

Birds on the Move

Ecology of Migration and Dispersal

Alice Boyle

Large-scale movements of birds are among the most impressive behaviors in the whole animal kingdom. Seasonal appearances and disappearances of birds have captured human imagination for at least as long as our written history. In Europe, observations of swallows foraging over lakes and ponds led to the belief that they burrowed into the mud under water during winter months (fig. 19.1). Other birds were believed to hibernate as many mammals do, and the replacement of breeding redstarts by overwintering robins in the same areas was thought to represent a “transmutation” or seasonal change in appearance of the same species (Aristotle). Ancient Mayans associated “rivers” of hawks passing over Central America as harbingers of the rainy season (Bassie-Sweet 2008). In the eighteenth century, naturalists proposed that birds went to the moon when they disappeared from Europe in winter. All of these observations instead represent large-scale movements of birds.

Movement is fundamental to interpreting most other aspects of avian biology because flight—the principal form of avian locomotion—is extremely costly (chapters 7 and 10). Thus, allocating energy and time to major movements can

constrain other parts of a bird’s life cycle, such as reproduction (chapter 16) and molt (chapter 9). The distance that birds fly influences the evolution of morphological traits such as wing and feather shape (chapter 6). The ability to fly also means that birds are among the most mobile animals in the world. Being able to fly means birds are better at crossing geographic barriers such as oceans and mountain ranges than many other taxa, permitting them to colonize every continent on Earth (chapter 4). Birds also take advantage of resources found at the highest latitudes and altitudes on earth, in part because of their ability to migrate seasonally away from those extreme environments.

Spectacular feats of long-distance movement are the most impressive of bird movements, but they represent only the most extreme examples of common behaviors. Movement types include foraging and other local movements within home ranges; one-way directional movements that we call **dispersal**; and cyclical, annual, return movements that we call **migration**. We refer to **nomadism** when birds engage in multiple, sequential dispersal events, and to **irruptions** when migratory tendency or distance varies a lot from year to year. Each of these movement types can occur over a wide span of distances, ranging from only a few tens of meters to thousands of kilometers.

While birds’ mobility allows them to take advantage of most of the earth’s surface, that same mobility imposes costs not experienced by more sedentary taxa. Some costs are a direct result of long movements—running out of energy while crossing inhospitable terrain, or colliding with human-made structures during nocturnal flights. Some costs are the indirect result of movement—risks associated with finding food and avoiding predators in unfamiliar sites en route, time spent in movement that precludes other activities, or lingering consequences of movement that affect future health and survival. Adaptations that enable a mobile lifestyle come at



Figure 19.1. Woodcut depicting fishermen hauling in “hibernating swallows” from a lake—an erroneous explanation proposed to explain the seasonal disappearances of birds, which is actually caused by their migration. From Olaus 1996.

evolutionary costs as well—investment in traits that enable long-distance movement constrains investment in clutch size, brain size, and behavioral flexibility. Determining the fitness costs and benefits of alternative strategies is essential to understanding why species exhibit different patterns of movement and why individuals sometimes engage in different movement strategies at different times of their lives. Studying bird migration and dispersal is difficult because the movements themselves take our study subjects away from earthbound researchers. However, technological advances are improving our understanding of movement patterns, making it an exciting time to study movement ecology.

In the pages ahead, we explore the incredible variety of patterns, distances, and gradients over which birds move. We then delve into migration and dispersal in greater detail, in each section highlighting studies investigating proximate and ultimate causes and ecological and evolutionary consequences of such movements. Final sections provide an overview of the major methods ornithologists have used to study migration, and the unique threats birds experience as a consequence of their mobility.

A TAXONOMY OF AVIAN MOVEMENTS

The diversity of animal movements (and indeed, even the dispersal of “sedentary” organisms like trees and fungi) can be understood as the outcome of differences in the animal’s

internal state that affect its motivation to move, navigational capacity, locomotion capacity, and the animal’s external environmental circumstances (Nathan et al. 2008). These factors ultimately determine the multiple types, scales, modes, and directions of movement a bird makes over its lifetime. Even the most sedentary of birds make local movements to find food, commute to roosting sites, and find mates (fig. 19.2). Local movements have not been as well-studied as other avian movements, but as technology increases our ability to document movement at fine temporal and spatial scales, detailed movement tracks of foraging and “ranging” behavior now allow us to test hypotheses explaining variation in those movements (box 19.1 on page 00). For small land birds, foraging movements may cover only a few hectares, but for others, notably pelagic seabirds such as Short-tailed Shearwaters (*Ardenna tenuirostris*), foraging trips routinely traverse more than 1,000 kilometers (Einoder et al. 2011). Even in species that do not travel long distances to find food, unpredictable excursions outside local areas probably occur more often than is generally appreciated. For instance, birds make long forays to avoid bad weather; in April 2013, Golden-winged Warblers apparently retraced 700 km of their migration journey only days after spring arrival just before severe storms hit their breeding sites (Streby et al. 2015). Birds can use long-distance forays to exploit ephemeral food resources or to gather information about the location of potential mates or high quality habitat. That information may later be used



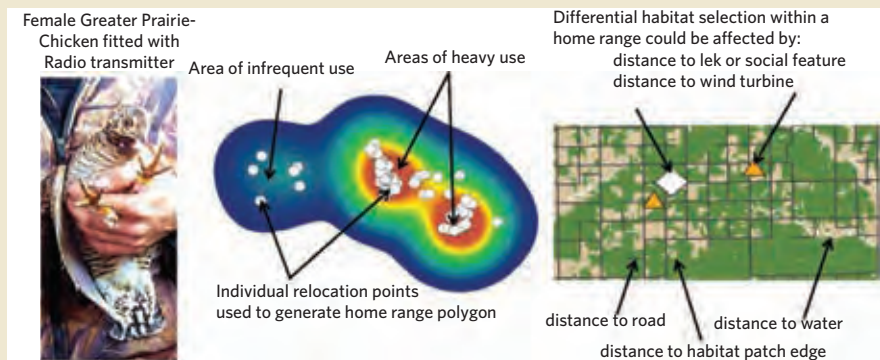
Figure 19.2. Most birds make many types of movement within their lifetimes. (1) Young birds disperse from their natal site to the site where they first reproduce (**natal dispersal**). (2) All birds make movements within their home ranges to forage, seek mates, thermoregulate, and avoid predation. (3) Sometimes birds make longer foraging excursions or **forays** well beyond the limits of their normal home range. (4) Although many species will breed in the same locations year after year, some species engage in **breeding dispersal**, which is a one-way movement to a new home range. (5) Seasonal, return movements between discrete breeding and nonbreeding areas are referred to as **migrations** in the ornithological literature.

TOOLS TO ANSWER THE AGE-OLD QUESTION: WHY DID THE CHICKEN CROSS THE ROAD?

By Virginia Winder

As the price and size of radio and satellite transmitters have decreased, ornithologists have been able to collect data on fine-scale movements of individual birds. Movement data are useful in linking habitat selection to demographic rates and generating vital information to inform conservation decisions. The outline of a home range provides information on *where* an animal is estimated to have been located, but space use within a home range is rarely uniform. Rather, some areas of the home range are heavily used, while others are infrequently used. Resource utilization functions (RUFs) allow researchers to link space use within an animal's home range to landscape features that can help determine *why* animals use certain areas more frequently than others (Marzluff et al. 2004). The analytical process includes four steps: (1) generate a home range polygon using movement data; (2) generate

a utilization distribution or "heat map," representing differential space use within the home range; (3) determine the landscape conditions at each cell within the home range for key resources hypothesized to predict habitat selection decisions; and (4) relate the intensity of space use to resource values on a cell-by-cell basis. We used RUFs to investigate how the installation of wind turbines affected space use decisions of female Greater Prairie Chickens (*Tympanuchus cupido*) in Kansas (Winder et al. 2014). Following construction of the wind energy facility, females avoided areas near wind turbines within their home ranges, even though they had shown no avoidance of eventual turbine sites prior to construction. Long-term persistence of avoidance behavior could result in extirpation of prairie-chickens from this site (see figure).



On left, a Greater Prairie Chicken is fitted with a radio transmitter. This threatened species is dependent on tallgrass prairie of the Great Plains. The central image represents the modeled space use of birds based on points of known occurrence (white dots), determined using telemetry. The warmer the color, the more frequently birds are predicted to use those areas. By overlaying such "heat maps" on the map in the right panel, we can relate hot spots of space use to landscape features such as patches of native grassland (green) and non-habitat (agricultural fields, beige), lek sites (orange triangles), roads (black lines), and wind turbines (white diamonds). Images © Virginia Winder.

to guide dispersal decisions. Some longer-range forays blur the boundaries between migration and dispersal—two immensely important types of movement for birds—which are the topics of the rest of this chapter.

Dispersal is a one-way movement that takes a bird permanently away from its previous home range, and is the only movement that results in gene flow between populations. Virtually all species engage in **natal dispersal**, a one-way move-

ment from the location of the nests birds fledge from to the site where they first reproduce. Some birds also engage in **breeding dispersal**, a one-way movement that takes place between nesting bouts. Both types of dispersal can result in species-level range shifts (often, confusingly, called "migration" in other branches of biology; box 19.2 on page 00). Key attributes of avian **migratory** behavior involves annual, cyclical, to-and-fro movements between different breeding and nonbreeding

ranges, with some element of predictability in the direction of movements and the timing of departures and returns. When all individuals in a species engage in similar, often innately controlled movements, those migration or dispersal strategies are often treated as species-level traits. However, within species, different populations and individuals often vary greatly in their movements. **Partially migratory** species or populations comprise some individuals that migrate and others that do not. **Differential migrants** are species in which identifiable

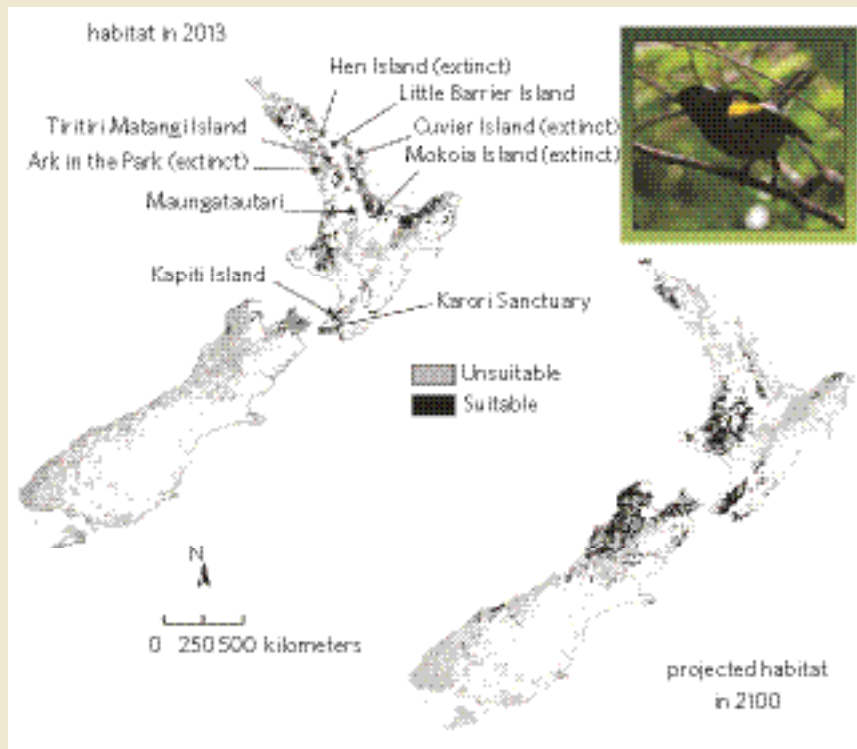
groups of individuals differ in migratory distance or timing, or both (Terrill and Able 1988). Even though annual, cyclical migrations can span very large spatial scales, migrants often have low rates of breeding dispersal, resulting in high **site fidelity**, meaning they return to the same site (or even the same territory) in successive years. Hence, migration does not necessarily result in gene flow, unlike dispersal movements.

Understanding many aspects of migration and dispersal ecology requires that we study the behavioral choices made

WHEN DISPERSAL CAN'T KEEP PACE WITH CLIMATE CHANGE

Assisted “migration” (or colonization) is human-assisted establishment of populations outside their current range. It is a highly controversial conservation tool that is becoming increasingly relevant for species endangered by shrinking areas of suitable climatic conditions and those unable to disperse to the new areas where those same climates will occur in future decades. Land managers help populations disperse using the same methods as they do in reintroduction programs, except with added risks because the species being moved was never historically part of the community to which they are introduced. Because birds are relatively good dispersers, they have less need of assisted migration than do less mobile organisms. However, birds like the endan-

gered Hihi or Stitchbird (*Notiomystis cincta*) may require such dramatic intervention in order to survive (Chauvenet et al. 2013). The Hihi was extirpated on all but one tiny island adjacent to the North Island of New Zealand and has subsequently been reintroduced to a handful of other small islands and sanctuaries. Because climate drives population dynamics of this species, and climate change is pushing suitable habitat southward, the species will likely not persist without translocations to safe sites where climates are expected to be appropriate well into the future. In the case of the Hihi, survival might be dependent on translocation to New Zealand’s South Island where they were not found historically (see figure).



As with many native New Zealand birds, the Hihi (inset) was driven nearly to extinction by predators that accompanied European settlers. They now exist in the wild in only five of nine historic populations (starred locations). Black shading in upper left map depicts current distribution of suitable habitat, and gray shading depicts other native forests that are currently unsuitable because of climate. The lower right map depicts the projected distribution of suitable climatic conditions in the year 2100 under a “middle of the road” climate change scenario. Very little suitable habitat is projected to remain by 2100 in areas where the bird currently persists, and more suitable habitat may be found in the South Island, well beyond the dispersal capabilities of this species. Hihi image © David A. Rintoul. Maps reproduced with permission from Alienor Chauvenet and John Wiley & Sons, Inc.

by individuals. Indeed, one definition of migratory movements is based on behavioral and physiological syndromes. Dingle (1996) defines migration as “persistent, straightened-out movement effected by the animal’s own locomotory exertions . . . [that] depends on some temporary inhibition of station-keeping responses, but promotes their eventual disinhibition and recurrence.” In other words, migrations differ from regular day-to-day movements by being more directional, and, while migrating, animals temporarily ignore cues (such as encountering a rich food source) that would normally cause them to stop moving. In birds, long-distance migrants almost certainly exemplify such behaviors in spades. Nevertheless, the application of Dingle’s criteria to classify movement in wild animals is challenging because we lack detailed knowledge of the patterns and mechanistic control of most movements. Furthermore, by emphasizing attributes of the movement path and responsiveness to cues, this definition does not distinguish between one-way (i.e., dispersal) and round-trip movements (i.e., migration).

The differences between migration and dispersal are important to the study of ecology, evolution, and conservation. Scaling up from individuals to populations, a key feature of migration to avian population biology lies in the sometimes huge mortality costs; vast numbers of birds die while migrating. In contrast, dispersal is central to population biology because it is the mechanism by which individuals move in and out of populations and colonize new areas. Population biologists need to know how many birds that disappear from a population dispersed (i.e., emigrated) away, rather than died, and the extent to which the influx of dispersing (i.e., immigrating) individuals “rescue” that population demographically. Scaling up from populations to species, we encounter new definitions and reasons to differentiate between migration and dispersal. Selection for dispersal behavior can occur on different traits and for different reasons than selection for migratory behavior. Species can be highly **philopatric** (the propensity for young to return to breed for the first time at their natal site—the inverse of natal dispersal) or have high **site fidelity** (returning in successive years to the same breeding site—the inverse of breeding dispersal), yet migrate thousands of kilometers between breeding seasons. Conversely, species can forgo round-trip migrations but exhibit low site fidelity. It is impossible to infer anything about dispersal from looking at a species’ range map, but range maps do tell us something about migration when breeding and nonbreeding ranges do not fully overlap—birds must be moving between areas seasonally for such geographic patterns to emerge. Classification of movement at broad geographic scales and at higher levels of biological organization becomes both more difficult and less

accurate. Do we classify species as migrants or nonmigrants when migratory movements occur entirely within their year-round distribution? Such challenges are typical when applying categorical labels to traits that vary continuously in nature. Categories can be useful, but movements are flexible, individual-level behaviors, and researchers must apply criteria to distinguish between behaviors that make the most sense in the context of their scientific questions.

MIGRATION

Patterns

How common is migration? Estimates of the proportion of the world’s bird species making migrations range from ~20 percent to over 50 percent (Fretwell 1972, Berthold 2001, Kirby et al. 2008). But those estimates represent minima for two reasons. First, the lower estimates are based on range-level characterizations (such as nonoverlapping breeding and wintering ranges), which eliminates all but the longest-distance, complete migrants. Second, the movements of many species are completely unknown. Thus, global estimates and most macroecological studies of migration do not include short-distance and partial migrants that constitute a large fraction of migratory bird diversity (Berthold 2001). The prevalence of migration varies geographically. In both the Old and New World, the proportion of migratory species increases steadily from subtropical latitudes toward the arctic (Newton and Dale 1996a, Newton and Dale 1996b, Kuo et al. 2013). Interestingly, the same patterns are not as strong in the Southern Hemisphere. Migration in southern continents (**austral migration**) tends to involve fewer complete, obligate, latitudinal migrant species, more partial migrants, and more complex spatial patterns (Chesser 1994; fig. 19.3). These hemispheric differences have been attributed to smaller landmasses of Southern Hemisphere continents, geographic idiosyncrasies of barriers and continental shape, and a stronger influence of precipitation on climatic seasonality in southern than in northern regions. Migrants are drawn from most major clades of extant birds, and most avian orders contain both migratory and nonmigratory representatives. However, certain clades, such as the New World Warblers (Parulidae) or shorebirds and plovers (Scolopacidae and Charadriidae) contain a preponderance of migrants, while others, such as the antbirds (Thamnophilidae) or the ratites are primarily nonmigratory.

