20641 Migration and Navigation in Birds

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Introduction

Migration is the movement of an animal between distinct habitats or home ranges; these movements are greater in scale than those that occur as part of the regular daily routines of animals (**Dingle and Drake, 2007**). Most commonly, migratory movements, including those of birds, take animals between a breeding location and non-breeding location or wintering ground. Although migration is itself an energetically demanding process, it allows animals to make use of resources that vary in space and time, such as food sources that are only available seasonally. For example, Gambel's white crowned sparrows (*Zonotrichia leucophrys gambelii*) breed at high latitudes such as in Alaska and northern Canada, where they can feed on insects that become abundant in the spring and summer. However, these high-latitude breeding sites become inhospitable in the winter. Therefore, the birds migrate to lower latitudes in the western US and Mexico for overwintering, where seeds, grasses and fruits are available to eat. In this way, migration allows birds to utilize resources that are available in a given area for only a limited period of time.

Types of Migration

Patterns of migratory behavior vary widely among species. The most well-known migrants are those species that make very predictable migrations that occur at the same times each year and move birds between the same locations each year. This type of migration is often called obligate, calendar, or to-and-fro migration. Most often birds move to breeding grounds in the spring and then to wintering grounds in the fall. Some species make an additional movement to a third location, such as a molt migration to a location for molting (i.e., replacing of the feathers). American redstarts, (*Setophaga ruticilla*,), black-headed buntings (*Emberiza melanocephala*), Gambel's white-crowned sparrows, Northern wheatears (*Oenanthe oenanthe*), and red knots (*Calidris canutus*) are just a few well-studied examples of obligate migrants.

However, not all birds move so predictably. Migrations that occur less predictably in space and/or time are called facultative migrations. One form of facultative migration is nomadic migration. Nomadic migrants typically move unpredictably between different locations each year, such that they rarely return to the same location. Nomadic migrations also tend to vary more in their timing from year to year, and nomadic migrants may forgo migration in some years. Banded stilts (*Cladorhynchus leucocephalus*), gray teals (*Anas gracilis*), pine siskins (*Spinus pinus*), red crossbills (*Loxia curvirostra*), and Tengmalm's owls (*Aegolius funereus*) are examples of nomadic migrants.

It is also important to recognize that many species of birds (or, in some cases only certain populations within a species) do not migrate; instead they remain in the same location year-round. Such birds are referred to as permanent residents. For such a strategy to be successful, resources, particularly food, must be sufficiently available in the same location year-round. House finches (*Haemorhous mexicanus*), spotted antbirds *(Hylophylax naevioides)*, and gray partridges (*Perdix perdix*) are all examples of species that are permanent residents in at least some parts of their range. Furthermore, some populations are composed of a mixture of birds that migrate and birds that remain resident. Such populations are said to be partially migratory. In some cases, individual birds within a partially migratory population remain either migrant or resident for their entire lives. This is the case for European blackcaps (*Sylvia atricapilla*) where being migratory or resident is an inherited trait. In other species, such as tropical kingbirds (*Tyrannus melancholicus*) and skylarks (*Alauda arvensis*), individuals can switch between being migrant and resident across years, depending on their body condition, social status, or prevailing environmental conditions.

In addition to nomadic migration, another form of facultative migration is fugitive or escape migration. Fugitive migrations are movements away from unpredictable and severe disruptions in the local environment, such as a severe storm or drought. They allow birds to escape these inhospitable conditions and return when the disruption subsides. Fugitive migrations can occur in any bird, regardless of their typical migratory pattern. Thus, obligate, nomadic, and partial migrants, as well as permanent residents, can all make fugitive migrations if necessary.

