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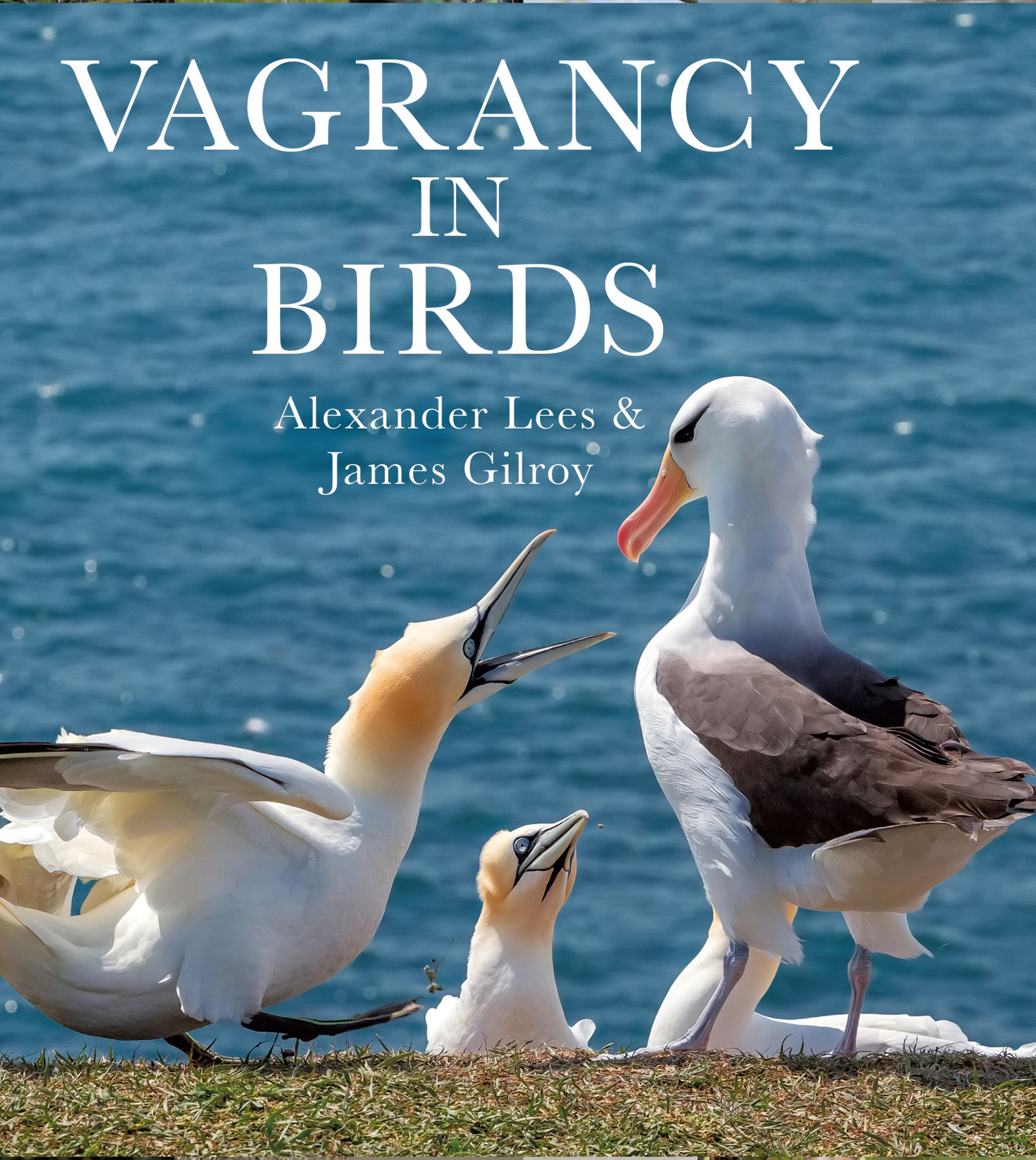
Alexander Lees &
James Gilroy



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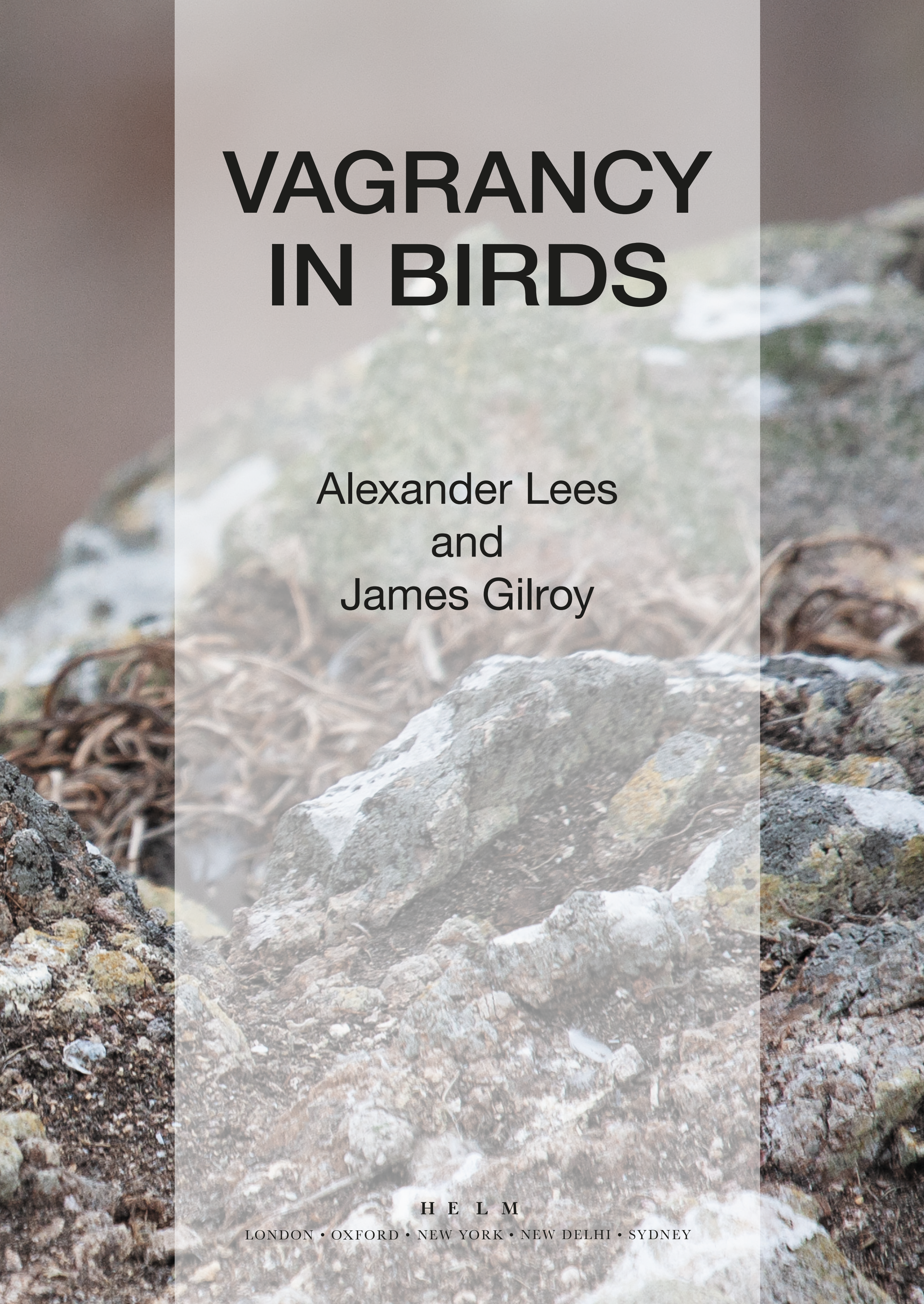

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Half-title image: Brown Shrike *Lanius cristatus*, Grutness, Shetland, Scotland 14 October 2019 (*Rebecca Nason*).

Title image: Connecticut Warbler *Oporornis agilis*, Southeast Farallon Island, California, United States, 14 September 2010 (*Matt Brady*).

