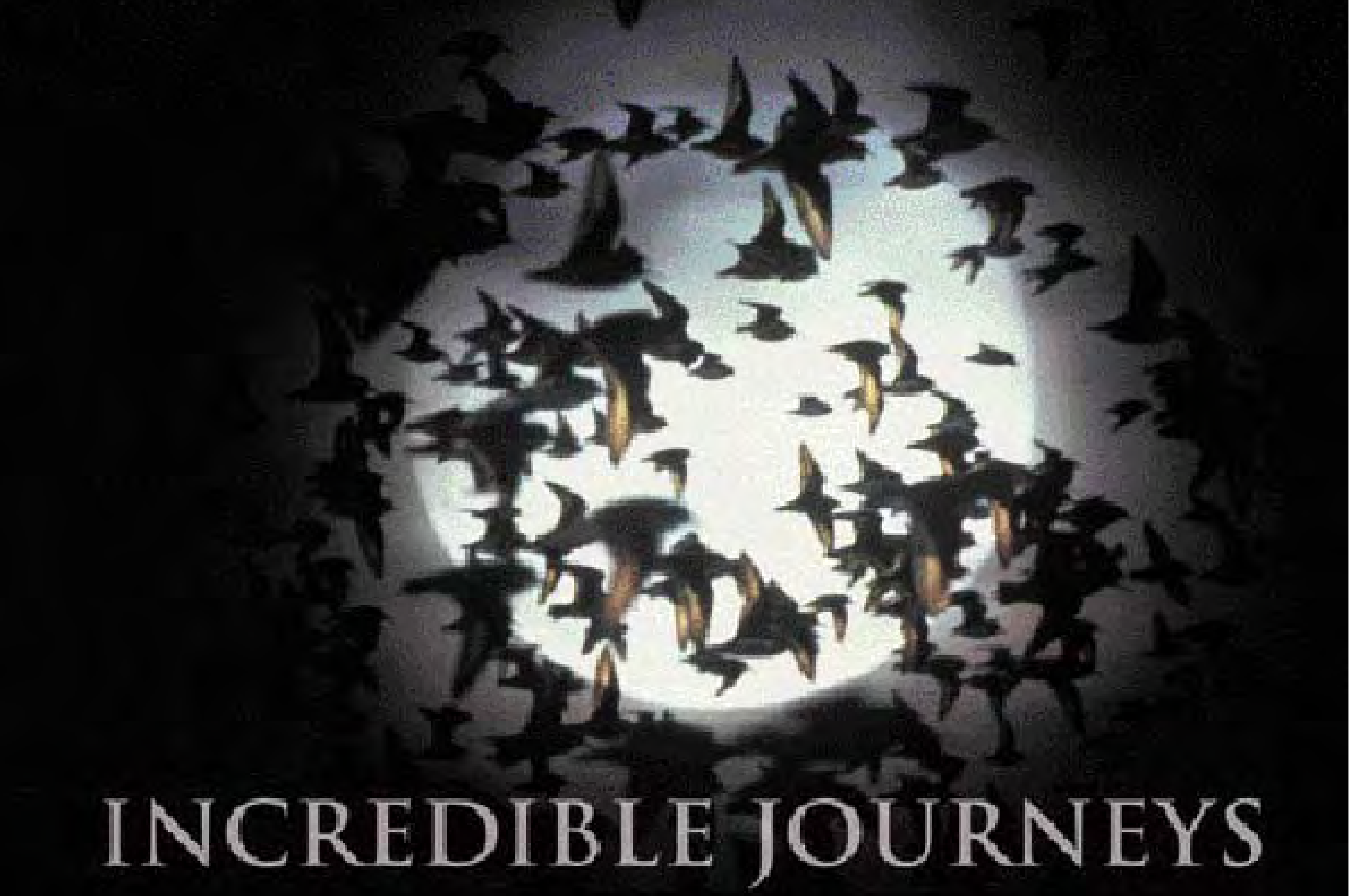
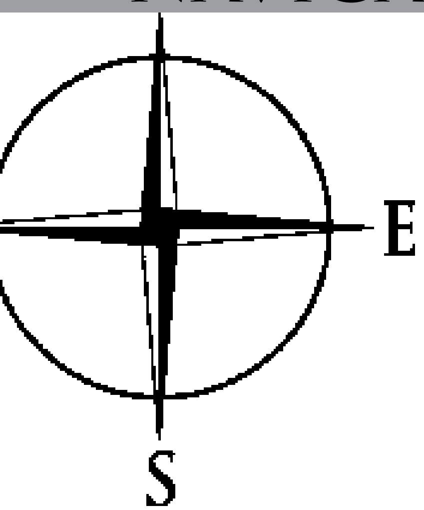