Bird migrations traverse many types of gradients. Latitudinal (i.e., north–south) gradients are the most common, but birds also migrate along elevational gradients. **Altitudinal** (or **elevational**) **migrants** move up and down between breeding and nonbreeding ranges along the slopes of all major

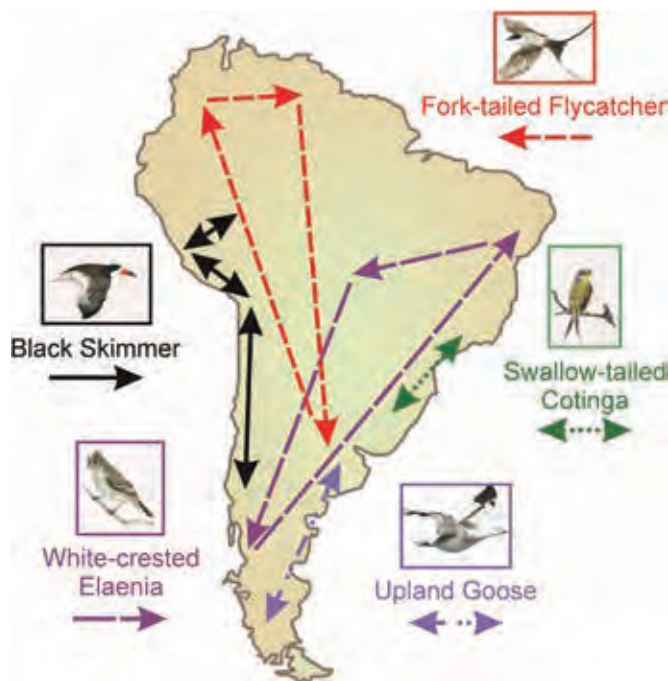


Figure 19.3. Examples of diverse patterns of seasonal migration within South America. References for each species are as follows: Fork-tailed Flycatcher (*Tyrannus savanna*, Jahn et al. 2013); Black Skimmer (*Rynchops niger*, Davenport et al. 2016); Swallow-tailed Cotinga (*Phibalura flavirostris*, Snow et al. 2016); White-crested Elaenia (*Elaenia albiceps*, Bravo and Cueto 2015); Upland Goose (*Chloephaga picta*, Carboneras and Kirwan 2016). Map by Alex E. Jahn; drawings by Caitlin Wiechman.

mountain ranges on every continent except Antarctica. In a few regions, ornithologists have estimated the percentage of species in a community that migrate altitudinally; those estimates are typically around 10–20 percent (Stiles and Skutch 1989, Johnson and Maclean 1994, Nosedal 1994, Burgess and Mlingwa 2000, Bildstein 2004, Boyle 2017). Rarely, birds migrate over longitudinal gradients, especially in regions with strong east–west precipitation gradients, such as in central North America (Prairie Falcons, *Falco mexicanus*), or in subtropical South America (Golden-rumped Euphonias, *Euphonia cyanocephala*; Areta and Bodrati 2010). The distance that birds migrate varies hugely, regardless of the gradients they traverse. In particular, some latitudinal migrants make migrations of as little as tens or hundreds of kilometers such as Lewis’s Woodpecker (*Melanerpes lewis*). Others, such as Bar-tailed Godwits (*Limosa lapponica*), migrate tens of thousands of kilometers in nonstop oceanic flights of nine days. When breeding and wintering distributions overlap, determining what individuals do in the zone of overlap is not straightforward: Are some birds year-round residents, while the birds that breed at high latitudes migrate past them to lower lat-

itudes in what is known as **leapfrog migration**? Or do all populations shift synchronously toward lower latitudes or altitudes, known as **chain migrations**? Both patterns occur. For instance, tundra-breeding Peregrine Falcons (*Falco peregrinus*) migrate to southern South America, passing by shorter-distance migrants and residents of the same species along the way. In contrast, the most northerly-breeding Dunlin (*Calidris alpina*) spend their winters at more northerly wintering locations than do Dunlins breeding farther south, resulting in a chain migration pattern (fig. 19.4A). The extent to which breeding populations of migrants intermix with others during the nonbreeding period is termed **migratory connectivity**; when all individuals of a population overwinter together in the same region, and each population of the species occupies different wintering areas, the populations have very high connectivity, whereas when breeding populations intermix completely during winter, they have low connectivity (Boulet and Norris 2006) (fig. 19.4B). Knowledge of migratory connectivity is crucial for understanding how events that occur during one season influence migrants in later season (termed **carryover effects**), and for implementing **full-life-cycle conservation** (Marra et al. 2015).

Species in which all individuals migrate every year are considered **complete migrants**. In contrast, species of **partial migrants** comprise both migrants and year-round residents. Variation in migratory behavior can occur within populations (i.e., some individuals migrate, others remain resident), or at the population level (i.e., some populations are completely migratory, others are completely resident). Even within complete migrants, age or sex classes often vary in the distance they migrate; this is called **differential migration**. For instance, female Western Sandpipers travel farther south than do males, and within sexes, younger birds winter farther from the breeding grounds than do adults (Nebel et al. 2002). Differential migration is often associated with **protandry**—the tendency of males to return to breeding grounds earlier than do females. Protandry is common in male-territorial species, in which a male’s reproductive success depends on the quality of the territory he can acquire and defend (chapter 16). Multiple variations on migratory behavior often occur within a single species. The common and widespread American Robin (which gets its scientific name *Turdus migratorius* for its migratory behavior) comprises long-distance latitudinal migrants that breed in Canada, altitudinal migrants that breed in mountains, and residents breeding in Mexico. Some robin populations are completely migratory, others are partially migratory, others do not migrate at all, and migration distances range from tens to thousands of kilometers.

Despite all the complexity and variation, latitudinal migrants often follow major “flyways” (fig. 19.5), which are

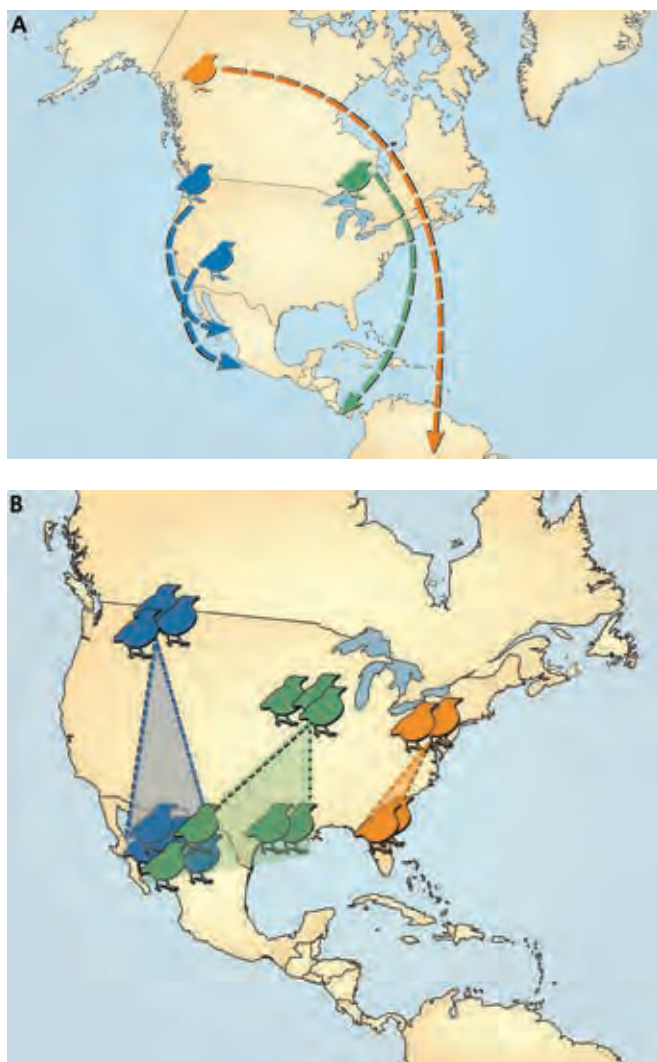


Figure 19.4. *Top:* Different breeding populations of the same species (e.g., blue birds) sometimes all migrate similar distances, with northern-breeding birds spending the nonbreeding seasons at more northerly wintering locations than southern-breeding birds. Such patterns of migration are termed chain migrations. Alternatively, birds can exhibit “leapfrog” migration patterns in which a more northern-breeding species or population (e.g., orange birds) migrate over both the breeding and wintering locations of more southern-breeding species or populations (e.g., green birds).

Bottom: The degree of migratory connectivity refers to the extent to which different breeding populations mix during the winter in their nonbreeding range. The orange breeding populations in this figure display high migratory connectivity—all birds migrate to the same wintering areas. Severe habitat loss to that one wintering site could potentially wipe out the whole breeding population in the orange part of the range. By contrast, the green breeding populations display weak connectivity—the birds breeding in one area spread out over multiple wintering areas. The blue breeding populations are intermediate. They spread out a bit on their wintering grounds, and mix with the green birds in some parts of their nonbreeding range.

equivalent to superhighways used by large numbers of individuals and species when crossing continents. Flyways are most clearly defined where routes are constrained by geographic features. For example, the mountain ranges running down the spine of the Americas create uplift exploited by a river of migrating raptors each fall and spring that attracted the attention of the ancient Mayans. The location of mid-continental wetlands also concentrate waterfowl into crucial **stopover** areas where birds refuel mid-journey. Some long-distance migrants spend over 30 percent of their lives migrating, and of that time, they can spend 70 percent at stopover sites, where they must avoid dying from predation, weather, or starvation; refuel to successfully complete their migrations; and do all this on a tight time budget (Hedenstrom and Alerstam 1997, Sillett and Holmes 2002). Small land birds funnel through land bridges linking Europe and Africa, such as the Strait of Gibraltar and routes along the coasts of Israel and Egypt. By doing so, birds avoid the risks of open-water Mediterranean crossings. The direction of prevailing winds affects migration routes and can lead to different northward and southward patterns. Tiny, 12-gram Blackpoll Warblers (*Setophaga striata*) travel north in spring through forests of eastern North America to breed in Canada’s boreal forests. Remarkably, their southward fall journeys trace a vast arc over the western Atlantic. Birds depart from the Maritime provinces and New England and do not make landfall until reaching the northeast coast of South America, exploiting northeasterly trade winds during the latter part of this journey (DeLuca et al. 2015). Such **loop migration** patterns are common, and can reflect seasonal and spatial differences in stopover habitat quality (such as food availability) as well as in-flight environmental conditions.

Proximate Causes and Control of Migration

Migration is controlled in different ways in different species. In some lineages, migration is culturally transmitted. Most waterbirds learn their migration routes from their elders—a fact that makes their migratory behavior very flexible in the face of changing environmental conditions. However, cultural transmission means that migratory behavior can be lost during severe population bottlenecks. One such loss occurred in the past century: all Whooping Cranes (*Grus americana*) today are descendants of only 15 migratory individuals alive in 1942. Through intensive captive-breeding, the species has recovered to a few hundred individuals. But when this species was first reintroduced to eastern North America, young cranes had to be trained to follow costumed caretakers in ultralight aircraft, eventually being led across the continent on their first migrations (Urbanek et al. 2010; fig. 19.6). Other types of **facultative migrations** do not involve cultural

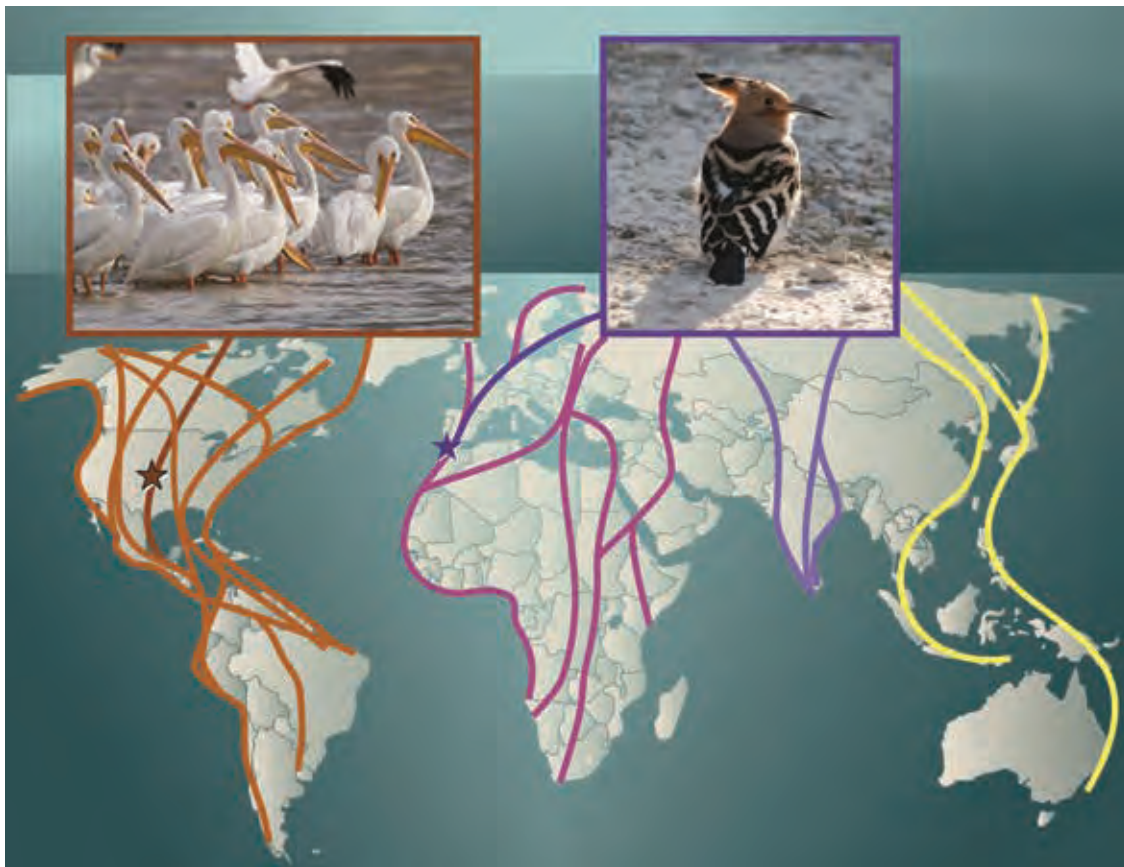


Figure 19.5. Examples of some of the major migratory flyways worldwide. Waterbirds such as American White Pelicans (*Pelecanus erythrorhynchos*, left) use isolated wetlands in the Great Plains as stopover sites in the central flyway (dark orange star). Hoopoes (*Upupa epops*, right), like many other European birds, converge on narrow land

bridges or geographic features (dark purple star) that offer short overwater routes around the Mediterranean to reach wintering areas in Africa. Photo of American White Pelicans by Mark Herse; Hoopoe image © 2005 David A. Rintoul.

transmission, but are similar to the above example in that they involve flexible responses to interacting sets of external and internal cues.

Obligate migrations are controlled endogenously via genetic programs. This means that young birds raised from the egg in the lab can successfully complete their first migratory journey without ever interacting with conspecifics. Indeed, the adults of many long-distance migrant songbirds and shorebirds depart breeding areas well before their offspring, leaving young to complete development and make their first migrations alone, often during nocturnal flights. Given the appropriate environmental cues, obligate migrants are hard-wired to migrate every year. Apparently, the most efficient way to package the complex information required to time migration and navigate over unknown territory is in a hard-wired genetic program. Such programs control integrated sets of physiological and behavioral adaptations that are turned on and off twice each year. In a series of classic experiments on Eurasian Blackcaps (*Sylvia atricapilla*), Ber-

thold (box 19.3 on page 00) demonstrated that migration can be a heritable behavior controlled by multiple genes. First, he brought individuals from completely migratory and completely resident populations into a “common garden.” Birds from the migratory population exhibited migratory tendencies (measured via expression of pre-migratory restlessness or *Zugunruhe*; box 19.4 on page 00) and those from the resident population did not. In doing so, he showed that environmental conditions are not the proximate cause of differences in migratory behavior in Blackcaps. Then, Berthold cross-fostered eggs from migratory individuals into the nests of residents and vice versa. Offspring of migratory parents still exhibited migratory tendencies, demonstrating that the causes of their behavioral differences were genetic. Berthold then interbred migrants and residents, creating a population that exhibited intermediate migratory tendencies. He performed a selection experiment, mating the most migratory individuals with each other and the least migratory together. In only six generations, he had fully migratory

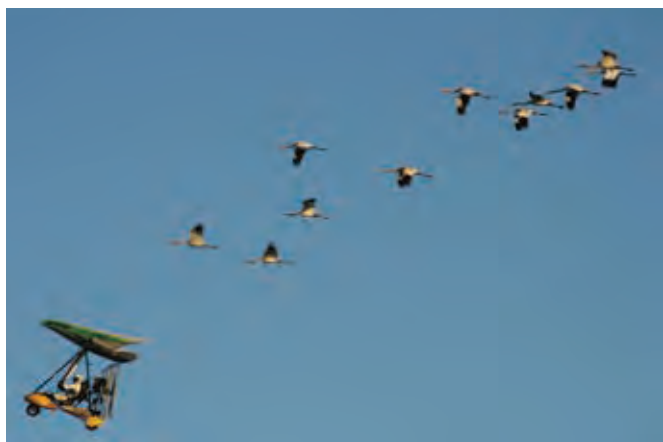


Figure 19.6. Captive-reared Whooping Cranes learning their migration routes from human trainers in ultralight aircraft. Photo by H. Ray, Operation Migration USA Inc.

and fully resident populations once again (Berthold 1999; fig. 19.7).

