CHAPTER 6

Migration and Navigation

Once birds evolved the ability to fly, migration and globe-trotting became possible. The movement of birds across the Earth is most pronounced in autumn and spring, when many species that breed in temperate and higher latitudes move toward (in autumn) or away from (in spring) lower latitudes, where they spend the winter. Such globe-trotting has required the evolution of sophisticated navigation and timekeeping skills, to allow birds to find their way and set off at the right time.

Some birds travel thousands of kilometres to and from their regular breeding and wintering areas on a fixed schedule, whereas others travel only when environmental conditions deteriorate and they are forced to find greener pastures. Variation in the timing, duration and direction of these usually seasonal movements for any given species occurs because the migrations are controlled by a combination of internal (genetic, physiological) and external (environmental) factors.

◀ Lesser snow geese (*Anser caerulescens caerulescens*).

Migration patterns

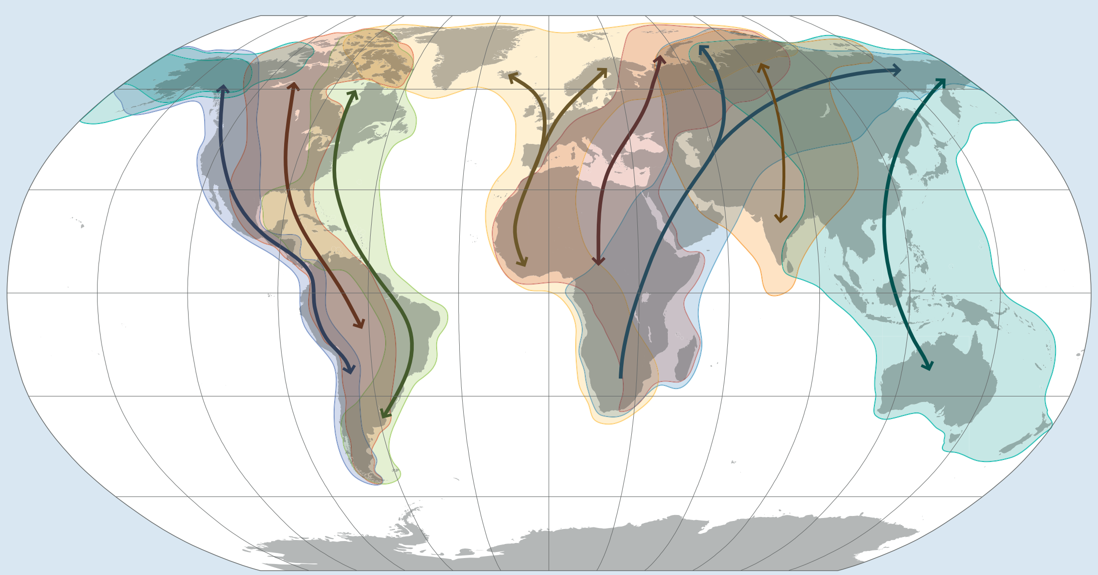
With few exceptions, almost every inch of our planet is overflown by a bird at some point in the year. During migration, most birds move along recognised flyways that have become defined over time by ecological barriers such as tall mountains, large deserts and oceans, and by prolonged glacial periods. Most major flyways are oriented north to south and are predominantly used in autumn and spring, when many species migrate between breeding and wintering grounds. In some areas, however, birds migrate in a wider variety of directions to benefit from wet or dry seasons, or for those species that breed on mountains, they simply move to lower altitudes during winter.

Obligate versus facultative migrants

The timing, duration and routes used by birds during their migrations all vary. However, our ability to track the movements of the full diversity of birds over the globe has become possible relatively recently with the development of very small tracking devices, many of which communicate via orbiting satellites. Some migratory birds traverse the full length of a given flyway (e.g. bar-tailed godwit, *Limosa lapponica*, seasonally move between western Alaska and New Zealand), whereas most move much shorter distances. Likewise, some migratory birds initiate and end migration on the same day each year; that is, timing of migration is principally controlled endogenously, or internally, and is quite independent of environmental conditions. Other migratory birds require certain changes in the environment (e.g. cold temperatures) to prompt their departure during a given season and hence the timing of their movements varies from year to year.

Like human snowbirds or grey nomads, who spend the winter in warmer places, most birds seasonally migrate to more benign areas on their own, even though many individuals may be moving from the same place at the same time. The general route taken by most migrating birds from breeding areas to/from wintering areas is inherited, although local environmental conditions (e.g. prevailing winds) and barriers (e.g. oceans for landbirds) influence the exact path an individual bird takes. Young birds migrating for the first time (usually well before they are a year old) can be found in unusual places, in part because the entire migration is across unfamiliar landscapes, and also because the inherited avian navigation system is not as precise as our Global Positioning System (GPS) .

Principal migration flyways of the world

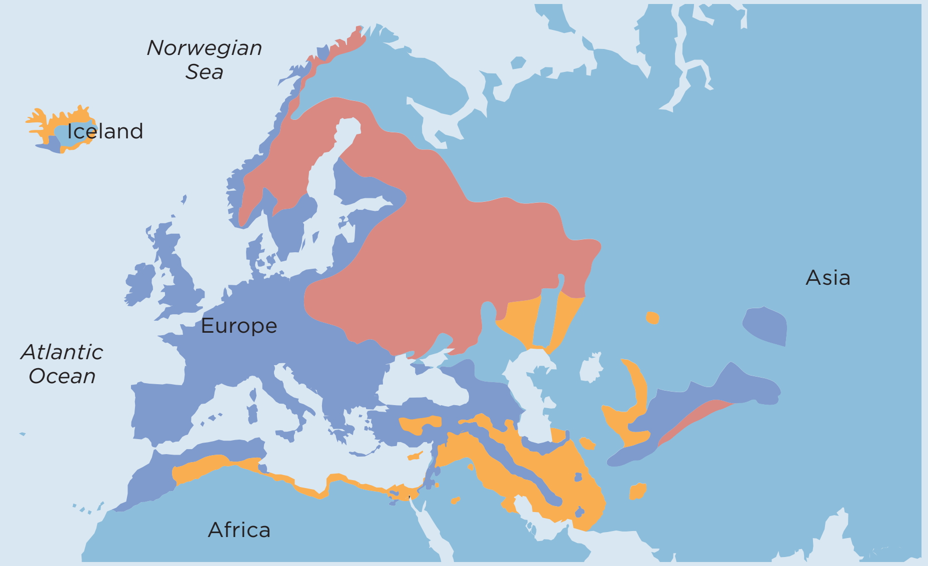


- Pacific Americas
- Central Americas
- Atlantic Americas
- East Atlantic
- Black Sea–Mediterranean
- East Asia–East Africa
- Central Asia
- East Asia–Australasia

◀ The major migratory flyways of birds are primarily oriented along a north–south axis.

