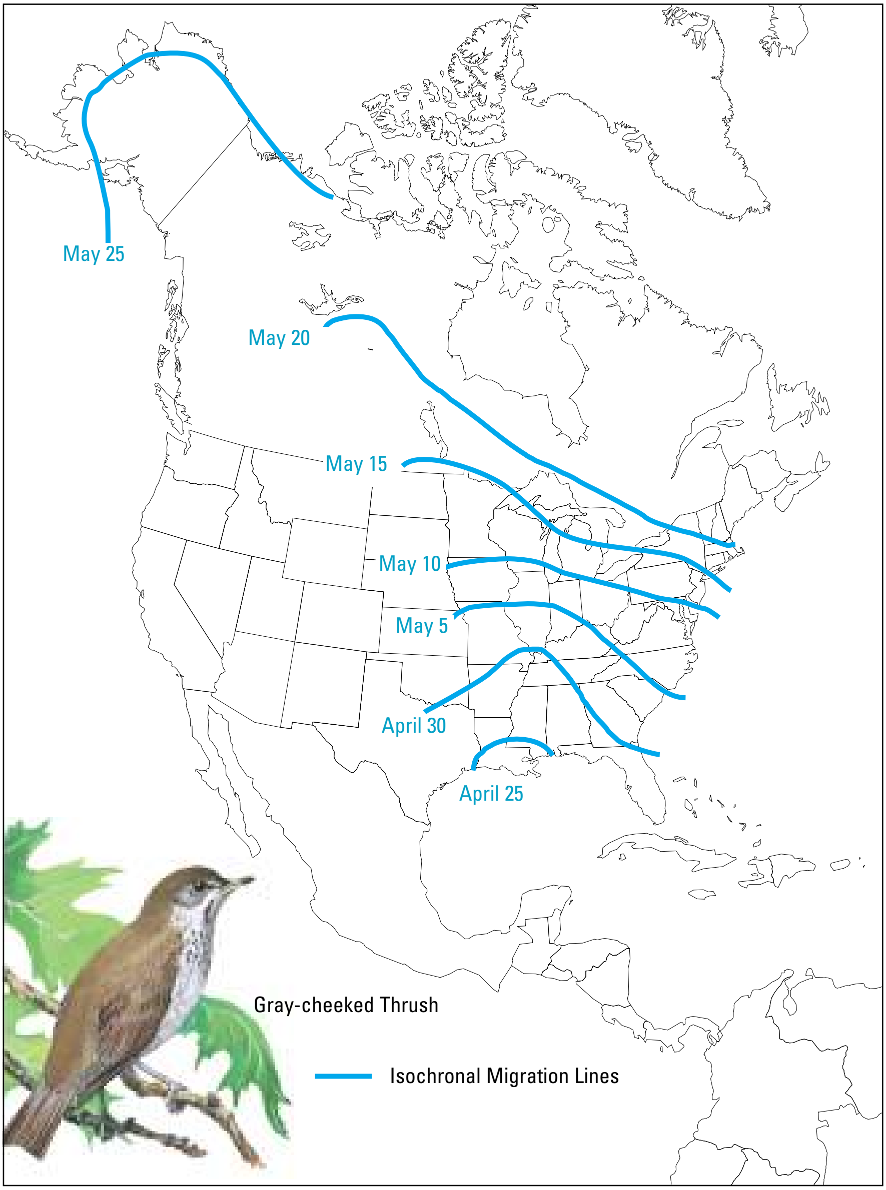

Figure 6. Isochronal migration lines of the Gray-cheeked Thrush, an example of rapid migration. The distance from Louisiana to Alaska is about 4,000 miles and is covered at an average speed of about 130 miles per day. The last part of the journey is covered at a speed several times what it is in the Mississippi Valley.

is crossed by advancing spring in 68 days. In this case, however, it does not necessarily mean that individual robins are slow. The northward movement of the species probably depends upon the continual advance of birds from the rear, so that the first individuals arriving in a suitable locality are the ones that nest in that area, while the northward movement of the species is continued by those still to come. There is great variation in the speed of migration at different latitudes between the Gulf of Mexico and the Arctic Ocean. The Blackpoll Warbler again furnishes an excellent example (Figure 3). This species winters in northwestern South America and starts to migrate north in April. When the birds reach the southern United States, some individuals fly northwest to the Mississippi Valley, north to Manitoba, northwest to the Mackenzie River, and then almost due west to western Alaska. A fairly uniform average distance of 30 to 35 miles per day is maintained from the Gulf to Minnesota, but a week later this species has reached the central part of the Mackenzie Valley, and by the following week it is observed in northwestern Alaska. During the latter part of the journey, therefore, many individuals must average more than 200 miles per day. Thirty days are spent traveling from Florida to southern Minnesota, a distance of about 1,000 miles, but scarcely half that time is used to cover the remaining 2,500 miles to Alaska. Increased speed across western Canada to Alaska is also shown by many other birds (Figures 2, 4, and 6). A study of all species traveling up the Mississippi Valley indicates an average speed of about 23 miles per day. From southern Minnesota to southern Manitoba, 16 species maintain an average speed of about 40 miles per day. From that point to Lake Athabaska, 12 species travel at an average speed of 72 miles per day, while 5 others travel to Great Slave Lake at 116 miles per day, and another 5 species cover 150 miles per day to reach Alaska. This change corresponds to variation in the isothermal lines, which turn northwestward west of the Great Lakes.

As has been previously indicated, the advance of spring in the northern interior is much more rapid than in the Mississippi Valley and on the Gulf coast. In the North spring comes with a rush, and during the height of migration season in Saskatchewan, the temperature in the southern part of the Mackenzie Valley just about equals that in the Lake Superior area, 700 miles farther south. Such conditions, coupled with the diagonal course of the birds across this region of fast-moving spring, exert a great influence on migration and are probably factors in the acceleration of travel speed.

MIGRATORY FLIGHT ALTITUDE

While factors regulating the heights at which birds migrate are not clear, there are many obvious reasons why flying at higher altitudes may be advantageous. High-altitude flight may be used to locate familiar landmarks, fly over fog or clouds, surmount physical barriers, gain advantage of a following wind, or maintain a better thermoregulatory balance.

In general, estimates of bird heights based on direct observation are quite unreliable except under special conditions. A Eurasian Sparrowhawk could be distinguished at 800 feet but disappeared from sight at 2,800 feet. A Rook (a European member of the crow family) could be recognized at 1,000 feet but disappeared from sight at 3,300 feet. An interesting experiment with an inflated model of a vulture painted black with a wing span of 7 feet 10 inches illustrated similar limitations. When released from an airplane at 4,700 feet, it was barely visible and invisible without binoculars at 5,800 feet. At 7,000 feet it was not picked up even when 12 power binoculars were used. Radar studies have demonstrated more accurately than human vision that 95 percent of the migratory movements occur at less than 10,000 feet, the bulk of the movements occurring under 3,000 feet.

Yet birds do fly at higher altitudes. Bird flight at 20,000 feet, where less than half the oxygen is present than at sea level, is impressive if only because the work is achieved by living muscle tissue. A Himalayan mountain climber at 16,000 feet was rather amazed when a flock of geese flew northward about two miles over his head honking as they went. At 20,000 feet a man has a hard time talking while running, but those geese were probably flying at 27,000 feet and even calling while they traveled at this tremendous height. Numerous other observations have come from the Himalayas. Observers at 14,000 feet recorded storks and cranes flying so high that they could be seen only through field glasses. In the same area large vultures were seen soaring at 25,000 feet and an eagle carcass was found at 26,000 feet. The expedition to Mt. Everest in 1952 found skeletons of a Northern Pintail and a Black-tailed Godwit at 16,400 feet on Khumbu Glacier. Bar-headed Geese have been observed flying over the highest peaks (29,000+ feet) even though a 10,000-foot pass was nearby. Probably at least 30 species regularly cross these high passes. Other accurate records on altitude of migratory flights are scanty, although altimeter observations from airplanes and radar are becoming more frequent in the literature. For example, a Mallard was struck by a commercial airliner at 21,000 feet over the Nevada desert. Radar observations have revealed that birds on long-distance flights fly at higher altitudes than short-distance migrants. It has been hypothesized that advantageous tail winds of greater velocity are found higher up and that the cooler air minimizes the demand for evaporative water loss to regulate body temperature under the exertion of flight. Radar studies also have shown that nocturnal migrants fly at different altitudes at different times during the night. Birds generally take off shortly after sundown and rapidly gain maximum altitude. This peak is maintained until around midnight, then the travelers gradually descend until daylight. Thus, there is considerable variation, but for most small birds the favored altitude appears to be between 500 and 1,000 feet. Some nocturnal migrants (probably shorebirds) fly over the ocean at 15,000 or even 20,000 feet. Nocturnal migrants also fly slightly higher than diurnal migrants. Observations made from lighthouses and other vantage points indicate that certain migrants commonly travel at altitudes of a very few feet to a few hundred feet above sea or land. Sandpipers, Red-necked Phalaropes, and various sea ducks have been seen flying so low they were visible only as they topped a wave. Observers stationed at lighthouses and lightships off the English coast have similarly recorded the passage of landbirds flying just above the surface of the water and rarely rising above 200 feet over the waves.

SEGREGATION DURING MIGRATION

As Individuals or Groups of Species

During the height of northward movement in spring, the woods and thickets may suddenly be filled in the morning with several species of wood warblers, thrushes, sparrows, flycatchers, and other birds. It is natural to conclude they traveled together and arrived simultaneously. Probably they did, but such combined migration is by no means the rule for all species.

As a group, the wood warblers probably travel more in mixed companies than do any other single family of North American birds. In spring and fall, the flocks are likely to be made up of the adults and young of several species. Sometimes swallows, sparrows, blackbirds, and some of the shorebirds also migrate in mixed flocks. In the fall, great flocks of blackbirds frequently sweep south across the Great Plains with Common Grackles, Red-winged Blackbirds, Yellow-headed Blackbirds, and Brewer's Blackbirds included in the same flock.

On the other hand, many species keep strictly to themselves. Common Nighthawks fly in separate companies, as do American Crows, Cedar Waxwings, Red Crossbills, Bobolinks, and Eastern Kingbirds. And it would be difficult for any other kind of bird to keep company with the rapid movements of the Chimney Swift. Besides flight speed, feeding habits or roosting preferences can be so species-specific as to make traveling with other species incompatible. Occasionally, a flock of ducks will be observed to contain several species, but generally when they are actually migrating, individuals of each species separate and travel with others of their own kind.

Even if different species do not migrate together, we often find many species passing through an area at the same time. If the different kinds of birds observed in a specific area are counted every day throughout the entire migration season, this count often rises and falls much like the bell-shaped curve exhibited when the number of individuals of a given species are counted through the same time period. Figure 7 shows two peaks in the number of species passing through the desert at the north end of the Gulf of Eilat (Akaba) in the Red Sea. These two peaks coincide with peaks in the numbers of individuals (mostly perching birds) traveling through the area. Therefore, in the latter part of March and again in April, there are not only more birds in the area, but also more species.

Closely related species or species that eat the same food are not often found migrating through the same area at the same time. In North America, peaks in the migration of the five species of spotted thrushes generally do not coincide. Dates of departure in these species have evolved so all the individuals of these closely related birds do not converge on one area at the same time and subsequently exhaust the food supply. By selection of staggered peak migration dates, the processes involved in evolution have distributed the members of this family more or less evenly throughout the entire season. Likewise, in the eastern Mediterranean area, we find a similar situation during spring migration for three closely related buntings; Cretzschmar's Bunting comes through first, followed a few weeks later by the Ortolan Bunting and, at the end of the migration period, the Black-headed Bunting appears (Figure 8). Many groups of migrating species like shorebirds, blackbirds, waxwings, and buntings maintain a close flock formation. Other species like Turkey Vultures, hawks, swifts, Blue Jays, swallows, and warblers maintain a loose flock. And still others, like shrikes, Belted Kingfishers, grebes, and Winter Wrens, ordinarily travel alone.

Just as flocking among resident birds provides group protection against predators and facilitates food finding, flocking of migrants probably serves the same purposes. The V-shaped flocks associated with Canada Geese and Double-crested Cormorants have a definite energy conserving function by allowing members of the flock to gain an aerodynamic advantage from the wing-tip vortices of the bird ahead. It has also been observed from

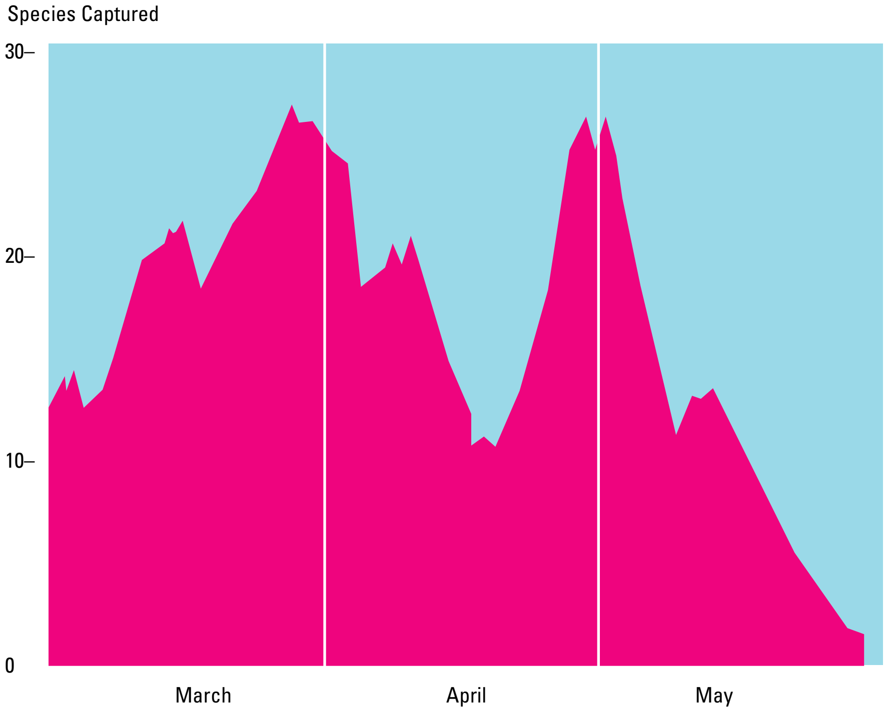

Figure 7. Average number of species captured daily in mist nets during spring migration at Eilat, Israel, in 1968. The number of species passing through an area on migration will rise and fall similar to the number of birds counted in the area. In this case two major movements came through about 1 month apart.

radar studies that day migrants fly in tighter formations than flocks migrating by night. This again may reflect a strategy to deter the effect of aerial predators.

By Age

The adults of most birds abandon the young when they are grown. This gives the parents an opportunity to renew their plumage and gain fat stores before starting for winter quarters. The young may move south together ahead of their parents, as has been documented in a number of species including Mourning Doves and the Common Swift and White

Cretzschmar's Bunting

Ortolan Bunting

Black-headed Bunting

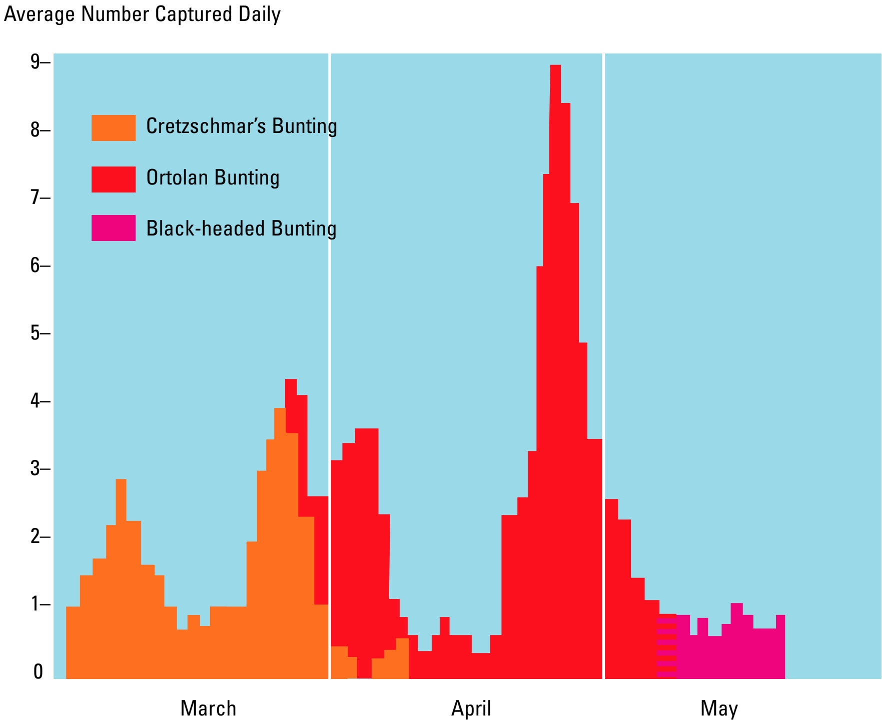

Figure 8. Average number of three species of buntings captured daily in mist nets during spring migration at Eilat, Israel, in 1968. Closely related species that migrate through the same area often appear at different times. Thus species that may eat the same foods do not compete with each other.

Storks in Europe. In Sharp-shinned Hawks passing through Wisconsin, the immatures are much in evidence during mid-September while the adults come through a month later. Far to the south in Antarctica, young Adelie Penguins depart for coastal wintering grounds much earlier than adults.

In a few species, adults depart south before the young. Adult American Golden-Plovers, Hudsonian Godwits, and probably most of the arctic breeding shorebirds leave the young as soon as they are capable of caring for themselves and set out for South America ahead of the juveniles. Likewise, data for the Least Flycatcher indicate adults migrate before the young, but this segregation does not occur in the closely related Hammond's Flycatcher. In Europe, adult Red-backed Shrikes are known to migrate ahead of their young. In contrast, geese, swans, and cranes remain in family groups throughout migration. The parent birds undergo a wing molt that renders them flightless during the period of growth of their young so that both the adults and immatures acquire their flight capabilities at the same time and are able to start south together. Large flocks of Canada Geese, for example, are composed of many family groups. When these flocks separate into small V-shaped units it is probably correct to assume an older goose or gander is leading the family. After female ducks start to incubate their eggs, the males of most species of ducks flock by themselves and remain together until fall. When segregation of the sexes such as this occurs, the young birds often accompany their mothers south.

By Sex

Males and females may migrate either simultaneously or separately. Although there are exceptions, generally passerine males arrive before females. Thus, in spring great flocks of male Red-winged Blackbirds reach a locality several weeks before any females. The first American Robins are usually found to be males, as are the first Song Sparrows, Rose-breasted Grosbeaks, Dickcissels, and Scarlet Tanagers. In Europe, the three buntings mentioned previously are also segregated as to sex during migration. Figure 8 shows two prominent peaks for both the Cretzschmar's and Ortolan buntings; during passage the first peak was primarily males while the second peak consisted mostly of females. This early arrival of males on the breeding grounds is associated with the establishment of territories in which each male defends a definite area from trespass by other males of his own kind, while announcing his presence to rival males and later arriving females by song or other displays. The female then selects the site where she wishes to nest. In the fall, Common and King eiders are sexually segregated during migration. During July, flocks crossing Point Barrow are composed almost entirely of males, while after the middle of August the flocks are almost all females. In the Chicago area, male Hermit Thrushes, Swainson's Thrushes, Gray-cheeked Thrushes, and Veerys arrive before any females and predominate during the first week of passage.

In a few species the males and females arrive at the breeding grounds together and proceed at once to nest. In fact, among shorebirds, ducks, geese, and the Osprey courtship and mating often takes place while the birds are in the South or on their way north, so that when they arrive on the northern nesting grounds, they are paired and ready to proceed at once with raising their families. Mallards and American Black Ducks may be observed in pairs as early as December, the female leading and the male following when they take flight.

In the Pacific-slope Flycatcher, the sexes appear to migrate in synchrony during the spring in contrast to migration of the closely related Hammond's Flycatcher in which the adult males usually precede the females. Both sexes of the Common Blackcap of Europe appear to migrate together at least across the eastern end of the Mediterranean during the spring (Figure 9).

Common Blackcap

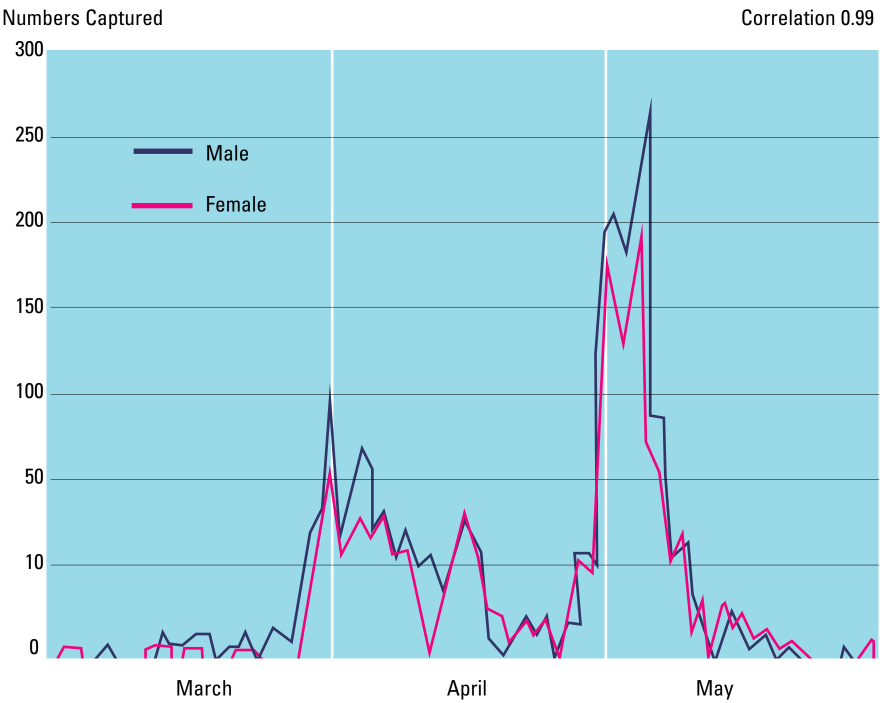

Figure 9. Numbers of male and female Common Blackcaps captured daily in mist nets during spring migration at Eilat, Israel, in 1968. At this point in their migration the sexes are passing through the area at the same time. In other species (e.g., the buntings in Fig. 8), the males often precede the females.