What exactly does a genetically controlled migratory “program” consist of? It is the interrelated navigational components controlling timing, distance, and direction. The correct **migratory phenology**, or timing of migratory journeys, is critical to a migrant’s fitness. Departing temperate breeding grounds too late puts birds at risk from possible death during early winter storms (Wellicome et al. 2014). Departing wintering areas too late can mean a late arrival to breeding grounds, compromising reproductive success (box 19.5 on page 00). Correct timing also operates at finer time-scales, such as deciding when to depart stopover areas for risky legs of migratory journeys. Traveling the correct distance involves ending migrations at the right time. This does not merely involve stopping flying, because most birds must stop regularly to refuel along the way. Migration requires, by Dingle’s definition, that birds stop ignoring the cues that would regularly induce them to resume “station-keeping” behavior. Ending migratory journeys involves responding to those cues once again. Migrating in the correct direction is of course key to going the correct distance, and requires that birds possess an internal compass. Navigational systems can involve serial sets of directions and distances can create an endogenous flight plan, but to integrate that plan, birds must also possess a refined map sense and a well-tuned internal clock. We know that birds use multiple sources of information to determine their locations, correctly sense direction, and regularly calibrate their navigation systems. These mechanisms include the ability to see and interpret information from polarized light and sun angles, sense geomagnetic sensitivities, and use celestial navigation, as well as possessing an accurate circannual clock and long-term

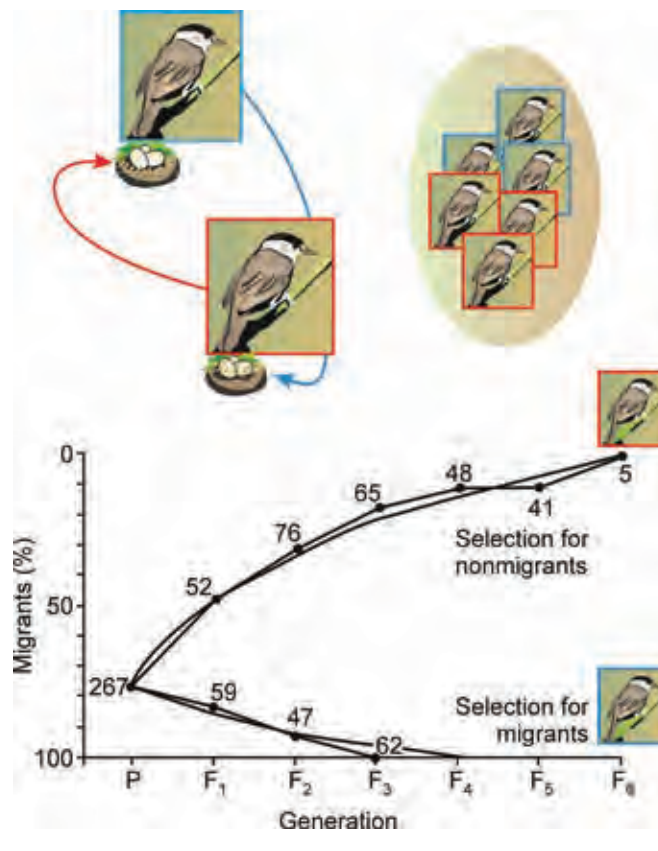


Figure 19.7. Some key experiments and results demonstrating the genetic basis for migratory behavior. Upper left, eggs from an obligate migrant population of Blackcaps (blue boxes) were reared by birds in a nonmigratory population (red boxes), and offspring exhibited the migratory tendencies of their biological rather than their adoptive parents. Upper right, birds from both migrant and nonmigrant populations were bred and raised in a common aviary, and offspring exhibited ancestral migratory tendencies. The lower panel depicts the outcome of selective breeding from a pool of hybrid individuals (crosses between migrant and resident populations) resulting quickly in fully migratory and resident lines. Selection figure reproduced from Berthold et al. 1990 with permission from Springer.

spatial memory (chapter 12). The extent to which different species use different navigational senses, and how birds integrate disparate sources of information, remains an area of active research (Alerstam 2006). The topic of avian navigation and orientation is a large and fascinating field of study (Wiltschko and Wiltschko 2003, Wiltschko and Wiltschko 2009, Deutschlander and Beason 2014, Holland 2014, Willemoes et al. 2015); unfortunately, a detailed discussion of this subject is beyond the scope of this chapter.

Beyond determining when and where to go, genetically controlled migratory programs also must include mechanisms that physiologically prepare birds for long flights and regulate and optimize moment-to-moment responses to internal and

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Professor
Dr. Peter Berthold. Photo
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Dr. Peter Berthold is a German ornithologist who, as a boy, became fascinated with birds, observing them with binoculars left over from World War II. By the age of 16, he had joined the German Ornithological Society; he proceeded eventually to a PhD at the University of Tübingen, embarking formally on the study of bird migration. He spent his long and illustrious career at the Vogelwarte Radolfzell and is best known for his groundbreaking research on the genetic basis for migratory behavior. This work involved, at one time, immense aviaries in which Berthold kept up to 2,000 Blackcaps. Berthold has been incredibly prolific, writing dozens of books and ~450 scientific articles on many topics in avian biology. His *Bird Migration: A General Survey* (Berthold 2001) synthesizes much of his life's research and learning on migration. In recent years, he has devoted a good deal of his attention to conservation (see figure).

external information. Birds are sensitive to environmental cues that trigger neuroendocrine pathways, which, in turn, result in suites of physiological and behavioral pathways (Ramenofsky et al. 2012). In obligate migrants, the cues that trigger migratory behaviors are rarely the same as the factors that ultimately shape those migrations. Obligate migrants typically depart before experiencing the severe winter weather or food shortages that can act as ultimate selective factors shaping migratory behavior. Consequently, effective proximate cues convey reliable information about future en-

vironmental conditions. Changes in day length are the most important of such cues. The hypothalamic-pituitary-gonadal axis (HPG) responds to changing photoperiod (chapter 8), and captive migrants housed under naturally varying photoperiod increase their *Zugunruhe* and fat deposition during the seasons in which they would normally migrate (chapter 7). Because many events in the annual cycle are controlled by photoperiod, the nature and sensitivity of a bird's photoperiod response is dependent on both completion of previous events (e.g., breeding) and time of year, which birds monitor via an internal **circannual** clock. Although other exogenous cues tend to provide less-reliable information about future conditions, they nevertheless modulate responses of obligate migrants. Examples of alternate cues include changes in food, social conditions, or weather. Responses to these less-predictable cues are mediated via a different neuroendocrine pathway, the hypothalamic-pituitary-adrenal axis (HPA). The proximate causes and mechanisms controlling facultative migrations are not well understood, but likely, the proximate cues and ultimate processes are more tightly coupled in facultative migrants than in obligate migrants (Ramenofsky et al. 2012).

Facultative and obligate migration can be viewed as extremes along a continuum of varying dependence on innate and flexible programs, both employing a combination of cues and pathways for responding adaptively to environmental variation. Obligate migrants combine strongly directional, repeatable, consistently timed phases of their migration with less predictable, facultative phases. Young obligate migrant birds apparently learn during their first journeys and make more accurate directional decisions as they age. Even in Whooping Cranes, some elements of the migratory program are probably innate, because after their first ultralight-guided southbound trip, groups of juveniles departed on their northward spring migration at the correct time without human assistance. At the same time, facultative migrants respond to changing photoperiods via the HPG in many of the same ways that obligate migrants do. Thus, obligate and facultative migrants may differ primarily in how sensitive they are to environmental stimuli; possibly obligate migrants have lower response thresholds to internal or external cues that trigger migration. In wild birds, this threshold model would translate into a continuously varying ratio of obligate to facultative phases in a bird's migratory pathway (Newton 2012).

Although much remains to be learned about the control of irruptive migrations, we know that several different control mechanisms operate, and that the relative importance of those mechanisms varies among species. The consistent, predictable part of movements includes southward fall movements and northward spring movements each year. However,

HOW DO WE STUDY MIGRATION IN THE LAB? EMLÉN FUNNELS AND BEYOND

Peter Berthold's classic experiments and many other important breakthroughs in migration ecology would not have been possible by only studying migration in the wild. Yet when we bring birds into the lab, we prevent them from migrating. So how do ornithologists measure migratory behavior in captive birds? In 1966, two brothers, Stephen and John Emlen, devised a simple device that allows us to quantify a bird's urge to migrate, and the direction of flight, were it not confined to a cage (Emlen and Emlen 1966). The device consists of a paper funnel covered with wire mesh, originally with an ink pad base but now consisting of thermal paper sensitive to abrasions (first figure). Nocturnal migrants get "antsy" when kept in cages overnight during migration seasons. When placed in an Emlen funnel, birds view the night sky through the mesh and they hop onto the paper funnel, leaving their tiny footprints behind. If birds can see the stars or a representation of the night sky, then their scratch marks cluster in a single direction. Researchers quantify the number and orientation of those marks to represent migratory urge and direction. New video-based techniques (rather than paper-based) are being developed to quantify the same behaviors (Delmore et al. 2016). In studies not aimed at understanding navigation and orientation, we can quantify the same nocturnal migratory restlessness, or *Zugunruhe*, by attaching electronic sensors to perches in normal bird cages, measuring nocturnal activity levels but not directions. In a few labs around the world, researchers can simulate real migratory flights by training birds to fly in wind tunnels. Huge fans create controlled airflow through a chamber roughly a meter wide and a few meters long. Some birds learn to fly for hours under these conditions (second figure). Researchers can then manipulate environmental conditions during flight, or diet, health, or other preflight treatments, measuring a response that

more accurately reflects the physical experience of migrating than proxies such as *Zugunruhe*.



Upper panel: Willow Warbler (*Phylloscopus trochilus*) in an Emlen funnel in Sweden. Photo by David Toews. Lower panel: Swainson's Thrush (*Catharus ustulatus*) flying in the wind tunnel at the Advanced Facility for Avian Research at Western University in London, Canada. Photo by A. R. Gerson.

in some years, large numbers of individuals spend the winter much farther south than usual. Instead of attempting to explain these irruptions as a unique behavior, we can focus instead on identifying the thresholds and specific combination of environmental cues that trigger birds to travel farther in some years than others.

The Origin and Evolution of Migration

Migration can involve feats of athleticism and navigation far beyond anything humans could ever achieve. How did such

a complex trait evolve? It would be natural to presume that migratory behavior would be strongly conserved, phylogenetically, arising a few times in avian evolutionary history and persisting in the descendants of those first migrants. The reality is just the opposite. Migration blinks on and off the avian tree of lifelike lights on a Christmas tree. Genera vary in migratory tendencies within families, species vary within genera, populations vary within species, and individuals vary within populations. We see sedentary lineages giving rise to migratory ones, and descendants of migrants becoming

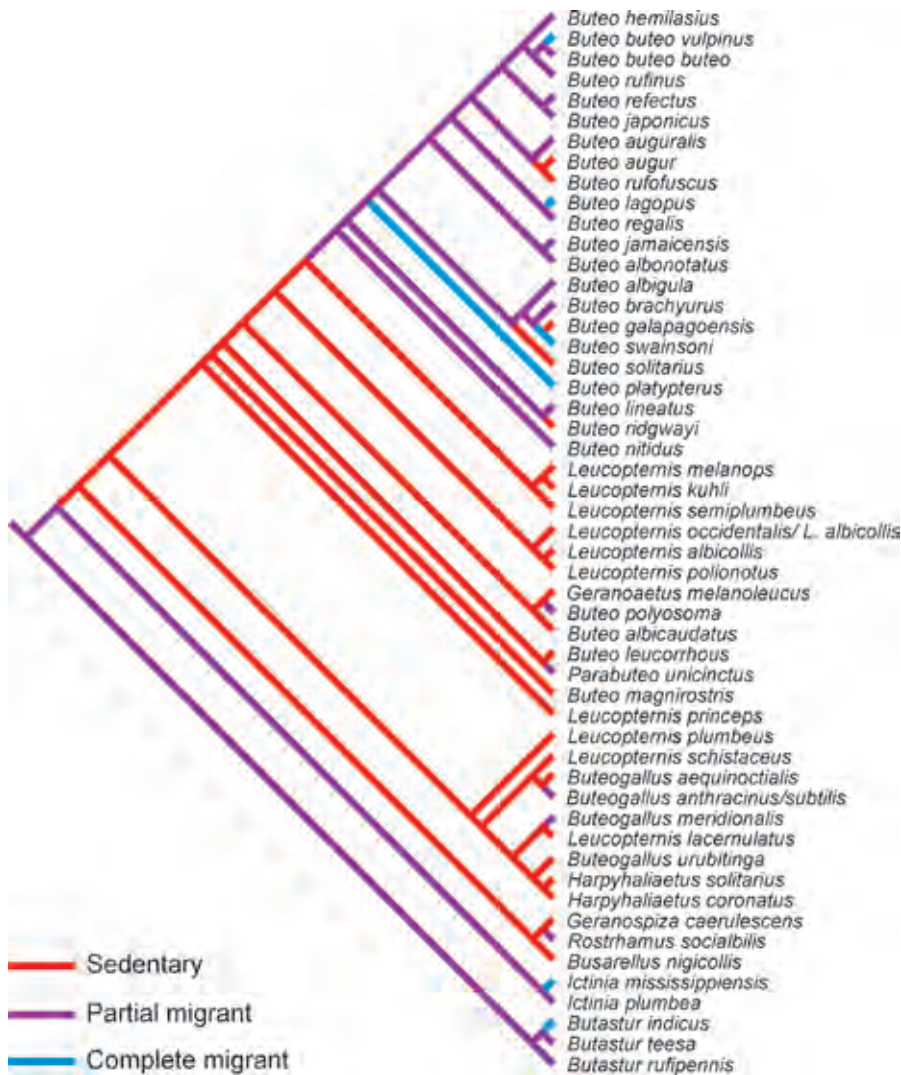


Figure 19.8. The migratory behavior of extant species varies between close relatives and changes rapidly over evolutionary time in the genus *Buteo* and its relatives (Amaral et al. 2009). In this phylogeny, many of the living species (names on right) and their ancestors (represented by the branches) are partially migratory (purple shading), and the most basal representative of this group was inferred to be a partial migrant. Partial migration gave rise to completely migratory species such as Rough-legged Hawks (*Buteo lagopus*), whose nearest relatives are all partial migrants. In other cases, the reverse happened and migratory behavior was lost entirely. For example, a partially migratory ancestor gave rise to the nonmigratory (red shading) Ridgway's Hawk (*Buteo ridgwayi*) endemic to Hispaniola. Redrawn with permission from Fabio Raposo do Amaral.

sedentary (fig. 19.8). For example, Hawaiian Hawks (*Buteo solitarius*) and Galapagos Hawks (*B. galapagoensis*) both likely descended from a migratory ancestor of Swainson's Hawks (*B. swainsoni*), which may have been blown off course during migration (Bildstein 2004). We have witnessed gains and losses of bird migration, even within the past few generations. Famously, a population of sedentary Californian House Finches (*Haemorhous mexicanus*) introduced onto Long Island, New York, became migratory, gradually increasing their migration distance over many generations (Able and Belthoff 1998). The urbanization of large parts of the world continues to affect migration behavior; urban populations of Eurasian Blackbirds (*Turdus merula*) are becoming less migratory, and this change in behavior is controlled genetically (Partecke and Gwinner 2007). Decreases in migratoriness are accompanied by physiological changes that allow earlier nesting by blackbirds living in cities than blackbirds living in forests.

Turning the migratory switch on or off is not the only way that birds respond evolutionarily in their migratory behavior. New migration routes can emerge rapidly as the result of changes in resource availability. Over only a few decades, about 10 percent of blackcaps breeding in Germany dramatically altered their migration direction, no longer departing in a SW direction to winter in Spain but departing in a west-northwesterly direction and overwintering in Great Britain, apparently in response to changing winter food availability caused by extensive bird feeding in England (Berthold et al. 1992; fig. 19.9). Selection can also act against evolutionary novelty in migratory behavior. Hybrid individuals at a zone of contact between genetically distinct western and eastern populations of Swainson's Thrush (*Catharus ustulatus*) exhibit intermediate migratory pathways over more mountainous terrain and different overwintering locations relative to the two parental populations—an outcome that may decrease fitness of hybrids (Delmore and Irwin 2014).