Eurasian distribution of the common blackbird

- summer distribution
- resident distribution
- winter distribution



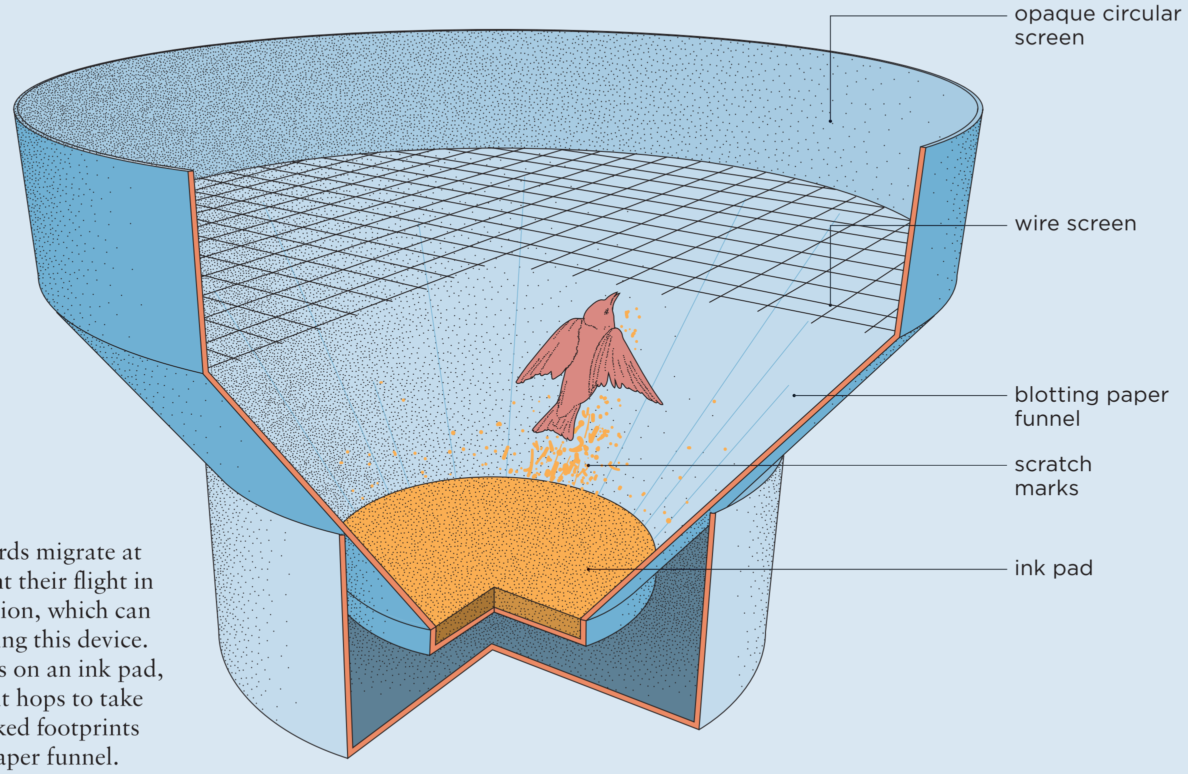
▶ The common blackbird (*Turdus merula*) is known as a partial migrant, in that some populations migrate between summer and wintering areas, whereas others do not migrate and instead remain resident year-round (purple shading).

◀ Innovations in transmitter technology allow the tracking of individual birds as they traverse the globe. Shown here is a transmitter with a small solar panel that charges a battery inside.

Birds that rely more on internal (inherited, physiological) regulation of migration are known as obligate migrants and tend to be much more predictable in the timing, duration and direction of their movements. Those that rely more on environmental factors are known as facultative migrants and are usually much less predictable in their patterns of movement. This mix of migration types can even be observed within a single species, in which case it is known as a partial migrant. For example, some common blackbirds (*Turdus merula*) are year-round residents in western Europe, but others are facultative or obligate migrants that breed further north and then move to more southerly non-breeding areas.

Common blackbird (*Turdus merula*)

Experimental determination of migration direction



▶ Most songbirds migrate at night and orient their flight in a certain direction, which can be recorded using this device. The bird stands on an ink pad, and each time it hops to take off, it leaves inked footprints on the white-paper funnel.

Controls of bird migration

How can we determine the extent to which the timing, duration and direction of migratory movements is controlled by internal, inherited factors versus external environmental factors? Documenting where birds go throughout the year has been a long-standing activity for bird researchers, but only recently have we learned about the physiological mechanisms that control bird migration. A particularly revealing set of experiments was conducted by the German ornithologist Peter Berthold in the 1970s and 1980s on the Eurasian blackcap (*Sylvia atricapilla*). These common warblers breed throughout Europe and include populations that are long- and short-distance migrants.

The researchers captured birds from a variety of different populations and kept them under normal daylight conditions in cages. Conveniently, when blackcaps and many other small songbirds are brought into captivity, they respond to natural changes in photoperiod just like free-living birds. For example, during shorter days in autumn they became active at night (a behaviour known by the German term *Zugunruhe*, meaning 'migratory restlessness'), and the extent of nocturnal activity corresponds to the duration of migration for that population. In addition, small songbirds like blackcaps preferentially orient their night-time activity in the direction in which they travel, and by placing the captive birds in large funnels (called Emlen funnels, after their designers) at night and recording the way they jumped and fluttered, the researchers could determine their preferred direction of travel.

The experiments revealed that blackcaps from populations that migrate in a southwesterly direction to cross the Strait of Gibraltar oriented their movements to the southwest, whereas birds from populations that migrate in a southeasterly direction to the Middle East oriented their movements in that direction. Remarkably, when blackcaps from these two populations were cross-bred, the hybrids migrated on average in an intermediate direction (directly south), which suggests that there is an important innate, inherited genetic component to their migration strategy. This has been confirmed in dozens of species and seems an essential guide for birds during their annual migrations.

Influence of environmental cues

Besides the innate component to migration determining the direction of travel, the other important finding from the blackcap experiments and many other similar studies is that photoperiod (the duration of daylight, from sunrise to sunset) provides a proximate, predictable environmental cue, instigating key hormonal changes that control the timing and preparation for migration (in addition to reproduction; see pages 148–53). Other cues supplement the information from day length, including temperature, food supply and social cues (e.g. the activity of conspecifics). In summary, the timing of seasonal movements such as the migration of birds, and much of the variation between species in the timing of migration, is the product of an interplay between photoperiodically induced physiological changes, coincident changes in certain other environmental cues (e.g. food, temperature), and an evolved endogenous annual rhythm. In addition, the direction and duration of migration is also inherited to various degrees, depending on the species and population.

Blackcap
(*Sylvia atricapilla*)

Migration pathways of blackcaps in Europe

▲ Eurasian blackcaps (*Sylvia atricapilla*) inherit a tendency to migrate in different directions depending on which population they are from. The coloured dots show preferred direction of travel of certain individuals, while the triangle indicates the average direction of travel of each group – in this case, either southwest (SW) or southeast (SE), or an intermediate direction (middle circle) when individuals from the two populations are cross-bred.

Migration connectivity and conservation

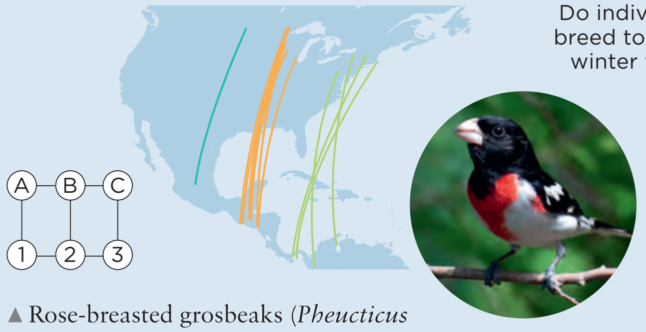
The fact that a species is migratory influences its populations and conservation. Most birds return annually to the same breeding areas, especially when they have bred successfully; faithfulness to wintering areas is less common. If individuals of a given species or population consistently use the same breeding and wintering areas, then this coordinated movement results in strong migratory connectivity. In contrast, weak migratory connectivity occurs when individuals from one breeding area have different wintering grounds, resulting in substantial mixing of birds and less population integrity.