The Migratory Phenotype

Migration involves profound changes to the morphology, physiology and behavior of a bird. Prior to migration birds undergo a period of preparation. This includes an increase in feeding (known as hyperphagia) and, in some species, a shift in diet such as an increase in fruit intake. These changes in feeding behavior in turn support fat deposition, which increases dramatically in many species (**Fig. 1**). Ultimately, these fat reserves provide the fuel for migration (**McWilliams *et al*., 2004**). Birds also increase muscle mass, particularly through hypertrophy, an increase in size, of the pectoralis muscles, which power the wing downstroke and are critical to sustained flight (**Fig. 1**). Birds may also undergo changes that facilitate oxygen transport during the intense exercise involved in migration, such as increasing the proportion of red blood cells in the blood. The intensity of these preparations (e.g., extent of fat deposition) can vary seasonally (fall vs. spring migration) and across species, and migratory preparations have been suggested to vary with factors such as the length of the migratory journey and expected conditions *en route*. Moreover, in some species, energy reserves that are deposited prior to migration or during stopovers may also provide energy for breeding efforts after arrival.

The preparatory period is followed by the expression of the migratory state. The immediate decision to begin a migratory flight is influenced by weather conditions such as precipitation, cloud cover, temperature and wind conditions, with warm weather, clear skies without rain, and no winds or tail-winds being most conducive to migration (**Richardson, 1990**). Time of day also influences when birds migrate. Many species of birds migrate at night, including numerous species that are otherwise diurnal in their activity patterns. Flying at night, rather than during the day, may occur because atmospheric conditions at night are more favorable for flight and/or for preventing dehydration and overheating (**Berthold, 1996**). Nocturnal flight may also be necessitated by the need to feed during the day. Despite these potential advantages of nocturnal migration, there are other species that migrate during the day.

In some species, such as bar-tailed godwits (*Limosa lapponica baueri*), migration occurs primarily as a single non-stop bout of flight, whereas in other species migratory flight is interrupted by frequent periods of stopover, during which birds refuel before resuming flight. Stopovers typically last a few days to a couple of weeks, during which time birds forage in order to replenish fat depots and prepare for further migratory flight. In selecting stopover sites, birds must select locations with sufficient food availability for refueling. The length of stay at a stopover site is influenced by the bird's condition when they arrive, as well as their ability to refuel at the site.

Once birds have arrived at their destination, migration terminates. This process of arrival and settlement is perhaps the least understood step in migration. In many species, arrival in the general geographic area of the destination is followed by a period of local movement as birds locate suitable habitats or sites before settling. Upon arrival birds may also maintain a degree of readiness to resume or continue moving if conditions are unsuitable or deteriorate (Ramenofsky and Wingfield, 2006).

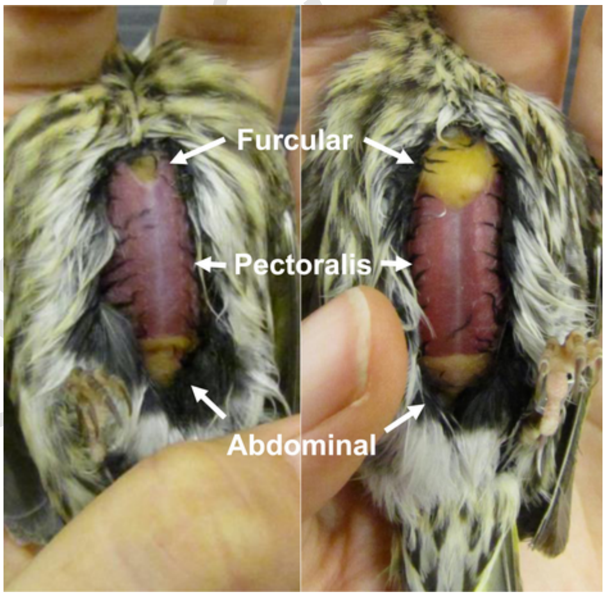

Fig. 1 Photos illustrating physiological preparations for migration. Subcutaneous fat deposition is visible in the furcular and abdominal regions as yellow tissue. The bird on the right has more extensive fat depots compared to the bird on the left. As premigratory fattening progresses, fat depots will even surpass those seen in the bird on the right. An increase in the size of the pectoralis muscles (muscle hypertrophy) can also be seen; on the right the muscles are bulging above the keel, this is not the case for the smaller muscles on the left. Photos are taken from pine siskins (*Spinus pinus*). Photos by H.E. Watts.