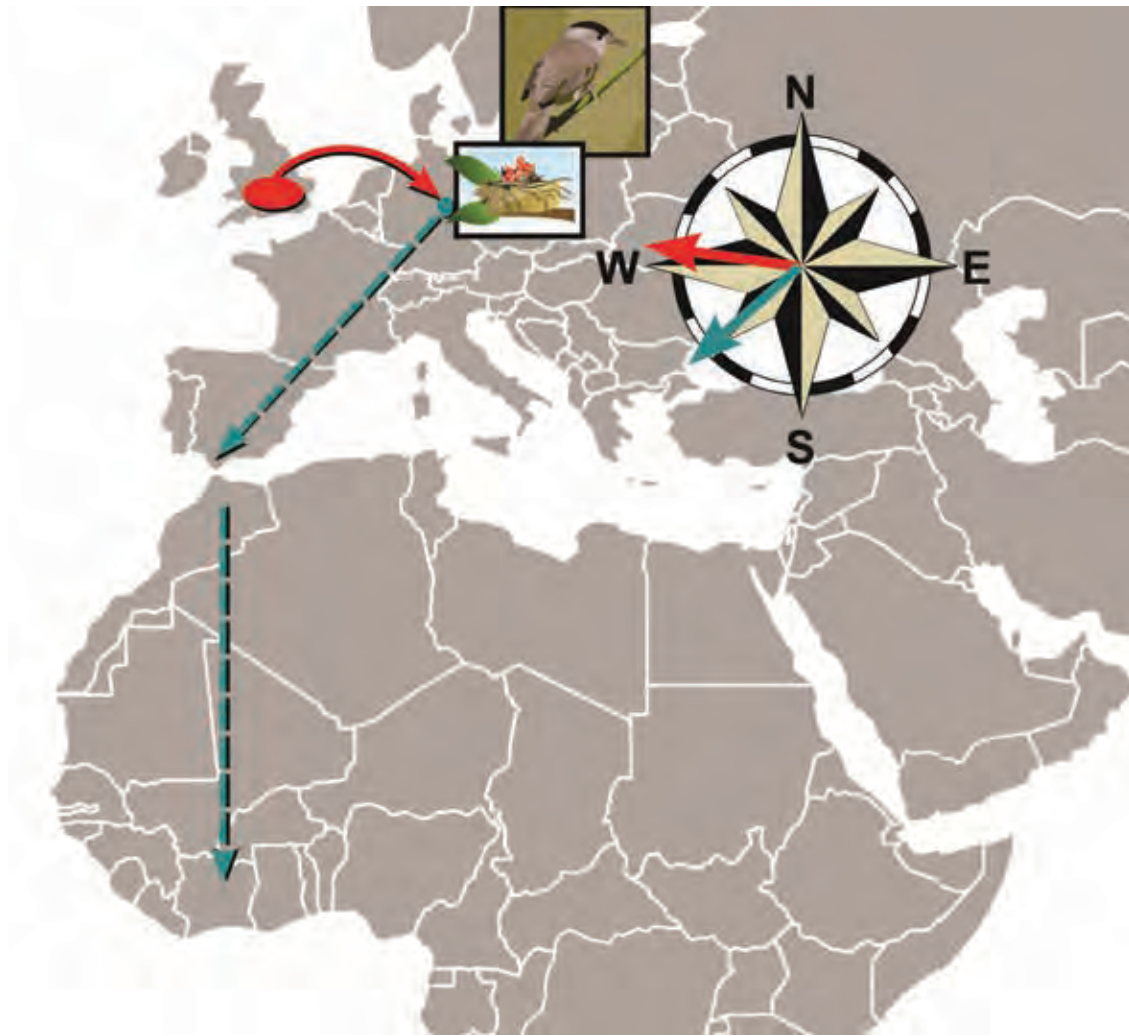


Figure 19.9. Experimental evidence that the orientation traits in Blackcaps exhibited rapid evolutionary change in recent decades. Birds breeding in Germany typically migrate southwest to Spain, and from there, south to Africa (green dashed arrow). Within recent decades, Blackcaps have begun overwintering in England. Berthold and colleagues captured birds during winter in England (red circle),

bred them in captivity in Germany, and then conducted experiments with those captive-reared offspring. Young captive-bred birds from “English” parents oriented to the west toward England during the fall migration period (red arrow on compass), whereas young wild-caught birds from the same site oriented southwest toward Spain (green arrow).

Rapid changes in endogenously controlled migrations suggest that the whole suite of behaviors required to successfully migrate doesn’t truly evolve independently over and over again. Rather, ornithologists are coming to the consensus that probably most, if not all, birds possess a migratory program that is easily switched on and off as ecological circumstances change (Zink 2011). Indeed, it is possible that some form of migration is ancestral for all of Aves. Avian fossil morphology suggests, however, that long-distance land-bird migration was not prevalent until 15–25 million years ago, more or less concurrent with the great diversification of passerine birds (Steadman 2005). Over the evolutionary history of extant birds, the earth has experienced tremendous

environmental fluctuations caused by glaciation events and longer-duration cycles of warmth and low seasonality alternating with cool, drier, more seasonal periods. With those climatic changes, birds have coped with major shifts in the distribution and extent of terrestrial habitats and extinction of other species (such as the Pleistocene megafauna or, more recently, Passenger Pigeons, *Ectopistes migratorius*) that profoundly influenced terrestrial communities. Many living genera including species of migrants and nonmigrants persisted through all these transitions with minimal morphological change, highlighting the extreme adaptability of birds and implying that migratory behavior must be flexible over longer time scales.

The extreme lability of migration has important implications for how we study the topic. For one thing, attempts to infer ancestral character states (required to map changes in migratory behavior onto a phylogeny; e.g., fig. 19.8) may not recover the full history of gains and losses of migratory behavior. If birds can change from being completely and obligately migratory, to being partially migratory, to resident in a handful of generations, then many changes in character state may have occurred since lineages diverged. In some ways, however, this possibility makes understanding the ecological drivers of migration easier. We can fairly safely assume that if migration persists today, then the behavior likely confers a fitness advantage under contemporary circumstances rather than being a product of past selection with few current fitness benefits.

For decades, ornithologists attempting to explain the ultimate causes of migration debated whether temperate-tropical latitudinal migrants were essentially temperate species that “vacationed” in the tropics, or essentially tropical species that made a quick jaunt up to more polar latitudes to take advantage of some temporarily abundant but seasonal resource. Theories of why and how migration evolves

frequently rely on one or the other scenario. For instance, Levey and Stiles’s (1992) “evolutionary precursor hypothesis” proposes that short-distance, facultative migrations within tropical regions was an intermediate step in the evolution of obligate, long-distance latitudinal migrations. Other theories assume northern ancestry; Bell (2000) invokes the fact that birds have less to gain by site fidelity during the nonbreeding season relative to breeding seasons, and that incipient migratory behavior is more likely to involve movements toward more climatically benign or less food-limited environments. We now know that both scenarios are true for different taxa. Hummingbirds, for example, originated and diversified in South America and reach astounding diversity within the Neotropics, particularly in the northern Andes. A few genera have evolved long-distance latitudinal migration and seasonally reach the high latitudes of North and South America (fig. 19.10). In contrast, North America’s emberizine sparrows probably diversified in temperate regions. Many of the contemporary temperate-breeding species now make latitudinal migrations, and some reach tropical and subtropical regions (Barker et al. 2015). Whether a bird now winters or breeds in its ancestral home contributes little to understanding the



Figure 19.10. Hummingbirds diversified within tropical South America, where a dazzling array of resident species live today, including the Sword-billed Hummingbird (*Ensifera ensifera*; lower right) from the high Andes. Tropical resident ancestors gave rise to many species evolving altitudinal migration up and down tropical mountains, such as the Snowcap (*Microchera albocoronata*), pictured upper right. Additionally, longer-distance migration into temperate regions of both South and North America has evolved from tropical resident ancestors. Pictured lower left is the Green-backed Firecrown (*Sephanoides sephanoides*) that breeds in Chile and migrates east across the Andes, wintering in Argentina. Upper left is the Rufous Hummingbird, a ~3.3 gram bird whose migration—if measured in body lengths—is probably the longest in the world. Rufous Hummingbirds breed farther north than any other hummingbird, reaching 61°N in Alaska, and winter in central Mexico. Images: Rufous Hummingbird © Ted Ardley Photography; Green-backed Firecrown courtesy of Wikipedia/Creative Commons Attribution-Share Alike 3.0 Unported license, https://commons.wikimedia.org/wiki/File:Picaflor_colibri_rubi.jpg; Swordbill and Snowcap photos by Richard C. Hoyer.

ultimate ecological selection pressures that shape migration patterns, because we must simultaneously explain both why birds depart their breeding areas during the nonbreeding season and why birds then do not remain on wintering grounds to breed.

Ultimate Costs and Benefits of Migration

The benefits of migrating result from spatial and/or seasonal variation in needs or the availability of one or a combination of factors, including food, predation risk (especially on the most vulnerable of avian life stages—eggs and nestlings), climatic conditions suitable for reproduction and survival, and sometimes, the availability of potential mates. Each of these major ecological factors can also influence migration via a variety of mechanisms. For instance, food availability could drive migration via simple changes in abundance such as huge midsummer pulses of arthropod prey at high latitudes. In addition, the time available to forage is very seasonal at high latitudes because of changing day lengths, so birds can potentially feed more young over short time spans because they can forage for more hours each day (Alerstam et al. 2003). True “availability” of a food source can change seasonally based on changes in the abundance and behavior of other competing species. Competition can also change seasonally because of changes in the energetic needs of conspecifics; birds require more food per capita while engaging in energetically costly activities such as reproduction and molt. Finally, many birds undergo seasonal changes in nutritional needs that drive food preferences, so even if one resource remains relatively constant in time and space, food could drive migration if the different resources they depend on at different times of the year are produced in different places. Similar variations exist in explanations that depend on variation in predation risk or climate. Some predators are only a risk to adults, whereas others target eggs and nestlings. Predator communities, abundances, and food requirements can vary seasonally. Birds’ vulnerability to predation changes seasonally based on molt and reproductive behavior. Birds’ physiological tolerances change seasonally, influencing the range of temperature and precipitation conditions under which they can thrive (chapter 7).

For migration to increase fitness, the benefits must outweigh the costs. Some costs are obvious. The act of migrating is risky and many (particularly young) birds die along the way. Landbirds sometimes die in large numbers when they encounter unanticipated bad weather, especially when making long overwater crossings. Opportunistic reports of mass mortality indicate just how risky weather can be: 1.5 million Lapland Longspurs (*Calcarius lapponicus*) died during a March

snowstorm in 1904; more than 10,000 Magnolia Warblers (*Setophaga magnolia*) caught in a storm off the Gulf Coast died in May 1951; 200,000 jays, thrushes, and warblers were killed over Lake Huron in May 1976; more than 20,000 corvids perished in dense fog off the Swedish coast in April 1985; and more than 40,000 birds of various species died in tornadoes off the Louisiana coast in April 1993 (Newton 2007b). Although it is difficult to document the magnitude of migration mortality during normal weather, an estimated half of all known deaths of satellite-tagged European-African migrant raptors occurred during migration, and mortality rates were six times higher during migration than during breeding or wintering (Klaassen et al. 2014). The ever-increasing human population is also increasing mortality risks for migrating birds. An estimated 6.8 million migrating birds die annually in the USA and Canada in collisions with communications towers (Longcore et al. 2012). Migrants also incur indirect mortality costs resulting from lack of familiarity with local conditions at stopover or upon arrival at their winter destination. Migrants may suffer disproportionately from predation risk or starvation than birds with more intimate knowledge of local resources and risks. Competition for food on tropical wintering grounds can **carry over** to influence migrants’ condition and ability to return to breeding areas in a timely fashion (Cooper et al. 2015) (box 19.5 on page 00). But migratory birds can also circumvent the costs of remaining resident. Extreme cold and food shortages kill many resident birds at temperate latitudes. To mitigate such risks, residents store fat as insurance against foraging uncertainty, which then makes them more susceptible to predation (Lima 1986, Rogers 2015).

Which of the many potential costs and benefits have been the most important in shaping bird migration behavior? Many combinations and variations have been proposed, particularly in the context of long-distance latitudinal migration. Predominant among those are the ideas of Cox (1968) and Von Haartman (1968), which postulate that resource competition—especially competition for food—underlies much of the interspecific variation in migratory behavior we see. Cox thought that migration evolved in species that were not as flexible in foraging behavior and used spatial segregation as a way to avoid competition during the times of year when food is scarcest. Alerstam and Enckell (1979) stressed that food limitation was likely to be most critical in species with relatively narrow foraging niches, because their specialization typically affords them a competitive advantage during the breeding season, and thus they can compensate for the costs of migration via high reproductive output. Fretwell (1980) argued that nest predation was the strongest driver of

BIRDS WITH BAGGAGE

By Henry Streby

Carryover effects are exactly what the name implies: conditions during one stage of a bird's life can carry over to affect the bird during a subsequent life stage. Studying these effects is a critical area of research because what happens to a bird during migration or winter helps us understand differences between individual breeding birds, or within the same individual over time. It is even possible that effort and energy expended during one breeding season can determine whether or how well a bird breeds in the subsequent year. Carryover effects are especially difficult to study in small migratory birds because of the challenges of observing individuals for more than one stage of their annual cycle. Therefore, ornithologists are often forced to piece things together from observations of different birds during different times of year or by inferring conditions from previous portions of the annual cycle using characteristics like current body condition or stable isotope analysis. Male American Redstarts (*Setophaga ruticilla*; see figure) that arrive later on the breeding grounds mate with females who lay smaller clutch sizes, and those pairs have lower nesting success generally (Norris et al. 2004a). However, those males then are more likely to interrupt fall migration to molt, and grow paler feathers—an important trait in mate attraction (Norris et al. 2004b). Males that control territories with less food on the wintering grounds end the winter in poorer condition and are late to leave wintering grounds on spring migration (Marra et al. 1998). Whether later migration departure leads to later spring arrival, or whether nesting success is a reliable measure of reproductive fitness, is yet to be determined in most songbirds, but if so, American Redstarts are an excel-

lent system in which to study carryover effects. There are plenty of pieces left to be placed in the puzzle of full-annual-cycle research in order to understand the frequency and importance of carryover effects in migratory songbirds. Lessons and models from nearly a century of full-annual-cycle research, conservation, and management in North American waterfowl provide an ideal starting point. Continued improvements in technology and the miniaturization of tracking devices are already making such work possible in some of the smallest songbirds. As such tools become ubiquitous in field data collection, the extraordinary work that has been completed to date, such as that with American Redstarts, will continue to be a fruitful area of research with important implications for the fields of evolution and conservation.



Male American Redstart. Photo by Geoffrey Hill.

variation in avian reproductive success, and competition for food was the strongest driver of mortality. Thus, high risks of nesting in the tropics would drive migration to temperate breeding areas. Subsequently, seasonal reductions in food that lead to intense competition drives the southward movements to less seasonal wintering areas (Fretwell 1980, 1985). In the “time allocation hypothesis,” Greenberg (1980) incorporated many of the same ecological processes by proposing that migrants trade off juvenile mortality resulting from migration in favor of higher adult survival during the non-breeding season. These ideas were derived from analysis of

interspecific variation in demographic rates consistent with the tropics being a good place to survive but a difficult place to reproduce.

Empirical Tests of Hypotheses Explaining Migration

Testing ultimate hypotheses for migration is particularly challenging in obligate, long-distance migration systems, both because of the huge spatial scales involved and because, when all individuals migrate, we cannot compare the fitness outcomes of migration and residency in the same species. However, in many species, individuals do vary in migratory

distance. Researchers studying arctic-nesting shorebirds took advantage of that variation and found that across 29° of latitude, a migrant shorebird might expect to enjoy a reduction of 3.6 percent in nest predation risk for every additional 1° she traveled north in the spring (McKinnon et al. 2010; fig. 19.11). This result is consistent with ideas of Fretwell: that a primary benefit of northward spring migration is to exploit the relative safety of temperate latitude habitats during the most risky phase of a bird's life—before it can leave the nest.

A rich body of empirical studies of the Dark-eyed Junco (*Junco hyemalis*) also exploited differences in migratory distance to determine the relative importance of different costs and benefits shaping migration patterns. Unlike shorebirds that differ in breeding distribution, juncos of different ages and sexes travel different distances from their breeding range to spend the winter at different latitudes: females travel farther than males, and adults travel farther than young birds. In perhaps the most thorough set of empirical evaluations of

alternative hypotheses explaining variation in migratory behavior, Ketterson and Nolan (1983) concluded that wintering distributions are most likely the outcome of groups of individuals optimizing migratory benefits and risks in ways that differ among age and sex classes. The mortality costs of longer migration are likely highest for young, inexperienced birds, which selects for shorter migrations. The benefits of remaining close to breeding areas and being able to return to them quickly and early in the spring are greater for males, as they are the sex that competes for territories (**arrival time hypothesis**; Myers 1981). Such benefits are likely strongest for young males because they have no prior territorial claims and must break into the competitive male hierarchy. Thus, the benefits of early arrival should select for shorter migrations in males and, particularly, in young males. Other factors, such as size-related differences in ability of birds to withstand cold and short-term fasting cannot explain the junco patterns because, although males are larger than females, smaller young birds would be expected to suffer greater costs of more northerly winter distribution and consequently migrate farther than adults (**body size hypothesis**; Ketterson and Nolan 1976). Likewise, if competition for winter food and dominance hierarchies dictates how far birds must travel to find wintering habitat, then, again, adults would be expected to winter farther north than the subordinate young (**dominance hypothesis**; Gauthreaux 1982). For groups of individuals whose costs of migration are relatively low, the benefits of traveling farther include reduced competition from conspecifics, or gradients in habitat suitability, with more southerly sites offering increased chances of survival because of food availability, climate, and/or reduced predation risk (Cristol et al. 1999). Such multifactor explanations are likely common to many, if not all, migrant species and highlight the importance of integrating the external factors that vary in space and time with internal factors (such as age and sex) that affect the fitness payoffs of different behaviors.