GEOGRAPHIC PATTERNS OF MIGRATION

Populations Within Species

Both length and duration of migratory journeys vary greatly between families, species, or populations within a species. Northern Bobwhite and other North American quails, Northern Cardinals, Canyon, Cactus and Carolina wrens, Wrentits, some of the titmouses and most woodpeckers are largely nonmigratory. These species may live out their entire existence without going more than 10 miles from the nest where they were hatched.

Song Sparrows, Eastern and Western meadowlarks, and Blue Jays make such short migrations that the movement is difficult to detect because individuals, possibly not the same ones, may be found in one area throughout the year while other individuals that move south may be replaced by individuals from the north. Information on movements of these partial migrant species can be gained by observing birds that are banded or color-marked. The American Robin, for example, occurs in the southern United States throughout the year, but only during the summer in Canada and Alaska. Its movements are readily ascertained from museum specimens. The breeding robin of the southeastern states is the southern race. In autumn most of the more northern nesters, such as those from Maryland and Virginia, move into the southern part of the breeding range or slightly farther south. At about the same time the northern American Robin moves south and winters throughout the breeding and wintering range of its smaller and paler southern relative. Thus, there is complete overlap of wintering ranges of northern and southern American Robin populations, although some individuals of the northern race winter in areas vacated earlier by the southern race.

Among many migratory species there is considerable variation among individuals and populations with respect to distances moved. Certain populations may be quite sedentary while others are strongly migratory, and certain individuals in the same population can be more migratory than others. For example, Red-winged Blackbirds nesting on the Gulf Coast are practically sedentary, but in winter they are joined by other subspecies that nest as far north as the Mackenzie Valley. In certain populations of Song Sparrows, males remain all year on their northern breeding grounds while the females and young migrate south. In Dark-eyed Juncos, adult females migrate the farthest south, while young males winter the farthest north. Adult male and young female juncos winter at intermediate distances.

Several species containing more than one distinguishable population exhibit "leap-frog" migration patterns. The eastern population of the Fox Sparrow breeds from northeastern Manitoba to Labrador, but during the winter it is found concentrated in the southeastern part of the United

States. On the west coast of the continent, however, a study of museum specimens indicated six subspecies of this bird breeding in rather sharply delimited ranges extending from Puget Sound and Vancouver Island to Unimak Island at the end of the Alaskan Peninsula. One of these subspecies breeds from the Puget Sound-Vancouver Island area northward along the coast of British Columbia. It hardly migrates at all, while the other races, nesting on the coast of Alaska, are found in winter far to the south in Oregon and California. Although much overlap exists, the races breeding farthest north generally tend to winter farthest south. This illustrates a tendency for migratory populations to pass over those subspecies so favorably located as to be almost sedentary. If the northern birds settled for the winter along with the sedentary population, winter requirements may not be as sufficient as in the unoccupied areas farther south (Figure 10). Among the differentially sized subspecies of Canada Geese, the populations of lowest body mass breed the farthest north but winter the farthest south, while the heaviest subspecies is a relatively permanent resident in the northern United States. This pattern is clearly related to the increased survival under cold stress afforded by large body size.

The Palm Warbler breeds from Nova Scotia and Maine west and northwest to the southern Mackenzie River valley. The species has been separated into two subspecies, those breeding in the interior of Canada and those breeding in northeastern United States and Canada. The northwestern subspecies makes a 3,000-mile journey from Great Slave Lake to the West Indies and Central America, moving through the Gulf States early in October. After the bulk of these birds have passed, the eastern subspecies, whose migratory journey is about half as long, drifts slowly into the Gulf Coast region and remains for the winter.

Short Distance Migration

Some species have extensive summer ranges (e.g., the Pine Warbler, Rock Wren, Field Sparrow, Loggerhead Shrike, and Black-headed Grosbeak) and concentrate during the winter season in the southern part of the breeding range or occupy additional territory only a short distance farther south. The entire species may thus be confined within a restricted area during winter, but with the return of warmer weather, the species spreads out to reoccupy the much larger summer range.

Many species, including American Tree Sparrows, Snow Buntings, and Lapland Longspurs, nest in the far north and winter in the eastern United States, while others, including Vesper and Chipping sparrows, Common Grackle, Red-winged Blackbird, Eastern Bluebird, American Woodcock, and several species of ducks, nest much farther south in the United States and Canada and move south a relatively short distance for the winter to areas along the Gulf of Mexico. In a few of the more hardy species, individuals may linger in protected places well within regions of severe cold. The Common Snipe, for example, is frequently found during subzero weather in parts of the Rocky Mountain region where warm springs assure a food supply.

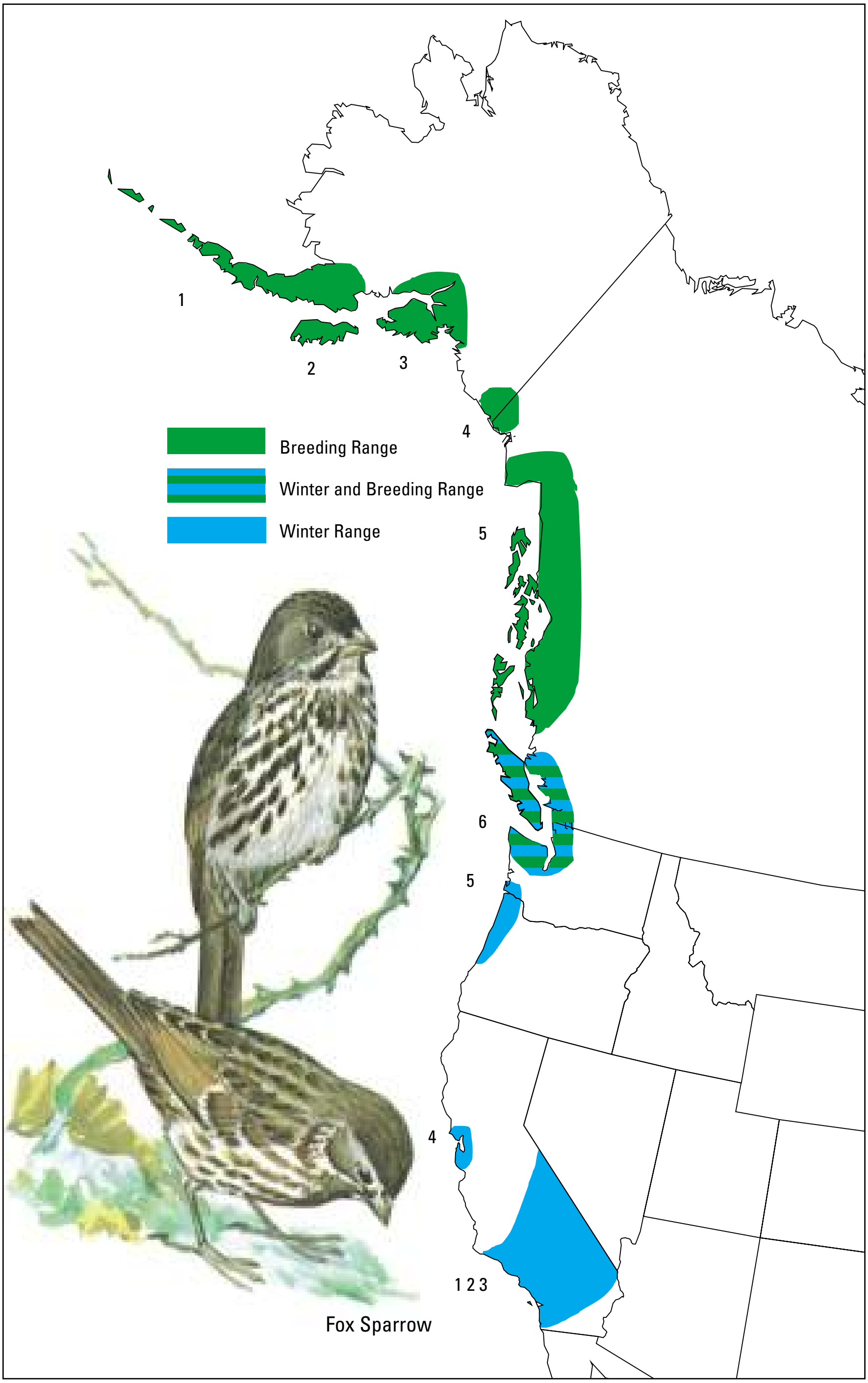

Figure 10. Migration of Pacific coast forms of the Fox Sparrows. The breeding ranges of the different races are encircled by solid lines, while the winter ranges are dotted. The numbers indicate the areas used by the different subspecies as follows: 1. Shumagin Fox Sparrow; 2. Kodiak Fox Sparrow; 3. Valdez Fox Sparrow; 4. Yakutat Fox Sparrow; 5. Townsend Fox Sparrow; 6. Sooty Fox Sparrow (after Swarth 1920).

Long Distance Migration

More than 300 breeding species leave the United States and Canada and spend the winter in the West Indies, Central America, or South America. For example, the Cape May Warbler breeds from northern New England, northern Michigan, and northern Minnesota, north to New Brunswick, Nova Scotia, and nearly to Great Slave Lake. In winter it is concentrated chiefly in the West Indies on the island of Hispaniola.

Some of the common summer residents of North America migrate even farther, pushing across the Equator and finally coming to rest for the winter on the Argentine pampas or in Patagonia. Common Nighthawks, Barn Swallows, Cliff Swallows, and thrushes may occupy the same general winter quarters in Brazil, but other nighthawks and Barn Swallows go farther south. Of all North American landbirds these species probably travel the farthest; they are found north in summer to the Yukon Territory and Alaska, and south in winter to Argentina, 7,000 miles away. Such seasonal flights are exceeded in length, however, by the remarkable journeys of several species of shorebirds including White-rumped and Baird's sandpipers, Greater Yellowlegs, Ruddy Turnstones, Red Knots, and Sanderlings. In this group, 19 species breed north of the Arctic Circle and winter in South America; six of these go as far south as Patagonia, a distance of over 8,000 miles.

The Arctic Tern is the champion "globe trotter" and long-distance flier. Its name "Arctic" is well earned, as its breeding range is circumpolar and it nests as far north as the land extends in North America. The first nest found in this region was only 7-1/2 degrees (518 miles) from the North Pole and contained a downy chick surrounded by a wall of newly fallen snow scooped out by the parent. In North America, the Arctic Tern breeds south in the interior to Great Slave Lake, and on the Atlantic coast south to Massachusetts. After the young are grown, Arctic Terns disappear from their North American breeding grounds and turn up a few months later in the Antarctic region, 11,000 miles away. For a long time the route followed by these hardy flyers was a mystery. Although a few scattered individuals had been noted south as far as Long Island in the United States, the species is otherwise practically unknown along the Atlantic coasts of North America and northern South America. It is, however, a migrant on the west coast of Europe and Africa. As a result of band recoveries, its migratory pattern was disclosed (Figure 11). Few other animals in the world enjoy as many hours of daylight as the Arctic Tern. For these birds, the sun shines most of the day during the nesting season in the northern part of the range, and during their winter sojourn to the south, daylight is almost continuous as well.

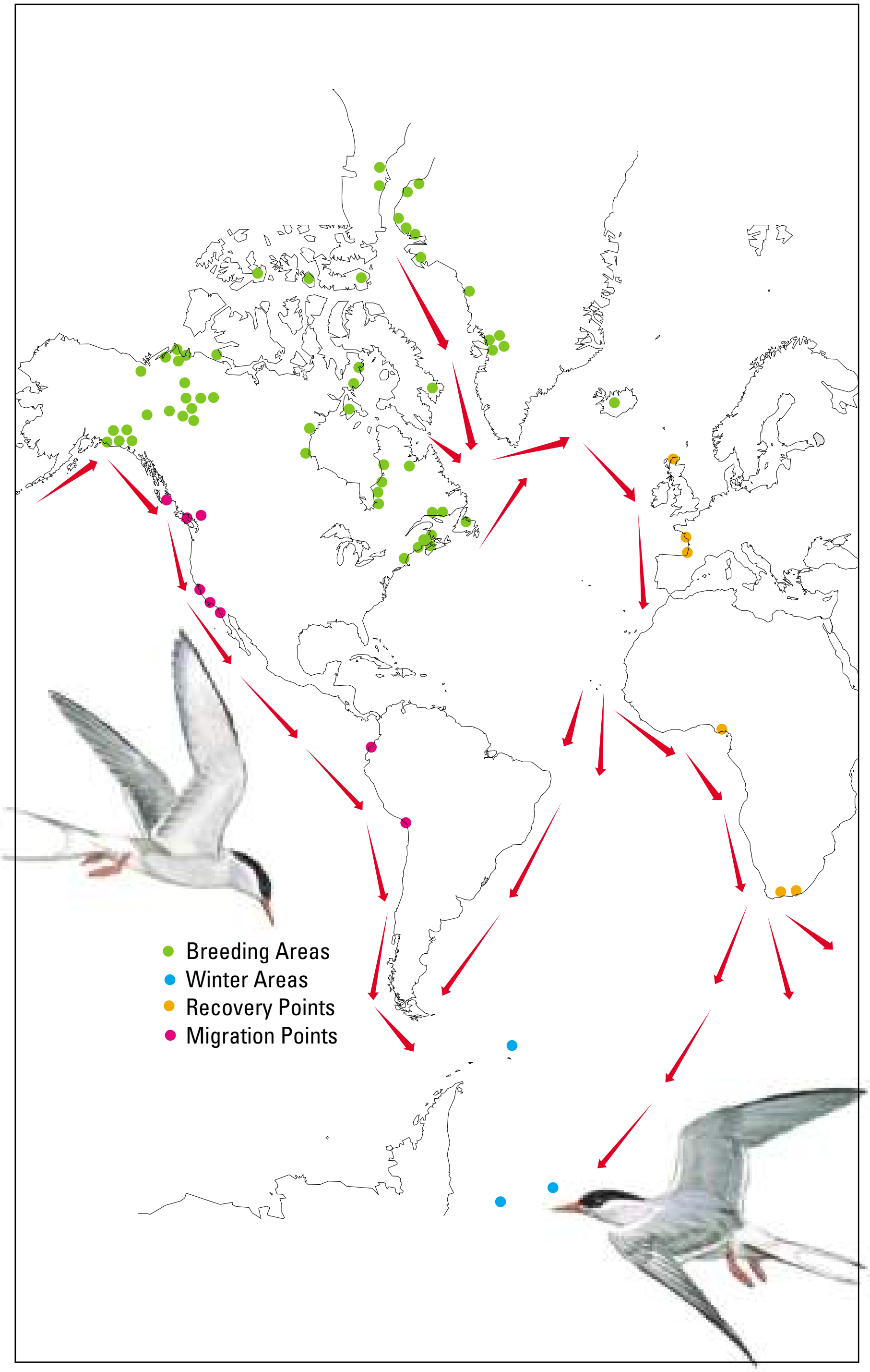

Figure 11. Distribution and migration of Arctic Terns. The route indicated for this bird is unique, because no other species is known to breed abundantly in North America and to cross the Atlantic Ocean to and from the Old World. The extreme summer and winter homes are 11,000 miles apart.

ORIENTATION AND NAVIGATION

Factors in a bird's environment select for the expression of migratory behavior, leading to the evolution of a migratory pattern or, on the other hand, to the loss of migratory abilities. Factors in the environment function to provide direct, proximal stimulation for the physiological preparation for migration. Factors in the environment also provide information that allows birds to navigate during migratory passage. Navigation requires knowing three things: current location, destination, and the direction to travel to get from the current location to the destination. Humans eventually learned to use both the sun and the stars to obtain this information. Recently we invented more precise satellite-based technologies that have made these celestial cues for determining geographic positions superfluous and developed electronic aids to navigation that allow orientation without reference to the natural environment. Birds have successfully navigated for eons using environmental information.

Birds are not alone in their ability to navigate long distances. Fish, mammals, and even insects make migratory journeys. But the clarion honking of geese moving in huge skeins across the vault of the heavens, the twittering of migrants filtering down out of the night sky, the flocks of newly arrived birds filling woodlands, fields, and mudflats makes us most aware of the seasonal movements of birds and fills us with awe and wonder as to how such a magnificent event can be accomplished season after season, year after year, with such unerring precision.

Of the three kinds of information necessary for navigation, we know something about the environmental cues that birds use to orient their migratory flight in the proper direction. On the other hand, there also is well-supported experimental evidence that birds use neither the positions of the sun or the stars to know where they are or where they are to go. It has been shown, however, that birds must learn both the location of the wintering area as well as the location of the breeding area in order to navigate properly, but we have no idea what information they are learning. Nor do we know what cues birds use to know the location of their migratory destination when they are in their wintering locale, often thousands of miles away. The recapture of banded birds at the same places along the route of the migratory journey in subsequent years suggests that some species also learn the location of traditional stop-over sites, but how they do that remains a mystery.

Vector Navigation

European Starlings pass through Holland on their migration from Sweden, Finland, and northwestern Russia to their wintering grounds on the channel coast of France and the southern British Isles. Perdeck transported thousands of starlings from The Hague to Switzerland, releasing these banded birds in a geographic location in which the population had never had any previous experience. The subsequent recapture of many of these banded birds demonstrated that the adults, which had previously made the migratory flight, knew they had been displaced and returned to their normal wintering range by flying a direction approximately ninety degrees to their usual southwesterly course. The juveniles, which had never made the trip before, in contrast, continued to fly southwest and were recaptured on the Iberian peninsula. These first-year birds "knew" what direction to fly, but did not recognize they had been displaced, thus ending up in an atypical wintering range. In subsequent years these now adult birds returned to again winter in Spain and Portugal. Coupled with another displacement of starlings to the Barcelona coast in Spain, Perdeck concluded that the proper direction of the migratory flight was innate, that is, inherited in their DNA, since the naive juveniles could fly that direction, and that the birds were also genetically programmed to fly a set distance. This is the same vector or dead-reckoning navigation program Lindberg used to fly from New York to Paris by maintaining a given compass direction (or directions) for a predetermined time (i.e., distance). But this study demonstrated that this navigation system is modified by experience, since adults knew they were not in Holland any longer and knew that in order to get to their normal wintering grounds they needed to fly a direction that they had never flown before! These results are truly amazing. And we don't know how they did it.

Displacement studies in the Western Hemisphere using several species of buntings also demonstrated that birds recognized they had been moved and could fly appropriate, yet unique, routes to return to their normal range. Yet adult Hooded Crows transported latitudinally by over 600 km from wintering grounds in the eastern Baltic to northwestern Germany failed to recognize this displacement. In the spring they oriented properly but migrated to Sweden, west of their normal breeding range. This species used vector navigation, but did not know the location of its traditional destination. Since it is generally accepted that migratory behavior evolved independently again and again in different bird populations, a single explanation to fit all cases perhaps should not be expected.

Orientation Cues

Most of the effort applied to understanding how birds make a migratory flight has been directed toward environmental cues that birds use to maintain a particular flight direction. These cues are landmarks on the Earth's surface, the magnetic lines of flux that longitudinally encircle the Earth, both the sun and the stars in the celestial sphere arching over the Earth, and perhaps prevailing wind direction and odors.

Landmarks are useful as a primary navigation reference only if the bird has been there before. For cranes, swans, and geese that migrate in family groups, young of the year could learn the geographic map for their migratory journey from their parents. But most birds do not migrate in family flocks, and on their initial flight south to the wintering range or back north in the spring must use other cues. Yet birds are aware of the landscape over which they are crossing and appear to use landmarks for orientation purposes. Radar images of migrating birds subject to a strong crosswind were seen to drift off course, except for flocks migrating parallel to a major river. These birds used the river as a reference to shift their orientation and correct for drift in order to maintain the proper ground track. That major geographic features like Point Pelee jutting into Lake Erie or Cape May at the tip of New Jersey are meccas for bird-watchers only reflects the fact that migrating birds recognize these peninsulas during their migration. Migrating hawks seeking updrafts along the north shore of Lake Superior or the ridges of the Appalachians must pay attention to the terrain below them in order to take advantage of the energetic savings afforded by these topographic structures.

Since humans learned to use celestial cues, it was only natural that studies were undertaken to demonstrate that birds could use them as well. Soon after the end of the Second World War, Gustav Kramer showed that migratory European Starlings oriented to the azimuth of the sun when he used mirrors to shift the sun's image by ninety degrees in the laboratory and obtained a corresponding shift in the birds' orientation. Furthermore, since the birds would maintain a constant direction even though the sun traversed from east to west during the day, the compensation for this movement demonstrated that the birds were keeping time. They knew what orientation to the sun was appropriate at 9 a.m. They knew what different angle was appropriate at noon, and again at 4 p.m. It has been recently shown that melatonin secretions from the light-sensitive pineal gland on the top of the bird's brain are involved in this response. Not only starlings but homing pigeons, penguins, waterfowl, and many species of perching birds have been shown to use solar orientation. Even nocturnal migrants take directional information from the sun. European Robins and Savannah Sparrows that were prevented from seeing the setting sun did not orient under the stars as well as birds that were allowed to see the sun set. Birds can detect polarized light from sunlight's penetration through the atmosphere, and it has been hypothesized that the pattern of polarized light in the evening sky is the primary cue that provides a reference for their orientation.

Using the artificial night sky provided by planetariums demonstrated that nocturnal migrants respond to star patterns. Quite analogous to Kramer's work on solar orientation, Franz Sauer demonstrated that if the planetarium sky is shifted, the birds make a corresponding shift in their orientation azimuth. Steve Emlen was able to show that the orientation was not dependent upon a single star, like Polaris, but to the general sky pattern. As he would turn off more and more stars so that they were no longer being projected in the planetarium, the bird's orientation became poorer and poorer. While the proper direction for orientation at a given time is probably innate, Emlen was able to show that knowing the location of "north" must be learned. When young birds were raised under a planetarium sky in which Betelgeuse, a star in Orion of the southern sky, was projected to the celestial north pole, the birds oriented as if Betelgeuse was “north” when they were later placed under the normally orientated night sky, even though in reality it was south!

