INCREDIBLE JOURNEYS

UNRAVELLING THE MYSTERIES OF BIRD MIGRATION

Every year, thousands of millions of birds pour into Africa from breeding grounds to the north, crossing en route **one of the most formidable natural barriers in the world – the Sahara. Millions more undertake shorter-distance migrations within Africa, and one species even travels between the Arctic and Antarctica.**

In a series of three articles Phil Hockey addresses some of the fundamental questions about this behaviour. Why does it occur? What are the costs and benefits of migration? Why are some species migratory and others not? How do they find their way – how much of the information they need is inherited and how much is learned?

LIOR RUBIN

Previous spread *White Storks on migration over Israel.*

Below *Seedeaters of the drylands, such as the Double-banded Sandgrouse, move opportunistically in response to rain; they are nomads rather than migrants.*

WARWICK TARBOTON

Man has been fascinated by the migrations of birds for more than 2 000 years, with written accounts dating back to Herodotus, Pliny and Aristotle. Some of the ponderings of these ancients were not entirely accurate: Aristotle, for example, believed that when Common Redstarts Phoenicurus phoenicurus disappeared from Europe at the end of the northern summer they had mutated into Robins Erithacus rubecula, changing back into redstarts the following spring! He also believed that some birds hibernated, an idea pooh-poohed until quite recently when it was discovered that the Common Poorwill Phalaenoptilus nuttalli, an American nightjar, does indeed go into deep torpor for several months. In a less scientific vein, the augurs of ancient Rome read mystical properties into bird migrations, using the shapes of migrating bird flocks to foretell Rome's chances in battle.

Our fascination with migration continues today and, while interpretations of the birds' behaviour might be tempered by greater scientific knowledge, there still remain half-answered questions that tease the minds of scientists across the globe.

WHAT IS MIGRATION?

Migration is often misinterpreted as meaning any movement undertaken by animals – many journeys are not migrations. Perhaps the simplest definition and one of the most widely used is that migrations are journeys repeated in space and time; that is, they are movements that are predictable in terms of when and where they take place. Recently, a subtle twist has been added to this definition, classifying migration as any journey that involves an animal bypassing suitable resource patches. These 'resource patches' could be suitable breeding or feeding areas that are ignored by the traveller.

The most common type of movement with which migration is confused is nomadism. The main distinction between the two types of movement is that migration refers to predictable movement in response to predictable conditions (such as the seasonal bloom of food in the Arctic summer), whereas nomadism is an unpredictable movement in response to unpredictable conditions. In an African, and indeed a global, context, nomadism is characteristic of birds that live in arid and semi-arid regions, such as the Karoo or the drylands of northern Kenya and Somalia. Many of these birds are seed-eaters (granivores), such as canaries and finchlarks, whose food supply is dependent on rain. The timing and distribution of rain is unpredictable, as are the movements of the birds.

A second type of non-migratory movement is dispersal. Dispersive movements are usually undertaken by young birds, typically when they are evicted from the territory of their parents. These movements are exploratory in nature and are not repeated later in the bird's life.

WHY MIGRATE?

By definition, the key to migration is mobility. Among the world's animals, birds are the most mobile and have, without question, evolved the most spectacular migrations. Almost without exception, the earth's landmasses experience seasonal changes in climate. This is true in habitats ranging from tundra to tropical rainforest. Such seasonal climate changes are reflected in seasonal changes in the abundance of food for birds, be this grass, seeds, fruit or insects. Because most birds are able to fly, they can exploit peaks in food availability at different times in different places. Thus, a Curlew Sandpiper Calidris ferruginea may experience pastures of plenty on the tundras during the brief Arctic summer and migrate to southern hemisphere estuaries to enjoy the flush of invertebrate food during the warm southern summer.

Although the benefits of migration are fairly easy to understand, such movements, because they are expensive energetically, also carry risks. Accepting the premise that a bird's lifetime objective is to leave behind as many offspring as possible, the nature of the cost-benefit equation that a bird must solve becomes clear. In any one year the number of young produced is determined by the number of breeding attempts that can be fitted into the breeding season and by the number of young that can be reared at each breeding attempt. Typically, birds that breed at high latitudes have a short breeding season, but many rear large broods relative to their tropical counterparts that have a longer breeding season. Thus, one of the benefits of breeding at high latitudes is the summer peak in food abundance. One of the disadvantages is that for several months of the year food abundance may be very low or the landscape ▷

Many birds migrate south at the onset of the northern winter. For most species, these movements are triggered by an impending shortage of food rather than by the direct effects of cold.