Cover images: Main image Black-browed Albatross with Northern Gannets, Heligoland, Germany (*Vincent Legrand*). Front cover, clockwise from top left: Yellow Warbler, Shetland Islands (*Hugh Harrop*); Squacco Heron, Somerset (*Rich Andrews*); Pallas's Warbler, Norfolk (*James Lowen*); Tengmalm's Owl, Shetland Islands (*Rebecca Nason*); Red-flanked Bluetail, Wiltshire (*Rich Andrews*); Long-billed Murrelet, Devon (*Shutterstock/Agami Photo Agency*); Black-throated Thrush, The Netherlands (*Shutterstock/Agami Photo Agency*); African Crake, Cape Verde Islands (*Shutterstock/Agami Photo Agency*); Siberian Accentor, Shetland Islands (*Stef McElwee*); Sandhill Crane, Japan (*Shutterstock/Agami Photo Agency*); Red-eyed Vireo, Easington, East Yorkshire (*Jake Gearty*); Sharp-tailed Sandpiper, California (*Shutterstock/Agami Photo Agency*).
Back cover, clockwise from top left: Ring-necked Duck, Durham (*Stef McElwee*); Woodchat Shrike, Somerset (*Rich Andrews*); Green Heron, Pembrokeshire (*Jake Gearty*); Siberian Rubythroat, Shetland Islands, (*Hugh Harrop*); Iceland Gull, Shetland (*Rebecca Nason*); Black Redstart, Northumberland (*Stef McElwee*); Black Stork, Tyne & Wear (*Stef McElwee*); Olive-backed Pipit, Shetland (*Stef McElwee*); Black-winged Stilt, Somerset (*Rich Andrews*); Lanceolated Warbler, Shetland (*Shutterstock/Agami Photo Agency*); Nutcracker, The Netherlands (*Shutterstock/Agami Photo Agency*); Blyth's Reed Warbler, Shetland Islands (*Jake Gearty*).

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▲ Hume's Warbler *Phylloscopus humei*, Easington, Yorkshire, England, 10 November 2019, an increasingly recorded vagrant to Europe, usually in late autumn (*Alexander Lees*).

SCOPE OF THE BOOK

‘Vagrants’, ‘accidentals’, ‘rarities’, ‘extralimitals’ and ‘casuals’ are all synonyms for unusual records of nominally ‘out of range’ individuals of a given bird species. Humans have long coveted records of these ‘lost’ individuals, and there is a rich ornithological literature that describes the various subcultures associated with their pursuit, from 19th-century collectors to 21st-century twitchers (Mearns & Mearns 1998, Wallace 2004). The obsession surrounding vagrant birds has been historically derided by some ornithologists, who argued that records of vagrants are of little biological relevance, but we share the contention of others (e.g. Grinnell 1922, Rose & Polis 2000, Newton 2008) that vagrancy is a powerful biological phenomenon whose study is fundamental to understanding the diversity of life on earth. This book will for the first time systematically explore the taxonomic and geographic patterns of extralimital avian occurrence globally and try to synthesise what we know about the processes that underpin these occurrences, based on the latest scientific discoveries.

▲ Icterine Warbler *Hippolais icterina*, Foula, Shetland, Scotland, 4 June 2008, an expected ‘scarce migrant’ in late spring in the Northern Isles but still out of habitat and out of range (*James Gilroy*).

Before we can embark on this study of pattern and process in avian vagrancy, we need to define what a vagrant is in the first instance. This is surprisingly more challenging than one might expect. If our starting assumption is that a vagrant of a species is an individual occurring outside of its normal geographic range, then defining vagrants is simply a matter of identifying the range edge – and any individuals that lie beyond it are vagrants. For example, Short-toed Treecreepers *Certhia brachydactyla* do not breed in Britain and are a strictly sedentary species – thus any individuals that appear in Britain are vagrants, even if they are only a few dozen kilometres from regular breeding sites on the near Continent, separated by the English Channel which is a significant barrier to their dispersal. Meanwhile Icterine Warblers *Hippolais icterina*, which breed equally close to Britain, are highly migratory and occur in small numbers regularly – are these individuals vagrants? Most British birders would label them as ‘scarce migrants’, but they do meet our criteria for being out of range, highlighting the fact that there is a smooth continuum between the rarest of vagrants to true ‘scarce migrants’ occurring at the edge of their normal migration routes. It is tempting to try and apply some sort of quantitative threshold to define vagrancy, but this is a major challenge, not least because geographic ranges are not fixed in time and space, and can change dramatically very quickly. However, a ballpark definition might be that the geographic range of a species should encompass something like 99.99 per cent of individuals of a species at a given time – anything outside this range, based on the density of the species, might be defined as a vagrant.

In case you are an all-round naturalist picking up this book and thinking, well ‘is this just a bird thing?’, it would be remiss of us not to point out that vagrancy is not just a bird-specific phenomenon. Vagrancy is most appreciated and celebrated in birds because of their high mobility, but taking Britain again as an example, natural historians have recorded vagrant butterflies, dragonflies and bats from North America, vagrant moths, grasshoppers and sea turtles from the tropics, and vagrant seals and cetaceans from the Arctic.

Most newspaper articles reporting on the latest ‘waif’ or ‘stray’, and the ‘hordes’ of birders who come to see it typically invoke the weather as the root cause of vagrancy – the oft repeated adage of ‘blown off course’. Weather is an important driver of vagrancy, but is far from the only one. The aforementioned Short-toed Treecreepers do not migrate and can’t realistically be blown ‘off course’, as they don’t have a ‘course’ to take; their appearance outside their normal range belies one of the many other different mechanisms for vagrancy, the description of which forms a substantial part of this text. Another old adage – sometimes heard from birders – is that ‘anything can turn up anywhere’. Although it might sometimes feel like this is the case, particularly at the height of exciting autumn migrations, this is demonstrably not true. Vagrancy is far more frequent in highly migratory species and

▲ Thousands of birders line the seafront at Dawlish, Devon, England, to see the first record for Britain of a Pacific seabird – Long-billed Murrelet *Brachyramphus perdix* – on 12 November 2006 (*Alexander Lees*).

migration span is a good predictor of both vagrancy likelihood (McLaren *et al.* 2006) and the distance that birds may travel in the 'wrong' direction – to reach places vast distances outside of their regular ranges. Sedentary species can occur as vagrants, but the distances involved tend to be far more modest. This in turn varies latitudinally – tropical forest understorey species, for example, may be the least vagrant-prone of all taxa, and many may be physically incapable of flying more than a few dozen metres before collapsing exhausted (Moore *et al.* 2008). As such, it is perhaps possible to encounter a species like Sanderling *Calidris alba* almost anywhere in suitable habitat on Earth, yet finding an Andean *Scytalopus* tapaculo more than a few hundred metres outside of its elevational range limit (and hence geographic range) would be an incredibly rare vagrancy event, as these species are extremely sedentary. The life history characteristics of birds are thus reliable predictors of their vagrancy likelihood, and we explore this variation across the avian 'tree of life' in the second part of the book.

Broadly speaking, vagrancy can arise through both *exogenous* factors (i.e. with an external cause) or *endogenous* factors (an internal cause). The Icterine Warblers that are drifted across the North Sea to eastern England during 'fall' conditions are thus exogenous and might even be termed 'exovagrants'. Vagrancy in Short-toed Treecreeper, although potentially assisted by favourable winds, is more likely to be driven by an endogenous impulse to disperse – making these nominally 'endovagrants'. These categories are simplistic, and in many cases vagrancy may stem from multiple processes occurring simultaneously – Icterine Warblers may appear in Britain primarily during ideal wind drift conditions, but a significant proportion of those individuals are probably following errant compass headings anyway. In this book we will explore in detail the various internal and external drivers of avian vagrancy, first looking at the mechanisms by which migratory species navigate, and how errors in these mechanisms can help explain patterns of vagrant occurrence.

◄ Tschudi's Tapaculo *Scytalopus acutirostris*, Bosque Unchog, Huánuco, Peru, 24 June 2013. Tapaculos are among the most sedentary of all bird species and hence the least vagrancy prone. Their poor dispersal capacity has contributed to the high endemism and species richness in the group, as populations easily become isolated from one another by relatively minor habitat barriers (*Alexander Lees*).

HOW BIRDS NAVIGATE

Birds have remarkable navigation capacities, with many species migrating tens of thousands of kilometres only to return with pinpoint precision to the same nesting site they used in the previous year. Understanding the basics of avian navigation is essential if we are to make sense of vagrancy patterns, both in terms of identifying how endogenous navigatory errors are made, and also understanding how exogenous forces like weather can inhibit avian navigational abilities and lead them to stray off course.