Radar studies have shown that birds do migrate above cloud decks where landmarks are not visible, under overcast skies where celestial cues are not visible, and even within cloud layers where neither set of cues is available. The nomadic horsemen of the steppes of Asia used the response of lodestones to the Earth’s magnetic field to find their way, and the hypothesis that migrating birds might do the same was suggested as early as the middle of the nineteenth century. Yet it was not until the mid-twentieth century that Merkel and Wiltschko demonstrated in a laboratory environment devoid of any other cues that European Robins would change their orientation in response to shifts in an artificial magnetic field that was as weak as the Earth’s natural field. Although iron-containing magnetite crystals are associated with the nervous system in homing pigeons, Northern Bobwhite, and several species of perching birds, it is unknown whether they are associated with the sensory receptor for the geomagnetic cue. An alternate hypothesis for the sensory receptor suggests that response of visual pigments in the eye to electromagnetic energy is the basis for geomagnetic orientation. It has been shown, however, that previous exposure to celestial orientation cues enhances the ability of a bird to respond more appropriately when only geomagnetic cues are available.

Radar observations indicate that birds will decrease their air speed when their ground speed is augmented by a strong tail wind. We also know that birds can sense wind direction as gusts ruffling the feathers stimulate sensory receptors located in the skin around the base of the feather. Since there are characteristic patterns of wind circulation around high and low pressure centers at the altitude most birds migrate, it has been hypothesized that birds could use these prevailing wind directions as an orientation cue. However, there presently is no experimental support for this hypothesis.

The sense of smell in birds was considered for a long time to be poorly developed, but more recent evidence suggests that some species can discriminate odors quite well. If the olfactory nerves of homing pigeons are cut, the birds do not return to their home loft as well as birds whose olfactory nerves were left intact. A similar experiment has demonstrated that European Starlings with severed olfactory nerves returned less often than unaffected control birds even at distances as great as 240 km from their home roosts. And even more interesting, when these starlings returned to the nesting area the following spring, the starlings with nonfunctioning olfactory nerves returned at a significantly lower frequency than the other starlings.

Considering the array of demonstrated and suggested cues that birds might use in their orientation, it is clear that they rely upon a suite of cues rather than a single cue. For a migrating bird this redundancy is critical, since not all sources of orientation information are equally available at a given time, nor are all sources of information equally useful in a given situation.

INFLUENCE OF WEATHER

Weather, especially temperature, affects that rate of premigratory preparation. A warmer, earlier spring accelerates the process, while a cooler, later spring inhibits the process. For example, the maintenance of body temperature under cold stress competes for energy that might be stored as fat in preparation for the migratory journey if temperatures were a little more salubrious. Additionally, there might be a more direct response from temperature receptors in the skin that direct impulses to the areas of the brain that regulate hormonal factors affecting the development of the migratory state. Thus in warm, early springs a species arrives earlier than average, while in cool, late springs they tend to arrive later.

During both spring and fall migrations, radar studies have demonstrated that weather has a defining role in determining when a bird will actually begin a migratory flight. The primary stimulus for departure is a following wind; in the spring this is a wind from the south, in the fall it is a wind from the north. Clear skies, presumably providing for celestial orientation cues, are of secondary importance, since major flights will occur under an overcast if adequate tail winds are blowing.

In the North Temperate Zone, migrations are concurrent with periods of rapid seasonal change. In the summer, warm, moist air masses dominate, but as fall approaches colder, drier air pushes southward to eventually bring the grip of winter to the land. The battle for domination of air masses is then reversed in the spring as the longer daylengths increase the heat load in the atmosphere, again giving the advantage to the northward expansion of warmer air. It is along this frontal boundary between these air masses that low pressure centers develop and move eastward, steered by the high velocity jet stream aloft. Winds flow in toward these low pressure centers in a counter-clockwise circulation, fed by air spiralling outward in a clockwise direction from intervening high pressure centers within the air masses. Thus, in the southeastern quadrant of a low pressure center, warm moist winds drive a warm front northward into the colder air, the warmer air being pushed gradually above the colder air forming large areas of cloud cover and widespread rainfall. In the northwestern quadrant of a low pressure center, cold dry air pushes a cold front southeastward into the warmer air mass, abruptly forcing the warm, moist air aloft, sometimes with violent and severe consequences.

Since prevailing wind direction determines whether a migratory flight will occur, the patterns of wind circulation around highs and lows affects migratory movement (Figure 12). During fall migration, the best passage of migrants usually occurs the day after the day of cold front passage with brisk north winds, dropping temperatures, a rising barometer, and clearing

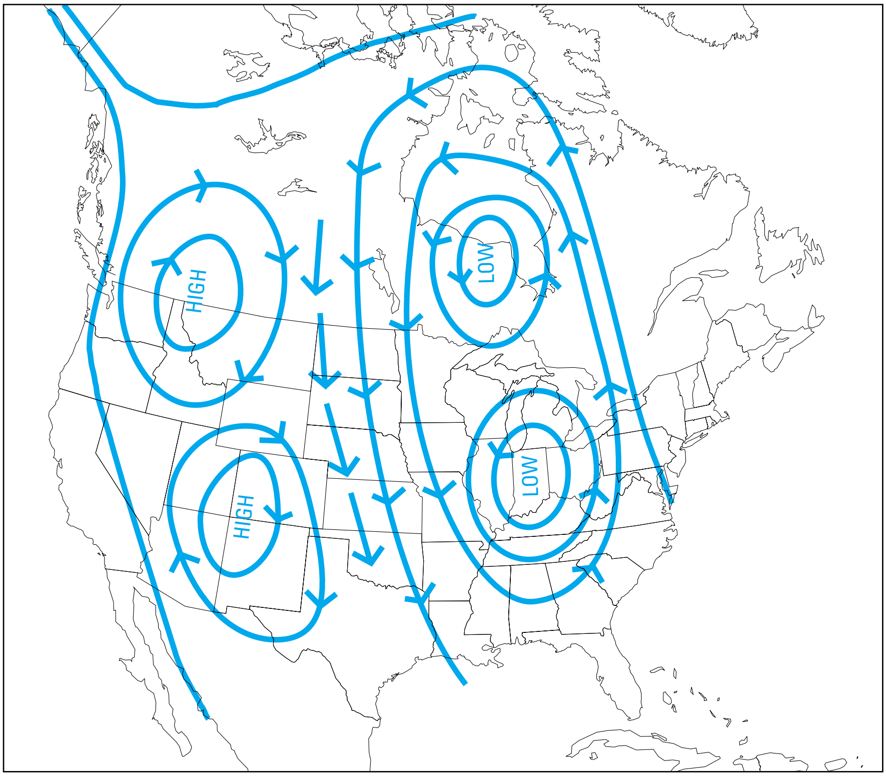

Figure 12. A hypothetical weather system that could be ideal for mass migrations of waterfowl in the fall. The strong southerly flow of air created by counter-clockwise winds about the lows and the clockwise rotation of air about the highs, aids the rapid movement of waterfowl from their breeding grounds in the Canadian prairies to wintering areas in southern United States.

skies. The intensity of this flight only wanes as migrating flocks become less and less influenced by the prevailing winds following the cold front as it moves eastward. Since wind direction becomes more variable and wind velocity decreases as high pressure begins to dominate, mass migratory flights are curtailed. This is the time birds stop and feed.

During spring, weather conditions in the southeastern or warm sector of a low pressure are conducive to movements of birds since the prevailing wind flows strongly from the south. But when these migrating flocks are overtaken by the cold front sweeping in from the west with its abrupt reversal of wind direction, towering clouds, turbulent air, and often torrential rain, migration stops, and the birds are grounded. If northward migrating flocks overtake the warm front, they are also faced with a shift in wind direction now blowing out of the east, increased cloud cover, and precipitation, but since the air is less turbulent, the wind shift less inappropriate, and the rains gentler, they will often continue northward awhile before they land and begin to forage.

The passage of low pressure system and the associated winds, often results in "waves" of migrants grounded by the storm being seen by observers. This is especially the case in the spring. This phenomenon reaches its superlative expression along the Gulf of Mexico if a cold front is positioned along or just off the coast. Then trans-Gulf migrants nearing the end of their flight from Central America and enjoying the advantage of a following wind must struggle against the adverse headwinds until landfall is reached, and the exhausted birds settle immediately to rest and forage in whatever habitat the coastal strand provides. It is a day to be remembered by any bird watcher. Orioles and tanagers by the dozens crowd the scrubby seaside bushes; Blackburnian and Cerulean warblers forage with Indigo and Painted buntings in the lawns of bayside homes. But if there is no front, there are no birds, the migrants having sufficient fat stores to continue flying northward on the following wind until they must stop to eat and drink.

Soaring birds such as hawks, Ospreys, eagles, and vultures are very dependent on proper wind conditions for migration. In the fall, often the best day to observe hawk migration along mountains in the eastern United States is on the second day after a cold front has passed, providing there are steady northwest to west winds to produce updrafts as the strong air currents are forced over the north-south oriented ridges. Migrants also soar on convective thermals that are generated by the differential heating of the Earth's surface. It has been estimated that the normal premigratory fat load of 100 grams in a Broad-winged Hawk would be exhausted in only five days of flapping flight. But by spiralling in the updrafts of one thermal and gliding down to the next to again to take advantage of the rising air currents, its stored fat would last 20 days, more than enough to provide energy for its 3,000 mile journey from the Neotropics.

INFLUENCE OF TOPOGRAPHY

The relation of the world's land masses to each other and the distribution of ecological communities within these land masses influence the direction birds migrate. Topography may aid, hinder, or prevent the progress of a migrant depending on the bird's particular requirements. Old World migrants must contend with east and west trending mountain ranges and deserts, and major migratory routes tend to be in a northeast to southwest or a northwest to southeast direction in order to circumnavigate these barriers. In the New World, however, migrants can proceed north and south across the land unimpeded, since the major mountain ranges and river systems are oriented in the same direction as the birds' migration.

Distinct features in the landscape, including rivers, mountain ridges, desert rims, or peninsulas appear to influence migratory travel by providing a landscape reference for orientation, especially when it is necessary to compensate for wind drift.

Large bodies of water constitute real barriers to soaring birds dependent on thermals, since water temperatures are usually less than land temperatures during both vernal and autumnal migratory periods and thus are characterized by subsidence of air rather than updrafts. The shoreline, then, may provide a guiding line, since onshore winds rise upward once they move across the warmer land. These conditions often concentrate Broad-winged, Rough-legged, Red-shouldered, and Red-tailed hawks migrating through the Great Lakes into restricted areas where numbers observed can be spectacular. It has been observed around Lake Ontario, for example, that maximum hawk flights occur when winds are from 10 to 25 miles per hour, but when winds exceed 35 miles per hour good soaring conditions are curtailed and hawk migration ceases. Similar conditions exist over the Bosphorus between the Black Sea and the Mediterranean where thousands of White Storks, eagles, and buzzards can be observed on a good day. For migrants not dependent upon soaring flight, on the other hand, large bodies of water do not affect their rate of migration or the routes they choose. The Gulf of Mexico, the Mediterranean Sea, and even the open Atlantic from the Maritime Provinces of Canada to the northern coast of South America are regularly crossed by many songbirds.

As previously noted, mountain ridges that parallel the line of flight offer updrafts to soaring birds. The highest and longest ridges deflect the horizontal winds upward better than the shorter ridges less than 1,000 feet high, and more birds are seen, on the average, along these higher ridges.

In summary, topography may help or deter a migrant in its passage. It affects different birds in different ways. In North America, migratory movements are continent wide, and no evidence indicates any particular part of the landscape influences all birds in the same manner. Certain bird populations may use regular geographic routes during migration, but they are usually not rigidly restricted to them because of topography.

PERILS OF MIGRATION

Migration is dangerous. Untold thousands of smaller migrants die each year from storms and attacks by predators. Indeed, the passage of migrants is so reliable that Eleonora's Falcon breeds in the fall to take advantage of the many songbirds crossing the Mediterranean as a source of food for its young. Mortality during migratory flight, of course, is one of the several costs that balance the increased production of offspring that migrants obtain by nesting in locations where food is more abundant and interspecific competition for most resources is lower.

Storms

Of all the hazards confronting birds in migration, storms are one of the most dangerous. Birds that cross broad stretches of water can confront headwinds associated with a storm, become exhausted, and fall into the waves. Such a catastrophe was once seen from the deck of a vessel in the Gulf of Mexico, 30 miles off the mouth of the Mississippi River. Great numbers of migrating birds, chiefly warblers, were nearing land after having accomplished nearly 95 percent of their long flight when, caught by a "norther" against which they were unable to make headway, hundreds were forced into the waters of the Gulf and drowned. A sudden drop in temperature accompanied by a snowfall can cause a similar effect.

Aerial Obstructions

Lighthouses, tall buildings, monuments, television towers, and other aerial obstructions have been responsible for destruction of migratory birds. Bright beams of lights on buildings and airport ceilometers have a powerful attraction for nocturnal air travelers that may be likened to the fascination for lights exhibited by many insects, particularly night-flying moths. The attraction is most noticeable on foggy nights when the rays have a dazzling effect that not only lures the birds but confuses them and causes their death by collision against high structures. The fixed, white, stationary light located 180 feet above sea level at Ponce de Leon Inlet (formerly Mosquito Inlet), Florida, has caused great destruction of bird life even though the lens is shielded by wire netting. Two other lighthouses at the southern end of Florida, Sombrero Key and Fowey Rocks, have been the cause of a great number of bird tragedies, while heavy mortality has been noted also at some of the lights on the Great Lakes and on the coast of Quebec. Fixed white lights seem to be most attractive to birds; lighthouses equipped with flashing or red lights do not have the same attraction.

For many years in Washington, D.C., the illuminated Washington Monument, towering more than 555 feet into the air, caused destruction of large numbers of small birds. Batteries of brilliant floodlights grouped on all four sides about the base illuminate the Monument so brilliantly, airplane pilots noticed that it could be seen for 40 miles on a clear night. On dark nights with gusty, northerly winds, nocturnal migrants seem to fly at lower altitudes and are attracted to the Monument. As they mill about the shaft, they are dashed against it by eddies of wind, and hundreds have been killed in a single night.

In September 1948, bird students were startled by news of the wholesale destruction of Common Yellowthroats, American Redstarts, Ovenbirds, and others against the 1,250 foot Empire State Building in New York City, the 491 foot Philadelphia Saving Fund Society Building in Philadelphia, and the 450 foot WBAL radio tower in Baltimore. In New York, the birds continued to crash into the Empire State Building for 6 hours.

More recently, television towers have become a major hazard. These structures are so tall, sometimes over 1,000 feet, they present a greater menace than buildings or lighthouses. Their blinking lights cause passing migrants to blunder into guy wires or the tower itself. Numerous instances throughout the United States indicate this peril to migration is widespread. Yet TV tower kills have been an excellent source of scientific information on the fat loads migrants carry, since they literally remove birds from out of the sky during their migration.

Exhaustion

The American Golden-Plover travels over a 2,400-mile oceanic route from Nova Scotia to South America in about 48 hours of continuous flight. This is accomplished with the consumption of less than 2 ounces of body fat. In contrast, to be just as efficient in operation, a 1,000-pound airplane would consume only a single pint of fuel in a 20-mile flight rather than the gallon usually required. Similarly, the tiny Ruby-throated Hummingbird weighing approximately 4 grams, crosses the Gulf of Mexico in a single flight of more than 500 miles while consuming less than 1 gram of fat.

One might expect the exertion required for long migratory flights would result in arrival of migrants at their destination near a state of exhaustion. This is usually not the case. Birds that have recently arrived from a protracted flight over land or sea sometimes show evidences of being tired, but their condition is far from being in a state of exhaustion, unless they have faced adverse winds. In reality, even small landbirds are so little exhausted by ocean voyages, they not only cross the Gulf of Mexico at its widest point but may even proceed without pause many miles inland before stopping. The Sora, considered such a weak flyer that at least one writer was led to infer most of its migration was made on foot, has one of the longest migration routes of any member of the rail family and even crosses the wide reaches of the Caribbean Sea. Observations indicate that under favorable conditions birds can fly when and where they please and the distance covered in a single flight is governed chiefly by the rate of dehydration and to a lesser degree, the amount of stored fat.

ROUTES OF MIGRATION

General Considerations

While certain flight directions are consistently followed by migratory birds, it is well to remember that the term "migration route" is a generalization, a concept referring to the general movements of a species, rather than an exact course followed by individual birds or a path followed by a species characterized by specific geographic or ecological boundaries. Even the records of banded birds usually show no more than the places of banding and recovery, and the details of the route actually traversed between the two points is interpolated. In determining migration routes, one must also constantly guard against the false assumption that localities with many grounded migrants are on the main path of migration and localities where no migrants are observed are off the main path.

There is also considerable variation in the routes chosen by different species. Differences in distance traveled, time of starting, speed of flight, latitudes of breeding and wintering grounds, all contribute to this great variation of migration routes among species. For example, waterfowl banding data not only indicate species differences, but also indicate considerable diversity in direction of movement by different breeding populations within a species as well as between individuals in the same population. Nevertheless, there are certain factors that serve to guide individuals or groups of individuals along more or less regular paths, and it is possible to define such lines of migration for many species.

Flyways and Corridors

Through plotting accumulated banding data obtained in the 1930's, investigators became impressed by what appeared to be four broad, relatively exclusive flyway belts in North America. This concept, based upon analyses of the several thousand records of migratory waterfowl recoveries then available, led Fred Lincoln to conclude that, ". . . because of the great attachment of migratory birds for their ancestral flyways, it would be possible practically to exterminate the ducks of the West without seriously interfering with the supply of birds of the same species in the Atlantic and Mississippi flyways, and that the birds of these species using the eastern flyways would be slow to overflow and repopulate the devested areas of the West, even though environmental conditions might be so altered as to be entirely favorable." Since 1948, this model has served as the basis for administrative action by the Fish and Wildlife Service in setting annual migratory waterfowl hunting regulations.

The notion of bird populations being confined to four fairly definite and distinct migration "flyways" is probably most applicable to those birds that migrate in family groups, namely geese, swans, and cranes, but does not appear to be very helpful in understanding the movements of the more widely dispersing ducks or most other groups of birds. Young geese will tend to return to breed in the area in which they were hatched, even though competition might be less in goose populations breeding in another flyway. Mating in many ducks occurs on the winter range and even though a male had come south on one flyway, it will return with the female, perhaps on a different flyway. Consequently, vacant breeding areas are more rapidly repopulated by ducks than by geese.

Although Lincoln's analysis was confined to ducks and geese, some thought that it applied to other groups of birds as well. Everyone now realizes that the concept of four flyways, designated as the Atlantic, Mississippi, Central, and Pacific Flyways, was an oversimplification of an extremely complex situation involving crisscrossing of migration routes that vary from species to species. Flyways can be considered meaningful only in a very general way, even for waterfowl, and not generally applicable to other groups of birds. By determining relative abundances of dabbling ducks east of the Rocky Mountains, Frank Bellrose of the Illinois Natural History Survey presented a more realistic picture (Figure 13). Yet the four "Flyway" areas have been useful in regionalizing the harvest of waterfowl for areas of different vulnerability to hunting pressure. Bellrose also mapped the corridors for the diving ducks and showed heavy traffic similar to that of dabbling species through the Great Plains and relatively heavily used corridors from these central arteries eastward across the Great Lakes area to the Atlantic coast, terminating particularly in the vicinity of Chesapeake Bay. A fairly well-used corridor also extends along the Atlantic coast.

With our present knowledge of bird migration, recognizing distinct broad belts of migration down the North American continent encompassing groups of distinct populations or species is not realistic. About all we can say for sure now is that birds travel between certain breeding areas in the North and certain wintering areas in the South; that a few heavily traveled corridors are used by certain species; and that more generalized are routes followed by other species.

Narrow Routes

Some species exhibit extremely narrow routes of travel. The Red Knot and Purple Sandpiper, for example, are normally found only along the coasts because they are limited on one side by the broad waters of the ocean, and on the other by land and fresh water; neither of these habitats furnish conditions attractive to these species.

The Ipswich race of the Savannah Sparrow likewise has a very restricted migration range. It is known to breed only on tiny Sable Island, Nova Scotia, and it winters from that island south along the Atlantic coast to Georgia. It is rarely more than a quarter of a mile from the outer beach and is entirely at home among the sand dunes with sparse covering of coarse grass.

The Harris' Sparrow provides an interesting example of a moderately narrow migration route in the interior of the country (Figure 14). This handsome sparrow is known to breed only in the narrow belt of stunted timber and brush along the northern limit of trees from the vicinity of Churchill, on the west shore of Hudson Bay, to the Mackenzie Delta 1,600 miles to the northwest. When this sparrow reaches the United States on its southward migration, it is most numerous in a belt about 500 miles wide between Montana and central Minnesota south through a relatively narrow path in the central part of the continent. Its winter range lies primarily from southeastern Nebraska and northwestern Missouri, across eastern Kansas

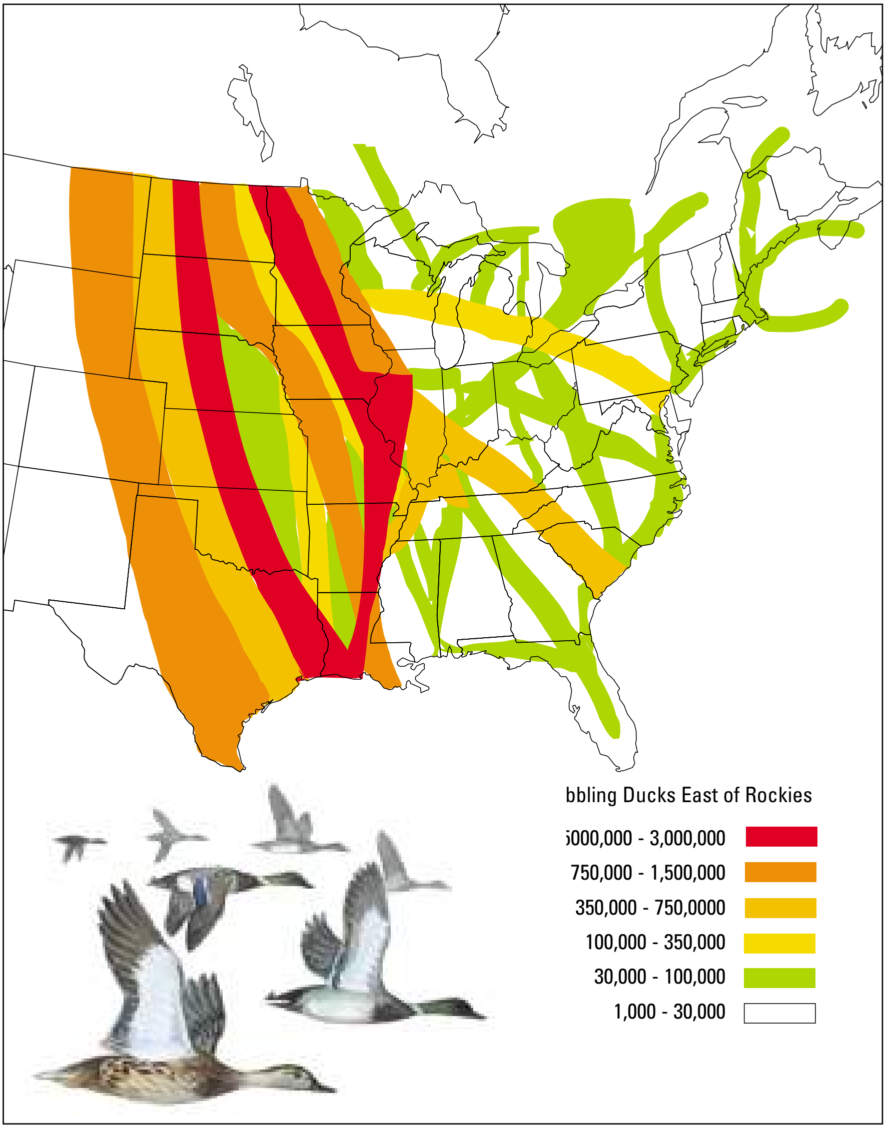

Figure 13. Migration corridors used by dabbling ducks east of the Rocky Mountains during their fall migration (after Bellrose 1968).

and Oklahoma, and through a 150 miles-wide section of eastern Texas. The habitat preference of Harris' Sparrows for the coniferous forest-tundra transition on its breeding range also characterizes the structure of its habitat choice of shrubby patches within grasslands on its wintering range. Consequently it's narrow migratory pathway is west of the eastern deciduous forest, and even with deforestation the species has not widened its wintering area.