FRANS LANTING/VIREO

INCREDIBLE JOURNEYS

NAVIGATION AND THE MIGRATORY BLUEPRINT



Understanding how migrating birds find their way has teased the minds of scientists for decades. How are they able to make these journeys with such pinpoint accuracy, returning to the same spot year after year? What are the cues that they use in finding their way? Which skills are inherited and which learned?

In this final article on migration, Phil Hockey explores some of the ingenious experiments that have been used to answer such questions.

Reduced to its bare essentials, migration can be considered as a vector with two components – distance and direction. For a migrating bird, distance can be substituted with a combination of flying speed and flying time. If a young bird inherited this very basic information from its parents, it could, in theory, set off on a migration with a reasonable chance of arriving in approximately the right place. Many young birds do not migrate with their parents, suggesting that this kind of information probably is inherited. The most convincing support for this idea, however, is provided by birds such as cuckoos that are not only migratory but are also obligate brood parasites. A young cuckoo has never even seen its parents, far less had the opportunity to migrate with them.

A young bird migrating for the first time cannot know precisely where it is going – it has never been there before. It may have a simple blueprint of distance and direction, but this is not superimposed on a genuine map of its journey. If something were to happen along the way to displace it, it would probably be unable to correct for the shift. Interestingly, juveniles account for a high proportion of vagrant birds, suggesting that youngsters are much more likely to get lost on migration than are adults. By the same token, this also suggests that adults are more capable of navigating accurately towards a known goal (termed 'goal-orientation').

This difference between the migratory abilities of adult and juvenile birds was effectively demonstrated in an experiment in the 1950s which involved European Starlings *Sturnus vulgaris*.

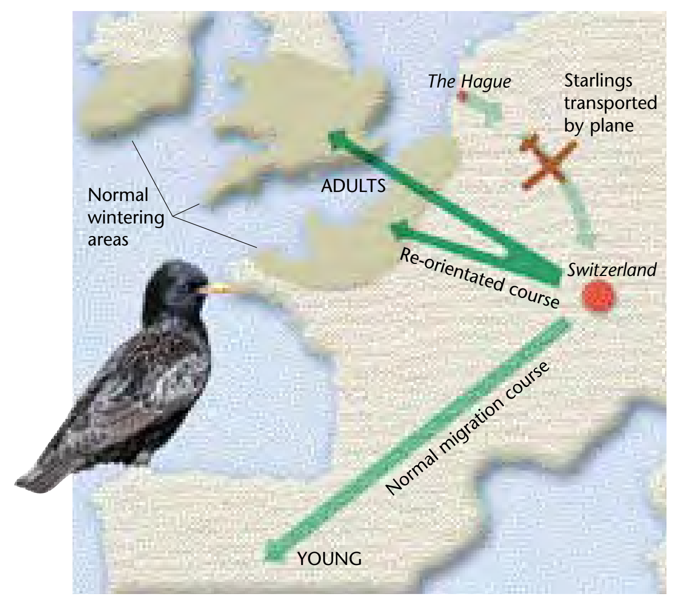
In the northern autumn, starlings that have bred in north-eastern Europe migrate in a south-westerly direction, passing along the coast of the Netherlands and continuing on to their non-breeding grounds in Britain and northern France. Researchers captured and ringed 11 000 migrating starlings on the Dutch coast and transported them south to Switzerland, where they were released. On release, the adult birds changed the direction of their migration to north-westerly and arrived at the 'correct' wintering grounds on either side of the English Channel. The juveniles, by contrast, continued in a south-westerly direction and ended their journey in southern France and Spain. If the juveniles had not been translocated, they would have ended up in the normal wintering range simply by following their south-westerly trajectory. However, it appears they had insufficient information to make the switch, following what is termed 'compass-orientation'. Adults on the other hand exhibited goal-orientation, that is, genuine navigation to a known end- point. Interestingly, in the following spring, the Spanish birds returned to their correct breeding grounds but continued to spend their winters in Spain. Thus, the experiment had resulted in their adopting a new migration route.