When humans think about navigation, we naturally conjure up maps of the world in our minds. This ability is not innate, however – we are fortunate that our predecessors have meticulously mapped the planet, providing us with visual resources that we can memorise and use to keep track of our location within the world around us. Our capacity for navigation thus depends almost entirely on learned information, much of which has been handed down from previous generations, as well as technological solutions like GPS – all of which are luxuries not afforded to most migratory birds. In the majority of bird species, the ability to navigate with precision to exact localities is not innate but is learned through gradual experience (Wiltshko & Wiltscko 2015). Migratory birds are apparently able to develop 'mental maps' during their early years of life, using cues they experience during their first migratory journeys, to allow them to assess exactly where they are in relation to specific localities such as former breeding locations, stopover sites or winter territories. However, when embarking on their first migration, most juvenile birds cannot rely on such a developed map sense. Unlike more experienced adults, juveniles are generally unable to determine exactly where they are, at any given point in time, relative to their origin and goal.

If we consider a juvenile of a migratory species that does not migrate in flocks – in other words, a species that cannot rely on following other individuals – it is clear that for the first migration at least, navigation must be done using only the innate instincts the bird has inherited from its parents. In many cases, such birds must embark on migration within weeks of fledging if they are to avoid being exposed to unsuitable environmental conditions as the seasons shift. Many migrants must also adjust their migratory headings multiple times over the course of their first migration to avoid barriers such as oceans or deserts. The fact that billions of naive juvenile birds successfully complete these journeys annually is genuinely remarkable. Without a map to guide them, how do they find their way?

Birds have evolved many different solutions to this problem, but research suggests that in general, juvenile long-distance migrants undertake their first migration using just two key tools – a clock (i.e. an ability to track the passage of time) and a compass. These tools are inherited genetically (Helbig 1992, Willemoes *et al.* 2014), and in theory they are all a young bird needs to complete its first migration entirely alone. Juvenile migratory birds typically inherit a migratory 'program' from their parents, which encodes both the direction and timing of

▲ Swainson's Thrush *Catharus ustulatus*, Norwick, Shetland, Scotland, 28 September 2014, the 33rd record for Britain (*Paul French*).

movements necessary to make a return trip to a suitable wintering area. The genetic heritability of this program is quite precise – a series of experiments with Eurasian Blackcaps *Sylvia atricapilla* revealed how interbreeding between individuals with different migratory programs produces offspring with intermediate strategies (Helbig 1992). This was further confirmed in a recent tracking study with Swainson's Thrushes *Catharus ustulatus* from a contact zone between two populations with different migration routes, where some offspring followed routes that were intermediate between their parents, whilst others adopted the orientation of one parent in autumn and the other parent the subsequent spring (Delmore & Irwin 2014).

From the point of view of understanding vagrancy, errors in any part of the inherited migratory program could result in first-year birds moving off in the 'wrong' direction. For example, a bird might inherit a perfectly functioning clock and compass (i.e. the machinery of navigation), but due to some mutation or other natural variation its directional or temporal 'instructions' differ from the rest of the population. Such an individual would theoretically be quite capable of understanding which way is north, but it will move in a very different direction than other individuals of its species. Alternatively, a bird might inherit a perfect set of directional 'instructions' but carry some mutation or variation of its clock or compass apparatus that prevents it from accurately implementing the movements encoded in its genes. Clearly, there are many ways that navigatory errors could lead to vagrancy – and this variability in part explains the vast diversity of observed vagrancy patterns. However, by examining recent advances in the scientific understanding of the mechanisms of bird navigation, it is possible to make some sense of just how and why vagrancy occurs. In the remainder of this section, we will summarise the current state of knowledge of how migratory birds inherit and implement their migratory programs. First and foremost, we will consider arguably the most fundamental component of the migratory apparatus, at least in terms of drivers of vagrancy: the compass sense.

◄ Chinese Leaf Warbler *Phylloscopus yunnanensis*, Zoige, Sichuan, China, 1 June 2011, a tired migrant 'out of habitat' (*James Eaton*).

The four avian compasses

Compasses have just one purpose – to tell the user where north is. Armed with such a tool, a naive juvenile bird should always be able to use north as a reference point, and then orientate itself by rotating its body to a point where it is in line with whatever desired migratory heading it has inherited from its parents. This basic compass orientation is thought to be the cornerstone of migration in naive juvenile birds and has been the subject of exhaustive scientific study. For decades, researchers have performed increasingly complex and elegant experiments to examine how birds 'read' their internal compass, and how they then use this information to orientate themselves. Many of these experiments have involved trapping wild birds (or raising them in the lab) and placing them in a cage apparatus – an Emlen funnel – overnight, where their desired target orientation can be evaluated from the pattern of marks they leave around the edges of the cage. By manipulating the information available to these birds – for example, by preventing them from seeing the stars above – researchers have been able to painstakingly unpick the different cues that birds use to orientate themselves.

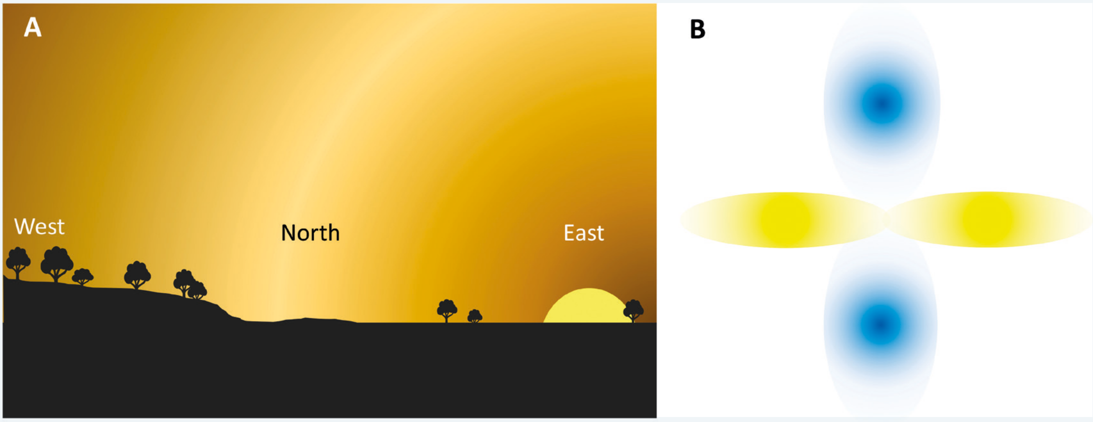
Thus far, research has identified four separate avian compass mechanisms, each using information from four different sources: 1) the Sun, 2) the pattern of polarised light, 3) the stars, and 4) Earth's magnetic field (Åkesson & Helm 2020). Interestingly, evidence suggests that most migrants have evolved to use at least two, and perhaps sometimes all of these compasses simultaneously, forming a hierarchy of tools that they can cross-reference to make the best judgements possible. Despite having this arsenal of compass mechanisms at their disposal, it is still clear that the system is fragile and prone to error – and thus potentially vagrancy – with each compass having its own particular weaknesses and complications.

The Sun compass was the first to be identified in birds; Kramer (1952) revealed how Common Starlings *Sturnus vulgaris* would show a very clear pattern of migratory orientation within their cages, but only on days when the Sun was visible. In a follow-up experiment, Kramer used mirrors to change the apparent position of the Sun above the Starlings and found that they duly shifted their orientation in line with this new position. Observing the position of the Sun at sunrise and sunset is the simplest solar compass, but this frame of reference is only available as two snapshots during each 24-hour period, which is clearly insufficient for a migrant that must keep track of its heading throughout the day. Research in 'homing pigeons' *Columba livia domestica* has revealed that they solve this problem using their high-precision internal body clock, allowing them to keep precise track of the Sun's arc of movement (the azimuth, or horizontal position) with respect to the passage of time (Wiltschko *et al.* 2000). In doing so, they can continually adjust their mental compass to ensure that they can always tell north from south.

Whilst this clearly provides an effective compass for diurnal migrants, there are two major drawbacks to reliance on the Sun compass in naive juvenile birds. One is that the time-adjustment method apparently requires a high degree of learning; evidence from pigeons suggests that they are only able to do it from around three months old and some individuals master learning it far better than others. The second issue is that the Sun must be clearly visible – the compass will not work when there is significant cloud cover. Clearly, a migratory bird must be prepared to move in cloudy conditions, and therefore relying solely on a Sun compass for navigation is not a safe strategy.

One way that some species have solved the problem of cloud cover blocking the Sun is to use the pattern of polarised light, rather than the Sun itself, as a compass cue. Polarisation describes the degree to which light waves coming from a source are either scattered or aligned – and helpfully for a migratory bird, light from the Sun always carries a consistent pattern of polarisation across the sky. The alignment of polarised light waves is most intense at an angle 90 degrees from the Sun, and most scattered at points either towards or away from the Sun itself (Figure 1). Importantly, this pattern is present even when the Sun is obscured by clouds or objects, meaning that any organism that can 'see' the polarisation of light can roughly identify the position of the Sun at any time of day.