Similar types of individualistic trade-offs seem to underlie altitudinal migrations. Although the major hypotheses proposed to explain migration were formulated in the context of long-distance, latitudinal movements, elevational and latitudinal gradients parallel each in many important ways. For instance, although temperatures typically decline along both geographic gradients, and nest predation risk seems to be generally higher in the lowlands than at higher elevations, the patterns and magnitude of climatic seasonality typically are similar along elevational gradients, unlike latitudinal gradients. The altitudinal migration of American Dippers (*Cinclus mexicanus*) of western North American mountains appears to ultimately be driven by competition for high-quality territories that provide rich food resources,

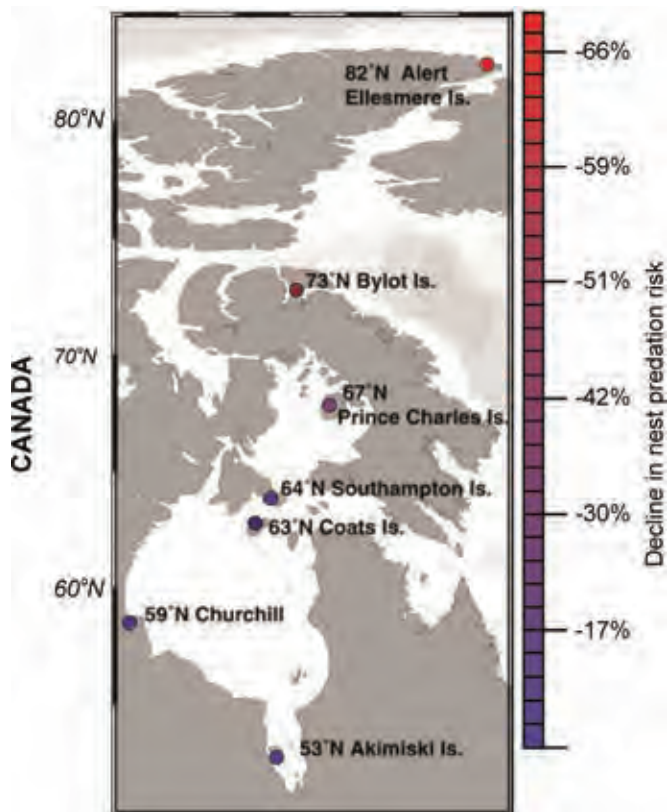


Figure 19.11. Shorebirds breeding at sites in the Canadian arctic may be trading off predation risk with the energetic costs and additional time constraints of flying and nesting farther north. Birds breeding at the northernmost site (Ellesmere Island, red dot) experience 66 percent lower nest predation risk than those breeding at the southernmost site at Akimiski Island (blue dot). Redrawn with permission from the American Association for the Advancement of Science.

consistent with the hypotheses of Cox (1968), Von Haartman (1968), and Alerstam and Enckell (1979). In Dippers, some birds remain resident on low-elevation streams year round, overwintering together with migrants who breed on high-elevation streams. The residents raise more young each season and survive equally as well as the migrants, implying that migratory behavior may be a direct result of heightened competition and increased food demands during the breeding season, combined with variation in individual quality (Morrissey 2004, Mackas et al. 2010, Green et al. 2015).

In contrast to the mechanism of seasonal changes in needs, seasonal changes in the relative availability of food over elevational gradients has been proposed to explain tropical altitudinal migrations, many of which depend primarily on fruit and nectar year-round (Stiles 1980, Stiles 1988). Although seasonal peaks in the abundances of frugivores often occur at the same time as peaks in food availability (Loiselle and Blake 1991, Solórzano et al. 2000; fig. 19.12), the timing and locations of migrations often take birds away from elevations of high relative food abundance (Chaves-Campos 2004). Instead of simple food availability, diet-migration relationships can result from interactions between seasonal variation in rainfall and high food intake rates dictated by the nutritional content of fruit and nectar. Like many tropical montane species, some White-ruffed Manakins (*Corapipo altera*) breeding in wet montane forests of Central America migrate to low elevations during the nonbreeding season, while others remain resident year-round. In contrast to the juncos, males are more migratory than females, and birds in compromised condition are more likely to migrate (Boyle 2008). Downhill migration is synchronous with storms, and many species are more migratory in the wettest years (Boyle and Sigel 2015). Birds experience storm as stressors, undergoing short-term fasts, especially at high elevations (Boyle et al. 2010). The birds that spend the nonbreeding season in the lowlands must cope with less food but benefit from better weather, experiencing storms only half as severe as at higher elevations. Migrating altitudinally likely confers a survival advantage, but migrant males are less successful than residents at gaining access to display sites and females the following breeding season (Boyle et al. 2011).

Constraints and Challenges Imposed by Migration

Migratory behavior—particularly long-distance migration—is associated with a host of other adaptations ranging from physiological innovations (chapter 7) to shifts in life history strategies (chapter 16). Birds such as Bar-tailed Godwits (*Limosa lapponica*) are able to depart spring staging areas in the Wadden Sea with body masses 90 percent higher than during nonmigratory periods because of their remarkable ability



Figure 19.12. Male Resplendent Quetzal (*Pharomachrus mocinno*) perched near fruits of *Nectandra cufodontisii* (Lauraceae, avocado family). Photo © Wes Hanson.

to rapidly deposit fat stores, known as **hyperphagia**. Birds achieve remarkably high rates of fat deposition by increasing foraging rates, increasing digestive efficiency, and/or by shifts in diet (Bairlein and Gwinner 1994). For example, most North American insectivores shift to a carbohydrate-rich diet of fruit prior to fall migration that enables them to rapidly deposit fat (Parrish 1997). Long-distance migrants modulate the mass of other tissues as well. Pectoralis muscle increases, while organs not needed during long migratory flights (e.g., stomach and intestine) atrophy immediately prior to departure (Piersma et al. 1999). Additionally, burning lean mass for fuel during migration may be common, and function primarily to avoid dehydration, because lean mass catabolism releases water, whereas burning fat does not (Gerson and Guglielmo 2011). At the proximate level, fine-scale modulation of body composition must be integrated temporally into mechanisms controlling migratory behavior. At the ultimate level, the benefits of large fat stores trade off with reductions in flight efficiency and agility when birds are atypically

heavy (Lima 1986, Rogers 2015). A fat bird is at greater risk from predators for the same reason that a “couch potato” runs more slowly than an Olympic athlete. Birds must integrate all benefits and costs when making a coordinated set of decisions, particularly during migratory stopover, where most birds accumulate the majority of their energy reserves and also spend much of the fuel they acquire (Cimprich et al. 2005, Cohen et al. 2014).

External and internal morphology differs between long-distance migrants and residents. Migrants have longer, more pointed wings, which increases the efficiency of long-distance flight at a cost to maneuverability (Mönkkönen 1995). A host of other less obvious morphological changes are also associated with migration; these include less graduated tails, shorter legs, lighter leg muscle mass, flatter skulls, and narrower bills (Winkler and Leisler 2005). Some adaptations can be interpreted as the outcome of trading off the mass of structures that support bipedal locomotion with those that support flight. Changes to skull morphology are related to overall reductions in brain size in migrants. Why might migrants, who have to find a way to thrive in multiple habitats over the year, have smaller brains than closely related residents, when big brains help birds cope with novelty (Sol et al. 2005)? Big brains are costly to grow and maintain, so the energetic demands of migration itself may constrain cognitive ability. Alternatively, or additionally, by moving between climatically benign locations the whole year, migrants may not require the same capacity for behavioral innovation as residents who must cope with whatever environmental challenges occur on their year-round home (Sol et al. 2010).

One major consequence of migration is the time constraints that movement imposes on annual cycles. Some migratory raptors spend as much or more time traveling to and from breeding grounds than they spend at either location (fig. 19.13). Because birds usually avoid multiple simultaneous, energetically costly activities, time spent in migration reduces time available for reproduction and molt. Even when the duration of migration is short, departing breeding grounds removes the possibility of more reproductive attempts for the season. Major consequences of temporal constraints on reproduction include fewer broods a female can raise each year and fewer renesting attempts following nest failure. A common pattern in landbirds is to molt following breeding but prior to southward migration. Attempting to both reproduce and molt during the short window of opportunity between spring and fall migration imposes further time constraints. In western North America, some species characterized as **molt migrants** reduce those constraints by breaking their fall migration and molting at an intermediate location (chapter 9). Still other species, such as Yellow-billed Cuckoos (*Coccyzus americanus*) sometimes



Figure 19.13. Swainson's Hawk (*Buteo swainsoni*). Photo by Geoffrey Hill.

circumvent the temporal constraints of migration on breeding by being **migratory double breeders**—these birds initiate fall migration after nesting in the north, then break migration to breed a second time in a more southerly location (Rohwer et al. 2009), a behavior that can also be characterized as long-distance, within-season breeding dispersal.

Time constraints are only one of several ways by which migration affects avian life histories. Conditions during previous seasons can influence when birds complete migratory journeys, the quality of breeding territories they are able to secure, the number of young they are able to raise, and even their chances of survival (e.g., Saino et al. 2004, Inger et al. 2010, Duriez et al. 2012, Catry et al. 2013). More types of these carryover effects are being documented as technology provides the means to gain detailed information on individuals over their complete annual cycles (box 19.5 on page 00). Migration also allows birds to avoid some of the fitness costs incurred by residents. Tropical resident species typically lie at the slow end of the life history continuum, with low reproductive output each year (small clutch size, high rates of nest failure) but high adult survival (Martin 1996). North temperate residents tend to lie near the fast end, having larger clutch sizes, higher nest success, but low adult survival probably caused by harsh winter climates (Sherry and Holmes 1995). Latitudinal migrants would be predicted to enjoy the reproductive benefits of northerly breeding and the survival benefits of more southerly overwintering, minus the costs of reduced allocation to reproduction and the mortality costs of migration itself. Indeed, in five species of North American sparrows wintering together, clutch size did increase with breeding latitude, but temporal constraints also meant that medium- and long-distance migrants were confined to raising fewer broods and had fewer opportunities to renest. Annual survival was not lower in species with longer migratory

journeys, indicating that the survival benefits of residency may only accrue when wintering ranges differ (Sandercock and Jaramillo 2002). While we know that migration is a major source of direct mortality, curiously, migrants exhibit slower rates of senescence after controlling for breeding latitude, age at first reproduction, and adult survival rate (Møller 2007). One potential explanation for this pattern is intriguing; the act of migrating may delay senescence as a by-product of physiological repairs following intensely athletic migratory journeys. We still have much to learn about the basic patterns of life history strategies for birds around the globe, migrants and residents alike. A better understanding of these patterns and the causes for regional and behavioral correlates in components of life history will undoubtedly reveal much about the rich diversity and multiple consequences of migratory behavior.

DISPERSAL

Patterns

Roughly half of the world's birds migrate, but all birds engage in some form of dispersal during their lifetimes. By far the most common type is natal dispersal—the permanent movement away from where a bird hatches to the site of first reproduction (Greenwood 1980). Indeed, natal dispersal is a “behavior” that birds share with most other organisms on earth, including those we think of as being sessile, such as plants or fungi. Less commonly, birds also engage in breeding dispersal—the one-way movement from one breeding site to another. In vertebrates, both natal and breeding dispersal is sex-biased. In birds, females usually are more likely to disperse, and to disperse farther than males (Clarke et al. 1997). For instance, young female Tree Swallows (*Tachycineta bicolor*) first breed an average of just over ~8 kilometers from the nest from which they fledged, whereas young males disperse on average fewer than 2.5 kilometers (Winkler et al. 2005). Subsequently, 14 percent of female Tree Swallows disperse between breeding sites, whereas only 4 percent of males make breeding dispersal movements (Winkler et al. 2004). Tree Swallows are typical for birds by displaying low **philopatry** while exhibiting high **site fidelity**—the inverse of natal dispersal and breeding dispersal, respectively (Greenwood and Harvey 1982). Despite making migrations of thousands of kilometers each year, many migrants return to within a few kilometers of their natal site to breed, and continue to do so, year after year. In some guilds and lineages, the sex bias in dispersal is reversed, most notably in many waterfowl (Clarke et al. 1997).

Dispersal tendency varies greatly among species. Great Reed Warblers (*Acrocephalus arundinaceus*) and Great Tits

(*Parus major*) in England both exemplify high philopatry and site fidelity—67–69 percent of young males recruit as breeders at their natal site, and 92 percent of adults are then site faithful to previous breeding localities (Hansson et al. 2002, Andreu and Barba 2006). In contrast, many North American grassland birds appear to be highly dispersive, with few to no young birds returning to breed at natal sites, and adult site fidelity is often less than 10 percent (Jones et al. 2007). Dispersal distance also varies greatly among species. Mallards (*Anas platyrhynchos*) only disperse up to 1 kilometer between breeding attempts (Clark and Shutler 1999), while some Razorbills (*Alca torda*) move more than 1,000 kilometers from natal sites and between breeding attempts (Lavers et al. 2007). Often natal dispersal is longer than breeding dispersal; Bobolink (*Dolichonyx oryzivorus*) and Savannah Sparrow (*Passerculus sandwichensis*) natal dispersal is four to eight times farther than subsequent breeding dispersal distances (Fajardo et al. 2009). However, the reverse is sometimes true: breeding dispersal of Oortolan Buntings (*Emberiza hortulana*) is four times farther than their typical natal dispersal distances (Dale et al. 2005).

Over evolutionary time, dispersal behavior appears to be less labile than migration, meaning that researchers must take phylogenetic relationships into account when testing for associations between dispersal and other traits (Paradis et al. 1998). Dispersal is also strongly associated with body size; large birds are more dispersive than small birds. Abundant species with large geographic distributions are among the most philopatric and site faithful, and migrants tend to be more dispersive than residents (Paradis et al. 1998). Even fine-scale habitat differences can strongly influence dispersal behavior. Tropical understory birds are remarkably unwilling to cross barriers such as small roads and rivers, making them the least dispersive guild of terrestrial birds; over eight years and nearly 6,000 telemetry locations, none of 30 tagged Afro-tropical understory birds ever crossed a forest gap more than 15 meters wide (Newmark et al. 2010; fig. 19.14). Such “gap-shy” behavior can seriously limit gene flow and affect large-scale biogeographic patterns. For instance, in a comparison of understory and canopy-dwelling South American birds living on both the east and west slopes of the Andes, the understory species had considerably higher levels of genetic divergence, consistent with extremely low rates of dispersal across the major Andean mountain barrier (Burney and Brumfield 2009).

Breeding dispersal typically occurs between breeding seasons in different years, which means that in migrants, the traveling phases (and potentially some of the costs) of dispersal may be subsumed by seasonal migration to and from wintering quarters; on their return journeys, some birds simply settle in a different breeding location than the one they



Figure 19.14. Radio-tracking data from tropical birds such as this Orange Ground Thrush (*Zootheragurneyi*; inset) reveal that forest fragmentation, such as in the East Usumbara Mountains of Tanzania, makes dispersal between forest patches extremely difficult. Photos by William Newmark.

occupied previously. Migratory movements may also provide information about the location of good breeding habitat useful in post-dispersal settlement decisions. However, breeding dispersal sometimes occurs within breeding seasons, between breeding attempts. In most cases, such within-year breeding dispersal movements are subject to more stringent time constraints because the climatic conditions suitable for breeding only last for a restricted period. Although we know relatively little about within-year dispersal, it appears that between- and within-year patterns of breeding dispersal are similar. For example, compared with between-year dispersal, the within-season breeding dispersal of Hoopoes (*Upupa epops*) is slightly less common and of slightly shorter distance (mean of ~0.5–0.8 versus ~1.5–2 kilometers), but shows the same patterns of sex bias (longer in females) and little relationship with previous reproductive success (Botsch et al. 2012).

Proximate Causes and Control of Dispersal

Like migration, the proximate factors that trigger dispersal involve both innate and facultative elements, and the flexibility in dispersal behavior varies among species. The ubiquity of natal dispersal, the highly conserved taxonomic patterns of sex-bias in dispersal tendency, and the heritability of dispersal and associated traits implies that the urge to disperse early in life is at least partially innate (Dingemanse et al. 2003). But to what extent are the timing, distance, and other elements of dispersal fixed rather than the outcomes of facultative decisions? When an individual's phenotype influences the costs and benefits of dispersal, and when those phenotypic

traits are heritable, then there is the potential for dispersal **syndromes** to emerge. Such syndromes integrate dispersal tendency with other behavioral and morphological traits and correlated genetic processes, resulting in individual-level differences in dispersal within species (Duckworth 2012) as described in a series of experiments with bluebirds (box 19.6 on page 00). Aggression is heritable but is also modulated by maternal effects: under high cavity availability, males hatched from eggs laid late in the clutch, and those males were non-aggressive and philopatric. However, when cavities were scarce, males hatched from early laid eggs and those young males were both aggressive and dispersive (Duckworth 2009; box 19.7 on page 00). Evidence for innate processes controlling dispersal decisions come from other birds as well. Snail Kites (*Rostrhamus sociabilis*) nest in wetlands either by lake-shores or in freshwater marshes. Young kites make natal dispersal movements of tens to hundreds of kilometers, but regardless of how far they moved, they usually selected the same kind of wetland in which to breed as that in which they themselves had been reared. Interestingly, such fixed preferences resulted in reproductive costs, not benefits; kites that dispersed to locations similar to their natal areas raised fewer young than kites that switched habitats (Fletcher et al. 2015).