Delineating migratory populations

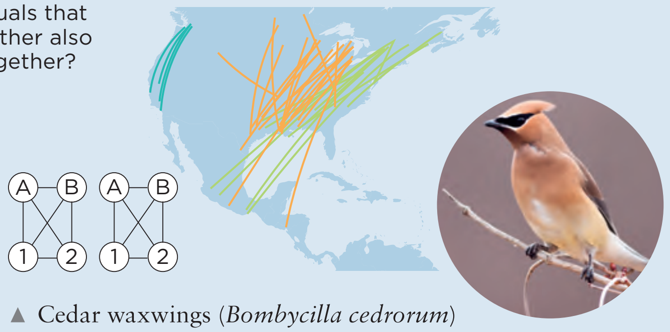
The pattern of site faithfulness and population connectivity of migratory species has consequences for how that species is managed. A classic example of the importance of accurately delineating populations for conservation purposes was the delayed recognition of 'migratory' and 'resident' Canada geese (*Branta canadensis*) along the Atlantic Flyway. Genetically distinct populations of these birds cannot be differentiated by appearance alone; rather, individuals from different breeding areas must be tracked to assess the extent of their movements. Prior to the 1990s, Canada geese in the eastern USA were managed as one large population, even though biologists recognised that there were breeding Canada geese throughout eastern Canada and all the way down the eastern coast of the US. Unfortunately, differential survival, breeding success and hunting pressures led to steep declines in the 'migratory' Canada geese that mostly bred in eastern Canada and wintered along the east coast of the US, while sedentary 'resident' populations that bred along the east coast of the US exploded to nuisance levels. Recognising this complex population structure, wildlife biologists changed the timing of the hunting season (an early September start to the season targeted the 'residents' and occurred before the arrival of the 'migrants'), which led to reductions in the harvest of 'migratory' Canada geese and the recovery of their populations.

Strong to weak migratory connectivity

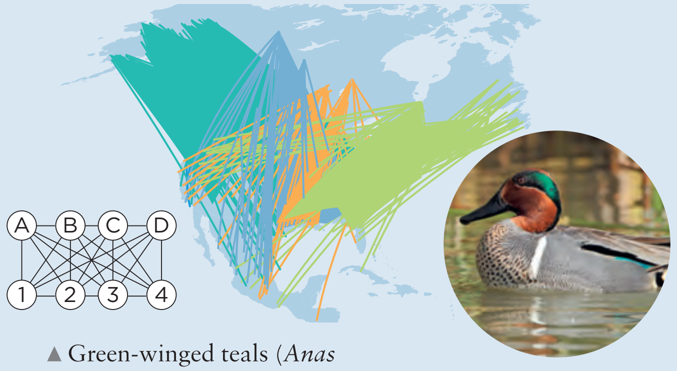
Do individuals that breed together also winter together?



▲ Rose-breasted grosbeaks (*Pheucticus ludovicianus*) from distinct breeding populations (A, B, C) tend to stay together during winter at distinct sites (1, 2, 3).



▲ Cedar waxwings (*Bombycilla cedrorum*) from several breeding populations (two sets of A, B) intermix and spend the winter in several wintering locations (two sets of 1, 2).



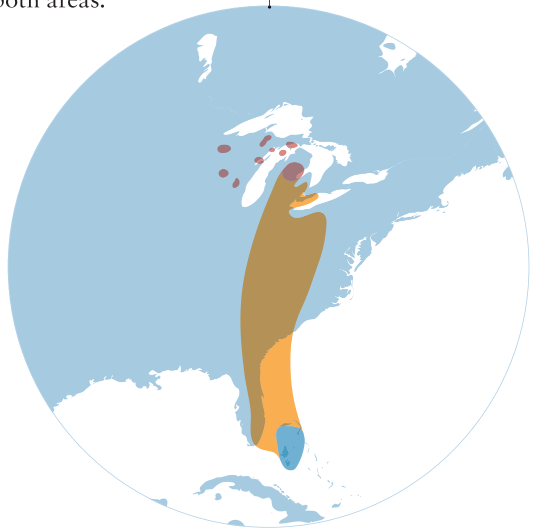
▲ Green-winged teals (*Anas carolinensis*) from many breeding populations intermix substantially during winter.

Managing migratory populations

Determining the key breeding and non-breeding areas of migratory birds has also led to the recovery of several threatened species. For example, the Kirtland's warbler (*Setophaga kirtlandii*) is a small songbird that was included on the very first US list of endangered species in 1967 under the Endangered Species Preservation Act of 1966. At that time there were fewer than a couple of hundred breeding pairs of Kirtland's warblers in the jack pine (*Pinus banksiana*) forests of upper Michigan and Wisconsin, and little was known about the reasons for their endangered status and where they went during the non-breeding season.

Initial efforts to help the Kirtland's warbler focused on enhancing breeding success, primarily by burning the jack pine forests to improve the extent and quality of the breeding habitat, and removing brown-headed cowbirds (*Molothrus ater*), a notorious parasitic species. Female cowbirds lay their eggs in nests of other species, including those of Kirtland's warblers, often at the expense of the host's own young. Although these management efforts enhanced the breeding success of the Kirtland's warbler, the population did not increase, suggesting that it was regulated by events during the non-breeding season. Not until the species' wintering areas in the Bahamas were discovered and also successfully managed did the population recover. Today, there are an estimated 2,000 breeding pairs, although the species depends on continuing management to establish young forest habitat and to reduce cowbird populations.

▲ Kirtland's warbler (*Setophaga kirtlandii*) is an endangered migrant with very limited breeding and wintering areas, and a strong migratory connectivity. Conservation relies on management in both areas.



Managing and protecting migration stopovers is also important for conservation, especially at key sites just before or after geographic barriers such as oceans or deserts, where birds are highly concentrated – for example, at Tarifa in Spain on the Strait of Gibraltar, at Falsterbo in southwestern Sweden and at Eilat in southern Israel. Illegal killing, habitat degradation, wind turbines and other threats can have disproportionately large impacts on migratory birds when they are concentrated in such sites.

In sum, the conservation of migratory birds requires coordinating efforts across their breeding, migration and wintering areas – no small task given that they move across almost every inch of our planet.

Finding home: navigation

Bird movements range from short-distance foraging trips to globe-spanning migrations that cross geographic barriers such as deserts, oceans and mountain ranges. Despite the massive scale of some bird movements, they are not random. After migrating hundreds or even thousands of kilometres, individual birds often return to breed within metres of their prior nesting location.