PHIL HOCKEY

may simply be uninhabitable because it is covered in snow and ice. It is not surprising, therefore, that at increasingly high latitudes the proportion of the species breeding there that is migratory, also increases.

For high-latitude species that have a short breeding season, survival between breeding attempts becomes critically important. One way to maximise survival is to spend the non-breeding season in as benign an environment as possible. For a breeder from the far north, such an environment may be found in the far south during the long days of the southern summer. One well-known example of a bird that has adopted this strategy is the Arctic Tern Sterna paradisaea. These birds breed on the edge of the Arctic Sea and migrate south to spend the non-breeding season around the fringes of Antarctica. Some Arctic Terns travel more than 50 000 kilometres on these annual journeys and also see more daylight during each year than any other animal on the planet.

Although the Arctic Tern is a well-touted example of a long-distance migrant, many other far northern breeders make similar journeys. Among those species that migrate from the Palearctic to Africa and between North and South America, there is a widespread tendency for those species that breed the furthest north to spend the non-breeding season the furthest south – a phenomenon known as 'leapfrog migration'. The pattern of migration between South-east Asia/Australia and the eastern Palearctic is rather different. Most of the land-bird species that follow both migration routes do not penetrate as far south in the East as they do in Africa and there is little or no evidence for any leapfrog migration, at least among land birds. One of the reasons why patterns in the East are so different to elsewhere is that of all the Palearctic-breeding land-bird species that migrate south, only four penetrate to Australia. It is very unlikely that this failure of most species to reach Australia results from their inability to cross the Torres Straits. Rather, it seems possible that the low-nutrient, highly leached soils of Australia do not support a prey base adequate for both residents and migrants.

The pay-off between chick production in one season and survival between breeding seasons was examined in a study of North American songbirds. Those that bred at high latitudes produced fewer young per year than those at lower latitudes. However, the high-latitude breeders migrated further south for the winter and had a greater chance of surviving until the following breeding season. The net result of the two strategies, balancing productivity and survivorship, was the same.

While we tend to think of migratory species as being high-latitude breeders, there are many species that migrate within the tropics and the subtropics. Among these are several species of kingfishers, cuckoos and nightjars. In almost all cases, these species migrate away from equatorial latitudes to breed, indicating that even a short trip into more temperate latitudes can be a worthwhile strategy in terms of finding more abundant food at the time of year when chicks have to be reared. Temperature is a key factor that drives birds away from polar latitudes in winter; among tropical birds, migrations are driven primarily by the seasonality of rainfall. In the Sahel savannas, immediately to the south of the Sahara, most rain falls during the northern summer and this is the time when tropical species move north from equatorial latitudes. These migrants are thus breeding at the same time of year as are those in the Palearctic. South of the equator most rain falls between November and March and the abundance of food associated with this is also exploited by tropical species moving south. This results in southern birds breeding at the same time of year as non-breeding migrants from the Palearctic are present.

WHAT ENVIRONMENTAL CONDITIONS PROMOTE MIGRATION?

When birds migrate to their breeding grounds, they are moving towards areas of high food availability at the warmest and/or the wettest time of year. Towards the end of the breeding season food availability decreases as temperatures fall or the dry season arrives. Some species do leave the breeding grounds when food is still fairly abundant – an enigma not fully explained – but many would be forced to leave soon afterwards because of either food shortage or extremely cold temperatures. Indeed, the average temperature of the coldest month of the year is a good predictor of the proportion of breeding species that are resident. At high northern latitudes in Europe, where the average temperature of the coldest month is between -15 and -20 °C, only 15–25 per cent of the species that breed there will remain through the winter. At lower latitudes where the coldest month averages about 15 °C, 80–90 ▷

'It would be interesting to discover what induces birds wintering in the more southern parts of Africa, where they are subjected to hardly any changes of climate, suddenly to leave these stations for their breeding homes in the north.' Heinrich Gätke, 1895

WARWICK TARBOTON

Most birds that search for insects among the leaf litter of the forest floor, such as the Natal Robin, do not need to migrate because their food is available throughout the year.

per cent of breeders are resident. Once temperatures exceed 20 °C, more than 90 per cent of breeders are resident.

Although temperature is a good predictor of the likelihood of migration, many birds do migrate away from latitudes where they would have no physiological problem in surviving. In the case of these species, there is little doubt that the proximate cause of migration is lowered food supplies.

Ambient temperatures are influenced not only by latitude (and altitude) but also by habitat. Habitats across a wide range of latitudes vary from forest or evergreen woodland to open heath-like and semi-desert environments. In general, those habitats characterised by tall trees and dense foliage do not experience such extreme temperature fluctuations as do open habitats. The degree to which habitat moderates climate is termed 'buffering': the more buffered the habitat, in general, the less the seasonal variation in food availability. One could predict, therefore, that well-buffered habitats are likely to have more resident species than are open habitats. This is well illustrated among the African Cuculidae (cuckoos and coucals). All of the resident species inhabit forest or perennial wetlands, whereas the migrants are typically found in more open savannas.