Navigation

For to-and-fro migrants, migration involves travelling between the same breeding and wintering grounds each year. How these birds find their way during migration has been a question of great interest to scientists. Although we do not yet have a complete picture of how this is accomplished, we do understand several mechanisms that birds use to navigate. Birds have at least three biological compasses that they can use to orient themselves in space. Birds are able to use (1) the sun and patterns of polarized light, (2) earth's magnetic field, and (3) stars to orient (**Berthold, 2001**). Moreover, evidence suggests birds may often use a combination of these cues. For example, thrushes belonging to the genus *Catharus* appear to use cues from the sun at twilight to determine a migratory direction and then use a magnetic compass to maintain that direction during their nighttime flight (**Cochran *et al*., 2004**). Each biological compass requires a sensory mechanism to detect the cue, which is then processed by the brain. Recent research has focused on understanding how birds detect and process magnetic information for orientation, and there is now evidence that both the eye and beak contain magnetoreceptors that could function in the magnetic compass (**Mouritsen and Ritz, 2005**). Although birds can determine direction using one or more of the biological compasses, a compass alone does not inform a bird about its relative location on the landscape. Although a number of potential mechanisms have been proposed by which birds might determine their location, few are well supported by empirical evidence. The best evidence for such a mechanism one is based on spatial cues that birds learn *en route* and at destinations in order to aid in navigation during subsequent migrations (**Mettke-Hofmann and Gwinner, 2003**). While such cues are useful for adults, young birds lack such cues on their first migration.

The first time a bird migrates from the breeding grounds where it was born to its wintering grounds, it must travel a route it has never taken to a destination it has never seen. To do this, birds make use of a genetically inherited migratory direction. This migratory direction sets birds off on a trajectory towards their destination and is coupled with a programed duration of migration. Together this use of direction and duration of migration, which is referred to as vector navigation or clock-and-compass orientation, leads juvenile birds to their wintering grounds (but see **Thorup *et al*. (2010)** for a discussion of the limitations of this explanation). In flocking species, juveniles may make use of the knowledge of experienced adults by following them. But even species that typically rely on experienced guides may also be able to vector navigate, presumably as a backup mechanism (**Mouritsen, 2003**). Once a bird has completed this initial journey, it has had the opportunity to gather information on the breeding and wintering grounds that it may use on subsequent migrations. A bird will also have been able to gather information *en route*. Therefore, it is possible that birds could make the return journey to the breeding grounds by retracing their outbound route. However, in many species, birds take a different migratory return route. Consequently, vector navigation is likely used in combination with information that was previously learned about habitat, latitude, or landmarks on the breeding grounds or *en route*. Once birds have completed the entire outbound and inbound migratory journey the use of learned spatial cues seems to take precedence in navigation, though birds continue to possess the ability to vector navigate (**Mouritsen, 2003**).

Timing of Migration and Connections to Reproduction

In many birds, reproduction and migration are tightly linked in the annual cycle (**Fig. 2**). Preparation for breeding often begins with migration to the breeding grounds, and the termination of breeding can be closely tied to the migratory departure to the wintering grounds. In order to prepare for breeding, most birds undergo seasonal development of the reproductive system, a process coordinated by activation of the hypothalamic-pituitary-gonadal (HPG) axis. The HPG secretes reproductive hormones leading to the development of a gonad capable of producing gametes. Although some species, typically those that move only short distances, do not undergo the process of gonadal development until after they arrive on the breeding grounds, many species undergo gonadal development during migration and arrive on the breeding grounds in a state of near-readiness to breed. In Gambel's white crowned sparrows, for example, initial activation of the HPG axis begins on the wintering grounds. By the time birds arrive on the breeding grounds, males are producing mature spermatozoa in the testes and females have enlarged ovarian follicles, though they have not yet begun yolk synthesis or deposition (**Ramenofsky and Wingfield, 2006**).