Philopatry

A high degree of site fidelity is known as philopatry, and most birds exhibit breeding-site philopatry. For example, males of numerous northern temperate-zone songbird species return to breed within metres of the same location each year, purple martins (*Progne subis*) winter in the Amazon basin and return to the same North American nesting colonies each spring, and in migratory Australian golden whistlers (*Pachycephala pectoralis*) 66 per cent of males return to the same nest site and 100 per cent pair with the same female. Most species exhibit very high philopatry to their first breeding site, but migratory common linnets (*Linaria cannabina*) breeding on the remote island of Heligoland in the North Sea return with almost perfect fidelity.

Although wintering philopatry is less studied, some species such as the Asian brown shrike (*Lanius cristatus*) are known to return to the same overwintering sites each year. Achieving such feats requires an accurate navigation system.

▼ Australian golden whistlers (*Pachycephala pectoralis*) exhibit remarkable philopatry. Males return to the same breeding territories and mate with the same female.

▲ Ultralight aircraft such as this have been used to teach migration routes to captive-reared cranes and geese.

First-time flyers

Birds have an amazing ability to navigate, finding their way to a known location from a variety of other locations. Especially revealing is the autumn migration of birds born in the summer, which must travel hundreds or even thousands of kilometres to a location they have never visited before. In some species that migrate in flocks during the day, such as geese and cranes, younger birds may learn migratory routes by following more experienced birds. Conservationists have tried to exploit this in order to teach captive-reared birds to migrate. For example, captive-reared whooping cranes (*Grus americana*) that imprinted on the humans who raised them were trained to follow ultralight aircraft to their wintering grounds in Florida. However, although these cranes did appear to learn their migratory route, their rearing in captivity and imprinting on humans may have affected other behaviours and the practice has been discontinued.

Many other species migrate individually and often at night, conditions that make it unlikely that young birds learn migration routes from older, experienced birds. As described above, studies have found that Eurasian blackcaps, independent of experience, become motivated to migrate in their first autumn for a set period of time, and the direction of their nocturnal migratory restlessness in captivity corresponds to that of their population of origin (see page 191). Another remarkable example of innate control of migration is provided by Eurasian common cuckoos (*Cuculus canorus*), which lay their eggs in the nests of other species, leaving the foster parents to raise their young. Despite being raised by parents of a different species, young cuckoos migrate to wintering areas in central Africa, irrespective of where their foster parents may travel.

These studies demonstrate that many birds have innate behavioural mechanisms that motivate them to fly in particular directions for particular durations on their first autumn migration. In subsequent years, birds often then use their learned experiences to navigate to and from their breeding grounds.

Navigation

Many birds exhibit true navigation: the ability to move to a known location from a variety of starting positions. In one study, white-crowned sparrows (*Zonotrichia leucophrys*) that were relocated thousands of kilometres from their wintering grounds in California one year returned to it the following winter. On a shorter scale, birds that are displaced tens or hundreds of kilometres from their nesting or breeding sites will readily find their way back.

This navigation ability exists naturally in all species studied to date and has been exploited in homing pigeons (*Columba livia domestica*), bred specially for racing and to carry messages. Navigation requires a sense of direction (compass) and a sense of location (map). Much of our knowledge of how birds navigate results from experimental studies of homing pigeons, wherein researchers manipulate the sensory input to the pigeons and determine how this affects their ability to return home. The main conclusion is that birds have multiple ways of sensing direction, and that these overlapping systems provide them with robust mechanisms for orientation and navigation. Virtually every sensory modality has been shown to play a role in navigation in birds, from olfaction to vision, hearing and magnetoreception.

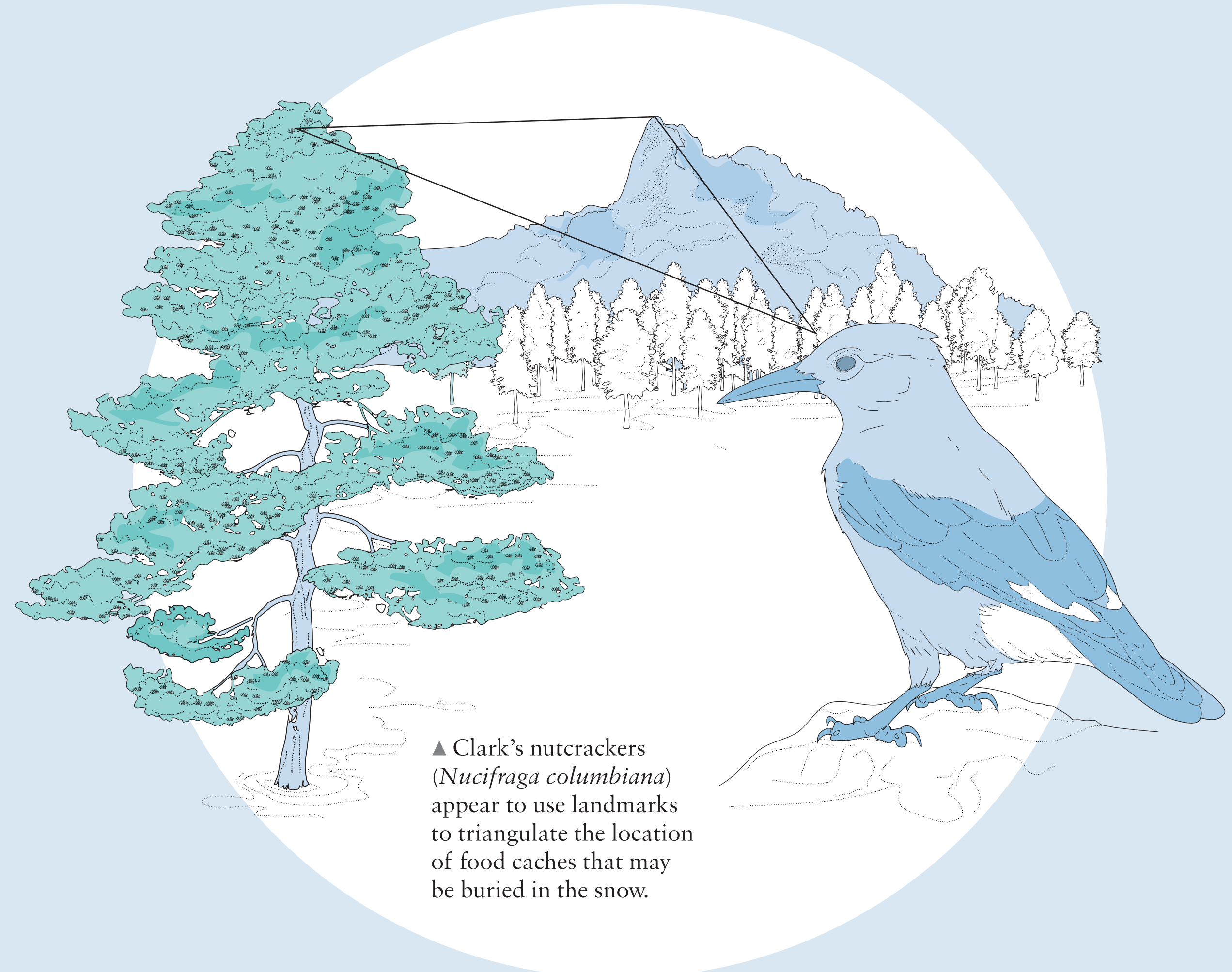
Maps and compasses

Cognitive maps are learned mental representations of the spatial layout of the environment. At least some birds are able to learn the arrangement of landmarks and features in their world and use a form of cognitive map. Studies of food-storing birds such as Clark's nutcrackers (*Nucifraga columbiana*) in the mountains of North America and willow tits (*Poecile montanus*) in Scandinavia demonstrate that birds use the spatial arrangement of visual cues to find hidden food. Remarkably, homing pigeons use olfaction to form a map-like representation of their environment. The spatial arrangement of volatile compounds and the direction of prevailing winds provide information to the pigeons about their location within their home range.