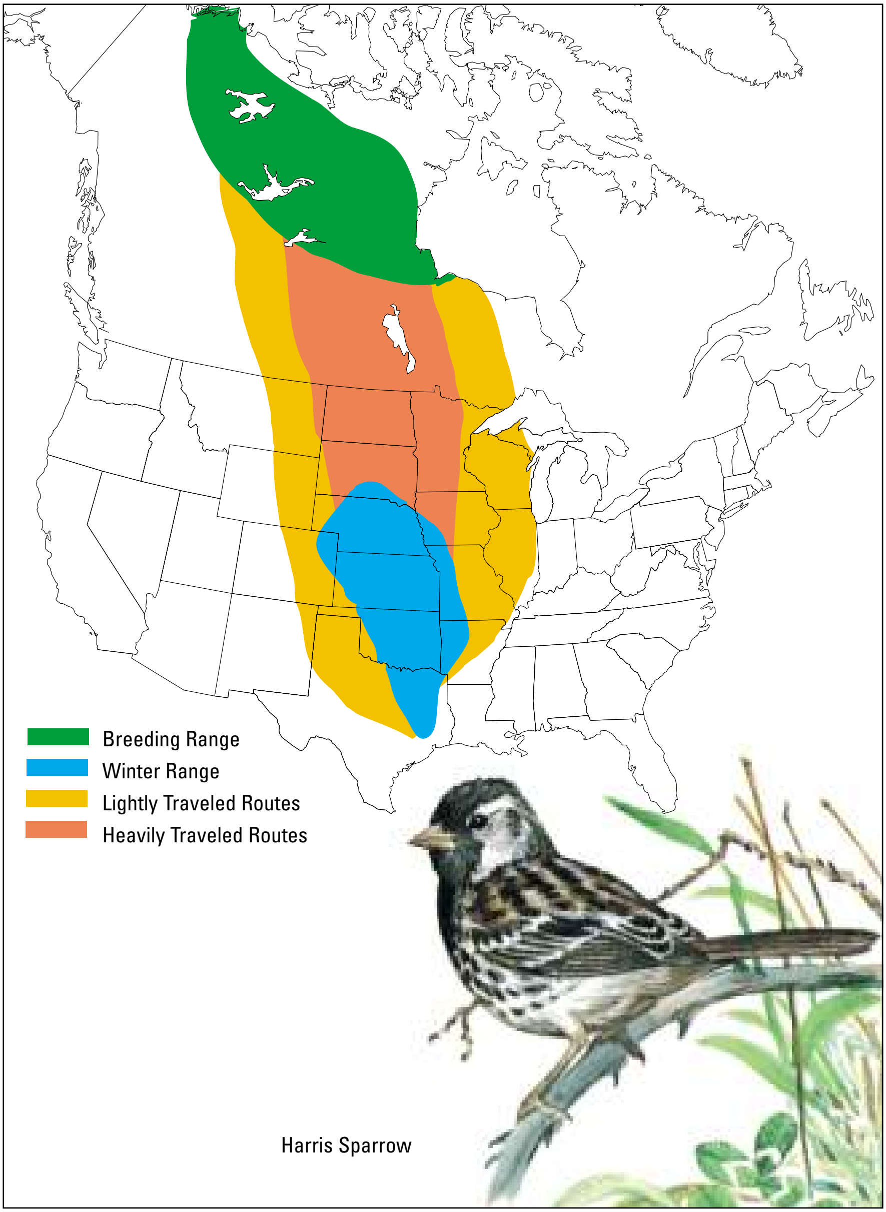

Figure 14. Distribution and migration of Harris' Sparrow. This is an example of a narrow migration route through the interior of the country.

Converging Routes

When birds start their southward migration, the movement necessarily involves the full width of the breeding range. Later, in the case of landbirds with extensive breeding ranges, there is a convergence of the lines of flight taken by individual birds owing, in part, to the conformation of the land mass and in part to the east-west restriction of habitats suitable to certain species. An example of this is provided by the Eastern Kingbird, which breeds in a summer range 2,800 miles wide from Newfoundland to British Columbia. On migration, however, the area traversed by the species becomes constricted until in the southern part of the United States the occupied area extends from Florida to the mouth of the Rio Grande, a distance of only 900 miles. Still farther south the migration path continues to converge and, at the latitude of Yucatan, it is not more than 400 miles wide. The great bulk of the species probably moves in a belt less than half this width.

The Scarlet Tanager presents another extreme case of a narrowly converging migration route starting from its 1,900 mile-wide breeding range in the eastern deciduous forest between New Brunswick and Saskatchewan (Figure 15). As the birds move southward in the fall, their path of migration becomes more and more constricted until, at the time they leave the United States, all are included in the 600-mile belt from eastern Texas to the Florida peninsula. The boundaries continue to converge to less than 100 miles through Honduras and Costa Rica. The species winters in the heavily forested areas of northwestern South America including parts of Colombia, Ecuador, and Peru.

The Rose-breasted Grosbeak also leaves the United States through the 600-mile stretch from eastern Texas to Apalachicola Bay, but thereafter this grosbeak crosses the Gulf of Mexico and enters the northern part of its winter quarters in southern Mexico and these lines do not converge. However, the pathway of those individuals that continue to South America is considerably constricted by the narrowing of land through Central America (Figure 16). Although the cases cited represent extremes of convergence, a narrowing of migratory paths is the rule for the majority of North American birds. Both the shape of the continent and major habitat belts tend to constrict southward movement so that the width of the migration route in the latitude of the Gulf of Mexico is much less than in the breeding range. The American Redstart represents a case of a wide migration route, but even in the southern United States this path is still much narrower than the breeding range (Figure 17). These birds, however, cross all of the Gulf of Mexico and pass from Florida to Cuba and Haiti by way of the Bahamas, so that here their route is about 2,500 miles wide.

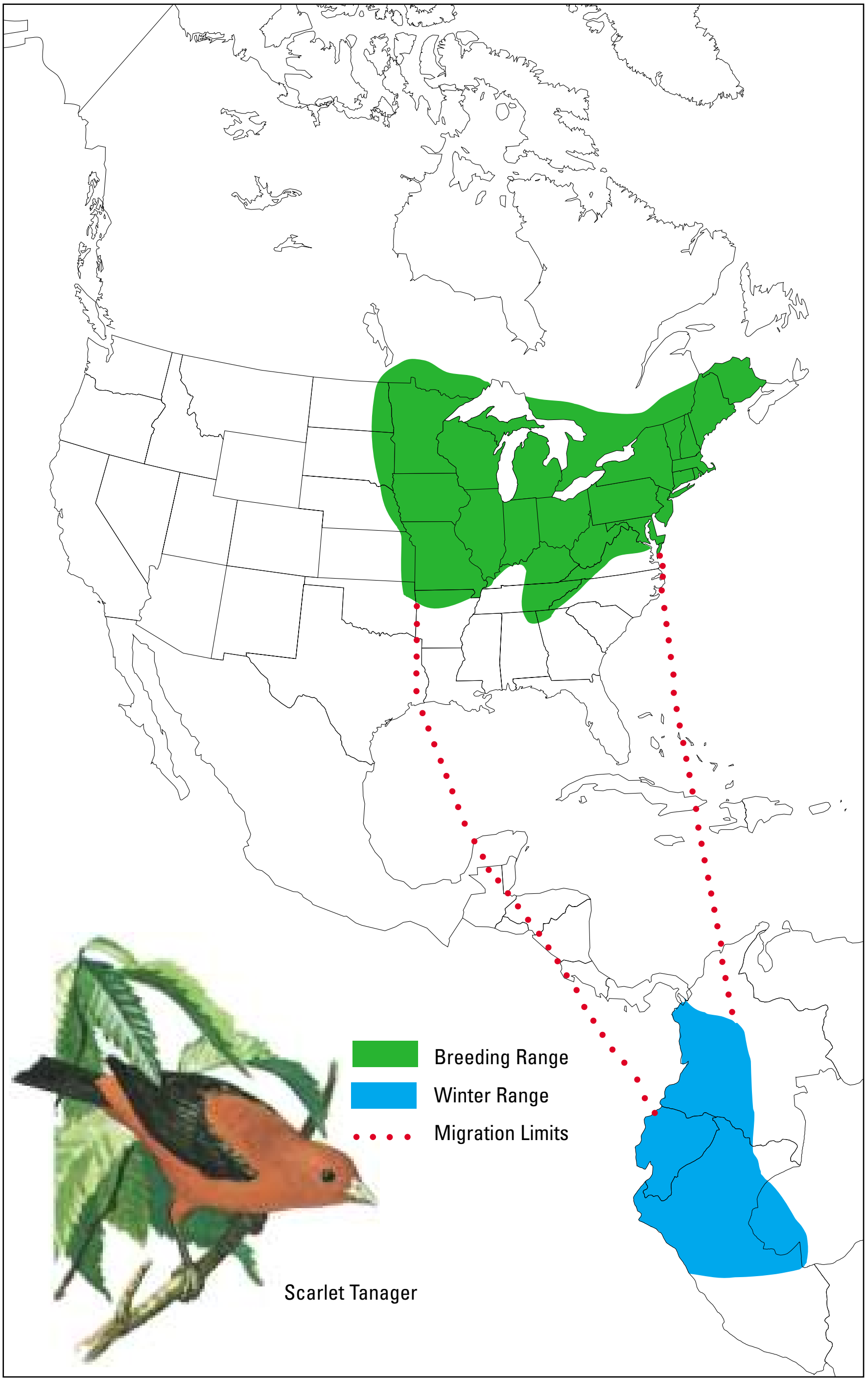

Figure 15. Distribution and migration of the Scarlet Tanager. During the breeding season individual tanagers may be 1,500 miles apart in an east-and-west line across the breeding range. In migration, however, the lines gradually converge until in South America they are about 500 miles apart.

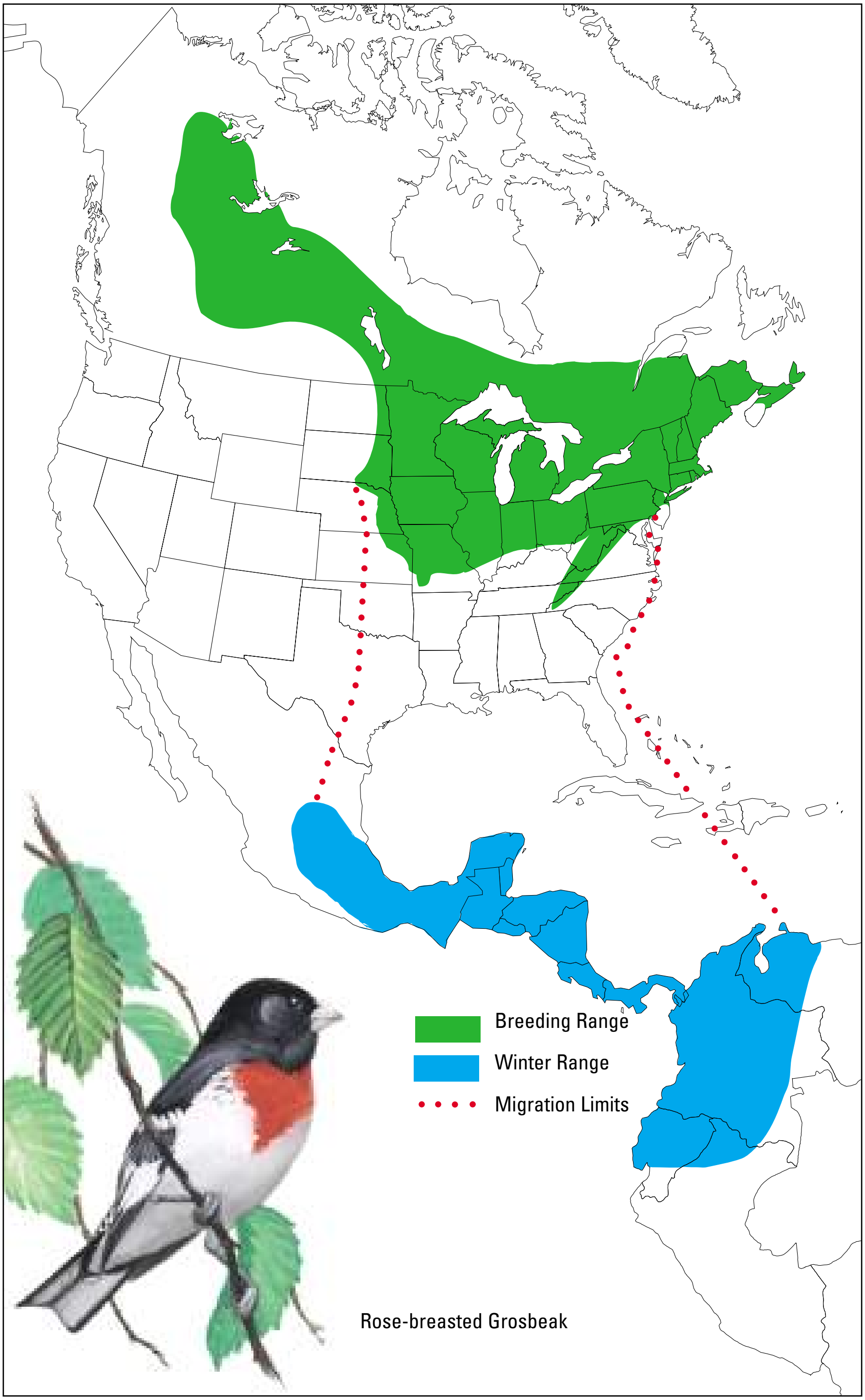

Figure 16. Distribution and migration of the Rose-breasted Grosbeak. Though the width of the breeding range is about 2,500 miles, the migratory lines converge until the boundaries are only about 600 miles apart when the birds leave the United States.

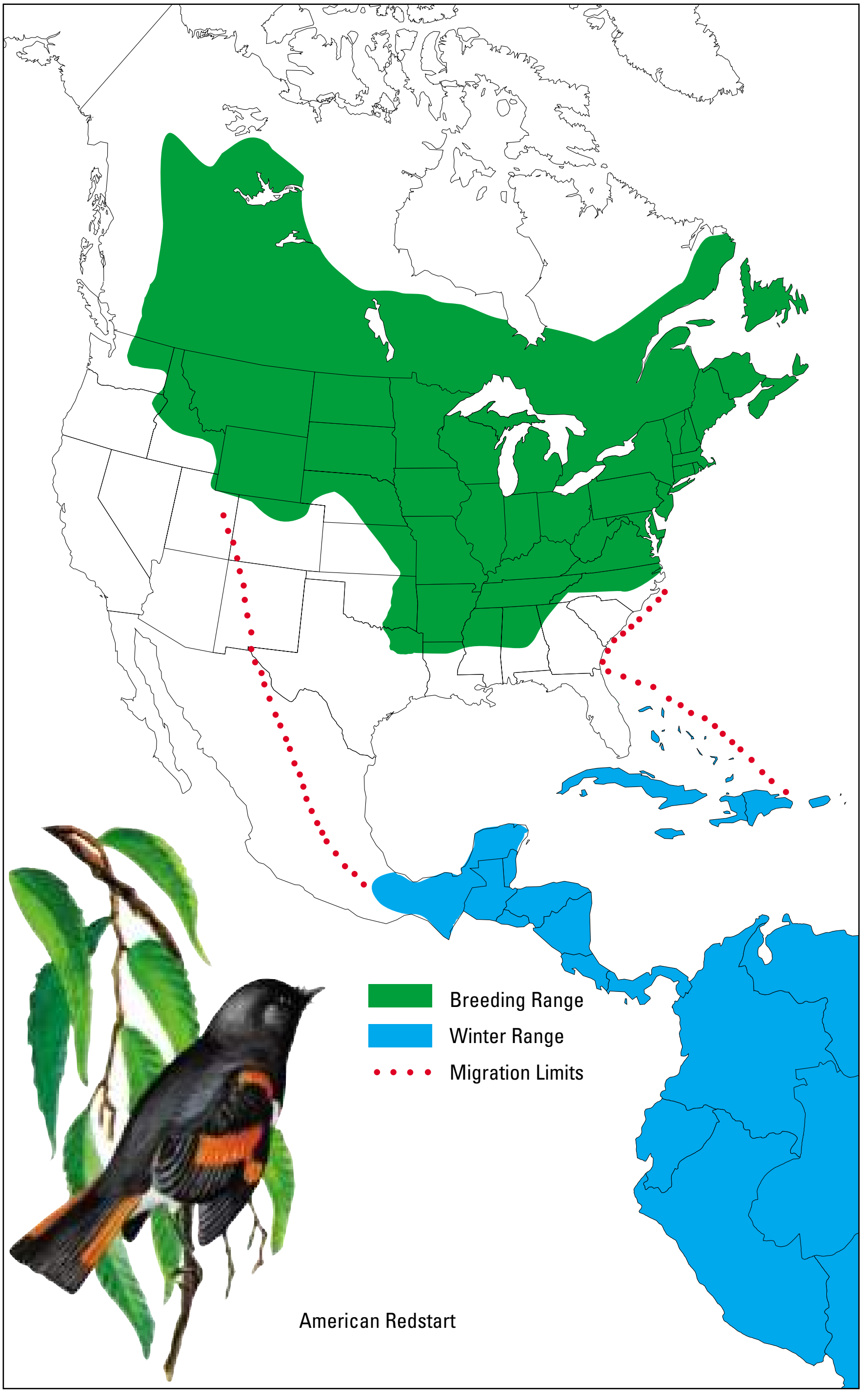

Figure 17. Distribution and migration of the American Redstart. An example of a wide migration route, birds of this species cross all parts of the Gulf of Mexico, or may travel from Florida to Cuba and through the Bahamas. Their route has an east-and-west width of more than 2,000 miles.

Principal Routes From North America

W. W. Cook identified seven generalized routes for birds leaving the United States on their way to various wintering grounds (Figure 18). The routes by which birds return northward in the spring are not as well known.

Atlantic Oceanic Route

Route No. 1 (Figure 18) is primarily oceanic and passes directly over the Atlantic Ocean from Labrador and Nova Scotia to the Lesser Antilles, then through this group of small islands to the mainland of South America. Most of the adult American Golden-Plovers and some other shorebirds use this as their fall route. These plovers may accomplish the whole 2,400 miles without pause, and in fair weather the flocks pass Bermuda and sometimes even the islands of the Antilles without stopping. As mentioned previously, radar has indicated strong fall movements of warblers from the New England coast out over the Atlantic to points south along this route. One of these, the Blackpoll Warbler has evolved a high level metabolic efficiency in order to make this extended overwater passage. This species looses only 0.06% of its weight per hour (essentially water and fat) compared to thrushes, warblers, and sparrows on overland routes which loose 1.2% of their weight per hour of flight. Since this route lies almost entirely over the sea, it is definitely known only at its terminals and from occasional observations made on Bermuda and other islands along its course. Some of the shorebirds that breed on the arctic tundra of the District of Mackenzie (Northwest Territories) and Alaska fly southeastward across Canada to the Atlantic coast and finally follow this oceanic route to the mainland of South America. Although most birds make their migratory flights either by day or by night, birds using this route fly both day and night.

The Arctic Tern follows the Atlantic Ocean route chiefly along the eastern side of the ocean in the eastern hemisphere. Likewise, vast numbers of seabirds such as auks, murres, guillemots, phalaropes, jaegers, petrels, and shearwaters follow this over-water route from breeding sites along coasts and on islands in the Northern and Southern Hemispheres.