The implications of this experiment were profound, and pointed strongly towards migration being under some form of ▷

RAY TIPPER

Above *Many cuckoos, including the Common Cuckoo* **Cuculus canorus***, are migratory. That the chicks have never seen their parents is strong circumstantial evidence for migratory behaviour being inherited.*

Opposite *Proof that some birds, such as these Sanderlings* **Calidris alba***, use the stars as a compass was provided by changing the night sky within a planetarium. By selectively removing constellations, scientists were able to prove not only that migrating birds use the stars, but also that some stars are more important to them than others.*



REDRAWN FROM BURTON, R. 1992. BIRD MIGRATION. AURUM PRESS, LONDON. PETER STEYN

Left *When adult and juvenile European Starlings were displaced from their normal migration route, the experienced adults were able to correct for the displacement, whereas juveniles making their first migration were not. This indicates that there is a learning component to true goal-navigation, but exactly how birds achieve this is unknown.*

genetic control. It was to be many years, however, before the proof of this genetic control was found.

DISCOVERING THE MIGRATORY BLUEPRINT

Rarely is it possible to undertake experiments on the scale of the one described above and, contradictory as it sounds, most experiments on the heritability of migration have been carried out on captive birds. This is possible because of a behaviour of migratory birds called *Zugunruhe* or 'migratory restlessness'. During the periods they would normally be migrating, birds hop backwards and forwards in their cages, often fluttering their wings. It was deduced some 200 years ago that the duration of *Zugunruhe* was correlated with the duration of the migratory journey and hence with migration distance. Willow Warblers *Phylloscopus trochilus* migrating from Europe to tropical Africa show *Zugunruhe* for about 120 days, whereas closely related Chiffchaffs *P. collybita*, which migrate only as far as the Mediterranean Basin and North Africa, show *Zugunruhe* for only about 80 days.

If *Zugunruhe* and migration distance are under genetic control, it could be predicted that the offspring of a hybridisation experiment involving one migratory and one non-migratory parent would show intermediate *Zugunruhe*. This experiment was performed with Blackcaps *Sylvia atricapilla*, by hybridising migratory individuals from southern Germany with non-migratory birds from the Cape Verde Islands. The offspring exhibited *Zugunruhe* intermediate between that of their parents, indicating genetic control. A more elaborate experiment to test this idea was performed with a partially migratory population of Blackcaps from southern France. In this population, about 75 per cent of birds are migratory and 25 per cent resident, but a single brood can contain both migrants and residents. Two experiments were performed, one in which birds exhibiting migratory behaviour were crossed with others showing the same behaviour, and another in which residents were crossed with residents. Even though a resident– resident cross can produce a migratory offspring, the results of the experiment were striking. Within three generations of selective breeding, residents were producing only resident offspring and the same result was found for migrants within six generations. Similar experiments with partially migratory populations of other species have produced the same result and it is now firmly established that migratory distance is heritable.

RAY TIPPER (2)

When migratory and non-migratory Blackcaps are hybridised, the migration distance of the offspring is intermediate between that of their parents, indicating that this component of migration is inherited.

