INCREDIBLE JOURNEYS Making the trip...

Weather patterns play a critical role in determining not only the timing of the birds' departure on migration, but also the best route for them to follow.

CARL ROESSLER/PHOTO ACCESS

Mountains, seas and deserts are all obstacles that migratory birds have to negotiate. They must also plan their journeys so that they arrive at and leave the breeding grounds at the right time. It is a juggling game of benefits and costs – when and how to start preparing, when to leave, what route to follow, how high to fly, how far to fly at a stretch and where and for how long to stop *en route*.

In this, the second of three articles, **Phil Hockey** provides an overview of the problem-solving processes involved in migration that lead birds towards optimal strategies.

ne might be tempted to think that migration routes are ancient and traditional phenomena, but this is not the case: they can change within a single generation. The migration paths of birds that travel to breed in the tundras of Siberia would have been very different 12 000–15 000 years ago when much of the land mass north of the Mediterranean was covered in ice.

The modern breeding range of the Northern Wheatear Oenanthe oenanthe is very extensive, stretching from the south-western Palearctic far to the east in Siberia. During the last glaciation, its range must have contracted greatly, probably diminishing to two little pockets - one in the south of the Iberian Peninsula and the other in the Near East, with both populations migrating to Africa after breeding. As the Ice Age drew to a close, the wheatears expanded their range northwards and eastwards, but nonetheless retained Africa as their sole wintering area. As a result, many wheatears today face a very long east-west migration before finally turning south to Africa. Other species underwent similar range expansions, but evolved new migration routes, in that birds from the east of the breeding range now migrate south at the end of summer to spend the non-breeding season in south-east Asia.

Breeding on the grassy tundras of Alaska is a population of Bar-tailed Godwits *Limosa lapponica* that has flown itself into the migratory record book. As the Arctic summer draws to



The migration routes of the Northern Wheatear have changed considerably as the species' breeding range has expanded following the retreat of the last Ice Age. a close, these birds fatten up to make a journey unmatched by any other creature on the planet. Departing the Alaskan coast, they travel south across the central Pacific, bypassing both the Hawaiian and Line islands on a nonstop flight of 11 600 kilometres to the coast of New Zealand's North Island, arriving at their destination little more than six days after leaving Alaska. None of the elaborate mathematical models of scientists would have predicted such a journey to be possible.

The migrations of most birds, however, take much longer than this and, for many species, preparing for and undertaking migrations are the most timeconsuming activities of their year. European Marsh Warblers Acrocephalus palustris, for example, leave their European breeding grounds in August, but many do not arrive in South Africa until December. They leave again in late February or early March, arriving back on the breeding grounds only in late May or early June. Thus, about eight months of their year is devoted to migration. The reason the journeys take so long is not that the birds fly slowly, but that they have to stop to refuel en route.

PREPARING FOR THE FLIGHT

Most birds set off on migration with a full fuel load – small birds may more than double their weight before departure and large birds may increase their weight by 50–60 per cent. The amount of extra weight that a bird can carry is limited by the laws of aerodynamics – the ratio of weight to power. For birds migrating to the breeding grounds. especially if

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LONGEST SPELL DURING WHICH A BIRD IS ABLE TO REMAIN ON THE WING WITHOUT TAKING SUSTENANCE OF ANY KIND.' Heinrich Gätke, 1895

> those breeding grounds are at high latitudes where the summer is short, it is critically important that they arrive at their destination on time. Late arrival may mean failure to find a mate or a territory or – just as risky – not having enough time to complete the breeding

cycle. The main factors influencing arrival time are the timing of first departure and the amount of time that has to be spent refuelling *en route* – both of these have to be factored into the birds' decisions.