Atlantic Coast Route and Tributaries

The Atlantic coast is a regular avenue of travel, and is well known for many famous locations for observing both land and water birds. About 50 different kinds of landbirds that breed in New England follow the coast southward to Florida and travel thence by island and mainland to South America (Figure 18, route 2). The map indicates a natural and convenient highway through the Bahamas, Cuba, Hispaniola, Puerto Rico, and the Lesser Antilles to the South American coast. Resting places are provided at convenient intervals, and at no time are these aerial travelers out of sight of land. It is not, however, the favored highway; only about 25 species of birds go beyond Cuba to Puerto Rico along this route to their winter quarters, while only six species are known to travel to South America by way of the Lesser Antilles. Many thousands of American Coots and American Wigeons, Northern Pintails, Blue-winged Teals, and other water-

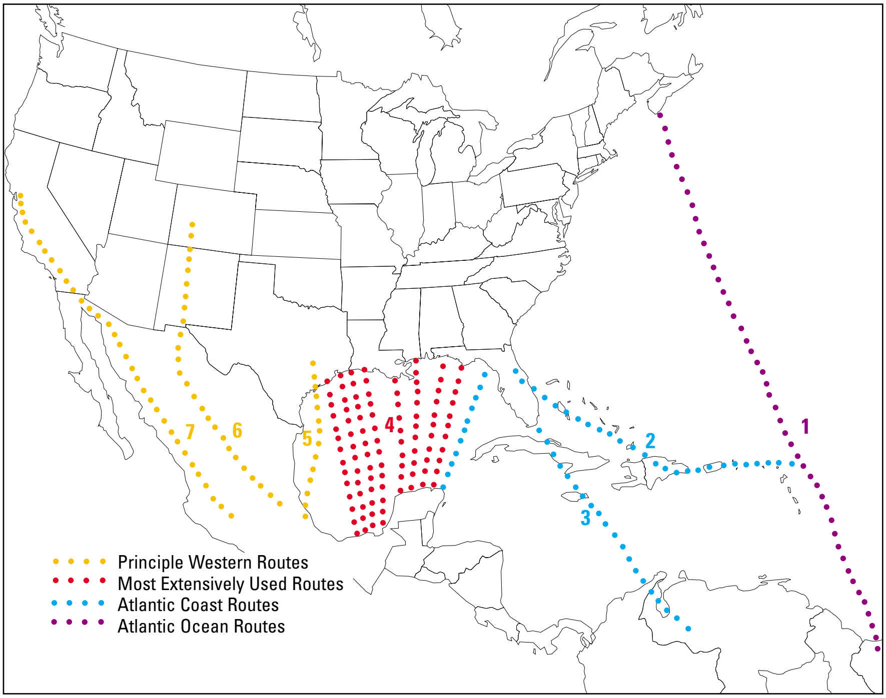

Figure 18. Principle migration routes by birds in passing from North America to winter quarters in the West Indies, Central America, and South America. Route 4 is the one used most extensively while only a few species make the 2,400 mile flight down Route 1 from Nova Scotia to South America.

fowl as well as shorebirds, regularly spend the winter season in the coastal marshes, inland lakes, and ponds of Cuba, Hispaniola, and Puerto Rico.

Route No. 3 (Figure 18) is a direct line of travel for Atlantic coast migrants enroute to South America, although it involves much longer flights. It is used almost entirely by landbirds. After taking off from the coast of Florida, there are only two intermediate land masses where migrants might pause for rest and food. Nevertheless, tens of thousands of birds of about 60 species cross the 150 miles from Florida to Cuba where many remain for the winter months. The others negotiate the 90 miles between Cuba and Jamaica but, from that point to the South American coast, there is a stretch of islandless ocean 500 miles across. The Bobolink so far outnumbers all other birds using this path that this route could be designated the "Bobolink route" (Figure 19). As traveling companions along this route, the Bobolink may meet vireos, kingbirds, and Common Nighthawks from Florida, Chuck-will's-widows from the Southeastern States, Black-billed and Yellow-billed cuckoos from New England, Gray-cheeked Thrushes from Quebec, Bank Swallows from Labrador, and Blackpoll Warblers from Alaska. Sometimes this scattered assemblage will be joined by a tanager or a Wood Thrush, but the "Bobolink route" is not used by the greatest number of migrants. Formerly, it was thought most North America landbirds migrated to Central America via the Florida coast, then crossed to Cuba, and finally made the short flight from the western tip of

Cuba to Yucatan. A glance at the map would suggest this as a most natural route but, as a matter of fact, it is practically deserted except for a few swallows and shorebirds or an occasional landbird storm-driven from its normal course. What actually happens in the fall is that many of the birds breeding east of the Appalachian Mountains travel parallel to the seacoast in a more or less southwesterly direction and, maintaining this same general course from northwestern Florida, cross the Gulf of Mexico to the coastal regions of eastern Mexico. They thus join migrants from farther inland in using route No. 4 (Figure 18).

Routes used by Brant in eastern North America merit some detail because their flight paths were long misunderstood. These birds winter on the Atlantic coast, chiefly at Barnegat Bay, New Jersey, but depending upon the severity of the season and the food available, many winter south to North Carolina. Their breeding grounds are in the Canadian arctic archipelago and on the coasts of Greenland. Careful studies have shown that the main body travels northward in spring along the coast to the Bay of Fundy, overland to Northumberland Strait, which separates Prince Edward Island from mainland New Brunswick and Nova Scotia. A minor route appears to lead northward from Long Island Sound by way of the Housatonic and Connecticut River valleys to the St. Lawrence River. After spending the entire month of May feeding and resting in the Gulf of St. Lawrence, the eastern segment of the Brant population resumes its journey by departing overland from the Bay of Seven Island area, flying almost due north to Ungave Bay and from there to nesting grounds, probably on Baffin Island and Greenland. A smaller segment travels a route slightly north of west to the southeastern shores of James Bay, although east of that area some of the flocks take a more northwesterly course by descending the Fort George River to reach the eastern shore of James Bay. Upon their arrival at either of these two points on James Bay, the Brants of this western segment turn northward and proceed along eastern Hudson Bay to their breeding grounds in the Canadian Arctic.

The fall migration of Brant follows the routes utilized in the spring. During this season, the eastern population appears only on the western and southern shores of Ungave Bay before continuing their southward journey to the Gulf of St. Lawrence and beyond. Most of the birds of the western segment, instead of following the eastern shores of Hudson and James bays, turn southwestward across the former, by way of the Belcher Islands, to Cape Henrietta Maria, and from there south along the western shore of James Bay by way of Akimiski and Charlton Islands. At the southern end of James Bay, they are joined by those that have taken the more direct route along the east coasts of the bays and all then fly overland 570 miles to the estuary of the St. Lawrence River.

The Atlantic coast wintering area receives waterfowl from three or four interior migration paths, one of which is of primary importance, as it includes great flocks of Canvasbacks, Redheads, Greater and Lesser scaup, Canada Geese, and many American Black Ducks that winter in the waters and marshes of the coastal region south of Delaware Bay. The Canvasbacks, Redheads, and scaup coming from breeding grounds on the great northern plains of central Canada follow the general southeasterly trend of

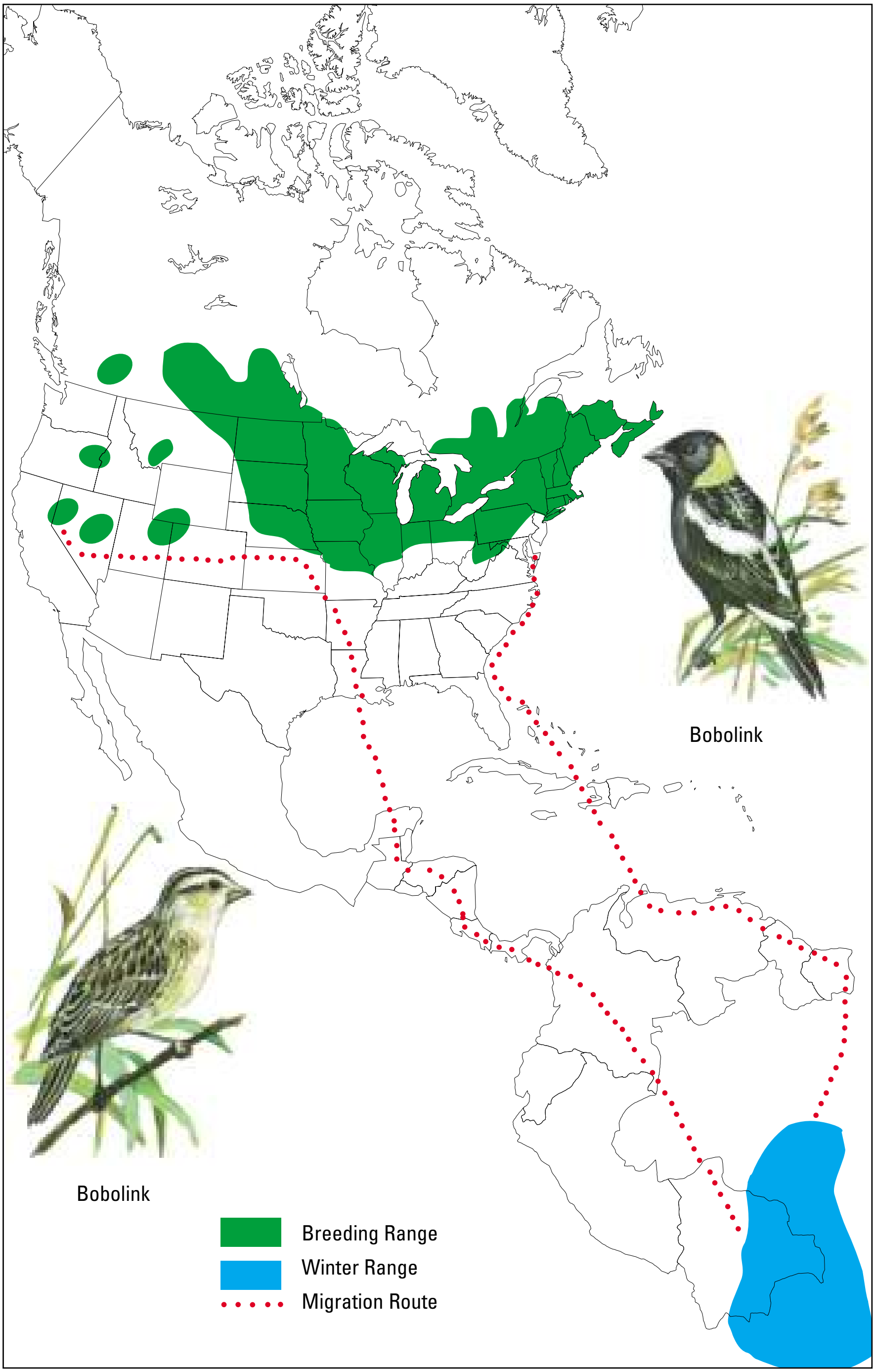

Figure 19. Distribution and migration of the Bobolink. In crossing to South America, most of the Bobolinks use route 3 (Fig. 18), showing no hesitation in making the flight from Jamaica across an islandless stretch of ocean. It will be noted that colonies of these birds have established themselves in western areas, but in migration they adhere to the ancestral flyways and show no tendency to take the short cut across Arizona, New Mexico, and Texas.

the Great Lakes, cross Pennsylvania over the mountains, and reach the Atlantic coast in the vicinity of Delaware and Chesapeake Bays. American Black Ducks, Mallards, and Blue-winged Teals that have gathered in southern Ontario during the fall leave these feeding grounds and proceed southwest. Many continue this route down the Ohio Valley, but others, upon reaching the vicinity of the St. Clair Flats between Michigan and Ontario, swing abruptly to the southeast and cross the mountains to reach the Atlantic coast south of New Jersey. This route, with its Mississippi Valley branch, has been fully documented by the recovery records of ducks banded at Lake Scugog, Ontario.

Canvasbacks migrate from the prairie pothole region of the central United States and Canada to many wintering areas in the United States. This duck has been the subject of careful study, and its principle migration routes based on recovery of banded birds have been shown. These principle routes travel from the major breeding area in the prairie provinces of Canada and the northern prairies of the United States southeastward through the southern Great Lakes area to Chesapeake Bay, the chief wintering area (Figure 20). Relatively few Canvasbacks proceed southward along the Atlantic seaboard. A less important route extends off from the main trunk in the southern Minnesota region and goes south along the Mississippi Valley to points along the river. Other individuals of the prairie breeding population fly southward on a broad front to the gulf coast of Texas and the interior of Mexico, while some proceed southwestward on a relatively broad path to the northern Pacific coast.

Mackenzie Valley-Great Lakes-Mississippi Valley Routes and Tributaries

The migration route extending from the Mackenzie Valley past the Great Lakes and down the Mississippi Valley is the longest of any in the Western Hemisphere. Its northern terminus is on the arctic coast in the regions of Kotzebue Sound, Alaska, and the mouth of the Mackenzie River, while its southern end lies in Argentina. For more than 3,000 miles, from the mouth of the Mackenzie to the delta of the Mississippi, this route is uninterrupted by mountains. In fact, the greatest elevation above sea level is less than 2,000 feet. Because it is well timbered and watered, the entire region affords ideal conditions for its great hosts of migrating birds. It is followed by such vast numbers of ducks, geese, shorebirds, blackbirds, sparrows, warblers, and thrushes that observers stationed at favorable points in the Mississippi Valley during the height of migration can see large numbers of many species.

When many of these species, including ducks, geese, American Robins, and Yellow-rumped Warblers, arrive at the Gulf coast, they spread out east and west for their winter sojourn. Others, despite the perils of a trip involving a flight of several hundred miles across the Gulf of Mexico, fly straight for Central and South America. This part of the route is a broad "boulevard" extending from northwestern Florida to eastern Texas and southward across the Gulf of Mexico to Yucatan and the Isthmus of Tehuantepec (Figure 18, route 4). This route appears to be preferred over the safer but

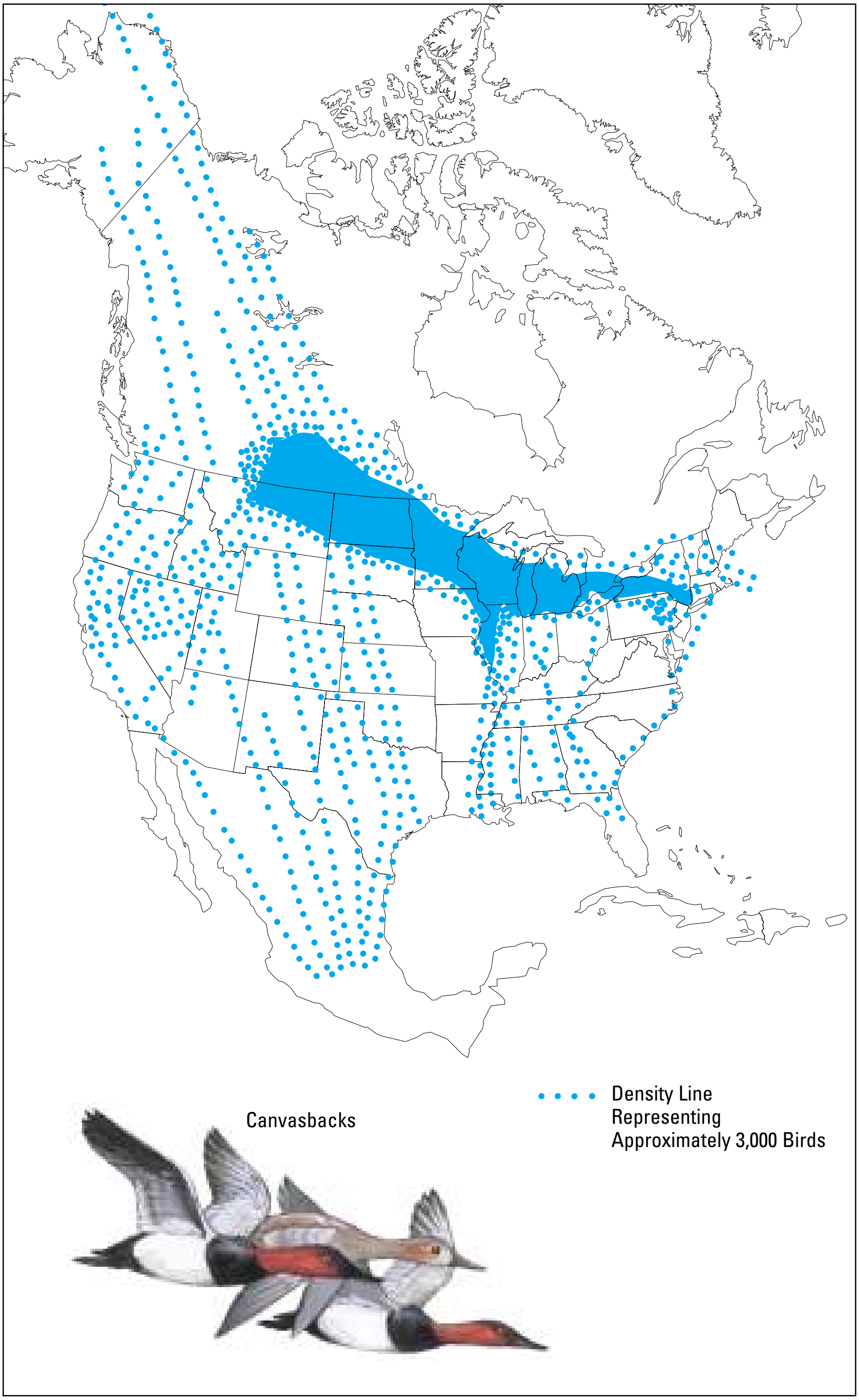

Figure 20. Principle migratory routes of the Canvasback. The major route of travel extends from breeding areas in central Canada southeast across the Great Lakes and either south down the Mississippi River or east to Chesapeake Bay (after Stewart et al. 1958).

more circuitous land or island routes by way of Texas or Florida. During the height of migration some of the islands off the coast of Louisiana are rewarding observation points for the student of birds, since the feathered travelers literally swarm over them.

Present detailed knowledge of the chief tributaries to the Mackenzie-Great Lakes-Mississippi Valley route relates primarily to waterfowl. Reference has been made already to the flight of American Black Ducks that reach the Mississippi Valley from southern Ontario. Some individuals of this species banded at Lake Scugog, Ontario, have been recaptured in succeeding seasons in Wisconsin and Manitoba, but the majority was retaken at points south of the junction of the Ohio River with the Mississippi indicating their main route of travel from southern Ontario.

A second route that joins the main artery on its eastern side is the one used by eastern populations of Snow Geese, including both blue and white phases, that breed mainly on Southampton Island and in the Fox Basin of Baffin Island. In the fall these geese work southward along the shores of Hudson Bay and, upon reaching the southern extremity of James Bay, take off on their flight to the great coastal marshes of Louisiana and Texas west of the Mississippi River delta.

Great Plains-Rocky Mountain Routes

This route also has its origin in the Mackenzie River delta and Alaska. The Sandhill Cranes, White-fronted Geese, and smaller races of the Canada Goose follow this route through the Great Plains from breeding areas in Alaska and western Canada. It is used chiefly by the Northern Pintails and American Wigeons that fly southward through eastern Alberta to western Montana. Some localities in this area, as for example, the National Bison Range at Moiese, Montana, normally furnish food in such abundance that these birds are induced to pause in their migratory movement. Some flocks of pintails and wigeons move from this area almost directly west across Idaho to the valley of the Columbia River, then south to the interior valleys of California. Others leave Montana by traveling southeastward across Wyoming and Colorado to join other flocks moving southward through the Great Plains.

Observations made in the vicinity of Corpus Christi, Texas have shown one of the short cuts (Figure 18, route 5) from the coastal bend of Texas to the shore of the Bay of Campeche that is part of the great artery of migration. Thousands of birds pass along the coast to the northern part of Veracruz, Mexico. Since coastal areas in Tamaulipas to the north are arid and unsuited for denizens of moist woodlands, it is probable that much, if not all, of this part of the route for these species is a short distance off shore. It is used by such woodland species as the Golden-winged, Worm-eating, and Kentucky warblers.

Pacific Coast Route

Although it does present features of unusual interest, the Pacific coast route is not as long or heavily traveled as some of the others described. Because of the equitable conditions that prevail, many species of birds breeding along the coast from the northwestern states to southeastern Alaska either do not migrate or else make relatively short journeys. This route has its origin chiefly in western Alaska, around the Yukon River delta. Some of the scoters and other sea ducks of the north Pacific region as well as the diminutive Cackling Canada Goose of the Yukon River Delta use the coastal sea route for all or most of their southward flight. Large numbers of arctic-breeding shorebirds also use this route. The journey of the Canada Goose, as shown by return records from birds banded at Hooper Bay, Alaska, has been traced southward across the Alaskan Peninsula and apparently across the Gulf of Alaska to the Queen Charlotte Islands. The birds then follow the coast line south to near the mouth of the Columbia River, where the route swings toward the interior for a short distance before continuing south by way of the Willamette River Valley. The winter quarters of this subspecies of Canada Goose are chiefly in the vicinity of Tule Lake, on the Oregon-California line, and in the Sacramento Valley of California, although a few push on to the San Joaquin Valley. A tributary of this flyway is followed by Ross' Goose, which breeds in the Perry River district south of Queen Maud Gulf and other areas farther east on the central arctic coast of Canada (Figure 21). Its fall migration is southwest and south across the barren grounds to Great Slave and Athabaska Lakes, where it joins thousands of other waterfowl bound for winter homes along the eastern coast of the United States and the Gulf of Mexico. But when Ross' Geese have traveled south approximately to the northern boundary of Montana, most of them separate from their companions and turn southwest across the Rocky Mountains to winter in California. In recent years more Ross' Geese have been found wintering east of the Rocky Mountains along with flocks of Snow Geese, a change that may be correlated with an eastward extension of their breeding range.

The southward route of long-distance migratory landbirds of the Pacific area extends chiefly through the interior of California to the mouth of the Colorado River and on to winter quarters in western Mexico (Figure 18, routes 6 and 7).

The movements of the Western Tanager show a migration route that is in some ways remarkable. The species breeds in the mountains from the northern part of Baja California and western Texas north to northern British Columbia and the southwestern headwaters of the Mackenzie River. Its winter range is in two discontinuous areas — southern Baja California and eastern and southwestern Mexico south to Guatemala (Figure 22). During spring migration the birds appear first in western Texas and the southern parts of New Mexico and Arizona about April 20 (Figure 23). By April 30 the vanguard has advanced evenly to an approximate east-west line across central New Mexico, Arizona, and southern California. By May 10 the easternmost birds have advanced only to southern Colorado, while those in the far west have reached northern Washington. Ten days later the northward advance of the species is shown

Figure 21. The breeding range, wintering range, and main migration route of Ross’ Goose. This is the only species of which practically all members breed in the arctic, migrate south through the Canadian prairie, and upon reaching the United States, turn to the southwest rather than the southeast. The southern part of this route, however, is followed by some Mallards, pintails, wigeons, and other ducks.

Figure 22. Breeding and wintering ranges of the Western Tanager. See Fig. 23 for the spring route taken by the birds breeding in the northern part of the range.