Zugunruhe can be used not only as an index of migration distance, but also as one of migratory orientation. Caged migratory birds do not hop in random directions, but spend a disproportionate amount of time hopping in the direction in which they would normally be migrating. Various types of cages, using either an ink pad in the centre and a paper lining or with perches attached to recording switches, have been used to quantify this hopping behaviour. An experiment with caged Garden Warblers *Sylvia borin* clearly showed that they had built-in information about when to change direction during migration. Garden Warblers that breed in Germany leave their breeding grounds in August, heading in a south-westerly direction until the end of September, by which time they have reached southern Spain and turn onto a southward heading for their journey into Africa. Caged birds showed exactly the same change in orientation at exactly the right time.

This, of course, did not prove that the information they had was inherited: to do this, it was necessary to perform more hybridisation experiments. Not only do Blackcaps have regional differences in migration tendency, they also have regional differences in migration routes. Birds breeding in Germany migrate southwestward to wintering grounds in the Iberian Peninsula and north-western Africa. Austrian birds, by contrast, migrate in a south-easterly direction to eastern and southern Africa. Hybridisation of the two produces offspring whose favoured migration trajectory is due south.

The above experiments indicate that migration behaviour within a species could change very rapidly – indeed, within a single generation – should something happen that forces populations with different migratory behaviour together or should one particular type of migration suddenly become favourable. This seems to have happened with German Blackcaps. Since World War II, an increasing number of Blackcaps have been migrating from their breeding grounds in west–central Europe to wintering grounds in Britain. This does not involve a huge directional change from their normal migration (west-north-west from west-south-west), and it is likely that some birds have always reached Britain. This migration is shorter than the traditional one and it may allow British-wintering birds to return to their breeding grounds earlier than Spanish-wintering birds and perhaps, as a result, obtain superior breeding sites and produce more offspring. This begs the question of why this migration has only evolved to be common in recent years if it confers such advantages. It has been suggested that the reason is the ever-increasing provision of supplementary food at bird tables – a relatively recent phenomenon. What it doesn't explain is why British-breeding Blackcaps continue to migrate south for the winter (at least for now!).

> 'To account for this remarkable phenomenon, scientists and observers sought refuge in the assumption of an "Instinctive Action" on the part of birds [that] adopted unconsciously the right road towards the attainment of an unknown goal. ...Later observers ... have rejected with contempt this explanation of a problem unsolved...' Heinrich Gätke, 1895

European Robins are able to orientate using the earth's magnetic field. If the nature of the magnetic field is changed using electromagnetic coils, captive robins become disorientated.

FINE-TUNING THE BLUEPRINT – FROM VECTOR NAVIGATION TO GOAL-FINDING

Vector navigation using inherited information can only get a bird so far – alone, it certainly cannot explain how an individual can navigate year after year to the same nesting tree or the same wintering territory. Indeed, it may be important only for an individual's first, outward migration when it has no knowledge of its destination. For all birds, however, there are at least three external cues that could assist them in maintaining direction (compasses).

Compasses

Homing pigeons and some nocturnal migrants are able to orientate using the earth's magnetic field – lines of magnetic force that humans are unable to perceive. Circumstantial evidence for the existence of this compass includes the ability of some nocturnal migrants to orientate at night in the absence of visual cues. The critical experimental test was performed using large electromagnetic coils to change the apparent position of magnetic north for caged European Robins *Erithacus rubecula*. The robins responded by changing their orientation. The magnetic compass is termed an 'inclination compass' because its use depends on detecting latitudinal differences in the angle of inclination of the lines of magnetic force to the earth. At the poles this angle is 90 degrees, at the equator it is 0 degrees. Thus, by monitoring the rate of change of this angle, flying birds are able to determine whether they are moving towards or away from the equator. The magnetic field alone will not help them differentiate between north and south: there is no evidence that they respond to the polarity of the magnetic field, which has changed several times.