As the time for migration approaches, physiological changes take place in birds. These changes are stimulated by changes in day length and are controlled, in a fairly complex way, by hormones. In order to gain weight, birds must take in energy (food) faster than they use it and must be able to convert the surplus energy into stored fuel. The 'overeating' is termed hyperphagia: recent research suggests that this behaviour is stimulated by the hormone prolactin, secreted by the pituitary gland. As migration time approaches, prolactin secretion increases, as do concentrations of another hormone, corticosterone. While prolactin stimulates hyperphagia, it is corticosterone that is responsible for the deposition of fat. Most of the surplus energy is diverted to fat stores beneath the skin. but some is diverted to the flight muscles to increase their capacity for the forthcoming flight. Fat is the most efficient fuel because, weight for weight, it contains far more energy than protein some five times as much. It is also much lighter than protein, hence is less costly to carry, and it releases water when converted back to energy, which reduces the risk of dehydration during long flights.

Birds are able to monitor their own body condition and their readiness to migrate. This was recently demonstrated in a study of several populations of Red Knots *Calidris canutus*. The knots wintering in tropical West Africa do not have a particularly rich food supply and cannot gain weight as quickly as, for example, South African birds. To compensate for this, the tropical birds start fattening earlier than their southerly relatives.

Once the flight has started, however, the eating machine must become a flying machine and the best way to achieve this transformation is to lose weight from parts of the body where it is not needed. This is achieved by the partial resorption of organs that will not be needed during the flight, such as the intestines and the liver. Very recent research has also shown that some birds are capable of lowering the costs of flight even further, by reducing the mass, and hence energy demand, of their flight muscles during the journey. This substantially increases their flight range, but may carry a cost in terms of reduced manoeuvrability. The principle is the same as overdrive in a car: they can maintain the same speed with lower fuel consumption, but are not able to accelerate as rapidly should trouble appear. These findings have helped us to understand how the Alaskan godwits might be able to make such a long non-stop flight.

As the accumulated fat dwindles during the flight, the costs of flight become progressively less. However, birds are eventually forced down to refuel. When this happens, the digestive organs once again increase in size and the transition from eating to flying machine is reversed.

READY TO GO - OR NOT?

For land birds whose migrations include sea crossings, departure condition is obviously critical – running out of fuel in mid-ocean is a fatal mistake! Experiments with migrants on the north shore of the Gulf of Mexico have shown that birds' orientation (which will be discussed in the next article in this series) changes depending on their body condition. Fat birds captured on southward migration immediately before their departure across the Gulf orientate in a southerly direction towards their goal. If the same birds are deprived of food \triangleright



Bar-tailed Godwit – the world recordholder for a non-stop flight. Some cover 11 600 kilometres in a single flight from Alaska to New Zealand. and start to lose weight, their orientation turns back northwards - in the direction of food resources inland. Birds that have set off on a sea crossing seem able to assess whether they run the

risk of not reaching the other side. If

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the risk is deemed too high because, for example, of adverse winds, they reverse direction and head back to their starting point. These reversals have been observed, using radar, for night migrants over the Mediterranean. Even the relatively short water crossing of the western mouth of the Baltic Sea can cause problems. In the early mornings of the northern autumn, tens of thousands of small passerines head south to sea from Falsterbo at the southern tip of Sweden. By mid-morning, many of these are returning to wait for more suitable flying conditions. Anyone arriving at Falsterbo in late morning could almost believe they were seeing the spring migration!

From time to time, adverse conditions may cause birds to abort their migration. In one study, Far Eastern Curlews Numenius madagascariensis in northern Australia were fitted with satellite transmitters before their migration to breeding grounds in the eastern Palearctic.

ed the South China Sea when they encountered a strong cyclone. Rather than battle the conditions, these birds turned around and flew back to Australia. where they remained for the rest of what would have been their breeding season. Similarly, in 1980, a large number of Red Knots failed to migrate north from Langebaan Lagoon, South Africa, even though most of them had attained full breeding plumage. In this case, the reason for failed migration was probably not so much to do with weather conditions as a local food shortage in the pre-migration period. Knots normally increase their weight by about 50 per cent before leaving South Africa: if food is short and they cannot gain sufficient weight by departure time, the risks of arriving late on their far northern breeding grounds may be so great as to make the journey worthless.