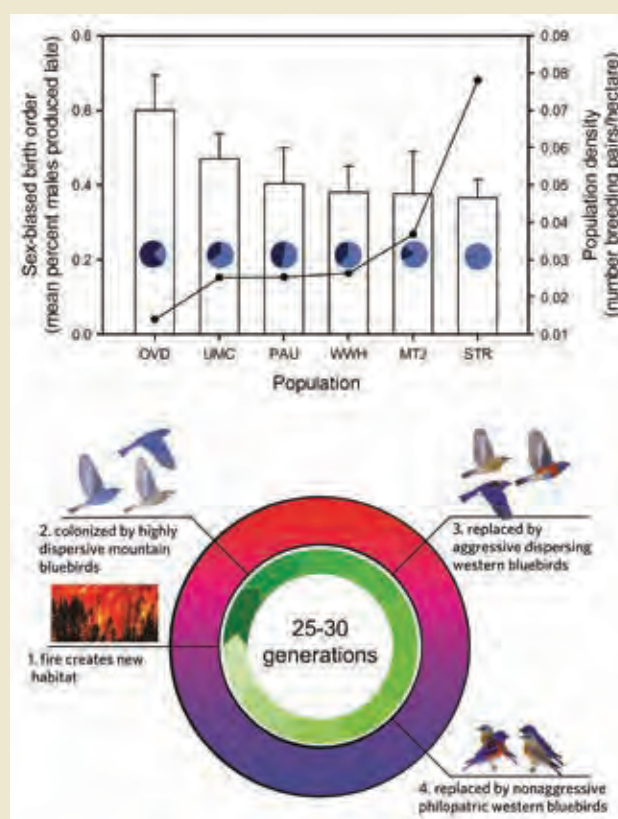
Plenty of evidence also exists for a strong facultative component to dispersal tendency, timing, and direction, particularly in breeding dispersal. Breeding dispersal tendency varies with quality of breeding habitat (Lecomte et al. 2008), density of competitors, and condition of the bird (Kim et al. 2007). The most common correlate of breeding dispersal tendency

GO WHERE MOM TELLS YOU! MATERNAL EFFECTS AND BLUEBIRD DISPERSAL

By Henry Streby

Generally speaking, a maternal effect is the influence of female phenotype on the phenotype of her offspring, and such effects can be genetic, environmental, or a combination of both. More specifically, maternal effects are often discussed as when females influence morphological or behavioral phenotypes of their offspring through some physiological or behavioral response by the female to current environmental conditions. One can imagine the potential fitness benefits of being able to produce more male offspring when a population is female-biased or to produce more or less aggressive offspring in response to population density or perceived competition for limited resources. Dr. Renee Duckworth described the nature of maternal effects in Western Bluebirds (*Sialia mexicana*) in an elegant series of manipulations to the habitat of wild populations (Duckworth et al. 2015). Duckworth demonstrated that female Western Bluebirds can change the order in which they produce male and female offspring within a clutch in response to the quantity of nearby available nesting cavities. When cavities are abundant, females produced male offspring later in the clutch, which results in less-aggressive males that do not disperse far from their natal territory. When cavities are scarce, females produced male offspring earlier in the clutch, which results in more-aggressive males that disperse farther from natal territories (see figure). Western Bluebirds are secondary cavity nesters that colonize open forested landscapes, often a few years after a forest fire. The cavities they exploit are an ephemeral resource because cavities are often abundant when Western Bluebirds colonize an area but become less abundant as other animals occupy them, snags containing cavities decay or fall, or cavities become unusable for any other reason. Colonization of an area by Western Bluebirds often follows colonization by Mountain Bluebirds (*Sialia curruoides*), a closely related species that is typically displaced by the relatively aggressive Western Bluebirds. There is a fitness benefit to being an aggressive Western Bluebirds when colonizing a new area, and a strong relationship between long-distance dispersal and aggression assures colonizing Western Bluebirds can outcompete Mountain Bluebirds. However, high aggression is also associated with reduced parental care by male Western Bluebirds, resulting in relatively low fitness for aggressive males compared with less

aggressive males once an area has been colonized. All of this means that females benefit when they can respond to high local cavity availability by producing males that are less aggressive, shorter dispersers, and better at parental care, and when they can respond to low cavity availability by producing males that are more aggressive, longer dispersers, but could maybe benefit from a parenting class or two.



Bars in the upper figure depict the proportions of males produced later in clutches of Western Bluebirds in six different populations. When the density of conspecifics (dots connected by lines) was high, and fewer territories were occupied by Mountain Bluebirds (dark blue portions of pie charts), female Western Bluebirds laid more of their male offspring early in the clutch, giving rise to more aggressive and dispersive individuals. These maternal effects shape the cycle of colonization and replacement of Mountain Bluebirds with Western Bluebirds in fire-adapted habitats as depicted in the lower panel (Figure 1 and Figure 3 from Duckworth et al. 2015). Images © Renee A. Duckworth.

RENÉE DUCKWORTH



Dr. Renée Duckworth. Image © Dr. Renee A. Duckworth.

Dr. Renée Duckworth is an associate professor in ecology and evolutionary biology at the University of Arizona. Dr. Duckworth investigates how behavior evolves and how evolutionary changes in behavior influence population dynamics and macroevolutionary processes. Her work is exceptionally successful at linking developmental and physiological processes to differences among individuals in behavior, then using that information to explain ecological patterns at broad spatial and evolutionary processes. Dr. Duckworth has received numerous early-career awards for her work on the evolutionary ecology of birds—particularly her bluebird research featured in this chapter.

is past reproductive success. Frequently, birds adopt a “win-stay, lose-switch” strategy in which adults that successfully fledge broods are site faithful, whereas those whose nests fail disperse to new breeding areas (Chalfoun and Schmidt 2012). Such a strategy implies that birds use past experience to predict future success and make movement decisions conditional on that likelihood. Facultative dispersal decisions are overlaid on fundamental differences among clades, guilds, and age and sex groups that likely reflect innate processes. Although few studies have explored how facultative and innate processes interact, species-level behavioral differences probably result from variability in cue-response thresholds, such as in migratory behavior.

Ultimate Causes of Dispersal

Because dispersal is a behavior common to all life on earth, a large body of theory exists to explain the selective advantages of such movements. The three general classes of dispersal

benefits are (1) inbreeding avoidance, (2) kin selection, and (3) variability in habitat quality or availability of mates (Clobert et al. 2009). Birds, as in other outcrossing, sexually reproducing organisms, have been selected to avoid mating with close relatives because inbreeding leads to the expression of rare, recessive alleles with adverse fitness consequences. Sex-biased dispersal can be an efficient way to maximize genetic benefits of inbreeding avoidance while minimizing costs, because only half the individuals disperse. Inbreeding avoidance is fundamental to explaining natal dispersal but is less applicable to breeding dispersal in most species; if a young female’s natal dispersal is effective in moving her to new neighborhoods far away from her father, brothers, uncles, and cousins, then she would have little to gain in terms of inbreeding avoidance by dispersing again later in life.

Kin selection can affect dispersal tendencies in two opposing ways. As classically formulated, dispersing to breed far away from kin reduces competition among relatives for resources such as food, breeding sites, or mates. Reduced kin competition increases the fitness of relatives and, thus, the disperser’s inclusive fitness (Hamilton and May 1977). In cooperatively breeding species, however, delayed dispersal may increase an individual’s inclusive fitness; by helping raise younger brothers and sisters, inexperienced birds can increase the odds of their genes being passed on to the next generation through their extended family (Koenig et al. 1992). Spatial and temporal variability in habitat quality (e.g., food or nest site availability, differences in predation risk, or microclimate) or social environment can also explain why animals disperse, either prior to or following first reproduction. Birds that require ephemeral resources for breeding sometimes make truly remarkable breeding dispersal movements. For example, the Australian Banded Stilt (*Cladorhynchus leucocephalus*) breeds along shallow inland salt lakes that form following unpredictable desert rains. Within a few days of heavy rains, birds arrive by the thousands from coastal areas hundreds of kilometers away (Pedler et al. 2014; fig. 19.15).

Sex-biased dispersal patterns may ultimately be shaped by mating system (chapter 17); the sex that has more to gain

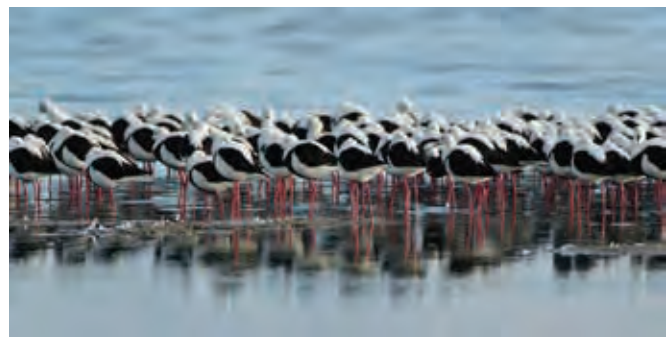


Figure 19.15. Banded Stilts. Photo by Stewart Monckton.

from familiarity with breeding areas and local social hierarchies should be more philopatric. In roughly 70 percent of birds, dispersal is female-biased, and in more than 90 percent of bird species, males compete for resources and females select males on the basis of territory quality. Males would benefit greatly from detailed local knowledge of habitat quality and previous interactions with neighboring males, whereas females' fitness would be most strongly affected by their choice of male (Greenwood 1980). Consistent with these ideas is the dispersal behavior of species without male territorial mating systems. For instance, in the polygynandrous Smith's Longspur (*Calcarius pictus*), neither sex defends territories, multiple mating opportunities exist in close proximity, and males and females are equally likely to be site faithful (Craig et al. 2015). Likewise, no evidence of sex-biased dispersal exists in Brown-headed Cowbirds (*Molothrus ater*), a species that defends no territories and lays its eggs in other birds' nests (Anderson et al. 2012).

Female-biased dispersal in male territorial mating systems is also consistent with an alternative explanation. In territorial species, males can select any unoccupied site in which to establish themselves, whereas females are much more restricted. Females can only choose from sites that (a) males have already selected, and (b) have not already been selected by other females. This imbalance in the availability of breeding sites, rather than sex-related differences in benefits of site fidelity, may cause females to typically disperse more frequently, and to disperse farther, than do males (Arlt and Part 2008). African Houbara Bustards (*Chlamydotis undulata*) provided an opportunity to test this explanation. Young male bustards make longer dispersal movements than do females, and males of this large, terrestrial bird display together in leks. While both sexes incur mortality costs of dispersal, males incur higher costs than females, especially when dispersing long distances (Hardouin et al. 2012). Lekking behavior may explain the reverse-sex bias in this species because male reproductive success is not dependent on defending resources. Likely male bustard breeding site options are limited. Females, on the other hand, may benefit from intimate knowledge of nesting areas and would not be as constrained in breeding sites as would females with male resource-defense mating systems.

The costs of dispersal overlap broadly with the costs of migratory behavior, including risks caused by lack of local knowledge of food or predation risks, opportunity costs of time spent traveling and establishing in new locations, and energetic costs of moving itself. Likewise, selection for dispersal abilities involves trade-offs with a wide variety of morphological, cognitive, and behavioral traits (Danchin and Cam 2002, Nevoux et al. 2013).

Empirical Tests of Hypotheses Explaining Dispersal

Empirical tests of the causes of natal dispersal have focused primarily on inbreeding avoidance and kin selection. Indeed, the tendency of adults to be highly site faithful while natal dispersal is so ubiquitous implicates inbreeding avoidance—if parents breed repeatedly in the same locations, then their offspring have little option but to go elsewhere if they are to avoid mating with relatives. In migratory Savannah Sparrows (*Passerculus sandwichensis*) breeding on islands in the Bay of Fundy, young birds disperse fairly short distances, mostly returning to the same small archipelago from which they fledged (Wheelwright and Mauck 1998). The dispersal distances of parents and young were uncorrelated, indicating that, at least at small spatial scales, natal dispersal has low heritability. However, birds managed to avoid mating with their relatives; young birds avoided breeding near parents of the opposite sex, and siblings raised together dispersed to different areas, resulting in lower within-pair relatedness than expected by chance. A key prediction of the kin selection hypothesis is that when competition among kin is high, natal dispersal should be more frequent and/or longer. English Great Tits (*Parus major*) exemplify this pattern; males disperse a distance corresponding to a greater number of territories (although not necessarily a greater absolute distance) when local territory density is high (Greenwood et al. 1979). Competition generally influences fine-scale dispersal movements in tits; population density affects resource availability, which results in spatial and temporal variation in habitat quality, which, in turn, influences dispersal behavior (Matechou et al. 2015).

Empirical tests of breeding dispersal have provided support for all major explanations for dispersal. However, most studies have emphasized the importance of habitat variability. For instance, Black-throated Blue Warblers (*Setophaga caerulescens*) breed in both high-quality shrubby areas, and lower-quality areas with fewer shrubs. Both sexes make shorter breeding dispersal movements when they breed in high-quality habitat. Additionally, males disperse shorter distances as they age, presumably because they secure higher-quality territories (Cline et al. 2013). Additionally, many birds use public information to inform their assessments of relative habitat quality when making breeding dispersal decisions. Colonial-nesting Black-legged Kittiwakes (*Rissa tridactyla*) judge nesting habitat based not only on their own nest success, but also on the nest success of their neighbors; experimental manipulations of perceived habitat quality by removing eggs from some birds' nests resulted in neighboring birds being more likely to disperse if their own nests failed (Boulinier et al. 2008). After deciding to disperse, birds also use social information to choose post-dispersal habitat.

Grasshopper Sparrows (*Ammodramus savannarum*) breeding in North American midcontinental tallgrass prairies are highly dispersive between and within years (Williams and Boyle in review). By broadcasting songs through loudspeakers, researchers experimentally manipulated the perceived density of territorial male sparrows. Relative to control plots, plots with loudspeakers attracted twice as many territorial males late in the breeding season. This result suggests that conspecifics may provide a signal of breeding habitat quality, especially in temporally constrained within-season dispersal (Andrews et al. 2015). Despite the importance of habitat variability, both inbreeding avoidance and kin selection can contribute to shaping breeding dispersal patterns. For instance, Red-cockaded Woodpeckers (*Leuconotopicus borealis*) are a communally breeding species that depend on old-growth longleaf pine in which to build nests that are used by cooperatively breeding groups of adults. In this system, both inbreeding avoidance and mate and habitat quality shape the dispersal decisions of females. Females disperse more frequently when their sons become breeders in their social group, consistent with females avoiding mating with close relatives. But females also disperse more frequently following nest failure, if they do not have helpers at their nests, and if their mates are of low quality. Thus, female Red-cockaded Woodpeckers may disperse to seek out better reproductive opportunities, independent of the presence of kin (Daniels and Walters 2000).

Consequences of Dispersal

Dispersal has many important consequences for other branches of avian biology. At the genetic level, the physi-

cal one-way movement of individual birds is a prerequisite to gene flow or **effective dispersal**. Dispersal does not ensure gene flow if post-dispersal breeding is unsuccessful, but gene flow cannot occur without dispersal of reproductive individuals. Only a few birds moving between populations each generation is sufficient to maintain high levels of genetic connectivity, and the rate of effective dispersal influences the potential of populations to adapt to local environmental conditions and, ultimately, to diverge into reproductively isolated species (Garant et al. 2005). Thus, differences in dispersal tendency and distance among lineages ultimately has a bearing on broad-scale patterns of species distribution and diversity patterns (Ghalambor et al. 2006).

The other main class of dispersal consequences is spatial. In the absence of dispersal, speciation could not happen for another, nongenetic reason: dispersal is the mechanism by which ranges expand to fill space and move into novel areas. This fact makes dispersal incredibly important for predicting distributional responses to ongoing climate change. For example, the latitudinal distribution of North American wintering bird species ranges is shifting north at roughly 1 km per year (La Sorte and Thompson 2007), the altitudinal ranges of Peruvian montane birds have shifted ~50 m uphill over 40 years (Forero-Medina et al. 2011), and New Guinean montane species have shifted 95–152 m uphill over a similar time period (Freeman and Class Freeman 2014; fig. 19.16). Dispersal is the mechanism by which distributional changes occur. Thus, while dispersal can swamp local adaptation when gene flow is high, thereby reducing speciation rates and diversification (Lenormand 2002, Claramunt et al. 2012), dispersal can also promote speciation via colonization of novel habitats.

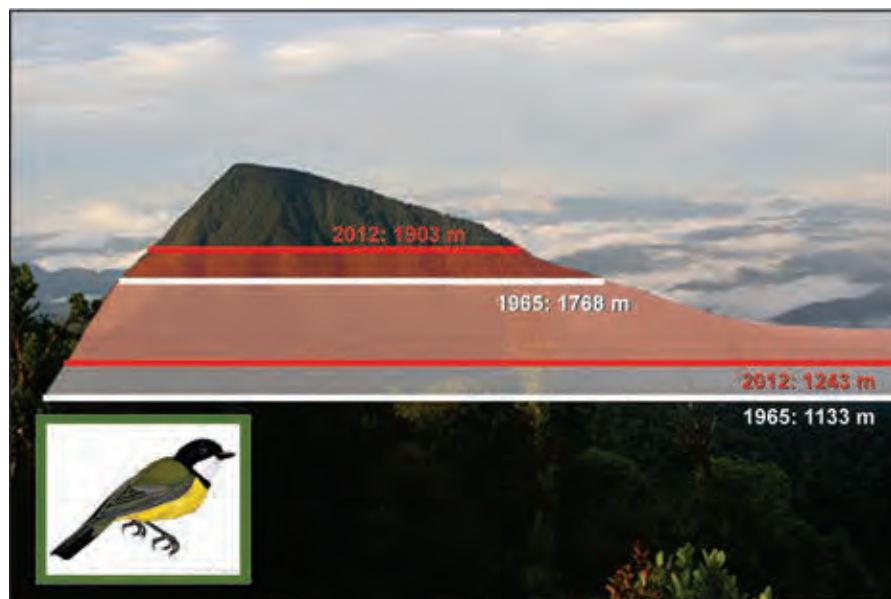


Figure 19.16. Sclater's Whistler (*Pachycephala soror*, inset) is one of many tropical species whose distribution has been shifting upslope as climates change. In 1965 on Mount Karimui in New Guinea, this species' elevational range extended from 1,133 m up to 1,768 m (white shading). By 2012, both lower and upper distributional limits had shifted upward, and the species now occupies elevational ranges between 1,243–1,903 m (red shading; Freeman and Class Freeman 2014). Background photo by Benjamin Freeman; image of Sclater's Whistler by Jessica Nguyen.