Appropriately timing events like migration and reproduction is critical to the survival and reproductive success of individual birds, and ultimately to the persistence of bird populations. If birds arrive on the breeding grounds too early, conditions may still be inhospitable and their survival may be threatened. On the other hand, birds that arrive too late may not have enough time to complete breeding, or they may miss peak food availability which could compromise their reproductive success. The question of how birds time their migrations has been best studied in obligate migrants. Therefore, that is the focus here, but for greater discussion of other migratory types see **Watts *et al*. (In press)**. Among obligate migrants increasing day length (photoperiod) in conjunction with an endogenous circannual rhythm are important mechanisms initiating spring migration (**Gwinner, 1996**), while other environmental conditions, such as temperature, can fine-tune the timing. Increasing photoperiod stimulates activation of the HPG axis, which is also important in preparation for breeding, and leads to increasing levels of circulating androgens, notably testosterone. In both males and females, increasing androgen levels are important in stimulating the behavioral and physiological changes associated with the transition to spring migration (**Wingfield *et al*., 1990**). Activation of thyroid hormone signaling pathways in the brain in response to increasing photoperiod is also critical in the spring migratory transition (**Pérez *et al*., 2016**).

The mechanisms triggering fall migration are not as well studied as those operating in the spring. As for spring migration, photoperiod (experienced in the fall as well as those experienced earlier in the year) and endogenous circannual rhythms likely play important roles. On the other hand, the endocrine mechanisms underlying the transition to a migratory state appear to differ from those in spring migration, though they are currently not well understood. The timing of fall migration tends to be more variable than spring migration, which likely reflects sensitivity to local environmental conditions (e.g., temperature, food availability) and differences among individuals in their progression

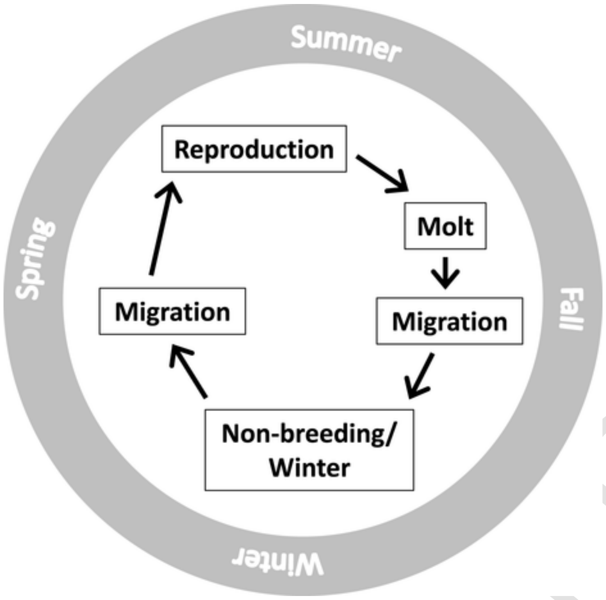

Fig. 2 Example of an annual cycle typical of many temperate zone birds.

through breeding and the feather molt usually needed before the migratory flight. For example, when breeding of mountain white-crowned sparrows is delayed due to heavy snow cover, birds subsequently delay the fall migratory departure (**Morton and Pereyra, 1994**).

Just as circumstances around breeding events can influence fall migration, so too can spring migration influence breeding. In many species, it has been found that birds arriving earlier on the breeding grounds enjoy greater reproductive success than later arriving birds. For example, in American redstarts (*Setophaga ruticilla*), which migrate from wintering sites in the Caribbean and Central and South America to breeding sites the United States and Canada, earlier arrival corresponds to greater reproductive success in males. The potential advantages of earlier arrival for redstarts and other species include access to more and/or higher quality territories and mates, as well as the potential to lay more clutches during the breeding season. Interestingly, studies across a variety of species have revealed that it is those birds in the best physical condition that arrive earliest. Among American redstarts, males that winter in better quality (in this case, wetter) habitats are in better physical condition at the end of the winter, depart for spring migration earlier, and arrive on the breeding grounds earlier than males that winter in poorer habitats (**Marra *et al*., 1998**). Given the correlation between migratory timing and physical condition, it is difficult to disentangle whether the superior reproductive success of early arriving birds is a result of their earlier arrival or their superior condition, or a combination of the two.