Some of these birds had already reach-

Whilst adults only rarely fail to migrate back to their breeding grounds, young birds often 'stay behind' for one, sometimes two years before returning - a behaviour termed 'deferred migration'. The probability of this happening increases with increasing size of the bird and increasing migration distance. Clearly these birds are capable of making the migration, because they have already completed the southward journey successfully. There are two main reasons behind their failure to migrate. Large birds tend to be long-lived and have delayed sexual maturity: they might thus be physiologically incapable of reproducing at one year old - so why waste all that energy flying to the breeding grounds? It is also true that the young of large birds generally take longer to learn how to forage efficiently than do the young of small birds. For example, in the pre-migration fattening period in South Africa, young Curlew Sandpipers walk and peck as fast as the adults when foraging, but only capture half as much food per unit time. It is thought that these youngsters do not migrate because they would have to spend so much time refuelling at stop-over points on the way that they would arrive late on the breeding grounds (and hence be unable to complete their breeding cycle before winter sets in). By contrast, many young Curlew Sandpipers that have spent the nonbreeding season in North Africa do



migrate: these birds have fewer refuelling sites - and thus a less delayed arrival because of the shorter journey.

MINIMISING THE COSTS

Although birds have physiological adaptations that help to reduce the energy costs of migration, they could obviously make further savings by choosing the shortest or least strenuous route and by making use of favourable winds. In Europe, most of the major mountain ranges run from west to east. Any bird wishing to cross these mountains in a direct line would therefore have to expend energy in gaining altitude. What happens, rather, is that birds tend to follow deep valleys through the mountains, even if these involve a slightly longer journey. This is carried to extremes by some of the small birds that migrate between Siberia and India. Between their breeding and their nonbreeding grounds rises the formidable massif of the Tibetan Plateau. Rather than tackle this obstacle head-on. most have opted for migration routes that take them around the plateau's edge. In the same way that a head wind slows aircraft, battling into a head wind **On cold and cloudy days, migrants that** is an energy-costly activity for a migrating bird. However, many of the world's wind patterns are fairly predictable and birds make use of tail winds wherever possible. Indeed, at the start of a migratory flight, there is some evidence that birds 'test' the wind at various different heights, selecting the migration altitude

RATHER THAN BATTLE THE CONDITIONS, THESE BIRDS TURNED AROUND AND FLEW BACK TO AUSTRALIA, WHERE THEY REMAINED FOR THE REST OF WHAT WOULD HAVE BEEN THEIR BREEDING SEASON

that gives them the strongest 'push'. For birds leaving Europe on their way to Africa, the start of their journey is determined by the relative positions of highand low-pressure cells. Both types of cell move from west to east, but the air flows in opposite directions around them, flowing clockwise around highpressure cells and anti-clockwise around low-pressure cells. Thus, when a highpressure cell follows a low pressure, \triangleright

Recent wind-tunnel experiments with Red

Knots have shown that the energy costs

of long-distance flight are smaller than

previously thought.

rely on thermals for lift, such as White Storks, may become temporarily grounded.



Seas and deserts are formidable barriers for migrating birds to cross and, for some, success or failure is balanced on a knife-edge. the prevailing wind direction between them is southerly and this is when the birds start their journey.

Given that mountain ranges and wind patterns are factors that shape the migration strategies of many birds, it is not surprising that many species have, independently, converged on the same migratory strategy and follow the same routes. These routes, like aeroplane lanes, are termed 'flyways'. One of the main flyways into southern Africa follows the Great Rift Valley down the east of the continent. The concentration of birds along flyways can best be seen along narrow land bridges, such as the isthmus of Panama, or where peninsulas of land reduce the length of water crossings. In the case of trans-Mediterranean crossings, for example, major concentrations of birds can be seen both at Gibraltar in the west and the Turkish Bosphorus in the east.