Even within a species' current distribution, the spatial consequences of dispersal are multifaceted. The rate of dispersal in and out of populations is a key parameter in metapopulation dynamic models. Within single populations, demographic studies either make assumptions about, or require independent estimates of, dispersal rates. Those estimates are rarely available, however, and, consequently, in populations where site fidelity is low, estimates of apparent survival are a poor estimate of true survival. Thus, dispersal severely inhibits the ability of wildlife managers to accurately estimate population growth rates and determine which parts of the annual cycle to target for conservation in order to achieve the most positive demographic response.

The dispersal of birds can have important implications for the species with which they interact. Dispersing birds can act as vectors for other taxa, such as in mutualist seed dispersal interactions. In the tropics, large, frugivorous birds are common, and most trees produce animal-dispersed seeds. While the plants themselves influence the movements of the birds through spatial variation in fruit production, the birds in turn shape the patterns of seed rain on the landscape (Levey et al. 2005). For example, highly mobile African Hornbills travel long distances, potentially moving the seeds of plants orders of magnitude farther than any other potential dispersers (Holbrook et al. 2002). Similarly, waterbirds routinely move propagules of aquatic plant species and macroinvertebrates between wetlands; a meta-analysis revealed that an astonishing one-third of duck and rail droppings contained at least one propagule, and one-third of those were viable (van Leeuwen et al. 2012). The resulting long-distance dispersal may be rare for plants, but may also be incredibly important for understanding population genetics and survival prospects in a changing world. Sometimes, however, bird movements result in the dispersal of taxa detrimental to humans or other bird populations. Avian dispersal and migration can move parasites and diseases between regions (Owen et al. 2006). Much remains to be learned about the importance of long-distance migrants in the spread of pathogens (chapter 23). While the physiological costs of long-distance movements may compromise or suppress birds' immune systems, long-distance movements may act to purge pathogens from populations when infection reduces survival (Altizer et al. 2011).

LINKS BETWEEN MIGRATION AND DISPERSAL BEHAVIOR

Migration and dispersal have been studied separately by ornithologists, likely because these two movement behaviors appear to vary independently among taxa. Both long-distance migrants and residents can be either incredibly site-faithful

or highly dispersive, and sometimes, different populations of the same species differ in one but not the other type of movement. However, as knowledge of the patterns, proximate causes, and constraints on both types of behaviors increases, intriguing relationships between migration and dispersal are emerging. At very broad spatial scales, the predominant north–south direction of long-distance migrations worldwide appears to constrain the spread of avian lineages, ultimately contributing to broad-scale avian biogeographic patterns. Despite the fact that birds are so mobile, birds have rarely dispersed east–west between the New World and Old World (Bohning-Gaese et al. 1998). At finer spatial and taxonomic scales, we do see migration-imposed constraints on dispersal. Dispersal of eastern European White Storks (*Ciconia ciconia*) is oriented along a southeast–northwest axis more frequently than would be expected by chance. The southeast–northwest axis aligns with the direction of spring migratory journeys, again providing evidence that migration may constrain dispersal. Such patterns could arise if dispersal happens when some individuals simply stop their migrations a little too early, or overshoot previous breeding locations, continuing along the same course (Itonaga et al. 2010).

Scandinavian- and Siberian-breeding migrants have smaller breeding distributions than do residents (Bensch 1999). A potential explanation for those smaller distributions is that, in obligate migrants, long-distance dispersal and expansion of breeding ranges into new areas may require considerable modification to migratory programs. To successfully navigate to good wintering areas, birds colonizing new breeding ranges would have to adjust the direction and possibly the timing of migratory trips, or locate new overwintering locations. Newton (2012) noted differences in dispersal tendency between obligate and facultative migrant species and proposed that such differences result from differences in the ways migration is controlled. Species with more facultative components to their migrations exhibit far greater inter-individual variation in migration directions and distances, and those movements are shaped by contemporary local conditions. Thus, dispersal to novel areas for a facultative migrant would impose fewer navigational costs than in an obligate migrant whose migrations are less flexible. The **serial residency** hypothesis extends these ideas and reconciles differences in natal and breeding dispersal within obligate long-distance species (Cresswell 2014). In long-distance, obligate migrants, young birds typically navigate their first migrations based on intrinsic map and compass senses that are subject to considerable error. If young birds successfully make the return trip and breed the following summer, then those individuals have now much to gain from locating the same breeding area in subsequent years. Thus, the capacity

to accurately retrace individual, migratory paths following a fairly haphazard journey made in their first year could be adaptive. Much evidence is consistent with predictions of the serial residency hypothesis. Many **vagrants**—birds that show up in unexpected places—are young birds making their first migratory flights (Newton 2007a). Additionally, long-distance migrant adults show remarkable individual-level consistency in their migration behavior (Stanley et al. 2012), yet population-level connectivity is often weak (Franks et al. 2012). The serial residency hypothesis can reconcile such individual predictability and population-level mixing if breeding populations are assembled from individuals ending up in the same place because of chance deviations in their innately controlled navigational systems. Finally, the serial residency hypothesis is consistent with there being no association between breeding dispersal and migration tendency within partial migrants, but longer natal dispersal in migrants than in residents (Alonso et al. 2000).

Nomadism

Nomadism has its own name and place in the avian movement literature, and the term is applied differently by different ornithologists. In some cases, species in which movements closely resemble migration are called nomadic. In other cases, the term refers to movements best considered as the most extreme expression of breeding dispersal. For example, individuals of some grassland-dependent species, such as Henslow's Sparrows (*Ammodramus henslowii*) and Cassin's Sparrows (*Peucaea cassinii*), breed in different locations each year, and even seemingly suitable habitat that was filled with song one year may be silent the following spring (Dornak et al. 2013). Likewise, many northern-breeding owls such as Boreal Owls (*Aegolius funereus*) routinely breed hundreds of kilometers from their previous territories. In such cases, individuals move independently and unpredictably from year to year. Birds may also sometimes be called nomadic when we lack sufficient information to understand and categorize patterns of individual- or population-level migration. For instance, Lawrence's Goldfinch (*Spinus lawrencei*) exhibits a generally east–west migration pattern at the species level, but the numbers of individuals and populations migrating varies from year to year, and even the direction of those movements is not consistent (Davis 1999). For many such “data-deficient” nomadic species, we may eventually understand the temporal and spatial patterns sufficiently to classify their movements more precisely.

Nomadism, as classically applied in the ornithological literature, refers to birds that engage in movements that are equivalent to spatially and temporally unpredictable migrations. Individuals move together in groups, resulting in negli-



Figure 19.17. White-winged Crossbill (*Loxia leucoptera*) on a Douglas-fir cone (*Pseudotsuga menziesii*). Photo by Kurt Kirchmeier.

gible genetic consequences, unlike dispersal. Birds of this type of nomadic species rarely breed in the same location twice, being incredibly flexible in their space use over time. Some of the best-studied avian nomads are the crossbill species inhabiting boreal forests of North America and Europe. Crossbills can breed at any time of year, and movements are triggered by changes in availability of conifer cones—the foods that have shaped crossbills' characteristic bill used in prying open cones to extract nutritious seeds (fig. 19.17). Crossbills can breed thousands of kilometers away from natal or previous breeding sites and exhibit seasonal irruptions driven by inter-annual variation in conifer seed production (Newton 2006). Birds reaching southern Europe during irruptions come from different breeding locations in different years but from similar breeding areas in the same year, meaning that breeding populations remain separate (Marquiss et al. 2012). Such cohesiveness is probably adaptive, because crossbill populations have differently shaped bills that match the traits of the conifer species on which they depend (Benkman et al. 2001). Thus, not only the availability of food but also the ability of crossbills to locate mates that share functionally important bill traits may be important factors shaping their movements (Smith et al. 2012).

STUDYING AVIAN MOVEMENTS

Studying the movement ecology of flying animals presents unique challenges because the behavior we want to understand takes our study organisms away from our study sites. Long-distance migrants often cross international boundaries and sometimes travel to different continents. Movement ecologists must cope with the logistical difficulties of deter-

mining where birds go when they leave our sites, the costs of our own travel, and sometimes language or cultural barriers that can impede collaborations between researchers at different ends of migratory journeys. Simply determining the patterns of movement remains a huge challenge for a majority of the earth's bird species, and determining the causes of differences in movements is even harder. Consequently, models of movement used in conservation are usually unreliable because of lack of detailed movement information (Beissinger and Westphal 1998). The need for better data on dispersal behavior, in particular, is frequently cited as a conservation priority (Donovan et al. 2002). The major methods we use to study movement differ in their resolution, cost, and effectiveness over different spatial scales, meaning that research questions and study species dictate the method most appropriate to any given study.

Humans have observed bird movements directly for as long as we have had written records. Ancient naturalists also noted the seasonal changes in local presence and absence of species that result from migratory behavior. Such observations are cheap and easily applied to most species, providing that observations are thorough and unbiased. Studies based on direct observations made by amateur ornithologists have made a resurgence because large-scale citizen science databases such as eBird (<http://ebird.org>) now capture unprecedented amounts of data (Sullivan et al. 2009). Direct counts of migrating raptors also continue to be an effective method for studying the spatial and temporal patterns of migration at the species level (Kim et al. 2015). Another form of direct observation that has been very useful in studies of migration for several decades is use of data collected by large-scale weather radars (fig. 19.18). Scientists have devised analytical tools to distinguish the signals of inanimate objects such as raindrops or hail from the radio signals reflected by animals, and even to be able to estimate body sizes, flight speeds, and wing beat frequencies (Gauthreaux and Livingston 2006). Although species-level identification is rarely possible, radar has provided a wealth of valuable migration data, particularly on nocturnal movements, for which other forms of direct observation are extremely difficult (Schmaljohann et al. 2007).

A problem with observation of unmarked birds is that we cannot learn much about individual behavior. While observation can provide species-level or, in some cases, population-level data of mass movements, such methods are not useful for studying dispersal or any kind of partial or short-distance migration involving individualistic movements. The practice of marking birds with uniquely coded leg bands, flags, patagial tags, or other markers and recapturing or resighting them elsewhere has transformed our knowledge of avian movements. The earliest records of movements of marked

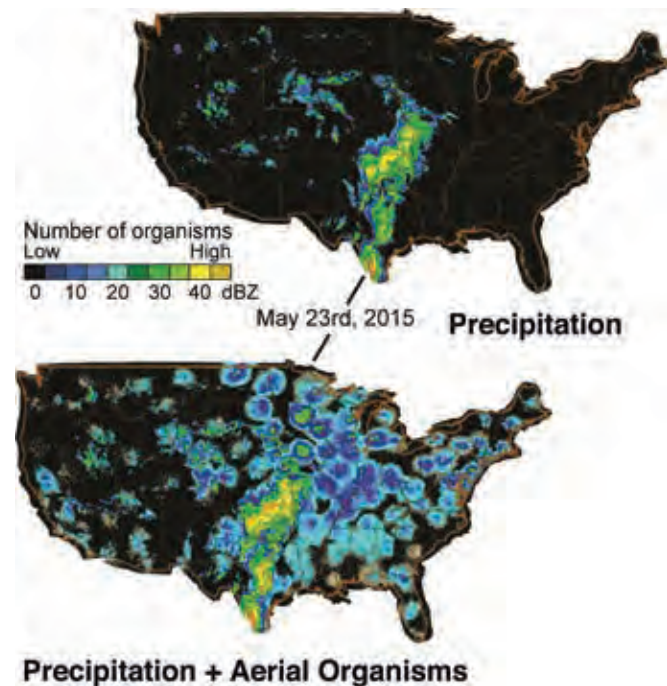


Figure 19.18. Weather radar images that you might find on your weather app have filtered data to only display precipitation (upper image). However, ornithologists can use the original, unfiltered data to visualize, quantify, and study the migration patterns of birds and other aerial organisms (such as bats and large insects). The blue circles visible in the lower image give an idea of the locations of the radar instruments, and show that on the evening of May 23, 2015, large numbers of migrant birds departed from stopover sites, especially in the Midwest and along the eastern seaboard as part of their spring migratory journeys. Images by Jeff Kelly.

individuals come from European falconers in the 1500s and 1600s whose birds turned up far from home. Bird banding began with Hans Mortensen in Denmark, who etched his return address on bands placed on the legs of waterfowl, starlings, and raptors. Mortensen's methods became the model for national or continent-wide banding schemes now in place throughout much of the world. Although only a small fraction of banded birds are ever recaptured, resighted, or killed, and reported, the sheer number of marked birds means that bird banding is still one of the most important sources of individual-based movement data available. For instance, band recoveries revealed how House Finches began to migrate latitudinally in the eastern United States (Able and Belthoff 1998) and the dispersal patterns of Smith's Longspurs (Craig et al. 2015), both described earlier in this chapter.

The primary problem with banding is that it is incredibly labor intensive. Consequently, indirect methods of studying individual movement behavior not requiring recaptures are often more cost-effective. Two primary indirect sources of

movement information come from population genetics and analyses of stable isotopes and other chemical tracers (chapter 31). Comparisons of allele frequencies between populations provide indirect estimates of the degree of effective dispersal and population connectivity. However, because it takes relatively few dispersal events per generation to result in significant gene flow, genetic and ecological measures of movement tendency can yield very different results. For example, a study of 118 radio-tracked White-tailed Ptarmigan (*Lagopus leucura*) living in disjunct alpine areas of Vancouver Island revealed that birds typically never dispersed more than 1 km. However, populations separated by more than 100 kilometers were identified as genetically cohesive clusters (Fedy et al. 2008). Population-specific molecular markers can also provide direct evidence of the movement of specific individuals from one population to another, or can discriminate the breeding populations of migrants on their wintering or stopover grounds, required to establish patterns of connectivity. For instance, region-specific molecular markers for migrating Red-tailed Hawks (*Buteo jamaicensis*) revealed that two temporal peaks in the number of observed migrants resulted from differences in timing of two genetically distinct populations breeding in California and the Intermountain West (Hull et al. 2009).

The application of stable isotope methods to studying animal migration and dispersal has taken off in recent decades. As an animal feeds, it incorporates the isotopic “signature” (i.e., the ratio of heavy to more common forms of elements) of the feeding location. Because those ratios vary spatially, when we capture an animal and sample tissue, we can infer past locations by matching the ratios in tissues to known geographic variation on the landscape. Consequently, every capture becomes almost equivalent to a “recapture” because we gain geographic information for two times in a single bird’s life. Bird migration and dispersal studies most commonly use the ratios of D:H (expressed as $\delta^2\text{H}$; chapter 31) and $^{13}\text{C}:^{12}\text{C}$ ($\delta^{13}\text{C}$). Ornithologists most commonly measure those ratios from information in feather samples, providing geographic information from a narrow window of time when feathers were molted, because feathers are inert once grown (Hobson 2005). Given sufficient knowledge of the timing of molt, feather tissues can be useful in linking breeding and nonbreeding ranges. When we need information on a bird’s location from a time of year other than during molt, then measuring isotopic ratios in continuously growing tissues that turn over at different rates is very useful. For instance, the claws of small birds turn over on the order of around three months, and red blood cells turn over every two weeks or so. Increasingly, ornithologists combine data from multiple isotopes and/or multiple tissues sampled from

the same individuals to gain better temporal and spatial resolution. For example, researchers analyzed $\delta^2\text{H}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in feathers, muscle, liver, and blood from three species of *Cinclodes* living in Chile. In combination, their data revealed both inter- and intraspecific variation in altitudinal migration patterns, as well as seasonal shifts in diet from marine to freshwater invertebrates (Newsome et al. 2015). Similarly, the combination of $\delta^{13}\text{C}$ data from blood and $\delta^2\text{H}$ from Black-and-white Warblers (*Mniotilta varia*) feathers sampled during stopover revealed not only the breeding destinations of those birds, but also that birds wintering in high-quality habitats migrated earlier than birds that wintered in arid, lower-quality habitats (Paxton and Moore 2015).

While genetic and isotopic data provide individual-level data without the need for recapture or resighting, both methods yield fairly imprecise geographic data. Isotope and genetic methods can allow us to assign birds to regions (e.g., at the scale of hundreds of kilometers) rather than specific locations (e.g., at scales of <10 kilometers). To gain fine-scale spatial data, ornithologists rely on attaching tags that transmit a signal and/or store geographic information. For decades, manual tracking using small radio telemetry tags has been a fundamental tool to obtain unbiased estimates of movement within small areas (e.g., box 19.1 on page 00). Radio telemetry revolutionized our knowledge of bird movement, but has limits because tag life and, to some extent, detection range are determined by battery size. Tag mass should not exceed ~3–4 percent of bird mass to minimize birds’ additional energetic costs and changes in behavior. Thus, both the duration and spatial scale of movement studies using standard radio telemetry is limited. Fortunately, tag technology is rapidly improving. Batteries are getting lighter, they last longer with micro-solar charging systems, and arrays of automated telemetry receivers placed on towers or other tall structures are greatly extending spatial scale. By strategically placing towers near migration corridors, we can now “see” small nocturnal birds departing on migratory flights and collect individual-level data on stopover duration (e.g., see discussion question 3 below) and other aspects of migration phenology (Bridge et al. 2011).