Many species, including birds, have an acute ability to see patterns of polarised light whenever at least some light is available. In fact, most humans can see polarisation patterns too – although until recently we have been largely unaware of this apparent 'extra sense' (Temple *et al.* 2015). Referred to as 'Haidinger's brush', human



▲ **Figure 1.** A) Birds can find north by viewing the pattern of polarisation across the sky at sunrise (shown here) and sunset. B) 'Haidinger's brush', a pattern of polarised light that is visible to the naked eye in most humans.

eyes have the capacity to see polarisation in the right circumstances – you can try it yourself using an LCD screen (e.g. a laptop or tablet). If you look at a blank white portion of the screen and tilt your head from side to side, you should see faint yellow and blue 'bow-tie' patterns (Figure 1B) appear at certain angles. With practice, you can also see the same pattern in the blue parts of the sky at 90 degrees from the Sun, particularly around sunrise and sunset. The long axis of this yellow 'bow-tie' will point approximately towards the Sun – it is likely that this is something akin to the polarisation compass used by birds to navigate. Although discovery of this capacity in humans was a surprise to modern science, Viking civilisations apparently discovered this more than 1,000 years ago, and even used quartz crystals (the enigmatic 'sun stone' of viking lore) to amplify the polarisation pattern for use as a compass tool (Le Floch *et al.* 2013).

Polarisation can provide a cloud-proof mechanism for identifying north, but its value as a universal compass for migratory navigation is limited. Evidence suggests that polarisation patterns are only likely to be strong enough to use at sunrise and sunset, and therefore may not be used for continual navigation throughout a flight. Moreover, knowing the precise position of the Sun at sunset is not sufficient for an individual to find north and south – the individual must also have a keen sense of time in order to compensate for changes in the Sun's position through the year. Again, this time-compensation ability appears to be a learned skill that is honed by developing birds over time – and thus may not be particularly accurate in a naive juvenile bird, and especially a late-fledged individual in a rush to embark on its first migration. For nocturnal migrants (which includes most passerines and many non-passerines), the stars provide another potential source of compass information. Some of the most elegant experiments conducted on bird navigation were carried out by Emlen (1970) using caged Indigo Buntings *Passerina cyanea* to examine their use of celestial cues. Emlen did this by taking caged buntings to Cornell University's planetarium, where he was able to measure how the migratory orientation of birds varied when he experimentally changed the patterns of stars in the night sky above them. The results were dramatic and conclusive – the birds did indeed use the stars to orientate, and in particular they used the point of axial rotation as their reference point (Figure 2). In the northern hemisphere this corresponds to Polaris, the North Star (Emlen 1970).

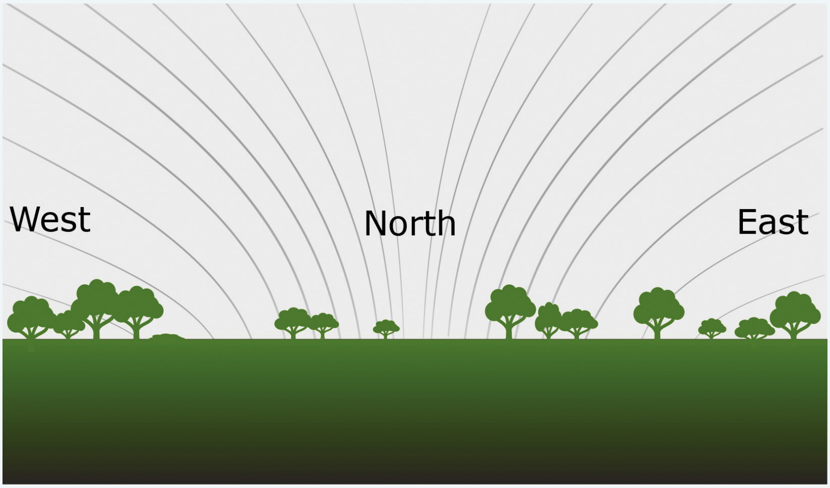
◀ **Figure 2.** Many migratory birds apparently memorise the pattern of star rotation around the poles during their first weeks of life, allowing them to identify north and south whenever sufficient clear sky is in view. Image reproduced with permission from the European Southern Observatory (ESO).

Emlen's experiments went on to show in detail how this mechanism worked. By changing the point of rotation in the planetarium from Polaris to Beetlejuice, he was able to prove that it was not the pattern of stars themselves that the birds used, but the point of rotation, as birds exposed to this new rotation point shifted their migratory orientations to reflect this new 'north' around Betelgeuse, moving in a different direction to those exposed to the fixed point of Polaris.

Another key insight from subsequent planetarium experiments was that much like the Sun compass, the star compass requires considerable learning and skill refinement on the part of juvenile birds to be useful. Specifically, individual birds must first identify the point of rotation itself, presumably through careful observation over multiple cloud-free nights. Then, the bird must learn the pattern of stars around the fixed point of rotation, so that they can then check and identify the north point at any moment during their subsequent journey – even if Polaris itself is obscured by clouds (Wiltshchko *et al.* 1987). This clearly represents an acute challenge for a recently fledged bird with only weeks between taking its first flight and embarking on its first full migration. Even after successfully internalising a star map, there are still many further pitfalls to the use of stars as a compass during an ongoing migration. Clearly, during flight itself, individuals must be able to continually assess their heading with respect to their compass – and yet this will not be possible whenever cloudy conditions mask the positions of the stars.

Prolonged cloudy conditions during a peak migration window – or indeed smoke from wildfires – could therefore cause significant problems for any birds relying largely on star-based or solar compasses to orientate. Also, as birds imprint on a star map based on the skies above them in their first weeks of life, the stars themselves will change considerably as the season progresses, and even more so as the bird begins to move across the planet during migration, with some constellations disappearing altogether whilst other new ones emerge on the horizon. The learned star map therefore must be updated continually during the course of a migration in order to remain usable as a compass (Muheim *et al.* 2014) – something that may be further inhibited by cloudy weather during the course of migration. It will also be made more difficult the shorter the timespan within which the migration takes place.

The stars, the Sun and polarised light therefore all appear to require some degree of learning, as well as being highly vulnerable to cloudy weather. The final tool in the avian compass toolkit, however, does not suffer from these weaknesses, and can apparently be used without the need for learning or skill development – the magnetic compass. It appears that most or even all species have evolved to use magnetic cues – and this likely represents the default 'fail-safe' compass among naive juvenile migrants.



► **Figure 3.** Hypothetical visualisation of how birds may view Earth's magnetic field, showing the apparent 'dip' towards the pole and away from the Equator, as 'seen' by birds such as European Robin *Erithacus rubecula*.

The avian magnetic compass was first discovered in European Robins *Erithacus rubecula* (Merkel & Wiltschko 1965), and our current best evidence suggests that it primarily works by inclination (the 'dip' of magnetic lines towards the pole) rather than polarity itself (Wiltschko & Wiltschko 1972; Figure 3). Just how birds perceive this 'dip' remains poorly understood, although it appears that at least two different mechanisms have evolved separately – one involving magnetic particles (magnetites) located in the sensory organs of the bird, and the other a light-based system involving specialised receptors in the retina that allow birds to literally 'see' the magnetic field around them. To use the magnetic compass, a bird must evaluate the point at which magnetic 'lines' dip towards the horizon – the steepest angle of this dip always points towards the magnetic pole (Ritz *et al.* 2009). As such, the magnetic compass seems relatively infallible – indeed, one might question why the other compasses are needed, if the magnetic compass can be used in any weather conditions and without any learning or imprinting. The fact that almost all migratory birds appear to have evolved the ability to use other compasses alongside their magnetic sense (Muheim *et al.* 2006) indicates that this cannot be the case – whilst evidently useful, it is apparent that the magnetic compass is not sufficient for orientation by itself.

◄ European Robin *Erithacus rubecula*, Mutsu, Tochigi, Japan, 26 February 2019, thousands of kilometres east of its normal range (*Yann Muzika*).