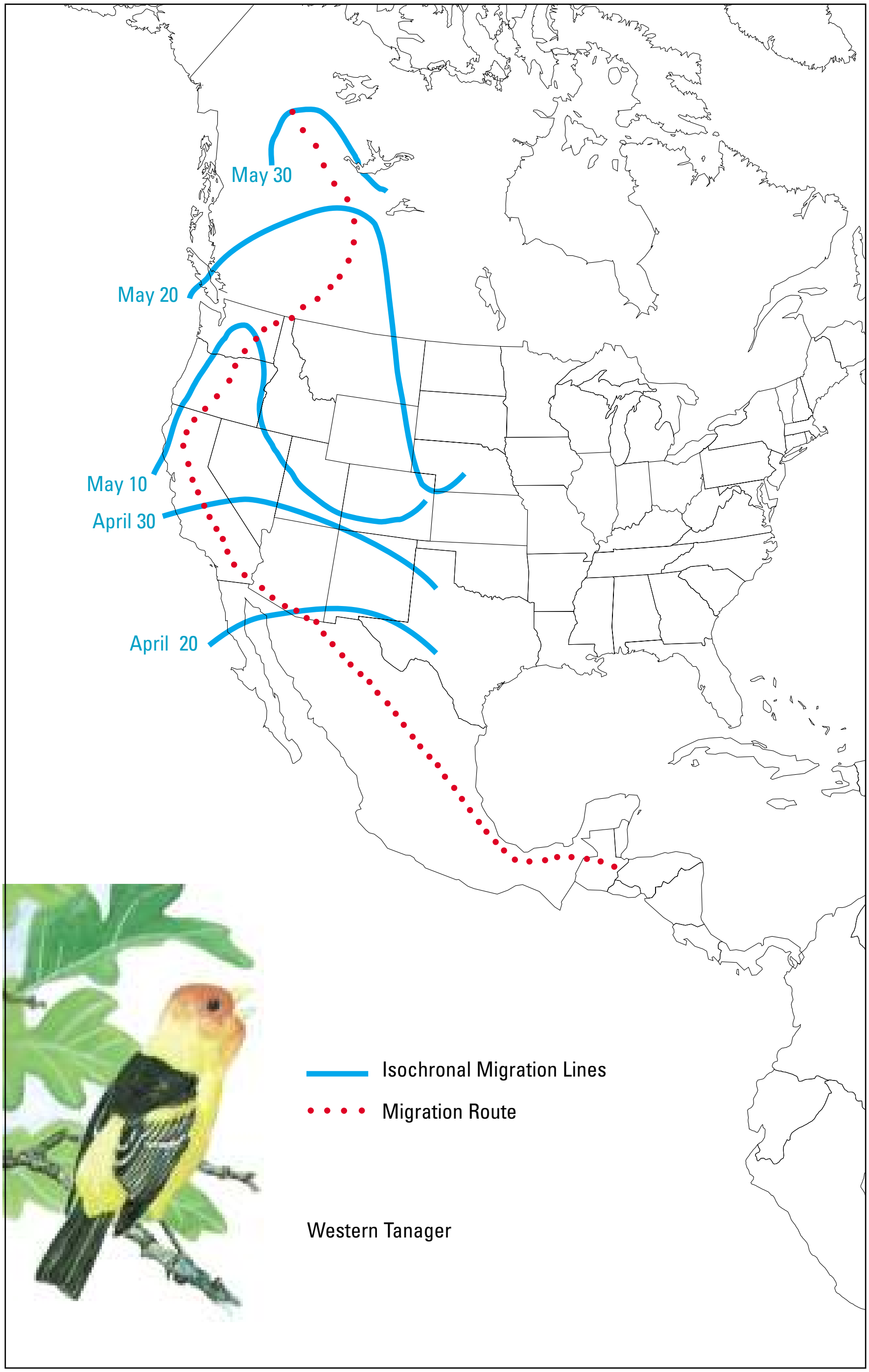

Figure 23. Migration of the Western Tanager. The birds that arrive in eastern Alberta by May 20 do not travel northward along the eastern base of the Rocky Mountains, because the vanguard has then only reached northern Colorado. Instead the isochronal lines indicate that they migrate north through California, Oregon, and Washington and then cross the Rockies in British Columbia.

as a great curve, extending northeastward from Vancouver Island to central Alberta and thence southeastward to northern Colorado. Since these tanagers do not reach northern Colorado until May 20, it is evident those present in Alberta on that date actually reached there by a route that carried them west of the Rockies to southern British Columbia and thence eastward across the still snowy northern Rocky Mountains.

Pacific Oceanic Route

The Pacific oceanic route is used by Pacific Golden-Plovers, Bristle-thighed Curlews, Ruddy Turnstones, Wandering Tattlers, and other shorebirds. The Ruddy Turnstones, migrating from the islands in the Bering Sea, have an elliptical route that takes them southward through the islands of the central Pacific and northward along the Asiatic coast. In addition, many seabirds that breed in the far northern coasts as well as on southern coasts and islands migrate across the Pacific well away from land except when the breeding season approaches. The Pacific Golden-Plover breeds chiefly along the arctic coast of Siberia and in limited areas of the Alaskan coast. Some of the birds probably migrate south through Asia to winter quarters in Japan, China, India, Australia, New Zealand, and the islands of Oceania. Others go south across the Pacific to Hawaii and other islands in the central and southern Pacific. Migrating golden-plovers have been observed at sea on a line that extends from the Aleutian Islands to Hawaii. While it seems incredible that any birds could lay a course so accurately as to make landfall on these small, isolated, oceanic islands, 2,000 miles south of the Aleutians, 2,000 miles west of Baja California, and nearly 4,000 miles from Japan, year after year Pacific Golden-Plovers make this transoceanic round-trip.

Arctic Routes

Some arctic nesting birds retreat only a short distance south in winter. These species include the Red-legged Kittiwake, Ross' Gull, Emperor Goose, and eiders. This latter group of ducks winter well south of their nesting area, but nevertheless remain farther north than do other ducks. The routes followed by these birds are chiefly parallel to the coast and may be considered as being tributary either to the Atlantic or Pacific coast routes. The heavy passage of gulls, ducks, and Brants at Point Barrow and other points on the arctic coast has been noted by many observers. The best defined arctic route in North America follows the coast of Alaska.
A migration route, therefore, may be anything from a narrow path closely adhering to a geographic feature, such as a river valley or coastline, to a broad avenue that leads in the desired direction and follows only the general pattern of the land mass. Oceanic routes appear to be special cases that are not fully understood. Also it must be remembered that all the main routes contain a multitude of tributary and separate minor routes. In fact, with the entire continent of North America crossed by migratory birds, the different groups or species frequently follow lines that may repeatedly intersect those taken by others of their own kind or by other species. The arterial or trunk routes, therefore, must be considered merely as indicating paths of migration on which concentration of birds is more noticeable.

PATTERNS OF MIGRATION

Band recoveries, netting records, and personal observations help to determine migration routes and probe more deeply into the origin and evolution of these pathways. Not surprisingly, certain deviations occur from the expected north and south movements. In the previous section, it was noted that some routes are not poleward at all, but proceed in many directions. After many years of gathering data, a pattern emerges for a particular population, species, or group of species. This section concerns some of the interesting or "eccentric routes," as Cooke referred to them, that birds travel from breeding to wintering grounds and back again.

Loops

Many species do not return north in the spring over the same route they used in the fall; rather, they fly a loop or ellipse. Cooke considered food as the primary factor in determining the course birds took between winter and summer ranges. He speculated that individuals returning by the same route and not finding sufficient food either did not return or did not breed; only the individuals that took a different course with adequate resources survived and left progeny. Assuming that there were genetic components to this variation in orientation and navigation, loop migration routes could evolve. Other investigators considered the prevailing winds to be the major selective factor, since a following wind would require less expenditure of energy. This would give an advantage to individuals who returned north on a different route if the prevailing winds were in more appropriate directions than along the path used during the southward flight.

Whatever the ultimate cause, loop migrations evolved separately in each species to satisfy its particular needs, and this pattern occurs throughout the world among unrelated species. The annual flight of adult American Golden-Plovers illustrates the loop pattern (Figure 24). In the fall, the birds fattened on the rich crop of berries along the coasts of Labrador and Nova Scotia depart south over the Atlantic Ocean to South America. They stop briefly on the coast and then continue overland to the pampas of Argentina where they remain from September to March. When these golden-plovers leave their winter quarters they cross northwestern South America and the Gulf of Mexico to reach the North American mainland on the coasts of Texas and Louisiana. Thence they proceed slowly up the Mississippi Valley and, by the early part of June, are again on their breeding grounds, having performed a round-trip journey in the form of an enormous ellipse with the minor axis about 2,000 miles and the major axis 8,000 miles stretching from the Arctic to the South Temperate Zone. The older birds may be accompanied by some of the young, but most of the immature birds leave their natal grounds later in summer after the adults and move

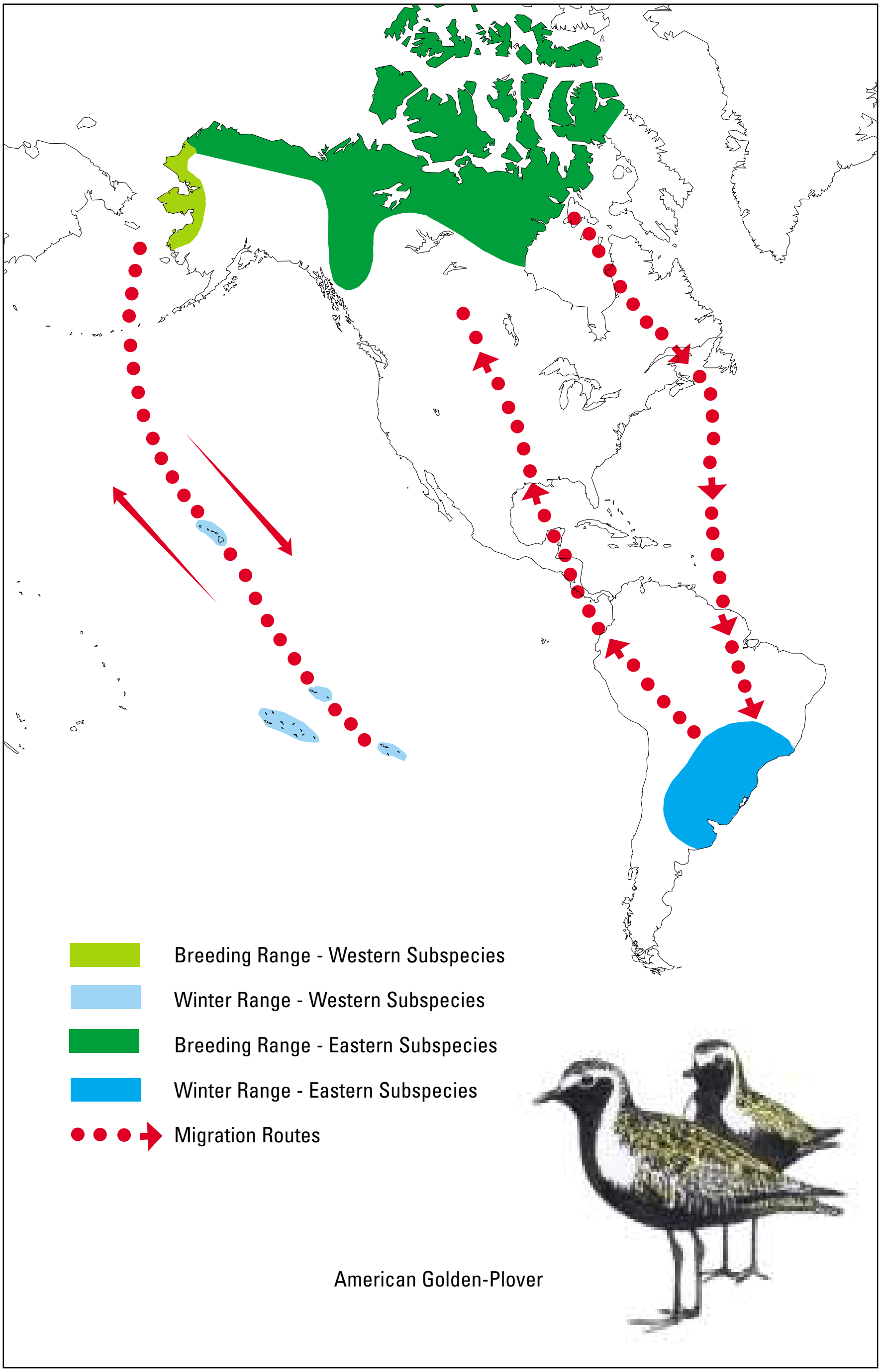

Figure 24. Distribution and migration of the American Golden-Plover. Adults of the eastern subspecies migrate across northeastern Canada and then, by a nonstop flight, reach South America. In spring they return by way of the Mississippi Valley. Their entire route, therefore, is in the form of a great ellipse with a major axis of 8,000 miles and a minor axis of about 2,000 miles. The western subspecies migrates across the Pacific Ocean to various localities including the Hawaiian and Marquesas islands and Low Archipelago.

southward through the interior of the country, returning in spring over essentially the same course. The oceanic route is therefore used chiefly by adult birds. A return by the oceanic route in the spring could be fatal. The maritime climate in the Northeast results in foggy conditions along the coast and the frozen soil would offer scanty food resources for the weary travelers. By traveling up the middle of the continent, a much better food supply is assured.

Other shorebirds follow loop migration routes. White-rumped Sandpipers fly from tundra breeding areas above the Arctic Circle eastward to the Atlantic coast of Labrador, Nova Scotia, and New Brunswick. From there they take the Atlantic Ocean route direct to the Surinam coast of South America, then fly overland to winter in Tierra del Fuego. They return to the arctic by a route through Venezuela and the Great Plains. As for the American Golden-Plovers, the interior route through the continent provides suitable resources while the Atlantic coast is still in the grip of winter. Some Western Sandpipers, instead of following most of their conspecifics southward along the Pacific coast, turn eastward at the Frasier River, moving beyond the Rockies to migrate through the Great Plains, then passing southeastward through Florida and thence to northern South America. In the spring they move westward to the Pacific coast, and the entire species follows the coast north to the tundra in Alaska and eastern Siberia.

Several North American warblers including the Connecticut Warbler (Figure 25) and the western race of the Palm Warbler follow circuitous migration routes. The Connecticut Warbler is not observed on the East coast in spring, but it is recorded farther inland during that season. Thus, this warbler proceeds down the East coast in the fall and up the interior of the continent in the spring. Similarly, the western race of the Palm Warbler moves from its breeding grounds directly east over the Appalachian Mountains before turning south along the Atlantic coast. Television tower kills in northern Florida indicate the population is very concentrated here at this time of year. In the spring this subspecies proceeds north through the interior. The eastern race of the Palm Warbler also proceeds south along the coast in the fall but returns north in the spring along the same path. Scientists had hypothesized that the western population initially migrates eastward to join the rest of the species moving south along the coast because this flight path retraces its past history of range expansion. An alternate hypothesis derived from radar observations, however, suggests that the disparity in seasonal flight directions of many migrants is a positive response to favorable wind directions at that time of year.

In the fall, the Short-tailed Shearwater is observed off the west coast of North America as far south as California. At this time the species is on the eastern leg of a tremendous figure-eight around the Pacific Ocean (Figure 26). The Subalpine Warbler and Red-backed Shrike perform loop migrations between Europe and Africa. Both pass much farther to the east in the spring than in the fall. The Arctic Loon travels south across inland Russia to southern Europe but returns to its arctic breeding grounds via the Gulf Stream in the Atlantic because this water is open while inland waterways are still frozen.

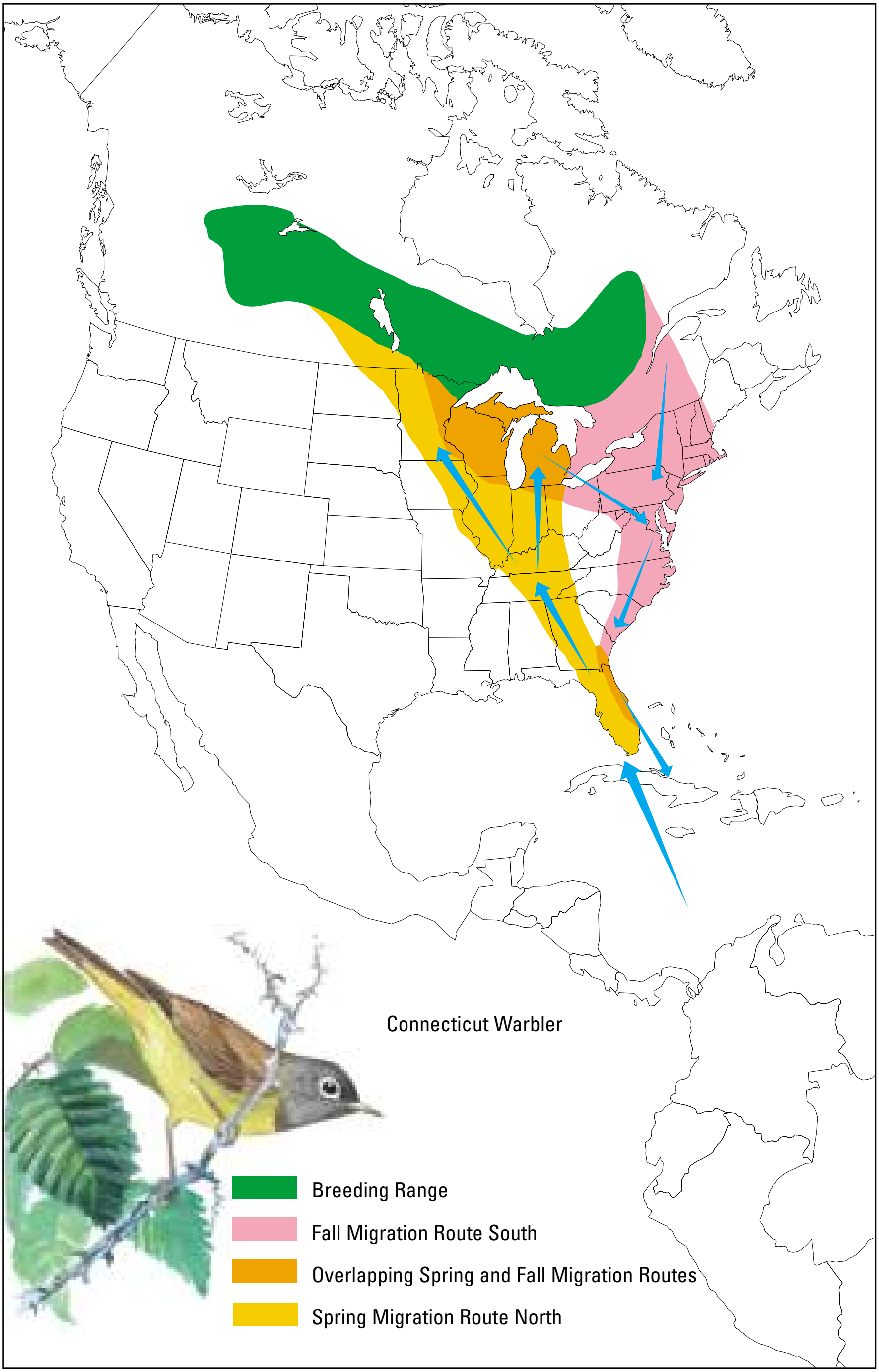

Figure 25. Breeding range and migration routes of the Connecticut Warbler. From the breeding range in northern United States and southern Canada, it migrates east in the fall to New England, then south along the Atlantic coast to Florida and across the West Indies to winter in south America. In the spring it does not return by the same route but rather completes a loop by migrating northwest across the Allegheny Mountains and the Mississippi Valley (adapted from Cooke 1915a)

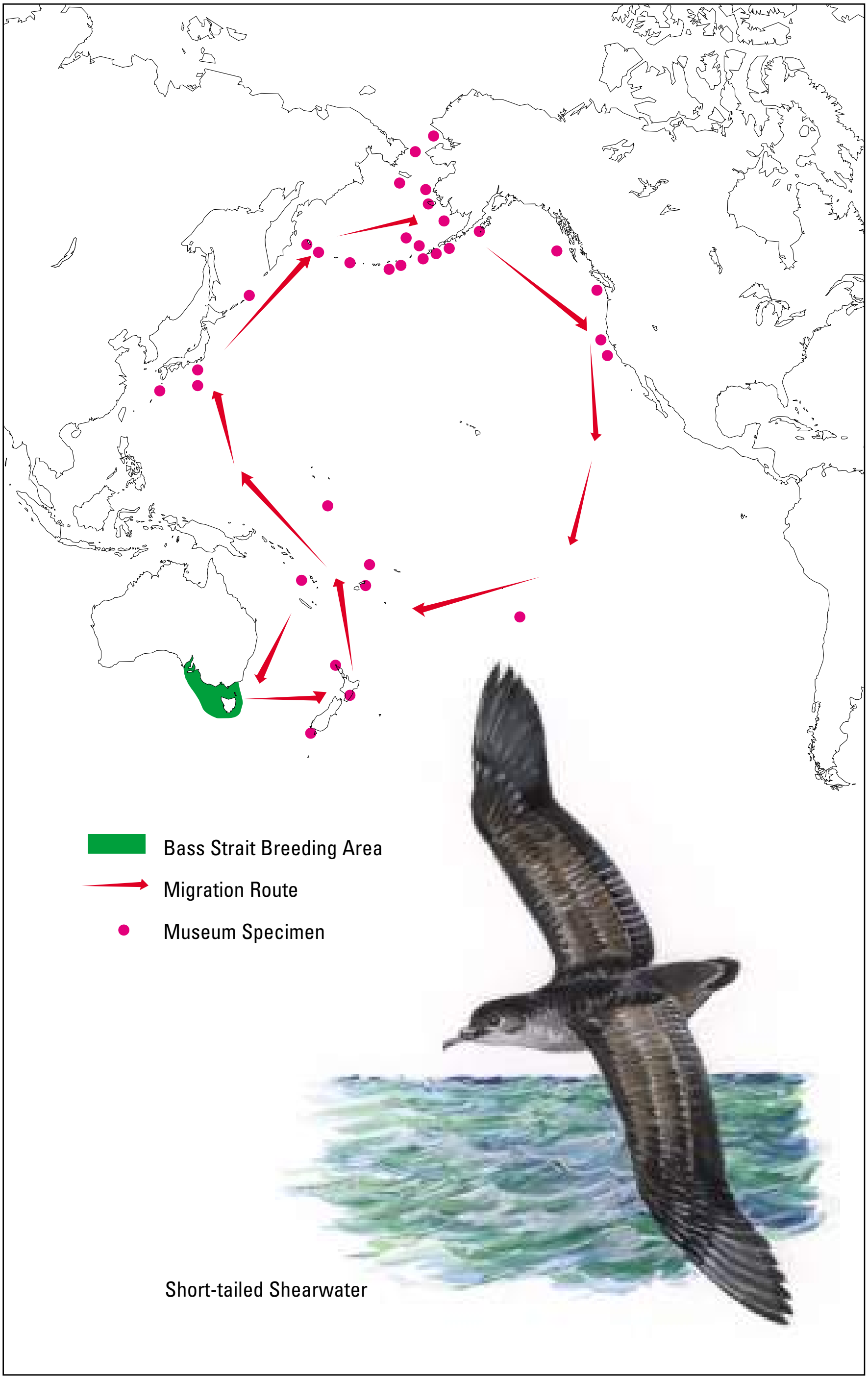

Figure 26. Migration route of the Short-tailed Shearwater. An example of an incredibly large loop migration pattern in a pelagic species. Breeding adults return to two islands in Bass Strait during the last part of October after completing a figure-eight circuit of the northern Pacific Ocean (from Serventy 1953).