Technical innovations are expanding the scope of telemetry-type markers in other respects (chapter 31). Large birds can be fitted with GPS devices that send location data to researchers’ email at preprogrammed intervals. Although costly, such devices provide very accurate spatial information practically anywhere in the world without requiring recapture. Thus, they are immensely useful for revealing the timing and patterns of migration and dispersal, and the inter- and intra-individual consistency of movements for larger birds (Therrien et al. 2014; fig. 19.19). However, such devices are too

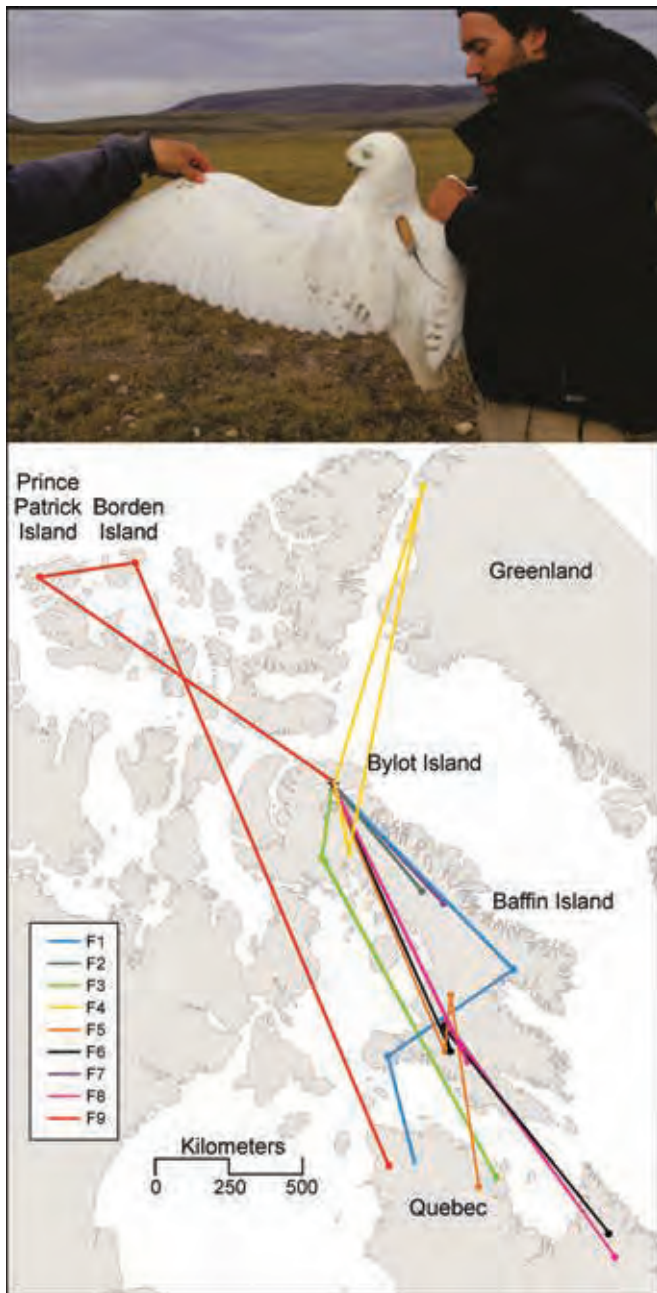


Figure 19.19. Satellite transmitter technology has transformed our ability to study the movements of larger birds, especially in remote locations. The photo shows a Snowy Owl (*Bubo scandiacticus*) fitted with a satellite tag in the Canadian arctic. The map shows the resulting data. Each of the nine dots is a breeding location of a different Snowy Owl (each individual is a different colored line) over four successive years (Therrien et al. 2014). All the birds were captured breeding at the point marked with a star. Only one owl returned to breed at that same site in the following three years (individual F4, yellow line) after breeding as far away as northern Greenland in intervening years. In addition to documenting breeding dispersal of up to 2,224 km, satellite data provides much detailed information on routes and timing that were impossible to study until recently. Map reproduced with permission from Jean-François Therrien. Snowy owl photo by Hilde Marie Johansen.

heavy for most birds. Those that are too small to carry satellite transmitters can often carry tiny light-detecting geolocators that record the time of daylight hours. The combination of date and time of sunrise and sunset allows us to infer (\pm a couple hundred kilometers) the latitude and longitude of the bird from deployment to eventual recapture and recovery of the tag. This technology has recently exploded in popularity because it finally allows ornithologists to document patterns of migratory connectivity, migration routes and stopover locations, winter movements, and migration phenology, all at the individual level (McKinnon et al. 2013). Smaller birds can also wear tags that allow researchers to preprogram a limited number of GPS fixes at specified times and dates. The device then stores information onboard, meaning that bird must be recaptured to retrieve data. Thus, like geolocators, their utility is limited to birds that are site-faithful to breeding or wintering areas but provides finer-scale spatial resolution.

MOBILITY AS A LIABILITY

Birds pose unique conservation challenges and opportunities as a consequence of their mobility. To ensure full-life-cycle conservation of migrants, we must protect far more habitat than we do for a sedentary animal. Migrants require not only different breeding and nonbreeding habitat, but stopover areas that provide food and safety from predators. Unfortunately, for many migrants, we don't always know where to focus our conservation efforts (Runge et al. 2015). While we usually have a good idea of species' breeding ranges, we know less about wintering ranges, and we have woefully inadequate information on stopovers. For instance, the wintering location of Black Swifts (*Cypseloides niger*) was only recently discovered in northwestern Brazil (Beason et al. 2012). Effective conservation must also support dispersal capabilities. For habitat specialists, fragmentation can increase the mortality costs of dispersing or effectively eliminate dispersal in cases where birds lack the behavioral or morphological capabilities to cross human-dominated landscapes lacking corridors between habitat patches (Ford et al. 2001). Experimental evidence in tropical understory species demonstrates that the willingness or ability to cross stretches of open water is positively associated with likelihood of occupying isolated islands in the Panama Canal (Moore et al. 2008). The flip side is that highly dispersive species may avoid some of the negative consequences of fragmentation. Despite near elimination of their native grassland, birds such as Henslow's and Grasshopper Sparrows have an uncanny ability to locate and breed in patches of newly restored habitat (Gill et al. 2006, Herkert 2007).

Even where suitable habitat allows for normal movements of migrants and dispersers throughout their life,



Figure 19.20. Building collisions are a major source of mortality for nocturnally migrating birds. The Fatal Light Awareness Program (FLAP) works to educate the public and policy makers on how to reduce bird-building collisions and rehabilitate injured birds. Volunteers collect dead and injured birds from near the bases of buildings during migration. This image shows a small fraction of the birds killed by building collisions in 2016, arranged with species experiencing strong population declines in the center. Photo used by permission of FLAP Canada.

human activities continue to make those movements more perilous (chapter 26). Nocturnally migrating long-distance migrants must cope with increasing light pollution. Cities, fishing boats, oil and gas rigs, communications towers, and fires now create nocturnal light environments very different from those in which avian navigational abilities evolved (Longcore and Rich 2004). Lights attract nocturnally migrating birds, especially on cloudy nights. Under certain weather conditions, migrating birds apparently become disoriented by lights and collide with lit obstacles in large numbers (fig. 19.20). Some of the species-level estimates of mortality are astounding—an estimated 9 percent of all Yellow Rails (*Coturnicops noveboracensis*), 8.9 percent of Swainson's Warblers (*Limnothlypis swainsonii*), and ~5 percent of Bay-breasted Warblers (*Setophaga castanea*) and Black-throated Blue Warblers (*Setophaga caerulescens*) are killed each year in collisions with communication towers alone (Longcore et al. 2013). An additional quarter of a million birds are estimated to die at monopole wind turbines each year in the United States, and those numbers are predicted to increase as turbines get taller (Loss et al. 2013). The number of birds killed each year by colliding with buildings and power lines in Canada is estimated at over 32 million, second only to the astounding 134 million birds killed by cats (Calvert et al. 2013). For a few species, re-

searchers have been able to estimate the relative riskiness of different phases of the annual cycle, and migration is clearly a dangerous business; roughly 85 percent of the annual mortality of Black-throated Blue Warblers occurs during migration (Sillert and Holmes 2002).

For birds that successfully complete their migratory journeys and find suitable habitat at their destination, anthropogenic disruptions to global climate systems can result in additional problems. When migrations are endogenously controlled, migration phenology is remarkably predictable from year to year (Fraser et al. 2013). Arrival time ultimately determines the timing of peak offspring demand for food. For species that breed at high latitudes, the timing of migration likely evolved in the context of matching the timing of reproduction and food availability. Syncing those two events is critical because short growing seasons mean that prey are abundant only for brief periods. Thus, there is widespread concern that birds and their prey will experience **phenological mismatch** as the emergence of prey shifts earlier in response to local warming, but migrants continue to depart wintering grounds on schedules controlled by unchanging day-length cues. Consistent with phenological mismatch, European migrant arrival dates are not advancing as much as is the climate, and the species that are less flexible in

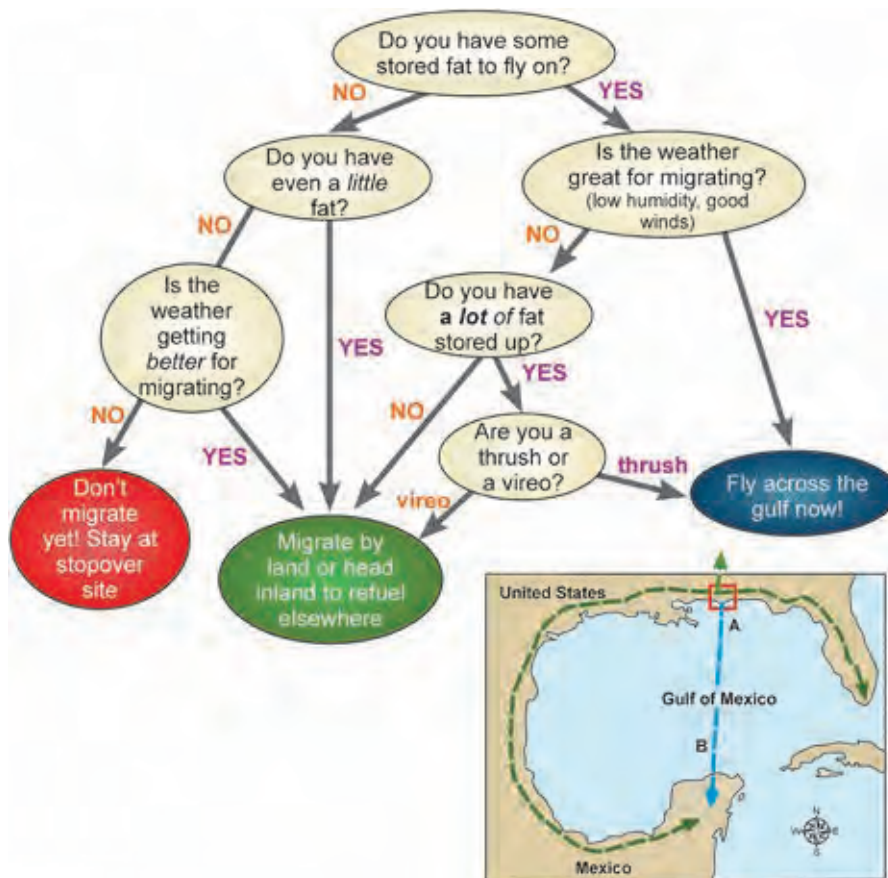


Figure 19.21. Successful migration requires that birds make good decisions. This flow chart represents the decisions made by migrating Swainson's Thrushes, Wood Thrushes, and Red-eyed Vireos. The map shows each of the possible outcomes (migrate over the Gulf of Mexico, blue; depart overland, green; or stay at stopover, red). Redrawn from Deppe et al. 2015 with permission from Jill Deppe.

migration timing are also those whose populations are declining (Saino et al. 2011).

Fortunately, variation in movement ecology within single species may buffer them from the myriad threats they experience over their annual cycle. In a study of 340 European-breeding species, partial migrants and species whose nonbreeding range is larger than their breeding range were less likely to be declining than either residents or migrants with small nonbreeding ranges (Gilroy et al. 2016). These results suggest that flexibility in movement behavior may allow birds to respond more quickly to novel challenges. Additionally or alternately, by spreading nonbreeding mortality risk over more areas, species may be more resilient to unpredictable risks affecting portions of their nonbreeding range. As both field and analytic methods improve, our understanding of the spatial scales and patterns of movement are increasing (Clark et al. 2004). As our knowledge of bird movements increases, ornithologists will be better equipped to manage bird populations and provide hope that movement strategies—the product of millennia of adaptation to ever-changing environmental contexts—will be flexible enough to cope with the current rapid pace of anthropogenic change.

KEY POINTS

- Birds are the most mobile creatures on earth; they exhibit an incredible diversity of movement patterns ranging from extremely long to very short distances, across gradients of latitude, elevation, and aridity, and those movements range from highly predictable, repeated movements, to one-time, unpredictable movements.
- Probably at least half of all bird species engage in annual, round-trip migrations; obligate long-distance migrants represent the most extreme of a continuum of behaviors, and most migrants are probably partial and/or facultative migrants.
- Migration has been “switched” on and off many times in the evolution history of birds, appearing when the ultimate benefits, such as availability of food, benign climatic conditions, or predator-free space, outweigh the considerable mortality risks, energetic costs, and temporal constraints.
- Dispersal differs from migration in being a one-way movement that can result in gene flow between populations; some members of all species engage in natal dispersal prior to their first breeding attempt, and in some species, birds make breeding dispersal movements between successive breeding attempts.
- Both migration and dispersal are controlled at proximate levels by both innate and facultative processes; knowing when to travel, where to go, and when to stop involves complex interactions between external cues, genetic predisposition, and physiological processes.
- While direct observation and bird banding have been extremely important sources of movement data, newer technology is rapidly increasing our ability to study movement at the individual level, making it possible to answer long-standing questions and revealing new and intriguing patterns.

KEY MANAGEMENT AND CONSERVATION IMPLICATIONS

- Because birds are so mobile, their migration and dispersal abilities mean that we must conserve far more land area than for resident animals, and we must maintain connectivity among fragmented habitats to maintain healthy populations.
- Full annual cycle conservation of migrants is particularly challenging, especially when birds cross geopolitical barriers requiring international partnerships—critical breeding, stopover, and wintering areas may be in different countries or continents.
- Climate change will likely affect movements in several ways, including promoting dispersal to new regions, affecting the match between of innately controlled migration phenology and food availability and, in facultative migrants, potentially leading to changes in the frequency, direction, or fitness payoffs of different strategies.
- Urbanization affects migratory behavior via selecting for less mobile strategies and impeding migrations by reducing habitat and increasing mortality through impacts with tall buildings and lighted structures.

DISCUSSION QUESTIONS

1. In contrast to birds, mammals exhibit male-biased dispersal—males typically disperse away from natal areas, whereas females remain near natal areas to breed. Discuss the potential causes for such a pattern, based on the ultimate causes of dispersal described in this chapter.
2. Some bird enthusiasts have been concerned that the practice of putting up hummingbird feeders in North America is leading to the loss of migratory behavior in some individuals. Use information in this chapter to argue both for and against the idea that human activities would affect migration in this way.

3. Successfully migrating long distances involves making a series of good decisions en route. How long to stay at stopover locations? When to leave? Which direction to travel? Decisions at key points can make a huge difference to a bird's immediate prospects of survival, how long it survives, and how many offspring it can produce in the future. Researchers placed radio transmitters on Red-eyed Vireos (*Vireo olivaceus*), Wood Thrushes (*Hylocichla mustelina*), and Swainson's Thrushes (*Catharus ustulatus*) at a stopover site in coastal Alabama (Deppe et al. 2015), detected departure times and directions using telemetry receivers along the Gulf Coast and detected arrival on the Yucatan peninsula. Birds chose to cross 1,000 km of open water to the Yucatan coast, or to depart overland, or to remain at stopover sites (fig. 19.21). The birds they studied made different decisions that depended on their fat stores, weather, and their species (vireos vs. two thrush species). Study the decision tree pictured here and discuss the following questions. What costs and benefits might birds be balancing when deciding whether to stay and increase fat stores to make the overwater crossing or depart, taking an overland route around the Gulf Coast? Low and dropping humidity is associated with favorable tail winds that may help explain the importance of weather variables in departure decisions. In what other ways might high humidity affect the costs of nocturnal flight? Vireos were less likely to cross the Gulf of Mexico than the thrushes. What might explain this pattern? (Hint: look up their range maps.)
4. Migration within the Southern Hemisphere is characterized by more facultative and shorter-distance migrations relative to birds breeding in the Northern Hemisphere. One potential driver of such differences is that precipitation patterns may be more important climatic drivers of Austral migrants because of generally milder and drier climates. No similar comparison of northern and southern dispersal tendencies yet exists for birds. If precipitation plays a greater role than temperature in shaping migrations in austral birds, then would you expect dispersal tendencies to also vary? Why or why not?
5. Migrant birds are among those in greatest decline in North America. Habitat destruction is the prime culprit in most species' declines, but migration confounds our ability to pinpoint problem locations and times during the annual cycle. Scientists have limited funds for research. Consider how you would decide how to spend funding if your goal was to conserve Dickcissels. Dickcissels breed in prairies of the midcontinental USA, wintering in Venezuela, where they eat grain crops and are persecuted by farmers. Dickcissels have moderate breeding

site fidelity and are parasitized heavily by Brown-headed Cowbirds. You can choose to learn only one of the following priorities for future research (Temple 2002): (a) whether or not birds rear second broods in more northerly parts of the breeding range after raising a brood further south earlier in the breeding season; (b) rates of survival during migration and on wintering grounds; (c) identity of nest predators; (d) the magnitude of financial incentives farmers in Venezuela might be accept in compensation for crop losses if they agree to avoid killing Dickcissels. Which research objective would you chose, and why?

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