There are various reasons why relying on magnetic fields alone would be risky – the angle of dip itself varies with latitude and may also become hard to discern in some regions, particularly towards the Equator. Another key feature of the avian magnetic compass is that it cannot truly differentiate between north and south – rather, it always points poleward from the Equator (Wiltschko & Wiltschko 1972). This means that if a bird moves across the Equator, its magnetic compass will 'flip', so a bird moving south out of the northern hemisphere will suddenly 'see' its magnetic compass pivot to point back towards the opposite pole. To counter this, transequatorial migrants must have some other mechanism to be aware that they have switched hemispheres, and thus adjust their orientation to control for the fact that their internal magnetic compass now points south.

Magnetic intensity itself varies, suggesting that the 'dip' pattern birds use to navigate may be very faint in some regions, making it difficult for birds to assess the precise point of maximum inclination. Another critical issue with the magnetic compass is that the orientation of the field varies from place to place (known as magnetic declination) meaning that in some areas the compass may become highly inaccurate. Across much of the globe this inaccuracy is relatively slight (between 0–20 degrees outside the true polar direction; Muheim *et al.* 2006), but at high latitudes the discrepancies between true and magnetic poleward orientation can be much more significant – up to 90 degrees in some cases. In the high Arctic, therefore, any bird naively using a magnetic compass to orientate could end up setting off in a direction up to 90 degrees outside the 'correct' orientation encoded in their genetic program (Alerstam *et al.* 2001).

Unsurprisingly, evidence suggests that migratory species breeding at high latitudes have evolved to rely much more heavily on other compasses – Arctic-breeding shorebirds, for example, follow routes that suggest they use a Sun compass almost exclusively, at least at high latitudes (Alerstam *et al.* 2001). For many other species, the favoured strategy appears to be to use a magnetic compass, which they then 'calibrate' using one or more other compasses at different stages of the migration. Strongest evidence for this comes from studies of Savannah Sparrows *Passerculus sandwichensis*, showing that despite breeding at high latitudes they do rely heavily on their magnetic compass, but prior to migration they correct for the declination effect by observing the 'true' north point using polarised light and use this to adjust the north point of their magnetic compass (Muheim *et al.* 2006). Having memorised this discrepancy, they can then apply it continuously as they begin to move (i.e. at night when the polarised light compass is no longer visible) to adjust their magnetic compass and find the true direction of north. This type of compass correction appears to be a common strategy – though some species might use other compasses as their reference category (solar or celestial cues). It provides an elegant way for birds to use their only compass that is always available – being visible day and night, and unaffected by weather conditions – despite that compass being 'flawed' in that it does not always point to true north. They do this by periodically working out how much they need to adjust their magnetic compass, by ground-truthing it against another compass during windows when weather conditions allow one of them to be used.

In light of this huge body of research, we can now go some way towards constructing a general picture of how the compass sense works in a typical juvenile migratory bird. It appears that to correctly develop the tools needed to robustly navigate on a first migration, a juvenile must go through two key steps:

- After hatching and prior to migration, a bird must develop a capacity to use at least one non-magnetic compass – either by memorising star maps (most important in nocturnal migrants) or developing a capacity to finely track the passage of the Sun and/or pattern of polarisation through the day (most important in diurnal migrants).
- Next, they must use these learned compass cues to calibrate their innate magnetic compass, ensuring they can use it to locate true north despite magnetic variability.

Clearly, failure to achieve both these steps during the early months of life could lead to a juvenile bird embarking on its migration without a robust method of navigation – placing it at risk of vagrancy. We would perhaps expect such a bird to wander almost randomly if it were unable to effectively orientate itself in its innate desired heading. Some vagrant occurrences do indeed fit a pattern of random movement, particularly in the case of vagrancy in very young juveniles that stray outside their normal distributions soon after the end of the breeding season (see page 55). Interestingly, however, many long-range vagrancy events fit much clearer patterns, with certain species appearing consistently as vagrants in particular areas and at particular times of year. This suggests that such vagrants are steadfastly moving in their chosen – but erroneous – direction, rather than randomly orientating from one flight to the next, as one might expect from a bird that has simply failed to develop a strong compass sense. In subsequent sections, we examine some of the most prominent hypotheses concerning how and why these erroneous orientations might arise. For now, however, we turn our attention to another key component of the navigatory process that may also play an important role in vagrancy – the ability to measure how far you have travelled.

▲ Purple Sandpiper *Calidris maritima* and Surfbird *Calidris virgata*, Playa del Borrego, San Blas, Nayarit, Mexico, 17 January 2015. This, the second record of Purple Sandpiper for Mexico and the first from the Pacific coast of North America, was presumably a misorientated individual, although it may have followed the Surfbirds south from the Arctic (*Steve Howell*).

The avian clock – deciding when to stop migrating

If we imagine that our inexperienced young juvenile is successfully able to orientate in the migratory direction given by its inherited genetic program, the only other barrier to successfully completing its first migration (assuming a simple straight-line scenario) is to judge when it has moved far enough to have reached its wintering grounds. This aspect of migration is perhaps less well understood than the compass component, but it is highly relevant to the question of vagrancy. Failure to stop on the first migration could lead individuals to overshoot their normal winter ranges – a phenomenon explored in more detail in the overshooting section on page 46. Perhaps more importantly from a vagrancy perspective, the mechanisms involved in sensing when to stop migrating may play an important role in determining how far an individual were to move if, for some reason, it set off in the 'wrong' direction. Many vagrants appear to move much further than their normal migration distances, suggesting some degree of failure in judging when to stop and thus continuing their migratory restlessness longer than necessary. Knowledge of the stopping mechanism can help us understand this intriguing component of avian vagrancy, although current research has yet to give a definitive answer as to how birds determine how far to migrate in their first year.

One possible cue that migrants may use to judge when to cease migration is time itself. Most animals possess an internal clock, and in birds the clock sense is known to be particularly advanced, with the capacity to keep track of time at high precision across daily and annual cycles (Åkesson *et al.* 2017). Key evidence concerning the role of the internal clock in determining migration distance came from experimental studies using captive Garden Warblers *Sylvia borin* that were kept for a year in light-sealed laboratories where day length was kept constant at 12 hours, and temperature and other environmental factors were controlled (Gwinner & Wiltschko 1978). Birds kept in these conditions therefore had no way of tracking the changing seasons, other than through their own internal circannual clock. Amazingly, these birds showed exactly the same patterns of migratory restlessness as birds exposed to natural light and weather – they became highly active and agitated at night during the precise spring and autumn periods where migration normally takes place. Even more remarkably, the direction of migratory orientation (assessed using Emlen funnels) shifted during the autumn, matching the shift in orientation expressed during the real migration as Garden Warblers pass through the eastern Mediterranean before turning south into East Africa.

▲ Garden Warbler *Sylvia borin*, Foula, Shetland, Scotland, 5 June 2008, a tired migrant resting on sea cliffs (*James Gilroy*).

This experiment, and others like it, revealed that the cues to start and stop migration appear to be hard-coded into the endogenous clocks of birds – in turn, we might expect that a vagrant would cease migration at a similar time to others of its species (and in turn at a similar distance from the breeding range). However, further experiments using another species, European Pied Flycatcher *Ficedula hypoleucos*, revealed an added wrinkle: here the expected changes in migratory orientation only happened in the laboratory-controlled birds when they were exposed to changes in magnetic fields, mimicking the magnetic environment they would have been moving through if performing real migration (Beck & Wiltshko 1982). This result strongly suggested that changes in the migratory program – in this case the direction of orientation – arise not only due to the internal clock of the bird, but also require some external confirmation that the bird has reached the target area to make the change. In this case, that information comes in the form of magnetic conditions, which change dramatically in field intensity and inclination at lower latitudes. Other cues could also be used, including changes in day length or other environmental features. Interestingly, magnetic cues are also apparently important in triggering switches between restlessness and fattening behaviour (Henshaw *et al.* 2006), indicating that birds may use a magnetic 'map' to determine when they have reached a stopover region, and thus to cease migration and fatten up before the next stage.

Crucially, these findings suggest that for migrants to move between the multiple phases of their migratory programs, they may need some cue to indicate that they have moved the correct distance and are ready to initiate the next phase. Magnetic cues appear to be favoured for this – and at some point, a final 'stopping' cue may indicate that the final phase is completed, and the migration can end, the destination reached.

A vagrant bird that has moved off in the wrong direction, or been displaced by weather, might therefore never encounter the correct cue to move to the next phase of migration. Such birds could become 'trapped' in a phase of the program, continuing along a single orientation potentially for much longer distances than would occur if they had set out along the correct heading. Migratory programs like those of Pied Flycatcher therefore could lead to individuals moving far longer than normal for their species, if their initial heading takes them along the wrong route, and so preventing them from ever encountering their genetically encoded 'waypoints' – which would indicate when to change course or stop.