The very same conditions and constraints that have promoted migration among birds have led to the evolution of migration in other groups of animals. These range from the daily vertical migrations of marine plankton to the longer-distance journeys undertaken by insects, fishes, turtles, whales and some large land mammals such as blue wildebeest and caribou.

WHAT TYPES OF BIRDS ARE MIGRATORY?

If migration is primarily a response to seasonal fluctuations in food availability, diet is likely to play a major role in influencing migration because it is unlikely that the food supplies of all birds, from grazers to carnivores, will fluctuate in the same way. Migration has been studied most intensively at high northern latitudes where seasonal weather extremes are so great that some of the more subtle factors, such as diet, that might influence different migration patterns are masked by the effects of cold. In Africa, however, there are some very obvious differences in patterns of bird migration that can be linked not only to the birds' food, but also to the way in which they capture that food. Considering land birds alone, frugivorous species are, almost without exception, resident. Even the frugivorous species that breed in the Palearctic do not migrate into Africa south of the Mediterranean Basin. The granivorous species, on the other hand, are typically nomadic and very few of them undertake migrations in the strict sense of the word. Migration among African land birds is very much the domain of the insectivores.

CHRIS VAN ROOYEN (2)

Among the insect-eaters, those that catch their food high in the sky, like the Red-breasted Swallow, are the most likely to be migratory.

Even among the insectivores, however, there are differences in migratory tendency depending on the types of insects eaten, and where and how they are caught. The least buffered and most seasonal habitat of all is the open sky, the hunting ground of swifts, swallows, nightjars and bee-eaters: these families of birds are highly migratory, moving towards the tropics at the approach of winter. Anyone who has spent a summer and a winter night on the South African highveld will have noticed how the abundance of aerial insects changes with the seasons. At the other end of the spectrum are the forest-floor insectivores such as robins and thrushes. Not only do these birds live in habitats with a dense canopy cover, but they also glean their prey from among leaf litter which adds another layer of buffering. Many of the invertebrates living on the forest floor are flightless and it is very probable that their abundance does not vary seasonally as much as that of flying insects. In the much colder woodlands of North America, the effects of habitat buffering are neatly demonstrated by woodpeckers. The grubs that these birds eat are buried in the wood of trees or below the bark – environments partially sheltered from temperature extremes. Whilst most of the insectivores that rely on flying insects or insects gleaned from the surfaces of leaves move south in winter, the woodpeckers are able to remain behind because their food is available in winter.

The influence of diet on migration is well illustrated by the three southern African alcedinid kingfishers. Two species, the Malachite Alcedo cristata and Half-collared kingfishers A. semitorquata are fish-eaters and are non-migratory. The third species, their very close relative the African Pygmy Kingfisher Ispidina picta, is a savanna-dwelling insectivore and is a migrant.

THE FRUGIVORES OF AFRICA AND THE NEW WORLD

Scientists are always searching for paradigms – those generalisations that are so widely applicable they can be elevated to the status of a global rule. Although the great divide between the migratory behaviour of frugivores and insectivores is very clear in Africa, this pattern is not mirrored in the Neotropics. Many of the frugivores in both regions are forest species: the Neotropics has much more tropical forest than Africa and many more species of fruiting trees, but it also has a great many migratory frugivores. Indeed it has even been suggested that migration in the Neotropics started with the frugivores.

In contrast to the rest of the world, very few, if any African frugivores, such as the Green Pigeon shown here, are migratory. The explanation for this remains a mystery.

So why don't African frugivores migrate? One possible explanation is that the living species of frugivorous birds in Africa are generalists that are able to eat different fruits at different times of the year, obviating the need to move in search of particular types of fruit. If this explanation holds, then it is necessary to explain why there are so many more specialised frugivores in the New World. Africa's tropical forests have experienced a dynamic history of expansion and contraction – during a dry period in the earth's history about 65 000 years ago, the forests of the Congo Basin shrank to a fraction of their present size. It is possible that this contraction was accompanied by an extinction of specialists, unable to cope as their food supplies dwindled.

Migration is a complex and finely tuned behaviour. It has evolved in a large number of bird species and is undertaken annually by thousands of millions of individuals. It occurs from the poles to the tropics and from the highest mountains to the lowest floodplains. The next two articles in this series will examine how birds find their way on these extraordinary journeys. □