Impacts of Climate Change on Migration

Changes in the earth's climate over the past century, including warming trends, are having considerable impacts on patterns of bird migration (**Carey, 2009**). Perhaps the most widely documented change has been in the timing of spring migration. In many species, birds are arriving on their breeding grounds earlier in the year. This may occur as birds adjust the timing of migration in response to conditions, such as warmer temperatures or advancing plant phenology, on their wintering grounds or *en route* (e.g., at stopover sites), though changes in the location of wintering grounds (see below) could also contribute (**Knudsen *et al*., 2011**). However, not all species or populations are showing such shifts in spring migratory timing.

The consequences of climatic shifts depend on the details of how conditions such as food availability are changing relative to changes in the timing of spring migration. In many species it has been found that the timing of arrival on the breeding grounds is becoming increasingly mismatched to the timing of food availability in the spring, a critical resource for successful reproduction. In some cases, this is occurring as species fail to advance their spring arrival. Pied flycatchers (*Ficedula hypoleuca*) in the Netherlands, for example, have advanced their spring breeding to some extent, but they are limited by arrival time, which has not advanced (**Both and Visser, 2001**). In other cases, birds are advancing the timing of their spring arrival but not enough to keep up with even greater advances in the timing of spring food availability. And in yet another scenario, birds are advancing their spring arrival but conditions on the breeding grounds have not advanced. For example, American robins (*Turdus migratorius*) in the Rocky Mountains have advanced their arrival on their high-altitude breeding grounds, presumably in response to conditions at their lower-altitude winter grounds. But the timing of snowmelt on the breeding grounds, which determines spring food availability, has not changed; the result is that robins must wait longer for food to become available (**Inouye *et al*., 2000**).

The effects of climate change on the timing of fall migration are not as well studied, but the effects seem to be even more varied than those on spring migration. Some species or populations are departing the breeding grounds earlier, while others are departing later, and yet others show no change. In addition to effects on the timing of migration, climate change is also altering the distances that birds migrate. The most common effect is for migratory distances to be shortened. Birds belonging to a number of species that breed in Europe have been documented overwintering at higher latitudes, closer to their breeding range, in recent decades compared to in the past. Furthermore, some populations are becoming increasingly sedentary, with fewer birds migrating and more birds remaining resident year-round (**Newton, 2010**).

Summary

Birds express a range of migratory patterns, from highly predictable obligate migration, to less predictable nomadic and fugitive migrations. Typically, spring migration moves birds from their wintering grounds to their breeding grounds, and fall migration returns birds to their wintering grounds. Frequently, migration is preceded by a period of physiological preparation, which can include increases in fat deposition as an energy reserve for migratory flight and increases in the size of the flight muscles. Once preparations are complete, the initiation of migratory flight is often influenced by weather conditions such as precipitation and wind. Many birds migrate at night, even species that are typically diurnal. As the migratory journey progresses, birds may make stopovers to refuel along the way. The process by which migration terminates once birds reach their destination is one of the least understood aspects of migration. In order to find their way on their migratory journey, birds may make use of several biological compasses, as well as inherited migratory programs, and learned landmarks on the landscape. Birds time their migrations using cues in the environment, most notably day length, and an endogenous circannual clock. Events during migration and breeding are often closely linked such that the timing or success of one stage is influenced by the other. Changes in the earth’s climate over the past century are having impacts on migratory timing and migratory patterns, as well as the extent to which the timing of migration matches the availability of key resources.

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