The use of migratory waypoints – magnetic field characteristics or other landscape features – is also central to the more advanced navigational abilities that apparently develop in adult birds after their first migration, allowing them to migrate with much finer precision to target locations (Alerstam 1978). The development of this mental map of waypoints apparently happens through the course of the first year of life and can involve a suite of different cues.

The avian map sense and 'true' navigation

A juvenile bird that is equipped only with a clock and compass cannot perform 'true' navigation – that is, it has no way of knowing its actual position relative to its goal, or to other waypoints around it during the course of its journey. Rather, a navigator using a clock and compass will blindly follow its set of instructions (in this case instinctive movement directions and timings) in the hope that these will lead it to the right place. A true navigator, on the other hand, will be able to keep track of its progress relative to other waypoints, and would be aware of any movement that takes it off course.

It is well known that many birds do indeed possess remarkable abilities to perform 'true' navigation – indeed, from ancient Egypt through to World War II, humans have taken advantage of this uncanny ability, pinning messages to the legs of pigeons that could be relied upon to return to specific locations from almost any starting point (Blechman 2007). Charles Darwin was one of the first to hypothesise on exactly how birds might do this – he suggested that they might have a capacity to memorise landscape features, and thus retrace an outward journey with precision (Darwin 1873). Since then, hundreds of scientists have explored this phenomenon, and thousands of experiments have been conducted to try to uncover how these feats are achieved. Despite this effort, however, much about the mechanics of 'true' navigation in birds remains a mystery.

One of the seminal works in the science of bird migration involved an experiment by Perdeck (1958) in the Netherlands, where he and his colleagues captured more than 11,000 migrating Common Starlings *Sturnus vulgaris* over the course of several years and shipped them via aeroplane to Switzerland – about 650km perpendicular to their normal NE to SW migration route. The aim of the experiment was to see whether the birds were able to detect this displacement, which effectively mimicked the impact of a strong side-wind, and adjust their migratory direction to get back onto the correct track. A bird equipped only with a clock and compass would not necessarily be able to do this, as detecting displacement would require having some frame of reference (i.e. a map) to know that your position had shifted relative to your goal. Their results showed unequivocally that juvenile Starlings failed to detect and adjust for their displacement – they continued to migrate in a southwesterly direction from Switzerland, heading toward Spain. Adult Starlings, however, were able to adjust their orientation to the north-west, and many migrated back toward their 'intended' wintering sites in north-west Europe. This was the first study to establish the capacity for 'true' navigation in a wild migratory bird – in other words, the ability to accurately assess their position relative to a goal – and also to demonstrate that this capacity comes only with age.

◄ Masked Wagtail *Motacilla alba personata*, Camrose, Pembrokeshire, Wales, 30 November 2016. This, the first British and fourth European record of this Asian subspecies in the White Wagtail complex, was thousands of kilometres out of range (*Chris Batty*).

The development of a navigational map sense has been studied in most detail in homing pigeons, where studies have revealed a complex and multifaceted process that individual pigeons use to build up maps of their world with which to navigate. It appears that these maps are formed by birds memorising gradients in environmental features, with intersections between these gradients acting like spatial waypoints to help birds triangulate their position in space (Cherntsov *et al.* 2017). The actual cues they use to build these gradients are still subject to debate, although there is now some conclusive evidence that a key part of the gradient map is magnetic intensity. Pigeons appear to be highly sensitive to variations in the intensity of the magnetic field in space – and these variations, caused by features of Earth's geography, may be fairly stable over time and allow birds to build up a 'magnetic map' of areas they have explored in relatively fine detail. Magnetic maps have since been detected among adults of many other migratory species (Cherntsov *et al.* 2017), suggesting that the magnetic field is extremely important not only for the avian compass sense, but also for mapping out the world around them.

Intriguingly, there is considerable evidence to suggest that another important component of the mental maps birds generate involves their sense of smell. Experiments with pigeons have pointed strongly towards this – with pigeons experimentally deprived of the sense of smell being consistently disoriented when released at unfamiliar sites. More surprisingly, a recent experiment demonstrated a similar phenomenon in adult Grey Catbirds *Dumetella carolinensis* (Holland *et al.* 2009). Researchers trapped a number of these birds and subjected some of them to a zinc sulphate treatment that removed their sense of smell. After flying the birds 1,000km east from Illinois to Princeton, they radio-tracked the birds from a light aircraft and found that their untreated control birds were able to correct for displacement and return to their appropriate heading, whilst the smell-deprived birds could not (Holland *et al.* 2009). Another study recently found that both the visual and olfactory areas of the brain become more active at night during the migratory period, while they are most active during the day when birds are not migrating (Rastogi *et al.* 2011). This again suggests that smell may play an important role in migration, at least in experienced adults that have been able to map out a 'smell-scape' over the course of their previous movements. Disruption to the olfactory sense, for example through exposure to pathogens, or exposure to abnormal smells, could therefore plausibly play a role in driving vagrancy in some birds, especially adults.

▲ Whooper Swans *Cygnus cygnus*, Fair Isle, Shetland, Scotland, 5 October 2018. The crashing of waves on Fair Isle's cliffs may have been audible to this group of Whooper Swans arriving from Iceland long before the cliffs themselves came into sight (*Alexander Lees).*

A final feature that may form part of the avian map sense is sound – and more specifically, the spectrum of low sounds known as 'infrasound', which can be audible over hundreds if not thousands of kilometres. Researchers have hypothesised that birds could use stable geographic sources of infrasound as navigational cues – for example, deep sounds generated by waves along a rocky oceanic coastline, or wind-scraping sounds along rugged mountain ranges. The remarkable capacity for oceanic islands to attract vagrants could thus in part be explained by birds orientating towards the sound of waves breaking on the island shore. Direct evidence for navigation using sound has so far largely been limited to studies of pigeons, whose homing performance can be severely disrupted by infrasound disturbance, including the frequent disruption of pigeon races by sonic booms of aircraft (Hagstrum 2000). However, an experiment that removed the cochlea of homing pigeons did not produce any deficits in homing performance (Wallraff 1972). This suggests that while infrasound can clearly be part of the map sense, it is perhaps not a central component.

An important question in the context of vagrancy – if adult birds typically possess such a finely-tuned mental map of their world – is why some adult birds still end up as vagrants? One possibility is that some birds reach adulthood without managing to accurately internalise a working map during their developmental years. There are likely to be significant cognitive challenges involved in this complex feat, and it is perhaps inevitable that some individuals fail to build an accurate working map during their first migration, particularly if they undergo spells of disorientation due to poor weather, or other factors that might interrupt their ability to perceive key gradients. Birds migrating during solar flares, for example, might see considerable interruptions to the magnetic field, scrambling or confusing their ability to map out stable patterns of magnetic intensity. Another intriguing possibility is that exposure to disease might inhibit the development of the map sense – migratory birds are almost uniquely susceptible to exposure to new pathogens as they move around the world, and therefore may be highly prone to conditions that might inhibit their senses – particularly the ability to detect olfactory cues.

Another important facet of the map sense to recognise is that it is likely to be built around a combination of environmental gradients and 'beacons' that an individual has mapped out through direct experience. The map might therefore cease to be useful if weather displaces the bird outside the zone it has previously inhabited. Whilst adult birds are often able to compensate for wind drift, they can only do this when winds are relatively light – strong winds may still see them drifted for large distances (see page 36). If this drift pushes an adult bird into a new region outside its experience-based map, its ability to navigate may be seriously compromised. Once outside the realm of their internal map, such birds may be forced to revert to their innate clock-and-compass program of navigation – this would allow them to resume a normal migration heading after the drift event, but they would still be moving outside their normal migratory range. Alternatively, displacement outside the map-zone could lead individuals to make more significant navigatory errors, particularly if they attempt to orientate using the cues that form their internal map sense (e.g. olfactory cues or infrasound). For a bird displaced by winds to a new area, these cues might place a bird on a very different heading than it would have followed prior to displacement.