Birds exploit a variety of cues to orient themselves, including visual references such as coastlines, mountain ranges and even man-made features like roads. Beyond visual landmarks, olfactory cues may be used by petrels and other birds to orient themselves toward food sources in the open ocean or to nesting burrows. Infrasound (very low frequency sound waves) can travel great distances and may provide birds with information about distant shorelines, mountain ranges or storm systems. Birds can also use cues from the Earth's magnetic field to determine direction. This field varies with respect to polarity (north versus south), intensity and inclination (angle of the field relative to the Earth's surface). In some cases, variation in the strength of the magnetic field may be used for a map sense for homing, but magnetic inclination is the cue most likely used as a compass, through magnetoreception in the beak and retina (see pages 120–1). The magnetic compass sense of nocturnally migrating songbirds appears to require calibration each night, with birds observing polarised light at sunrise and sunset in order use magnetic cues to orient themselves effectively.

◀ Clark's nutcrackers (*Nucifraga columbiana*) can store, and then later retrieve, up to 100,000 food items.

Triangulation by Clark's nutcracker



▲ Clark's nutcrackers (*Nucifraga columbiana*) appear to use landmarks to triangulate the location of food caches that may be buried in the snow.

▼▼ White storks (*Ciconia ciconia*) migrate in flocks numbering in the hundreds or thousands.

Celestial cues for navigation

Throughout human history we have used the sky for navigation. The positions of the sun and the stars provide us with compass directions, and when these are combined with the time of day we can calculate latitude and longitude. Birds have been using these same celestial cues for navigation since before the evolution of humans, relying on the sun as a compass during the day and attending to the stars at night.

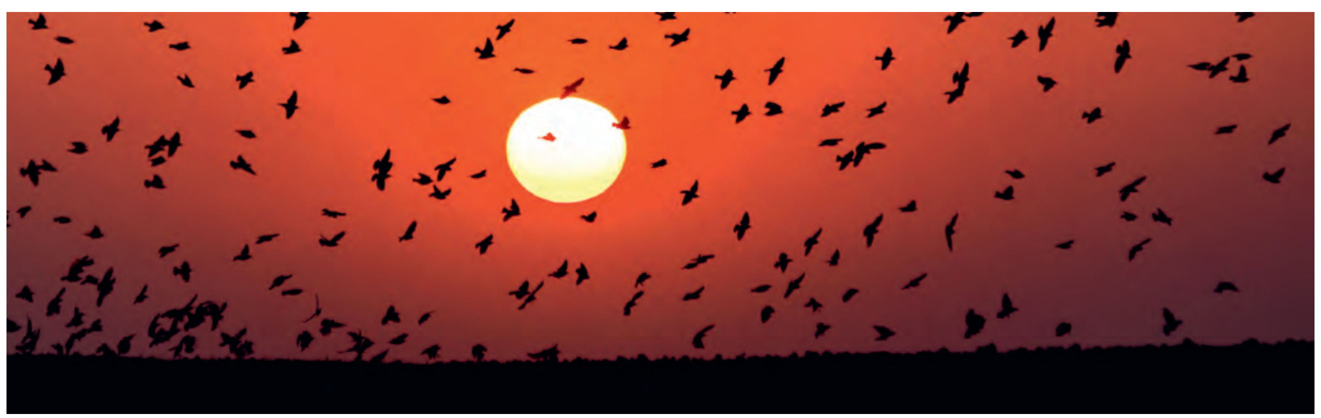
Sun compass

Birds use sky-based cues to determine direction. If the time of day is known, the position of the sun provides a solar compass. Experimental studies have used mirrors to 'move' the sun's direction, or have phase-shifted birds using artificial lights to make light phases (dawn and dusk) earlier or later relative to natural cycles. These studies have clearly demonstrated that homing pigeons and common starlings (*Sturnus vulgaris*) use the position of the sun for orientation and, because birds do not have watches, they rely on their internal circadian clock to correct the sun's position relative to the time of day. Remarkably, pigeons need to learn the path of the sun in order to use it as a compass. Scientists know this because birds reared indoors that had only ever seen the position of the sun in the morning were unable to use the afternoon sun to orient themselves.

Star compass

Nocturnally migrating birds use a star-based compass. However, rather than learning particular constellations, songbirds appear to pay attention to the general rotation of the night sky in order to determine which direction is north. Experiments on young American indigo buntings (*Passerina cyanea*), in which the birds were housed in a planetarium, demonstrated that they observe the slow rotation of the night sky and learn the location of Polaris, the North Star or Pole Star, relative to other constellations. During their autumn migration, after they have gained this knowledge, they orient themselves away from Polaris to move southward. When indigo buntings were experimentally raised in a planetarium where the night sky artificially rotated around a different star (Betelgeuse), they oriented themselves away from this star during their first migration. It is likely that many other species of night-migrating birds use star compasses in a similar fashion.

▼ Many birds, including these common starlings (*Sturnus vulgaris*), use the position of the sun as a compass, correcting for the time of day.



► American indigo buntings (*Passerina cyanea*) observe the night sky to learn the position of the North Star. When migrating south, they head away from this star.

Physiological challenges of migration

Even if the navigation system of birds keeps them from getting lost, a complete migration for most species involves periods of flying and fasting alternating with periods of resting and refuelling at stopover sites, repeated multiple times. Successful migration therefore requires overcoming a series of physiological challenges, including finding a way to store and carry enough energy, nutrients and water for the long-distance flight, avoiding fatigue and other damaging by-products of intense exercise, and then somehow rapidly restoring the necessary reserves at stopovers for the next stage of migration.

Preparing for the long journey

Birds store fat in preparation for migration by eating lots of food – as much as two to three times more than when they are not migrating – and by being picky eaters. A bird that is ready for migration may have doubled its body weight, of which 50–60 per cent will be fat. As explained in the previous chapter, fat is the best choice in the trade-off between energy and weight saving because stored fat contains much more energy per unit of weight in comparison to either protein or carbohydrates. For this reason, many birds preparing for migration choose foods that facilitate fattening (e.g. high-fat fruits and seeds) and that contain a certain fat quality (i.e. fatty acid composition). Specifically, changes in the diet of birds primarily determines seasonal changes in the quality of their stored fat. During migration, birds have a higher proportion of monounsaturated fats (like those in olive oil) relative to polyunsaturated fats, especially linoleic acid (an omega-6 fatty acid) and linolenic acid (an omega-3 fatty acid), both of which are 'essential' fatty acids for birds, meaning they cannot produce them and so must acquire them from diet. During their autumn migration, birds obtain these important omega-3 and omega-6 fatty acids by eating certain fruits, which has led to the habitat conservation and management practices of providing plenty of fruiting shrubs at important stopover sites used during migration.

◄ Red-winged blackbirds (*Agelaius phoeniceus*) gather in large flocks as they prepare for migration.