Dog-legs

Dog-leg migration patterns are characterized by a prominent bend in the route. Studies have shown some of these indirect pathways connecting wintering and breeding areas are the result of tradition much like the lineage of crooked streets in Boston which can be traced back to old cowpaths. When species have extended their range, many species continue to follow the old route from the original range even if the new areas are not on the same axis as the earlier route. The new extended routes are simply added to the old pathways.

This crooked traditional path can be seen in the routes taken by Old World species extending their ranges into the New World from Europe and Asia. For example, the Northern Wheatear has extended its range into Greenland and Labrador where the local breeding population has become a separate race. When the Labrador individuals depart from their breeding grounds, they proceed north to Greenland, their ancestral home, then east to Europe and south to Africa, the traditional wintering area for all wheatears. Alaskan breeding wheatears migrate to Africa in the opposite direction via Asia where the Alaskan population presumably originated. Alaskan breeding Arctic and Willow warblers and Bluethroats also migrate westward into Siberia and then southward on the Asiatic side of the Pacific Ocean. Some investigators believe the Arctic Tern colonized the New World from Europe because when this bird departs for the south it first crosses the Atlantic to Europe, then moves down the eastern Atlantic coast to Africa and either back across the Atlantic to South America or continues south down past South Africa (Figure 11). To get to South America from the eastern arctic, it would be shorter to follow the American Golden-Plover's flight path straight down the Atlantic or along the east coast of the United States but the fact that no Arctic Terns have been observed in the Caribbean indicates that they do no follow that route.

In western United States, California Gulls nest in various colonies around Great Salt Lake and Yellowstone Park. Banding records indicate these populations winter along the California coast (Figure 27). Instead of traveling southwest by the shortest distance to the wintering grounds, they proceed down the Snake and Columbia rivers and reach the coast around Vancouver. From there they proceed south along the coast to Oregon and California. In the spring the adults return over the same course rather than taking the shorter flight northeast in April across the deserts and mountains; this route would be largely made over a cold and inhospitable country.

Several dog-leg patterns are apparent in the eastern and western populations of the Tundra Swan (Figure 28). In the eastern population, a sharp change in direction occurs at their major feeding and resting areas in North Dakota. After the birds arrive from the arctic breeding grounds, they proceed east-southeast to their wintering grounds on Chesapeake Bay. In the western population, thousands migrate from the Alaskan breeding grounds to the large marshes along Great Salt Lake. Then after a major stopover, this population heads west over the mountains to California.

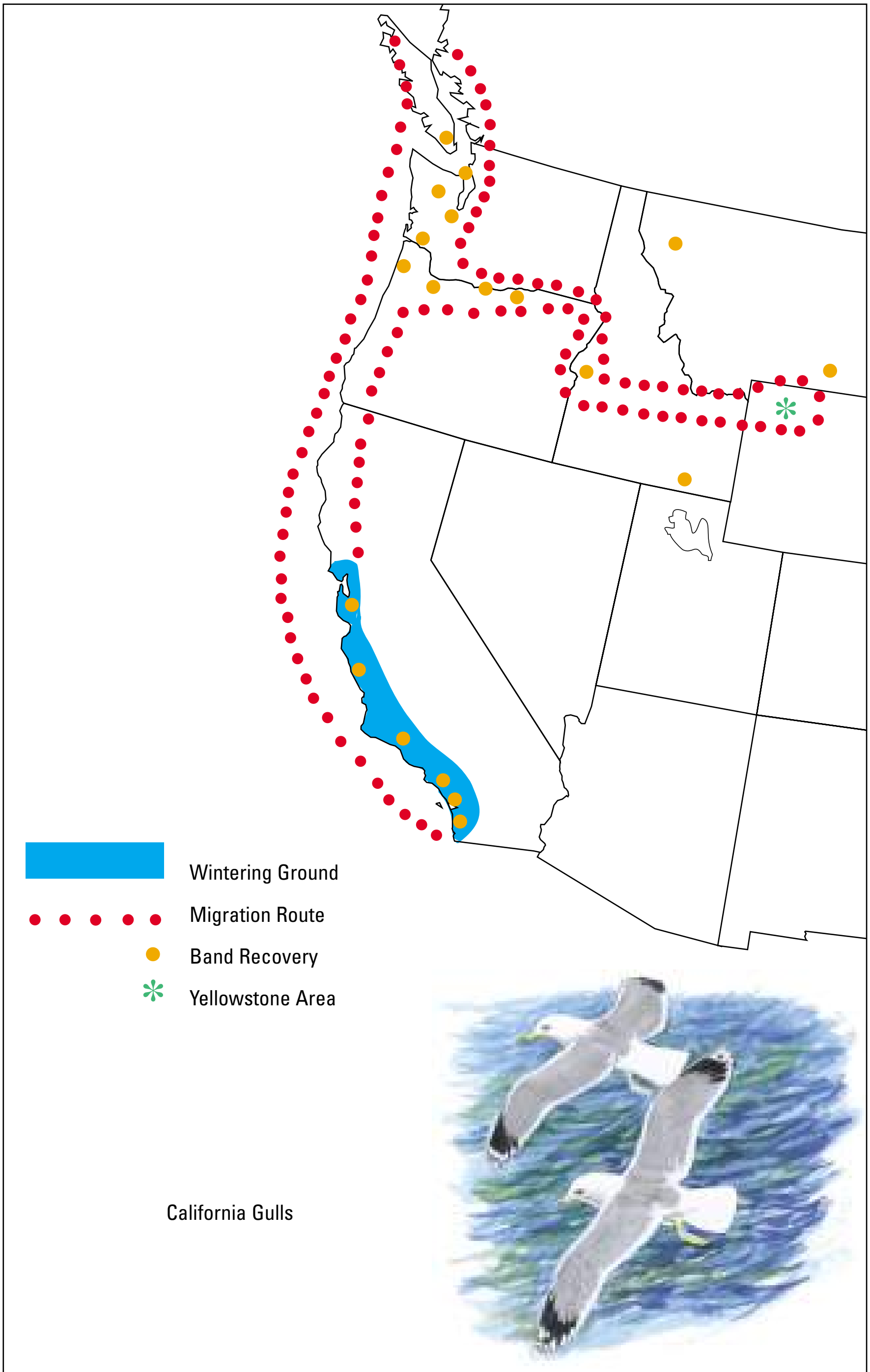

Figure 27. Migration route and wintering grounds of California Gulls banded in northwestern Wyoming. During fall migration, the birds proceed west from the breeding grounds to the Pacific Ocean before turning south to wintering areas in California. A more direct route across Nevada would entail a trip through relatively barren country (after Diem and Condon 1967).

The general trend of migration in most northern populations of North American birds is along a northwest to southeast axis. This again is a reflection of eastern species having extended their ranges by pushing westward. For example, in the Stikine River Valley of northern British Columbia and southwestern Alaska the Common Nighthawk, Chipping

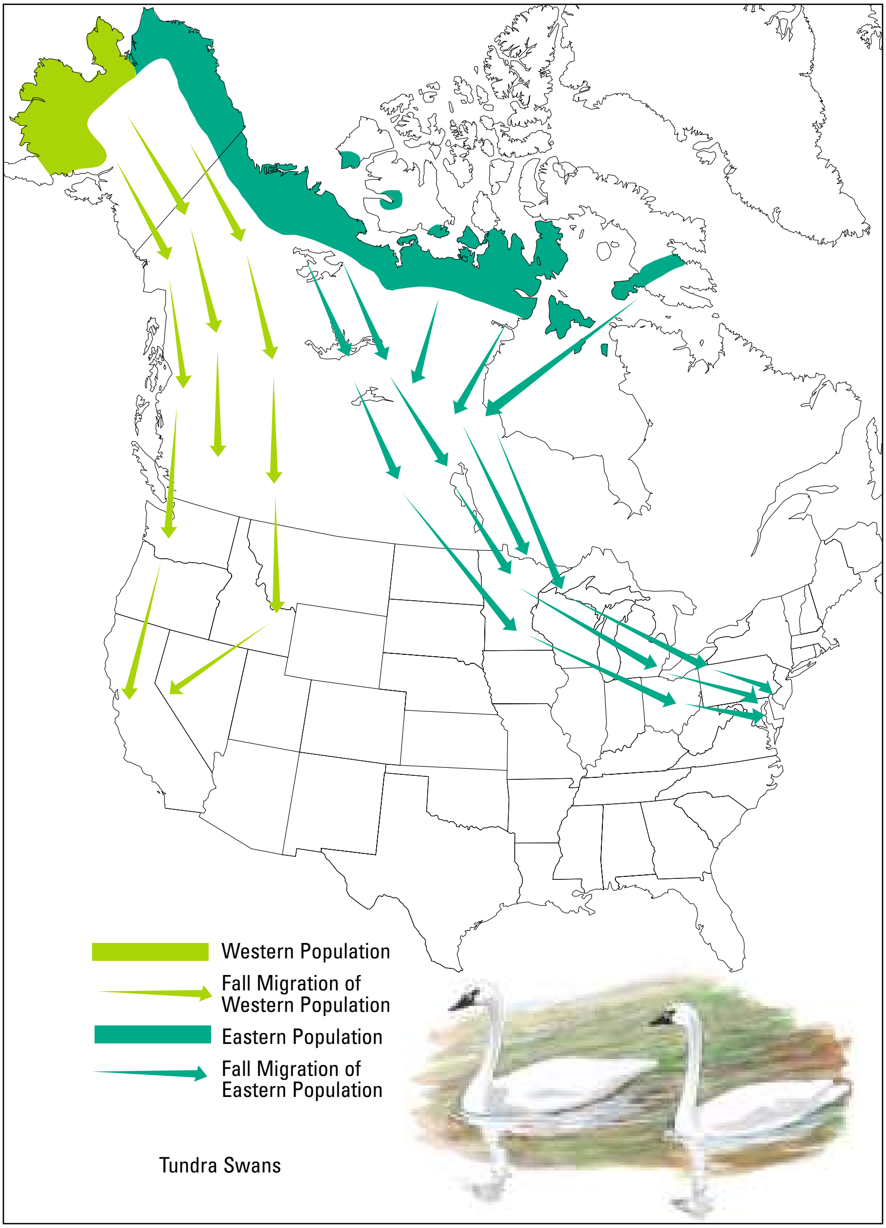

Figure 28. Distribution and migration routes of Tundra Swans in North America. Birds from the central arctic head south to North Dakota before proceeding east to Chesapeake Bay, while many Alaskan breeders migrate to Great Salt Lake before turning west to winter in California (after Sladen 1973).

Sparrow, Rusty Blackbird, Yellow Warbler, and American Redstart have established breeding populations in areas that are just 20 to 100 miles from the Pacific Ocean. The American Robin, Northern Flicker, Dark-eyed Junco, Blackpoll Warbler, Yellow-rumped Warbler, and Ovenbird, all common eastern species, also are established as breeding birds in western Alaska. The Ovenbird has even been detected on the lower Yukon River, and the Sandhill Crane, Pectoral Sandpiper, and Gray-cheeked Thrush have moved across the Bering Strait into Siberia. Yet these birds continue to migrate through the eastern part of the continent. Instead of taking the shortest route south, they retrace the direction of their westward expansion and move southward along the same avenues as their more eastern relatives.

The Red-eyed Vireo is primarily an inhabitant east of the Great Plains, but an arm of its breeding range extends northwest to the Pacific coast in British Columbia (Figure 29). It has been suggested that this range extension has taken place comparatively recently via deciduous woodland corridors, and the invaders retrace in spring and fall the general route by which they originally entered the region.

In the case of the Bobolink, a new extension of the breeding range and a subsequent change in the migration of the species has taken place since settlement by Euroamericans (Figure 19). Because the Bobolink is a bird of damp meadows, it was originally cut off from the western states by the intervening arid Great Plains, but with the advent of irrigation and the bringing of large areas under cultivation, small colonies of nesting Bobolinks appeared at various western points. Now the species is established as a regular breeder in the great mountain parks and irrigated valleys of Colorado and elsewhere almost to the Pacific coast. These western pioneers fly long distances east and west to join the western edge of the route followed by the bulk of the Bobolinks that breed in the northern United States and southern Canada.

Pelagic Wandering

Many of the pelagic birds observed off our coasts appear to be nomadic when they are not breeding. These movements are not necessarily random, because there is usually a seasonal shift in the population, often for great distances and in specific directions, away from the breeding area after completion of the nesting cycle. Also the return from the sea to nesting areas is at a definite time of year.

Observations on the movements of pelagic birds are difficult at best and accurate records are few. We do know some of these species have regular routes (e.g., Arctic Terns) and specific patterns of migration (e.g., the loop in the Short-tailed Shearwater). As more knowledge is accumulated on the "nomadic" species, we may actually find they, too, have regular migration routes.

Movements of some of the tubenoses (albatrosses, fulmars, shearwaters, and storm-petrels) have been correlated with ocean currents, prevailing winds, temperature, and water fertility. Commercial fishermen have long

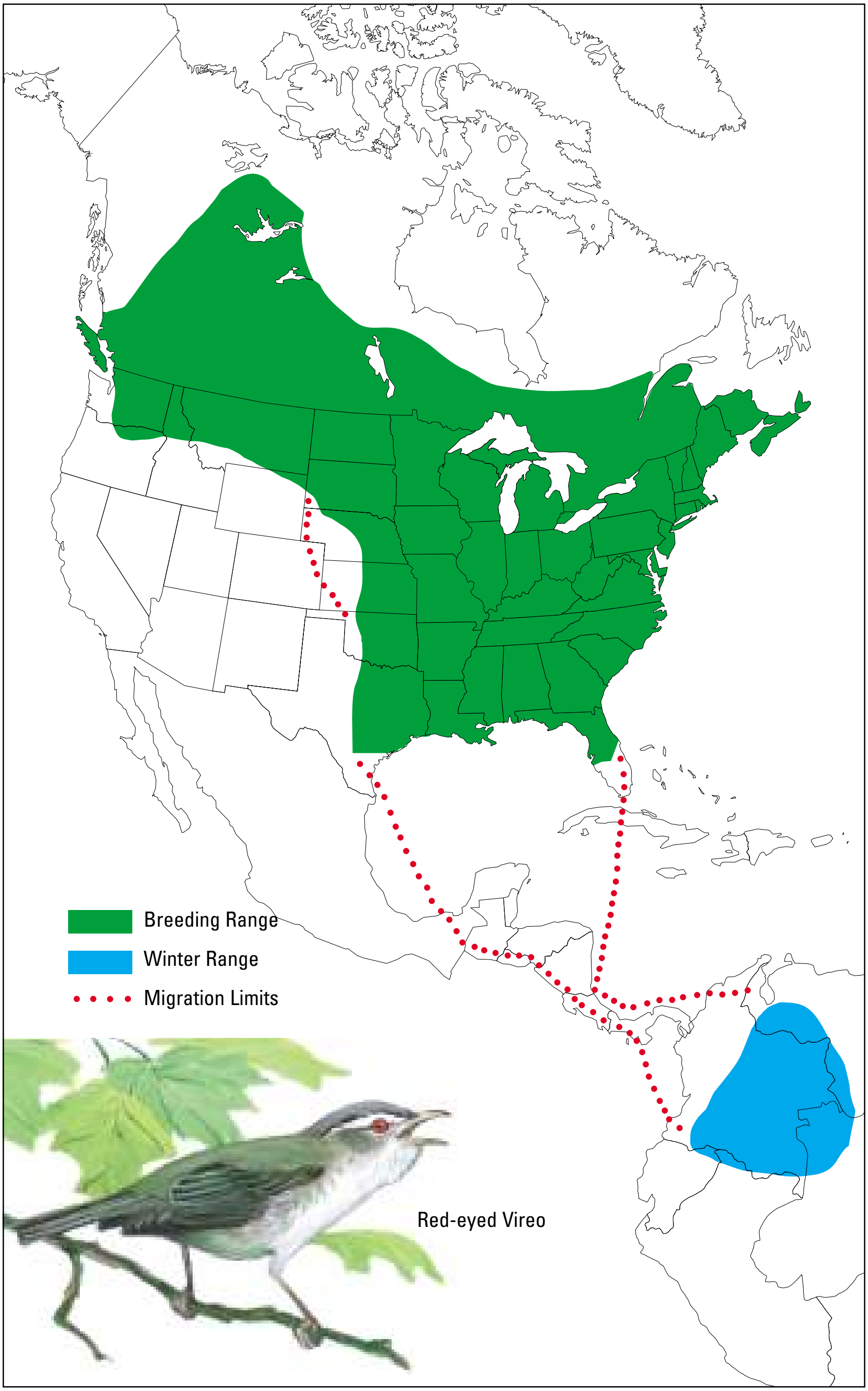

Figure 29. Distribution and migration of the Red-eyed Vireo. It is evident that the Red-eyed Vireo has only recently invaded Washington by an extension of its breeding range almost due west from the upper Missouri Valley. Like the Bobolink (Fig. 19), however, the western breeders do not take the short cut south or southeast from their nesting grounds but migrate spring and fall along the route traveled in making the extension.

known ocean currents are very important factors in the supply of nutrients, plankton, and forage fish for larger fish. These same foodstuffs often attract pelagic birds as evidenced by the tremendous concentrations of birds off the Peruvian coasts where there is an upwelling of cold, nutrient-bearing water. The migration routes of many albatrosses are over temperate marine waters of high biological productivity; that of the Laysan Albatross is correlated with cold currents, while the Black-footed Albatross occurs over warm currents. Many Southern Hemisphere pelagic species have been extremely successful by migrating across the equator to exploit rich northern waters during the North Temperate summer.

Leap-frogging

When two or more races of the same species occupy different breeding ranges on the same migratory axis, the races breeding the farthest north often winter the farthest south. Thus, a northern race "leap-frogs" over the breeding and wintering range of the southern populations. This has been well documented in the Fox Sparrow discussed previously (Figure 10) and has been demonstrated for populations of the Eastern Bluebird.

Vertical Migration

In order to find winter quarters furnishing suitable conditions, many North American birds fly hundreds of miles across land and sea. Others, however, are able to reach satisfactory areas merely by moving down the sides of a mountain. In such cases, a few hundred feet of altitude corresponds to hundreds of miles of latitude. These vertical or altitudinal migrations occur worldwide wherever there are large mountain ranges. Aristotle (cited by Dorst) first mentions vertical migration, ". . . birds in winter and in frosty weather come down to the plains for warmth, and in summer migrate to the hills for coolness . . . "

In the Rocky Mountain region vertical migrations are particularly notable. Chickadees, rosy-finches, juncos, Pine Grosbeaks, Williamson's Sapsuckers and others nest at high altitudes and move down to the lower levels to spend the winter.

The Dark-eyed Juncos breeding in the Great Smoky Mountains and northward to the Blue Ridge make a vertical migration, but other members of the species, breeding in the eastern north woods make an annual north-south migration of hundreds of miles. The young of mountain-breeding juncos work down to the lower levels as soon as the nesting season is over, while the adults come later. The sudden increases in numbers of birds in the foothills are particularly noticeable when cold spells with snow or frost occur at the higher altitudes. In the Dead Sea area of the Middle East, some birds that breed in this extremely hot desert move up into the surrounding cooler hills during the winter.

The vertical migrations of some mountain-dwelling gallinaceous birds (for example, Mountain Quail and Blue Grouse) are quite interesting because the annual journey from breeding to wintering grounds is made on foot.

Mountain Quail make this downward trek quite early in the fall well before any snows can prevent them from reaching their goal. Blue Grouse perform essentially the same journey in reverse. During midwinter, these birds can be found near timberline eating spruce buds protruding above the snow.

Premigratory Movements

Recent banding studies have demonstrated many migrants, especially young of the year, have a tendency to disperse after fledging. These premigatory movements have also been called post-fledging dispersal, reverse migration, and postbreeding northward migration. Demonstration of this phenomenon is especially important as it relates to locality-faithfulness (philopatry), range extension, and gene flow between populations. These movements cannot be considered as true migrations even though they are repeated annually by the species between breeding grounds and some other area, since these movements are generally repeated by the same age class in the population but not the same individuals.

Nevertheless, these regular northward movements are quite striking, especially in herons. The young of some species commonly wander late in the summer and fall for several hundred miles north of the area in which they were hatched. Young Little Blue Herons as well as Great and Snowy egrets are conspicuous in the East as far north as New England and in the Mississippi Valley to Minnesota and Michigan. Black-crowned Night-Herons banded in a large colony at Barnstable, Massachusetts have been recaptured the same season northward to Maine and Quebec and westward to New York. In September most of them return to the south.

These movements have been noted in several other species as well, for example, the northward movement of Bald Eagles along the Atlantic coast (Figure 30). Birds banded as nestlings in Florida have been retaken that summer 1,500 miles away in Canada. Postbreeding northward movements are also shared by Wood Ducks, Yellow-breasted Chats, Eastern Bluebirds, and American White Pelicans.