Another interesting wrinkle concerning the avian map sense relates to species that perform a loop migration, whereby the autumn migration route differs from that taken in the subsequent spring. Many species migrating between Europe and Africa perform looped routes – tracking studies of Common Cuckoos *Cuculus canorus*, for example, revealed that birds from central Europe take a very specific and circuitous route through western Africa during their southbound migration but follow a much more direct trans-Saharan route when returning in spring (Willemoies *et al.* 2014). For these species, the mental map developed during the autumn migration would be of little use in the following spring, as the return migration would not pass through the same regions – any waypoints or mapped gradients they have internalised would be irrelevant. The first spring migration must therefore be completed using the same error-prone clock and compass mechanism used in the first autumn. An interesting prediction from this is that spring vagrancy may be more prevalent in species that perform a loop migration, compared to equivalent species that retrace their autumn route the following spring – the latter would be able to navigate using their experience-based map sense and thus may be less prone to navigational errors, as well as more able to control for wind drift. To our knowledge, this prediction has yet to be empirically tested.

Finally, it is also worth noting that our broad generalisation of true navigational abilities being present in adult birds but not juveniles may in fact be far from clear-cut. There is compelling evidence that in some long-distance migrant species, juveniles do indeed show compensatory behaviour after being experimentally displaced, suggesting that they have some sense of where they have been moved to, relative to their previous position (Åkesson *et al.* 2005; Thorup & Rabøl 2007). Perhaps more compellingly, some of the migration routes undertaken by juveniles would appear simply impossible without some sense of where the individual is relative to its goal (i.e. a true map sense) – examples include species such as Marsh Warbler *Acrocephalus palustris,* which spread out over large areas of Eastern Africa during their southbound migration but later converge into narrowly defined routes, suggesting birds were aware they had reached some form of waypoint that triggers a complex and directed switch in orientation (Thorup & Rabøl 2001). For juvenile birds to perform such migrations alone, this implies that some form of innate map sense may be genetically encoded in the migratory program of these species, beyond the simple clock-and-compass program that is usually assumed.

◄ Marsh Warbler *Acrocepalus palustris*, Moscow, Russia, July 2007. The circuitous migratory route of this species across Africa involves multiple changes in orientation – the fact that inexperienced juveniles can navigate this successfully suggests they may be able to track their progress using an innate 'mental map', perhaps based on geomagnetic cues (*James Gilroy*).

VAGRANCY THROUGH COMPASS ERRORS

It is understandable that laypeople frequently assume that vagrant birds are usually ‘blown off course’ by adverse weather, but even the most cursory analysis reveals that a significant proportion of long-range vagrancy events cannot be explained by exogenous factors like winds alone. Vagrancy events are near constant, global and often entirely uncorrelated with weather patterns, indicating that there are invariably other factors at play – and indeed it is likely that most incidences of long-distance vagrancy are driven by factors that are endogenous to the birds themselves. Failures in the compass system are perhaps the most obvious and pervasive mechanism that could cause birds to stray from their normal ranges – even humans equipped with satellite GPS can still find navigation difficult and frequently get lost! It is therefore unsurprising that birds, especially inexperienced juveniles, commonly get their navigation wrong. And if embarking on a journey that spans continents, as many migratory birds do, even a small error in your initial bearing can lead to a very big error when the miles start to accumulate.

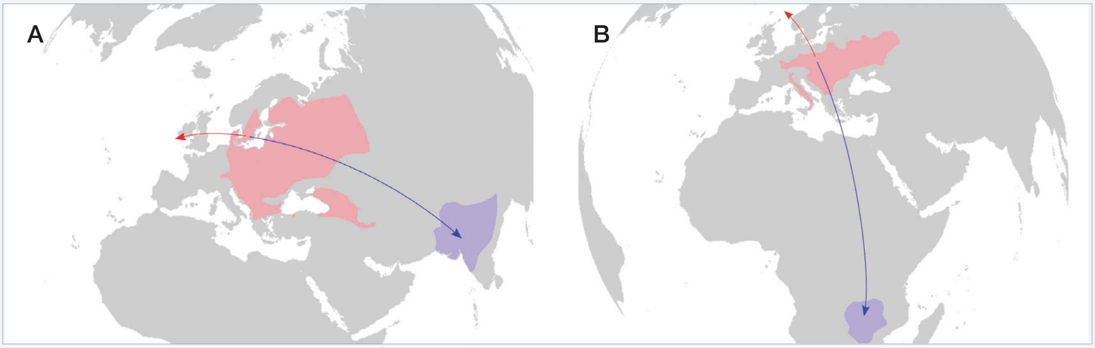
Many previous authors have considered the types of compass errors that might explain the patterns of vagrancy we observe, and several key candidates are often invoked – most prominently the associated phenomena of ‘reverse migration’ and ‘mirror-image misorientation’. Whilst these two candidate mechanisms should feature prominently in any analysis of vagrancy causes, in reality they form part of a far broader spectrum of errors that could arise from the hierarchy of navigational tools that birds use. In this section, we will examine vagrancy scenarios arising from these errors, and consider their relative likelihood in light of recent research on the nature and mechanisms of avian navigation. To begin, we will focus on the mechanism that has arguably received most attention from scholars of vagrancy worldwide and is sometimes invoked as a blanket explanation for vagrancy among inexperienced migratory birds: reverse migration.

Reverse migration as a cause of vagrancy

When a migrating bird sets out on a migratory flight solo, it must make a decision about which direction to fly in, and subsequently ensure that it continues in that direction for the duration of the flight. Two steps are involved in this process – the first is to identify a reference point on the compass (i.e. north), and the second is to angle itself correctly with respect to that reference point, such that it is facing its genetically determined migratory direction (see page 9). In other words, a bird must ‘think’ something along the lines of “*OK, I know that north is that way, and I need to point myself 55 degrees to the right of north*”. Mistaking south for north in step 1 – a simple error to make – would therefore lead our bird to migrate in the opposite direction to its innate heading, assuming it applied step 2 correctly with respect to this erroneous reference point. If the bird made this same error consistently throughout each migratory hop, the result would be a full reversal of its normal migration route.

► Red-breasted Flycatcher *Ficedula parva*, East Hills, Holkham NNR, Norfolk, England, 16 September 2009, a scarce passage migrant to the British Isles whose regular arrival in autumn many authors have attributed to reverse migration (*Alexander Lees*).

There is reasonable evidence that this form of reverse migration – i.e. individuals consistently mistaking north for south each time they check their migratory orientation – is a potentially significant cause of vagrancy, particularly among juveniles in their first migration. Patterns of relative abundance for vagrant species can often be explained reasonably well by models that assume reverse migration to be the principal causal mechanism of vagrancy – most classically, the occurrence of Siberian passerine migrants in north-west Europe each autumn (Thorup 1998). In the European context, a seminal example was put forward by Cottridge & Vinicombe (1996) involving the autumn occurrence patterns of two closely-related flycatcher species – Red-breasted Flycatcher *Ficedula parva* and Collared Flycatcher *Ficedula albicollis*. Both species breed in the temperate forests of central and eastern Europe, but they have very different migratory routes and wintering grounds. European populations of Red-breasted Flycatcher migrate south-eastwards in autumn to reach wintering grounds in southern Asia, whilst Collared Flycatchers from the same breeding regions migrate broadly due south to winter in East Africa. A reversal of the latter's migration route would take vagrants into eastern parts of Scandinavia and Russia but would be unlikely to carry them to north-west Europe (Figure 4). For the former, however, a reversed route would see individuals moving north-west towards the British Isles (Figure 4). As predicted under reverse migration theory, Collared Flycatcher is practically unknown in the British Isles in autumn, whereas Red-breasted Flycatcher is a frequent visitor with dozens or even hundreds recorded annually.



▲ **Figure 4.** Reverse migration routes (red) and normal migration routes (blue) for Red-breasted Flycatcher *Ficedula parva* (A) and Collared Flycatcher *Ficedula albicollis* (B). Only the former is a regular autumn vagrant to the British Isles.

Many other patterns appear to fit well with the reverse migration model. At vagrancy hotspots in Alaska, numerous frequently occurring autumn Siberian vagrants appear to be following direct reversals of their normal migratory routes from breeding areas in eastern Siberia and Kamchatka towards Indochina (Howell *et al.* 2014). The roll-call of autumn Old World vagrants to Japan and the Pribilof and Aleutian Islands of Alaska is long. It includes numerous species that would seem at face value extremely unlikely ever to reach the Pacific – including such species as Spotted Flycatcher *Muscicapa striata*, Wood Warbler *Phylloscopus sibilatrix* and Sedge Warbler *Acrocephalus schoenobaenus* which are largely restricted to western Eurasia as breeders, with wintering quarters exclusively in Africa. Despite the apparent remoteness of their ranges from the north-west Pacific, a reversal of the expected migration route from their westernmost breeding populations would indeed bring birds directly to the Bering Sea islands (Howell *et al.* 2014).