'No final solution of the problem has yet been arrived at. Nor, indeed, is it likely that such will ever be the case, since the performances of birds during their migrations are raised entirely beyond the range of man's mental and intellectual faculties.' Heinrich Gätke, 1895

There are two visual compasses used by migrating birds, namely the sun and the stars. Circumstantial evidence for the existence of a sun compass is the disorientation of daytime migrants on cloudy days. The same effect is observed in caged birds if they are prevented from having a view of the sun. Analogous to the coils used to change the magnetic field, the acid test of the existence of a sun compass was to change the apparent position of the sun by using mirrors. This experiment was carried out on European Starlings back in 1950 and was the first proof of an essential orientation cue in animals.

Use of a sun compass requires that birds have an internal clock that enables them to make allowances for the lateral movement of the sun caused by the earth's rotation. The existence of this was demonstrated in homing pigeons by changing their internal clock using artificial day/night regimes that were incorrect for the time of year: when released, the experimental pigeons orientated incorrectly.

The orientation ability of many nocturnal migrants is compromised on overcast nights, prompting researchers to hypothesise the use of a star compass. The existence of this compass was proved experimentally more than 30 years ago by placing American Indigo Buntings *Passerina cyanea* in a planetarium at the time of their southward migration. Under the correct night sky, they orientated south. If the sky was rotated by 180 degrees, they switched their orientation to north. Selective removal of stars from the sky showed that the birds were most responsive to stars within 35 degrees of the North Star, the sky's apparent centre of rotation where the star configuration remains static. A subsequent experiment demonstrated further that the ability of birds to use the star compass (as is the case with the sun compass) is something they develop rather than inherit as an innate skill. In a clever experiment, young birds were reared in a planetarium environment where the sky had been set to rotate around one of the stars in the Orion constellation (Betelgeuse) rather than around the North Star. When these birds were ready to migrate, they chose their departure direction using this artificial pivotal point.

JOHN GRAHAM

Some migratory birds, including many seabirds such as this Wilson's Storm Petrel* Oceanites oceanicus*, have a well-developed sense of smell. It has been suggested that they might use 'scent gradients' to help them on migration, but as yet there is no proof of this.

As yet, precise compasses have been identified experimentally for very few of the world's migratory birds. It is not known whether it is common for birds to have multiple compasses or whether birds might switch from one compass to another between their first and subsequent migrations – much still waits to be learnt.

Navigation aids

Many displacement experiments have been performed whereby birds are released from locations they have never visited. Time after time they have shown remarkable abilities to find their way home: the rapid return of rehabilitated African Penguins *Spheniscus demersus* from Port Elizabeth to Cape Town (see *Africa – Birds & Birding* 6:4) is a case in point. Manx Shearwaters *Puffinus puffinus* taken 4 000 kilometres from the east to the west Atlantic managed to find their way home in less than two weeks. Just how they do this still lies more in the realms of speculation and hypothesis than on the podium of proof.

Several hypotheses, of varying degrees of complexity and credibility, have been proposed to explain true navigation, some of which are claimed to have support, but none of which has been demonstrated to be adequate as a 'general rule'. Vector navigation is convincing for young birds – but after they have completed their first migration, both the breeding and nonbreeding sites are known and a new navigation technique might kick in based on this information. Some of the hypotheses involve memory – of a 'topographical map', a previous position of the sun, every twist and turn of the outward route, a scent map or a scent gradient. Others require almost unbelievable sensitivity on the part of the bird. One proposed that birds were able to generate a navigational map using a combination of the earth's magnetic field and the Coriolis force. In order to use such a system, birds would have to measure electric fields on their bodies to an accuracy of one-millionth of a volt and perceive a sideways force of one six thousandth of the earth's gravitational acceleration, even under windy conditions. When these requirements were pointed out, this idea was consigned to the scrapyard of science!

The combined efforts of scientists over the past 30 years have dispelled several of the myths surrounding bird migration. While many questions have been answered, these answers in turn have spawned new questions and hypotheses. Even today, scientists continue to debate fundamental questions about how, where and when migration evolved. Many of migration's costs and benefits are fairly well understood, but the explanation of how birds navigate with such extreme accuracy remains one of the great unsolved mysteries of the natural world. □