▲ Many songbirds, including the fieldfare (*Turdus pilaris*), eat plenty of nutrient- and energy-rich fruit during their autumn migration.

The dramatic increase in feeding (called hyperphagia) and fattening in preparation for migration is associated with dramatic increases in the size and function of digestive organs such as the gizzard and small intestine. These concomitant increases in food intake and digestive organs allow birds to maintain the efficiency of digestion and thus maximise nutrient and energy gain, at the same time loading their bodies with fuel for migration.

Although stored fat provides much more energy when metabolised than either protein or carbohydrates, compared to these alternative fuels the metabolism of fat provides very little water, requires more oxygen and produces more oxidative by-products that can cause damage at the cellular level. Birds therefore have to metabolise some protein to satisfy their water needs while migrating, and as noted in Chapter 5, their respiratory and circulatory systems are designed to satisfy the elevated requirements for oxygen for metabolism at this time. Migratory birds contend with potentially damaging oxidative by-products generated during increased metabolism and flight by building up their antioxidant system (see pages 166–7).

During a migratory flight

One of the more remarkable aspects of migration is that the vast majority of birds do not eat or drink during a migratory flight because they are aloft and typically away from sources of food and water. A single migratory flight can last from many hours to several days for small songbirds such as New World blackpoll warblers (*Setophaga striata*) and Old World northern wheatears (*Oenanthe oenanthe*), and as long as a week or more for some larger shorebirds such as the bar-tailed godwit (*Limosa lapponica*). As discussed earlier, fat provides the vast majority of fuel for such migratory flights, but many other aspects of a bird's body composition are modulated during migration.

Digestive organs are among the most costly in the body (only the brain has a higher metabolic rate); thus, it might be expected that during a migratory flight, when most birds are not eating or drinking, these organs would decrease in size and function. Indeed, the digestive organs exhibit remarkable flexibility, increasing in size as the need arises and birds eat large quantities of food in preparation for migration, then decreasing in size when they are fasting during flight. However, it has been shown that such remarkable flexibility in the digestive and other organs of the body (e.g. heart, flight muscle) are more closely related to intrinsic differences in the turnover rates of these tissues rather than their function (e.g. loss of digestive organs while fasting). Furthermore, some of this 'lost' digestive tissue is used as an important source of protein and metabolic water during a migratory flight.

Refuelling at stopover sites

The refuelling process at a given stopover site along the migration route is somewhat similar to the preparations for the migration journey – birds carefully select what to eat and consume large quantities of food. However, birds at stopover sites must contend with a few unique physiological challenges. First, as they arrive after a migratory flight they cannot immediately eat lots because the reduced size of their digestive organs (see above) constrains food intake. Thus, the digestive organs must be rebuilt before birds can feed at maximum capacity, which can take a few days depending on the duration of the prior migratory flight.

Second, birds that have just completed a migratory flight must contend with any oxidative damage that has occurred, while also rebuilding their antioxidant capacity in preparation for the next flight. Birds can increase their antioxidant capacity by increasing production of endogenous antioxidant enzymes (e.g. superoxide dismutase) and by increasing their consumption of dietary antioxidants. During autumn migration, birds acquire dietary antioxidants such as vitamin E and anthocyanins from fruits, which also contain the specific types of fatty acids they need for fuel. The relationship between plants and the birds that eat their fruits is usually mutualistic, meaning that fruit consumption benefits both the bird (which receives nutrients and energy) and the plant (through seed dispersal), and many fruits are both widely available and easily consumed. Unfortunately, we know little about the source of dietary antioxidants for birds during spring migration, when fruits are much less abundant and birds must also begin preparations for reproduction.

◄ During migration, all birds – including these evening grosbeaks (*Hesperiphona vespertina*) – must consume large quantities of food to fuel their journey.

▲ Large-bodied, long-lived species such as this common crane (*Grus grus*) usually travel with their juveniles (rusty-brown heads) during their autumn migration, literally showing them the route.

Other bird movements

Although seasonal migrations between wintering and breeding grounds are often the most impressive and conspicuous movements birds make, they exhibit a variety of other movement patterns that span a range of geographic scales. These include natal dispersal (movement of young birds away from the nest location where they were hatched) and breeding dispersal (movement of adults between breeding attempts), as well as nomadic movements and irruptive behaviour.

Dispersal

In almost all species, young birds move away from the location at which they hatched, a process called natal dispersal. For most temperate-zone birds that breed in spring, this dispersal occurs in late summer and early autumn. Young birds roam tens of kilometres or more away from their parents' breeding territory, possibly in search of breeding sites for the following spring. When these birds begin their first breeding attempt, it is typically at a site some distance from their hatch location. The range of natal dispersals typically has a skewed distribution, with most birds moving a short distance from their hatch site and relatively fewer dispersing greater distances. In addition, there is a sex difference in most species, with females dispersing further than males. For example, in lovely fairywrens (*Malurus amabilis*) of tropical Australia and New Guinea, males disperse only 0.1–0.4 km, whereas females disperse 2–5 km. This sex difference of greater natal dispersal by females has been reported for numerous species and is in direct contrast to the pattern typically seen in mammals, where males disperse further than females.

▼ In Australia, male lovely fairywrens (*Malurus amabilis*) are homebodies, settling close to where they were born. Females disperse further, settling several kilometres from their natal home.

▲ Female Eurasian black kites (*Milvus migrans*) are more likely than males to move nesting locations between breeding seasons, thus showing higher breeding dispersal.

In addition to natal dispersal, birds may engage in breeding dispersal, or movement between breeding attempts, although most move only short distances. In territorial songbirds, dispersal between breeding seasons may result from competition for the highest-quality territories. As with natal dispersal, females often have greater breeding dispersal distances than males. For example, female black kites (*Milvus migrans*) are also more likely to move breeding territories than are males. Other factors leading to breeding dispersal are failure of a nest due to weather or predators, or the death of a mate.

Dispersal may result in the range expansion of a population or species. When rapid colonisation of a new area occurs, adults typically disperse into an unoccupied region, and further generations of offspring then continue to disperse into unoccupied breeding sites. North American western bluebirds (*Sialia mexicana*) nest in cavities and tend to breed in clusters of suitable habitat, often tree stands damaged by forest fires and then excavated by woodpeckers. Male western bluebirds that are more aggressive tend to disperse further and thereby colonise new areas of suitable habitat.

Prospecting

Prospecting involves exploratory movements by birds as they search for suitable habitats. Some birds prospect for suitable breeding sites well before they actually breed – it may even occur during the hatch year, with young birds roaming and exploring habitats before migrating south. In other species such as Old World collared flycatchers (*Ficedula albicollis*), some individuals are non-breeding owing to a lack of available nest sites. The non-breeders pay attention to nearby breeding flycatchers and are more likely to breed in subsequent years at sites where others successfully raised young. Similarly, black-legged kittiwakes (*Rissa tridactyla*) are more likely to return to a site to breed following their own nest failure if they observe that their neighbours' nests are successful. Thus, prospecting is not random and involves birds gathering information about the suitability of locations for future reproductive success.

► Snowy owls (*Bubo scandiacus*) are irruptive migrants, appearing unpredictably in large numbers in more temperate zones during the winter, possibly driven by population cycles and food availability.