A somewhat different type of postbreeding migration is the molt migration exhibited by many species of waterfowl. These birds may travel considerable distances away from their nesting area to traditional molting sites where they spend a flightless period in eclipse plumage. At such times they may move well into the breeding ranges of other geographic races of their species. These movements may be governed by the availability of food or a reduction in the chances for predation while they are flightless, This is counteracted in the fall by migration that carries those birds from more northern latitudes after the nesting period back to their normal wintering homes in the south.

Vagrant Migration

The occasional great invasions beyond the limits of their normal range of certain birds, especially species breeding in the far North, are quite differ-

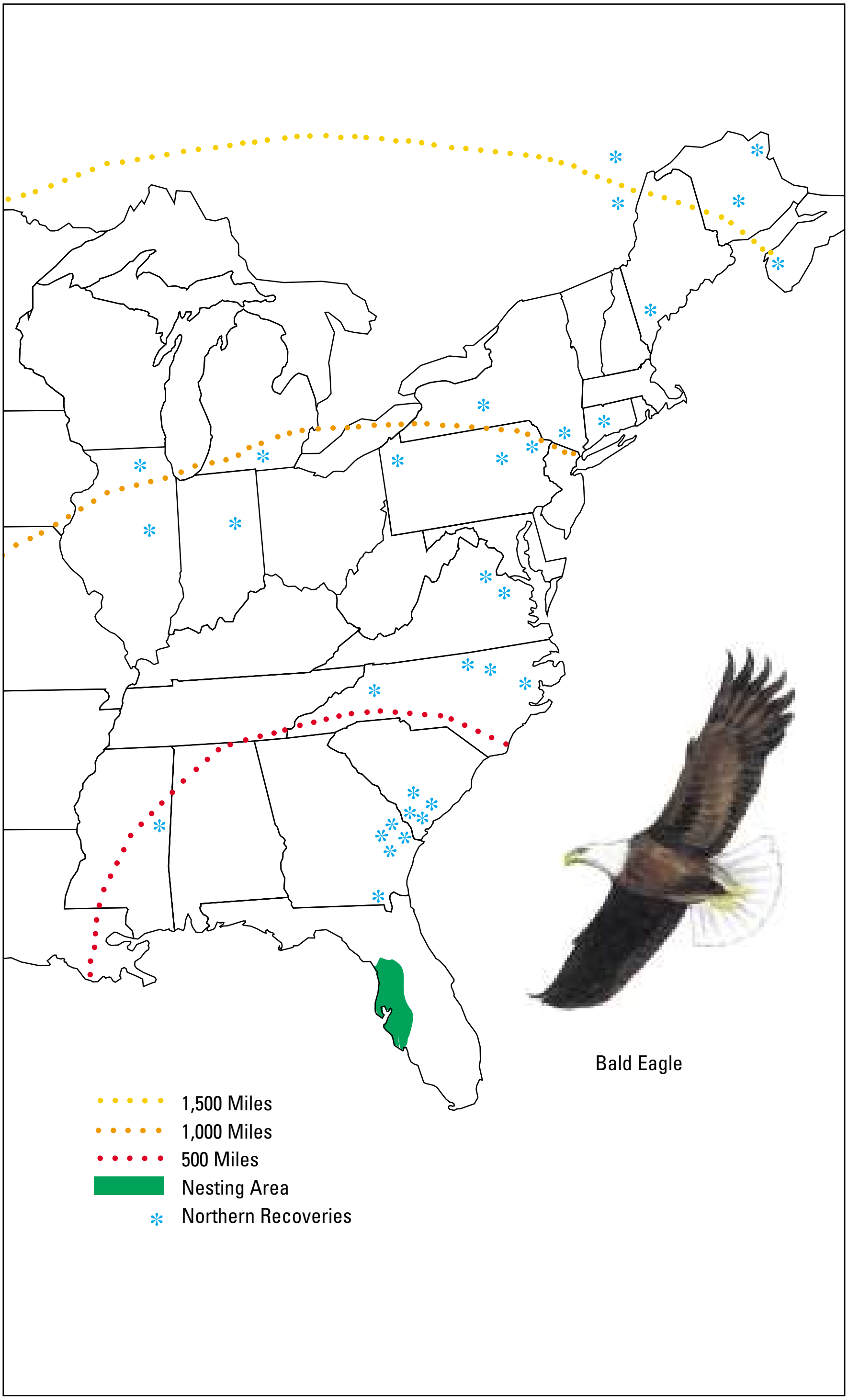

Figure 30. Northern recoveries of young Bald Eagles banded as nestlings in Florida. The birds sometimes "migrate" over 1,500 miles up the coast during their first summer before returning south (from Broley 1947).

ent from migration patterns discussed previously. Classic examples of such invasions in the eastern part of the country are the periodic flights of crossbills. Sometimes these migrations will extend well south into the southern States.

Snowy Owls are noted for periodic invasions that have been correlated with declines in lemmings, a primary food resource of northern predators. The interval between these incursions varied from 2 to 14 years, but nearly half were at intervals of 4 years. A great flight occurred in the winter of 1926-27 when more than 1,000 records were received from New England alone, but the largest on record was in 1945-46 when the “Snowy Owl Committee” of the American Ornithologists’ Union received reports of 13,502 birds, of which 4,443 were reported killed. It extended over the entire width of the continent from Washington and British Columbia to the Atlantic coast and south to Nebraska, Illinois, Indiana, Pennsylvania, and Maryland. One was taken as far south as South Carolina.

In the Rocky Mountain region, flights of the beautiful Bohemian Waxwing are occasionally recorded. The greatest invasion in the history of Colorado ornithology occurred in February 1917, when it was estimated that at least 10,000 were observed in Denver. The previous large occurrence of waxwings in Denver was in 1908.

Likewise, Evening Grosbeaks illustrate similar wanderings. In addition to occasional trips south of their regular range, they will also travel east and west for considerable distances. Evening Grosbeaks banded at Sault Ste. Marie, Michigan have been recaptured in winter on Cape Cod, Massachusetts and in the following breeding season were back at the original banding location. Banding records and museum specimen identifications demonstrate that this east-and-west trip across the northeastern part of the country is sometimes made also by Purple Finches, Red Crossbills, and Mourning Doves.

FUTURE DIRECTIONS

The mystery that formerly cloaked the periodic travels of birds for the writer of Jeremiah has been partly dispelled through our discovering the extent and times of seasonal journeys of most species. Even though we understand more, we still share with the ancients the awe and wonder as we contemplate these twice annual global movements. Indeed, in some ways, what we have learned only makes the phenomenon of migration more amazing! But many gaps still remain in our knowledge. Some of which, like the nature of the bicoordinate system that birds use to identify geographic positions, have barely been explored. Other hypotheses, like the use of olfactory cues for orientation need further verification.

We study migration because we are curious. That suffices as a rationalization for our efforts. Yet there are practical implications of what we discover. Clearly the regulation of hunting pressure on many game animals is dependent upon knowing the patterns and intensities of migratory movements. The protection of nongame bird populations for which our society has recognized its responsibility must similarly rely upon understanding migration. There are even direct economic aspects. Studies have indicated, for example, that local, nonmigratory populations of various blackbirds cause nearly all of the rice damage in southern States, and that "hordes from the North" contribute very little to the losses. In addition, the transport of arborviruses by long distance migrants has direct implications for human health.

While the habitat requirements sought by migratory species on their breeding areas have been the focus of much research and some attention also has been paid to the habitat selection of these species on their winter ranges, we are largely ignorant of the habitat requirements of these species during their migratory journeys. To what extent are the migratory pathways described in this book a reflection of continental habitat patterns that provide the resources necessary at stop-over sites used during migration? Is habitat selection during migration based on the same criteria the species uses on the wintering range or the breeding area? How important to the success of migrating passerines are the forested corridors along major river systems? How important is the density and spatial distribution of wetlands in the migration of waders and waterfowl? If important, how large an area is required to sustain these species during the periods of passage?

The nature and extent of environmental modifications wrought by humans throughout the world are readily apparent, and yet we have little understanding of how migrants are affected by changes in land use or habitat degradation. Extensive forests have been burned or cut away. Rolling prairies have been turned over by the plow and planted in monocultures of tame grasses and row crops. Natural landscapes continue to be obliterated by urban sprawl. Air pollutants carried by continent-spanning winds rain acid depositions on fields, mountains, lakes and forests. Wetlands are drained or filled. Riparian vegetation is lost as rivers disappear under the intensive mining of ground water by irrigators in the arid West. The once slow but now rapidly increasing concentrations of carbon dioxide, methane, and other greenhouse gases generated by human activities will alter global climates, even if we cannot predict with assurance the directions these changes will take.

Migratory pathways evolved over the eons in expectation of a moderately stable environment with sufficient food and cover along appropriate corridors that connected sustaining winter ranges with suitable breeding areas. Still, the environment has always been changing. Except for catastrophic events that punctuated the history of life from time to time, change occurred at gradual rates. This rate of change was slow enough that the processes of evolution allowed bird populations to make compensatory modifications that ensured continued existence. But human impacts on the environment generate rates of change that exceed many species' ability to adapt. A wetland long-used by shorebirds as a critical foraging site on their extended journey from South America to the arctic tundra is drained and cultivated during the short interval between spring and fall passages. Warblers return from the tropics to find clear-cut mountainsides with no other suitable habitat open for their use. Weedy fields that persisted in the floodplains of major rivers and offered cover and food for communities of wintering sparrows down from the north now greet their fall arrival with orderly rows of stuble or the asphalt and lawns of industrial parks. We know that the birds cannot use these altered habitats, but we do not know the consequences of these events on migrant populations. If we decide that we must ameliorate the impacts of these changes, we must first of all know the consequences of these changes.

Not all species are negatively affected by our impact on the environment. While warblers and thrushes breeding in forest interiors may decrease with increased forest fragmentation, edge species will take advantage of the more open habitat and increase. As towns form tree-dominated islands across the Great Plains, many eastern species like the Baltimore Oriole expanded their ranges westward. Feed-grains sustain larger numbers of blackbirds than would not have naturally survived the stress of winter before the development of a large cattle feedlot industry. Dredge spoil offers dependable nesting sites for terns along the Atlantic and Gulf coasts. Airports in the northeast provide perennial grasslands for Upland Sandpipers that traditionally had to rely on limited larger patches on the coastal plain or the ephemeral meadows of forest succession. Yet, the general trend of our effect on the environment is toward uniform sameness; we have reduced the heterogeneity of the landscape. This, in turn, reduces the richness of bird species we experience in our daily lives. And since we as a species have thrived on the diversity in our environment, our quality of life suffers.

The Federal Government of the United States has recognized its responsibility to migratory birds under these changing conditions. Enabling acts allow for carrying out migratory bird treaty obligations in cooperation with other countries, and now most species have legal protection under regulations administered by the U.S. Fish and Wildlife Service. Refuges have been established to foster migratory species. Environmental laws enacted during the latter half of the twentieth century have helped to retard and even thwart environmental degradation. Nongovernmental organizations and state agencies have come to play an increasing role in the protection of migratory birds. Yet the effectiveness of conservation efforts is increased in the same measure that we, the people, become acquainted with migratory bird resource and interest ourselves personally in the well-being of the various species. We are faced with a two-fold challenge. Firstly, our challenge is to develop an ethic that recognizes our stewardship of these resources and that motivates the economic and political choices we make so that we may balance our immediate needs against a sustainable quality of life for future generations. And secondly, we are challenged to gain the understanding that is necessary to implement the good stewardship we desire.

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LIST OF BIRD SPECIES MENTIONED IN TEXT

COMMON NAME	SCIENTIFIC NAME
Albatross, Black-footed	*Diomedea nigripes*
Albatross, Laysan	*Diomedea immutabilis*
Blackbird (European)	*Turdus merula*
Blackbird, Brewer's	*Euphagus cyanocephalus*
Blackbird, Red-winged	*Agelaius phoeniceus*
Blackbird, Rusty	*Euphagus carolinus*
Blackbird, Yellow-headed	*Xanthocephalus xanthocephalus*
Blackcap, Common	*Sylvia atricapilla*
Bluebird, Eastern	*Sialia sialis*
Bluethroat	*Luscinia svecica*
Bobolink	*Dolichonyx oryzivorus*
Bobwhite, Northern	*Colinus virginianus*
Brant	*Branta bernicla*
Bunting, Black-headed	*Emberiza melanocephala*
Bunting, Cretzchmar's	*Emberiza caesia*
Bunting, Indigo	*Passerina cyanea*
Bunting, Ortolan	*Emberiza hortulana*
Bunting, Painted	*Passerine ciris*
Bunting, Snow	*Plectrophenax nivalis*
Canvasback	*Aythya valisineria*
Cardinal, Northern	*Cardinalis cardinalis*
Chat, Yellow-breasted	*Icteria virens*
Chuck-will's-widow	*Caprimulgus carolinensis*
Coot, American	*Fulica americana*
Cowbird, Brown-headed	*Molothrus ater*
Cormorant, Double-crested	*Phalacrocorax auritus*
Crane, Sandhill	*Grus canadensis*
Crossbill, Red	*Loxia curvirostra*
Crow, American	*Corvus brachyrhynchos*
Crow, Hooded	*Corvus corone cornix*
Cuckoo, Black-billed	*Coccyzus erythropthalmus*
Cuckoo, Yellow-billed	*Coccyzus americanus*
Curlew, Bristle-thighed	*Numenius tahitiensis*
Dickcissel	*Spiza americana*
Dove, Mourning	*Zenaida macroura*
Dove, Turtle	*Streptopelia turtu*
Duck, American Black	*Anas rubripesh*
Duck, Wood	*Aix sponsa*
Eagle, Bald	*Haliaeetus leucocephalus*
Egret, Great	*Ardea albus*
Egret, Snowy	*Egretta thula*

COMMON NAME	SCIENTIFIC NAME
Eider, Common	*Somateria mollissima*
Eider, King	*Somateria spectabilis*
Falcon, Eleonora's	*Falco eleonorae*
Falcon, Peregrine	*Falco peregrinus*
Finch, Purple	*Carpodacus purpureus*
Flicker, Northern	*Colaptes auratus*
Flycatcher, Hammond's	*Empidonax hammondii*
Flycatcher, Least	*Empidonax minimus*
Flycatcher, Pacific-slope	*Empidonax difficilis*
Godwit, Black-tailed	*Limosa limosa*
Godwit, Hudsonian	*Limosa haemastica*
Golden-Plover, American	*Pluvialis dominicus*
Golden-Plover, Pacific	*Pluvialis fulva*
Goldfinch, American	*Carduelis tristis*
Goose, Bar-headed	*Anser indicus*
Goose, Cackling	*Branta canadensis minima*
Goose, Canada	*Branta canadensis*
Goose, Emperor	*Chen canagica*
Goose, Ross'	*Chen rossii*
Goose, Snow	*Chen caerulescens*
Goose, Greater White-fronted	*Anser albifrons*
Goshawk, Northern	*Accipiter gentilis*
Grackle, Common	*Quiscalus quiscula*
Grosbeak, Black-headed	*Pheucticus melanocephalus*
Grosbeak, Evening	*Coccothraustes vespertinus*
Grosbeak, Pine	*Pinicola enucleator*
Grosbeak, Rose-breasted	*Pheucticus ludovicianus*
Grouse, Blue	*Dendragapus obscurus*
Gull, California	*Larus californicus*
Gull, Franklin's	*Larus pipixcan*
Gull, Ross	*Rhodostethia rosea*
Hawk, Broad-winged	*Buteo platypterus*
Hawk, Cooper's	*Accipiter cooperii*
Hawk, Red-shouldered	*Buteo lineatus*
Hawk, Red-tailed	*Buteo jamaicensis*
Hawk, Rough-legged	*Buteo lagopus*
Hawk, Sharp-shinned	*Accipiter striatus*
Hawk, Swainson's	*Buteo swainsoni*
Heron, Little Blue	*Egretta caerulea*
Hummingbird, Ruby-throated	*Archilochus colubris*
Jay, Blue	*Cyanocitta cristata*
Junco, Dark-eyed	*Junco hyemalis*
Kingbird, Eastern	*Tyrannus tyrannus*
Kingfisher, Belted	*Megaceryle alcyon*
Kittiwake, Red-legged	*Rissa brevirostris*
Knot, Red	*Calidris canutus*
Lark, Horned	*Eremophila alpestris*
Longspur, Lapland	*Calcarius lapponicus*
Loon, Arctic	*Gavia arctica*
Mallard	*Anas platyrhynchos*

COMMON NAME	SCIENTIFIC NAME
Martin, Purple	*Progne subis*
Meadowlark, Eastern	*Sturnella magna*
Meadowlark, Western	*Sturnella neglecta*
Nighthawk, Common	*Chordeiles minor*
Night-Heron, Black-crowned	*Nycticorax nycticorax*
Oriole, Baltimore	*Icterus galbula*
Oriole, Black-headed	*Oriolus xanthornus*
Oriole, Black-naped	*Oriolus chinensis*
Osprey	*Pandion haliaetus*
Ovenbird	*Seiurus aurocapillus*
Owl, Great Horned	*Bubo virginianus*
Owl, Snowy	*Nyctea scandiaca*
Pelican, American White	*Pelecanus erythrorhynchos*
Penguin, Adelie	*Pygoscelis adeliae*
Phalarope, Red-necked	*Phalaropus lobatus*
Pigeon (Homing)	*Columba livia*
Pintail, Northern	*Anas acuta*
Poorwill, Common	*Phalaenoptilus nuttallii*
Quail, Migratory	*Coturnix coturnix*
Quail, Mountain	*Oreortyx pictus*
Redhead	*Aythya americana*
Redpoll, Common	*Carduelis flammea*
Redstart, American	*Setophaga ruticilla*
Robin, American	*Turdus migratorius*
Robin, European	*Erithacus rubecul*
Rook	*Corvus frugilegus*
Sanderling	*Calidris alba*
Sandpiper, Baird's	*Calidris bairdii*
Sandpiper, Pectoral	*Calidris melanotos*
Sandpiper, Purple	*Calidris maritima*
Sandpiper, Semipalmated	*Calidris pussilla*
Sandpiper, Upland	*Bartramia longicauda*
Sandpiper, Western	*Calidris mauri*
Sandpiper, White-rumped	*Calidris fuscicollis*
Sapsucker, Williamson's	*Sphyrapicus thyroideus*
Scaup, Greater	*Aythya marita*
Scaup, Lesser	*Aythya affinis*
Shearwater, Short-tailed	*Puffinus tenuirostris*
Shearwater, Sooty	*Puffinus griseus*
Shrike, Loggerhead	*Lanius ludovicianus*
Shrike, Red-backed	*Lanius collurio*
Siskin, Pine	*Carduelis pinus*
Snipe, Common	*Gallinago gallinago*
Sora	*Porzana carolina*
Sparrow, American Tree	*Spizella arborea*
Sparrow, Chipping	*Spizella passerina*
Sparrow, Field	*Spizella pusilla*
Sparrow, Fox	*Passerella iliaca*
Sparrow, Harris	*Zonotrichia querula*
Sparrow, Savannah	*Passerculus sandwichensis*

COMMON NAME	SCIENTIFIC NAME
Sparrow, Song	*Melospiza melodia*
Sparrow, Vesper	*Pooecetes gramineus*
Sparrowhawk, Eurasian	*Accipiter nisus*
Starling, European	*Sturnus vulgaris*
Stork, White	*Ciconia ciconia*
Strom-petrel, Wilson's	*Oceanites oceanicus*
Swallow, Bank	*Riparia riparia*
Swallow, Barn	*Hirundo rustica*
Swallow, Cliff	*Hirundo pyrrhonota*
Swan, Tundra	*Cygnus columbianus*
Swift, Chimney	*Chaetura pelagica*
Swift, Common (European)	*Apus apus*
Tanager, Scarlet	*Piranga olivacea*
Tanager, Western	*Piranga ludoviciana*
Tattler, Wandering	*Heteroscelus incanus*
Teal, Blue-winged	*Anas discors*
Tern, Arctic	*Sterna paradisaea*
Thrush, Gray-cheeked	*Catharus minimus*
Thrush, Hermit	*Catharus guttatus*
Thrush, Swainson's	*Catharus ustulatus*
Thrush, Wood	*Hylocichla mustelina*
Turnstone, Ruddy	*Arenaria interpres*
Veery	*Catharus fuscescens*
Vireo, Red-eyed	*Vireo olivaceus*
Vulture, Turkey	*Cathartes aura*
Warbler, Arctic	*Phylloscopus borealis*
Warbler, Blackburnian	*Dendroica fusca*
Warbler, Blackpoll	*Dendroica striata*
Warbler, Black-and-white	*Mniotilta varia*
Warbler, Black-throated Blue	*Dendroica caerulescens*
Warbler, Cape May	*Dendroica tigrina*
Warbler, Cerulean	*Dendroica cerulea*
Warbler, Connecticut	*Oporornis agilis*
Warbler, Golden-winged	*Vermivora chrysoptera*
Warbler, Kentucky	*Oporornis formosus*
Warbler, Palm	*Dendroica palmarum*
Warbler, Pine	*Dendroica pinus*
Warbler, Subalpine	*Sylvia cantillans*
Warbler, Willow	*Phylloscopus trochilus*
Warbler, Worm-eating	*Helmitheros vermivorus*
Warbler, Yellow	*Dendroica petechia*
Warbler, Yellow-rumped	*Dendroica coronata*
Waxwing, Bohemian	*Bombycilla garrulus*
Waxwing, Cedar	*Bombycilla cedrorum*
Wheatear, Northern	*Oenanthe oenanthe*
Wigeon, American	*Anas americana*
Woodcock, American	*Philohela minor*
Wood-pewee, Western	*Contopus sordidulus*
Wren, Cactus	*Campylorhynchus brunneicapillus*
Wren, Canyon	*Catherpes mexicanus*

COMMON NAME	SCIENTIFIC NAME
Wren, Carolina	*Thryothorus ludovicianus*
Wren, Rock	*Salpinctes obsoletus*
Wren, Winter	*Troglodytes troglodytes*
Wrentit	*Chamaea fasciata*
Yellowlegs, Greater	*Tringa melanoleuca*
Yellowlegs, Lesser	*Tringa flavipes*
Yellowthroat, Common	*Geothlypis trichas*

* For all North American species the author has followed nomenclature in the 1983 edition of the A.O.U. Check-list of North American Birds and subsequent supplements. For other parts of the world I have used the most authoritative sources available.