The main energetic cost of flight is the flapping motion, when muscles have to power the down-stroke of the wings. Any bird that could migrate by gliding would therefore dramatically cut its travel costs. Many broad-winged soarers do exactly this, including several birds of prey and storks. An inevitable consequence of gliding in still air is a loss of altitude. This, however, can be counteracted by the use of thermals – rising columns of warm air – to supply the lift. Such

migrants typically glide from thermal to thermal. However, thermals are not available everywhere or all the time, so there are constraints placed on both the migration route and the speed of travel. Gliding migrants are destined to travel by day and almost exclusively over land because thermals do not form at night or over the sea. Even during the day, thermals are generally absent until mid-morning, explaining the large flocks of White Storks Ciconia ciconia gathered in the early morning in large acacia trees on the East African savannas. White Storks, among other species, can also be highly opportunistic about finding thermals, even using the updrafts from burning oil wells on the Arabian Peninsula.

Because gliding migrants have a limited time available for flying during the day and expend little energy while flying, there is less need for them to fatten up before and during migration. This 'budget air fare' however is only available to those birds which have the right wing structure.

WHEN TO FLY – Day or Night?

Most long-distance migrants travel both by day and night; this is probably necessary to ensure they reach their destinations on time. Some birds, including soarers, are exclusively diurnal migrants, whereas a great many birds that normally are active only by day migrate under the cover of darkness. There are several possible reasons for this, and it is not easy to disentangle their relative importance. By coming to ground during daylight, these birds are able to forage and refuel. Furthermore, the air at night is cooler, denser and calmer than it is by day. Flying in dense air is more energy-efficient than flying in the warm, thin air of day, and night flying may help conserve water and prevent overheating. All the above explanations relate to the efficient use of available energy. It has also been suggested that night migration may be effective in reducing predation from raptors. However, it seems that most birds are subject to greater predation pressure when on their breeding and non-breeding grounds than during migration, suggesting that it is unlikely for predation to have driven the evolution of nocturnal migration.

WHEN IT ALL GOES PEAR-SHAPED. . .

Although birds have highly advanced navigation systems, as will be discussed in the next article, long-distance journevs can be fraught with danger. These dangers range from failure of the food supply at a refuelling site to being blown off course by unexpected winds or meeting extreme weather conditions. Mass mortalities of swallows and passerines during droughts in the northern Sahel provide one of the most spectacular examples of food shortage. This is a critical area for many species which, having crossed the Sahara, are on an energetic knife-edge, totally dependent on the Sahelian refuelling point. During a cycle of wet years between the 1930s and the early 1960s, nomadic agriculturalists moved north in the Sahel to grow crops. With them, of course, went their domestic livestock. The stage for disaster was set as the livestock systematically destroyed the natural vegetation on which the insects that would provide food for the birds depended. As the wet cycle came to an end and drought conditions intensified in the late 1960s, the agriculturalists moved south, leaving behind a wasteland to greet southwardmigrating birds. Starved and weak, hundreds of thousands, perhaps millions of birds perished in the Sahel after successfully crossing the greatest natural barrier to bird migration on the planet.

Whilst there are advantages to arriving early on the breeding grounds, there is also a risk in as much as the retreating winter may have one last curved ball to throw. Late snowstorms and freezing conditions can prove catastrophic. In one night in March 1906 near Worthington, Minnesota, more than 1.5 million migrating Lapland Buntings *Calcarius lapponicus* were killed in a snowstorm – an event that became known locally as the 'great bird shower'.

It is clear that optimising migration patterns involves solving some complex cost-benefit equations. Major benefits can be derived from migration, but not all birds get it right all of the time. What is certain, however, is that our scientific understanding of the phenomenon has increased greatly in recent years. One of the great observers of migration patterns was Heinrich Gätke, warden of the Heligoland Bird Observatory in the late 19th century. In his book on the birds of Heligoland, published in 1895, Gätke described migration as 'a strange and mysterious phenomenon'. Although many mysteries still remain, researchers are constantly discovering more about what an extraordinarily complex phenomenon bird migration really is. The final article in this series investigates one of its great wonders – how birds find their way with such amazing accuracy.

Soaring and gliding is a very energyefficient way to travel, but migrants such as these Great White Pelicans are constrained to migrating over land and by day.