Nomadism

In contrast to the predictable seasonal to-and-fro migration of most migratory birds, nomadic species engage in large-scale movements that may be unpredictable in both time and space. Nomadic species often move to track fluctuating resources, a behaviour that is most common in birds that breed at high latitudes (tundra and boreal forest), in high steppes or in arid tropical regions. Snowy owls (*Bubo scandiacus*) on the Arctic tundra forage on lemmings that have unpredictable population cycles, these varying both from year to year and place to place. As a result, the owls may move thousands of kilometres between breeding attempts to track these resources.

In central Australia, various bird species – ranging from songbirds to ducks – move nomadically to regions that have recently had rainfall, to take advantage of a flush of plant growth and associated insects. For example, grey teal (*Anas gracilis*) may fly hundreds or thousands of kilometres to regions that have had recent rain or flooding. How they can detect the change in conditions from such great distances is unknown. In North America, Europe and Asia, red crossbills (*Loxia curvirostra*) use their specialised crossed bills to pry open pine cones. However, the cones are not abundant on a regular seasonal schedule, and bumper crops emerge unpredictably at different locations (called mast years). Thus, crossbill flocks will breed at sites with sufficient cones for a period of time, and then move on to search for new sites with abundant cones. In Africa, red-billed quelea (*Quelea quelea*) similarly live in nomadic flocks searching for unpredictable grass-seed crops following periods of rainfall that vary from year to year. Nomadism is thus most common in those species that rely for breeding on food resources that are temporally or geographically unpredictable.

▲ Red-billed quelea (*Quelea quelea*) can live in vast flocks. In some parts of Africa these flocks move nomadically in response to rains and can become crop pests.

Irruptions

Irruptions are dramatic increases in the local abundance of a nomadic species. Nomads can be thought of as skimming the cream, moving from location to location and thus benefiting from abundant food resources. Successful reproduction in such an area can lead to rapid population growth, and thus available food supplies can be depleted, with relatively less food per individual. In these circumstances, nomads or facultative migrants dramatically shift their home range, leading to an irruption. For example, in some years large numbers of Arctic-nesting owls and finches move southward for the winter in periodic irruptive migrations, much to the delight of birdwatchers who live in these southerly latitudes. Bohemian waxwings (*Bombycilla garrulus*) that breed in Scandinavia and Russia can also irrupt into the UK and Europe. Sometimes, these irruptions follow multi-year cycles – common redpoll (*Acanthis flammea*) abundance in the northeastern USA fluctuates on an approximately two-year cycle. By tracking food resources and population numbers at higher latitudes, many birdwatchers attempt to predict irruptions.

Migration risks: light at night

Birds die more often during migration than at any other time of the year – even when they are literally 'sitting ducks' during summer nesting, or when they are trying to stay warm in winter. High mortality during migration indicates that travelling long distances, which for many species takes place at night under the cover of darkness, is a risky business.

The risk of predation

Migrating birds face many challenges, from poor weather carrying landbirds out to sea, to predation by raptors such as peregrine falcons (*Falco peregrinus*) and Merlins (*F. columbarius*), which often time their own migrations to coincide with those of their bird prey. Recent studies have suggested that many migratory shorebirds – including American western sandpipers (*Calidris mauri*) – have changed their behaviour and even the regulation of their body mass in response to the recovery of raptor numbers (following the ban on the use of DDT in the US in the early 1970s) on shared migratory flyways.

To make matters worse, humans have modified environments on grand scales (e.g. climate change), constructed barriers (e.g. tall glass buildings, cellphone towers with cable tethers) and lethal attractants (e.g. city lights), and introduced predators (e.g. cats), all of which further increase mortality rates for birds during migration. And even though we humans know of many ways to reduce these avian mortalities, unfortunately we rarely take these preventative measures.

City lights and nocturnal migration

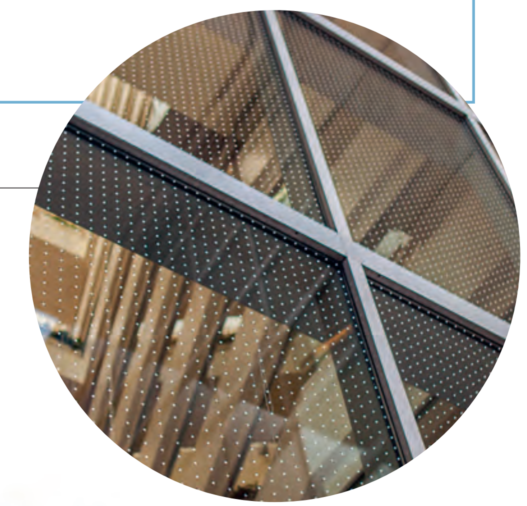
Given that birds use photoperiod, or day length, to time key events in their lives, such as when to breed and when to migrate, it might be expected that extensive city lighting at night would interfere or influence this. Indeed, this does appear to be the case, but the effect of artificial light at night on breeding birds is different than on migrating birds. For example, common blackbirds living in cities in Germany breed and moult as much as one month earlier than those living in nearby naturally dark forests, and blackbirds brought into captivity and exposed to dim city lighting at night also breed earlier. During avian migrations, city lights attract birds as they fly at night and can cause them to become disoriented, such that they collide with buildings and/or waste energy, leaving them vulnerable to other urban threats.

▼ Humans light up the otherwise dark night, creating a variety of problems for the billions of night-migrating birds.

BIRD-FRIENDLY GLASS

Given that millions of birds perish each year when they collide with windows or glass buildings, many bird-advocacy groups have funded studies to determine how glass can be modified to make it more apparent to birds so that they can avoid these lethal obstacles. Taking inspiration from spider webs, manufacturers have added ultraviolet (UV) patterns within glass and/or film coatings to the outside. Birds can see this wavelength of light, whereas we cannot, so such an addition is visible to them but the glass looks no different to us. UV coatings or decals can also be added to glass to increase its visibility to birds – this is most effective if the coatings or markings are spaced 5 cm apart horizontally and 10 cm apart vertically across the glass surface.

Given that most migration occurs over just a few nights each autumn and spring, conservationists have worked with some of the large cities along key migration flyways to turn off or dim the lights in buildings for short stretches. Scientists are also studying whether certain colours of artificial lighting affect birds less during night-time migration.



feather friendly glass

▲ Carcasses of birds found killed by window collisions on a single university campus over an eight-month period.

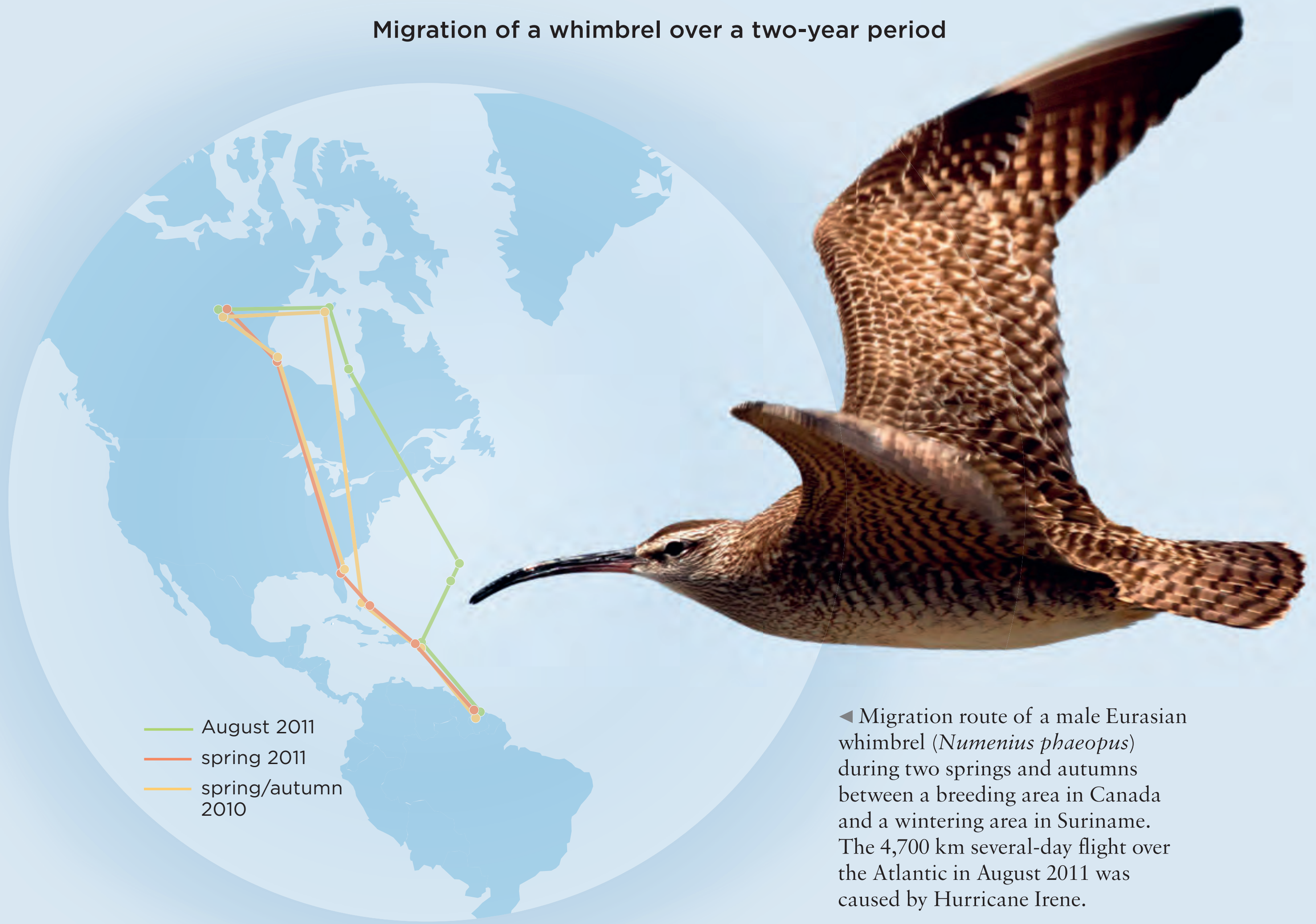
Migration risks: storms

Migratory birds pay close attention to prevailing winds and rain, and time their movements to take advantage of favourable conditions. However, they cannot forecast the weather along their entire migratory route, and at times they must cope with storms and even hurricanes.

Coping with storms

Many birds that migrate over land simply stop (fall-out) if they encounter bad weather. When such fall-outs occur along coastlines, thousands of birds, of many different species, may congregate – a boon for local birdwatchers. Similarly, islands in large bodies of water, including offshore oil platforms and large ships, can often provide refuge for large numbers of birds during bad weather.

▼ In stormy weather birds can be blown off course and out over the ocean. For those that cannot swim, human-made structures such as boats and oil rigs can provide a critical refuge.



◀ Migration route of a male Eurasian whimbrel (*Numenius phaeopus*) during two springs and autumns between a breeding area in Canada and a wintering area in Suriname. The 4,700 km several-day flight over the Atlantic in August 2011 was caused by Hurricane Irene.

Some birds try to remain aloft during storms and confront them directly. For example, a satellite telemetry study of whimbrels (*Numenius phaeopus*) breeding in Canada and wintering in South America documented how some of these strong-flying shorebirds deal with hurricanes in the Caribbean during their autumn migration. In 2011, one whimbrel named Chinquapin flew *into* Hurricane Irene's dangerous northeast quadrant and shot out the south side, while another bird named Goshen flew through the storm's outer edge. The previous year, Chinquapin successfully flew around the edge of Tropical Storm Colin, whereas a second tagged whimbrel perished in the same weather system. Smaller migrating birds can become trapped inside large storms. For example, a large flock of migrating chimney swifts (*Chaetura pelagica*) was swept up by Hurricane Wilma in 2005, the most intense hurricane ever recorded to date in the Atlantic Basin. The swifts rode the storm from the eastern US over to western Europe, much to the delight of birders there, who were very excited to see these New World vagrants.

An additional threat of climate change is that shifting weather patterns, caused by rising ocean temperatures and variation in the jet stream, result in more intense and more frequent storms. Thus, although birds' high mobility provide some capacity for them to cope with climate change, the migration patterns of some species will be affected and they may experience population declines as a result.

Climate change and migration

Climate change poses a threat to birds in several ways beyond increasing the frequency of major storm events such as hurricanes. As global temperatures increase due to human production of greenhouse gases, the leafing and flowering of plants, and the emergence of the insects that feed on them, are occurring earlier and earlier each year. Because many migrant birds rely on cues such as photoperiod to time their annual migrations, they may therefore arrive back at their breeding grounds too late to take full advantage of the peak abundance of food resources in spring.

Mismatched timing

The start of the breeding season in European pied flycatchers (*Ficedula hypoleuca*) in northern Europe has been advancing in recent years, but the emergence of the main insect species they depend on to feed their young has been advancing even more rapidly. The local insects are responding more quickly to the warmer local climate than the flycatchers because the birds cannot detect conditions on the breeding grounds from their wintering grounds in Africa. Large-scale studies of North American songbirds have demonstrated steady advances in spring migration timing, but whether these advances are sufficient to take advantage of advancing spring food resources is not yet known.

Range shifts

In addition to mismatches in timing of migration, climate change is driving range shifts in plant and insect species, which in turn is driving range shifts in breeding birds. Birds are highly mobile, and shifts in their range can be facilitated by natal and breeding dispersal. However, range shifts can also induce costs, such as when the suitable breeding and wintering habitats of a species move further apart. For example, it has been estimated that the migration distance between the wintering and breeding habitats of thrush nightingales (*Luscinia luscinia*) – in eastern Europe and western temperate Asia, and in sub-Saharan Africa, respectively – will increase by about 800 km, or five days' travel, in the forthcoming decades.

Thus, many species will need to increase the distance they migrate in addition to adjusting the timing of their spring migration if they are to cope with climate change. Another threat is that range expansions may become limited. For example, as cold-adapted plant and insect species move to higher altitudes in the mountains in response to warming temperatures, the high-altitude breeding birds that track these insect resources must also go higher; however, eventually even the mountain peak may become unsuitable and species will become locally extinct.

▲ Timing of breeding in pied flycatchers (*Ficedula hypoleuca*) has advanced with climate change, but at a slower pace than their insect prey, creating a timing mismatch.

► Thrush nightingales (*Luscinia luscinia*) must increase the distance they migrate as their preferred deciduous forest breeding areas move north with climate change.