Given the apparent power of the reverse migration model to explain patterns of autumn vagrancy, it is interesting to consider just how such an error might arise. Clearly, reverse migration would involve mistaking north for south – effectively reading the compass upside down. As explained in the previous section, however, even naive juveniles should have between two and four different compass mechanisms at their disposal, each of which should be available to act as a fail-safe against erroneous readings from the others. If birds have multiple different sources of information at hand to help them find north and south – why is it that some birds apparently make this same consistent error, time and again, across all these compass sources?

One potential answer to this question may come from studies examining the way birds respond when their various different compass mechanisms each give conflicting indications of where north is. Experiments with caged birds show that exposing a young bird to conflicting signals – for example, a misaligned magnetic field alongside the correct star map for their location usually leads to birds focusing on one compass sense as a 'default' and ignoring the others (Muheim *et al.* 2006). Prior to the start of migration, it appears that this default

► Wood Warbler *Phylloscopus sibilatrix*, Gongendo Park, Satte, Saitama, Japan, 29 Oct 2016 – a major rarity in the Eastern Palearctic and candidate 'reverse migrant' (*Yann Muzika*).

is usually the star compass, but once birds start moving, they switch to trusting the magnetic compass above the others. A bird that has some fundamental problem with its magnetic compass could therefore consistently make compass errors throughout its migration, as it would inevitably get strongly conflicting indications from its different compass senses and would instinctively default to the erroneous magnetic sense every time it takes flight. Interestingly, there are further lines of evidence to suggest that the magnetic compass may play a particularly important role in causing reverse migration. As described in the previous section, the magnetic compass functions by birds 'viewing' the magnetic field around them using specialised structures in their retina (and/or magnetic particles in other sensory organs). This field 'flows' between the north and south magnetic poles, forming lines that are apparently visible in almost all conditions except complete darkness (Ritz *et al.* 2009). However, at any given moment, it may not be so obvious to the bird which 'end' of the magnetic line points towards the pole, and which points to the Equator. To determine this, a bird must evaluate the angle of the lines with respect to Earth's surface, and calculate the point where the lines 'dip' towards the horizon, rather than incline away from it (Ritz *et al.* 2009) – this being the poleward direction. Errors made in evaluating this dip angle could cause individuals to mistake north for south – and they may plausibly then do this consistently throughout migration (Muheim *et al.* 2006).

Another possible explanation for reverse migration relates to the way that the migratory program is encoded in young birds genetically. It is likely that this program must contain navigatory instructions for both the autumn migration and that of the subsequent spring. One possibility is that some individuals erroneously follow the migratory program for the wrong season, following the innate bearing that would be appropriate for their spring migration. These birds are therefore able to correctly read their various compasses, but they end up following the wrong innate heading for the season they are in (Pfeifer *et al.* 2007). Such an error would lead to reverse migration, provided that the innately encoded spring migration route of the species directly retraces that of the autumn. Many species follow a loop migration, however, whereby a different route is used in spring – such species might therefore follow a very different route than a reversal of their expected autumn migration under this hypothetical mechanism.

We can propose one further possible explanation for reverse migration, this time relating to another facet of avian migration that is quite commonplace, but seldom considered as a potential cause of long-distance vagrancy: the short-term reversal of orientation that birds often make in response to adverse weather. This phenomenon is often noted at migration hotspots worldwide, where in some conditions very large numbers of migrants appear to move *en masse* in the 'wrong' direction (Shamoun-Baranes & van Gasteren 2011). Usually, these events correspond with conditions that are unsuitable for onward migration; periods of very cold weather in spring, for example, often result in significant reverse flights of migratory birds in northern Europe (Lindström & Alerstam 1986). Radar studies have further confirmed the size and frequency of these events, with mass reversals often resulting in huge numbers of migratory birds temporarily moving 'backwards' along their normal route after encountering bad weather (Shamoun-Baranes & van Gasteren 2011).

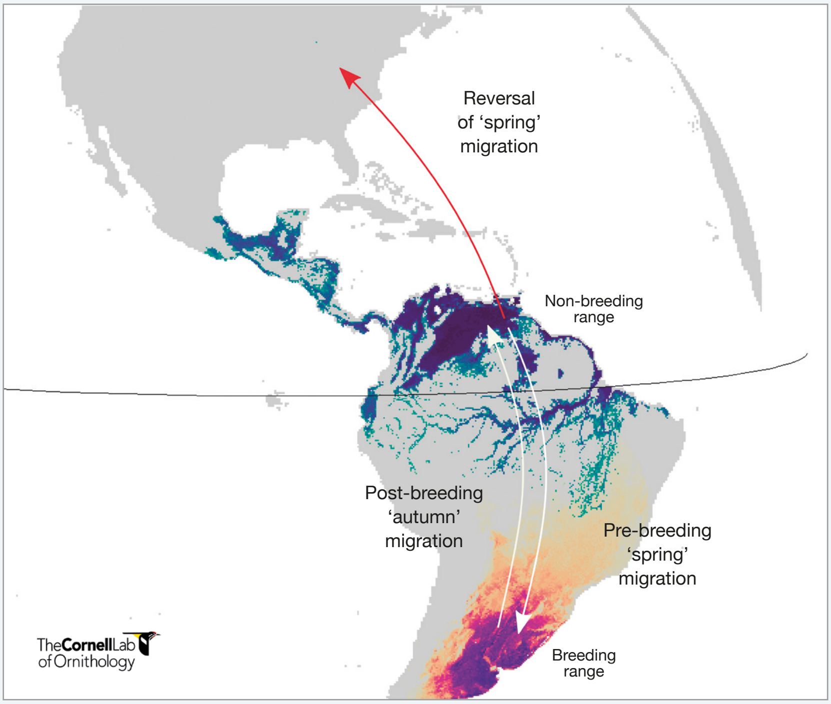
These mass reverse flights are unlikely to lead to vagrancy by themselves – radio tracking suggests that such reverse flights are usually short-lived, with individuals moving tens to hundreds of kilometres backwards before stopping to rest and feed, prior to continuing in the correct direction once conditions improve (Nilsson & Sjöberg 2016). One intriguing possibility, however, is that the behavioural mechanism that underpins short-term reversal is also at play in driving vagrancy through sustained reverse migration. Several studies have shown that short-term reversal is strongly linked to the condition of the bird – birds in lean condition are far more likely to exhibit temporary reversed orientation than birds carrying fat reserves (Deutschlander & Mulhelm 2009). This suggests a strong innate response in migrants that run low on energy reserves, where a certain trigger causes them to switch their migratory orientation 180 degrees and 'back-track', helping them find better feeding conditions and avoid competition in coastal areas where large numbers of migrants may be grounded. Responses such as this are often referred to as 'reaction norms' – when a particular cue (weather conditions or body fat) reaches a certain level, a reaction is triggered – in this case the migratory orientation switches by 180 degrees. It is plausible that some individuals might become trapped in this reaction state, with their orientation system effectively stuck in reverse, even if the conditions that triggered the reaction return to normal. Such a scenario could hypothetically explain why some individuals consistently follow a reverse heading, despite having multiple compasses as fail-safes and multiple opportunities to detect their orientation error throughout the course of a migration.

Reverse migration in spring

Reverse migration is commonly invoked as a cause of vagrancy during autumn migration, but there is also compelling evidence that the same phenomenon can occur among individuals making their return migration in spring. Apparent examples of this phenomenon include the appearance of numerous Palearctic-Afrotropical migrants as vagrants in South Africa or even on subantarctic islands in the northern hemisphere spring, when birds should be returning northwards to their breeding grounds. A study of vagrant passerines on Marion and Prince Edward Islands in the far south of the Indian Ocean revealed remarkable records of many Eurasian species such as Barn Swallow *Hirundo rustica*, Common Whitethroat *Sylvia communis* and Willow Warbler *Phylloscopus trochilus*, with individuals often reaching this remote archipelago during the months of April and May (Oosthuizen *et al.* 2009). The trajectory of these birds is consistent with a reversal of the correct spring migration route from their wintering grounds. The frequent occurrence of Siberian vagrants on islands off northern Australia during the northern hemisphere spring might also fit this pattern (Clarke *et al.* 2016). Birders have recently uncovered a number of vagrancy hotspots, such as Ashmore Reef, Queensland, Australia, where it may be possible to find many Siberian species that normally winter in equatorial South-east Asia but have apparently reversed their northbound migration in spring to find themselves moving deep into the Southern Hemisphere. There is, however, also the possibility that some may have wintered further south in Australia and are being detected returning north, rather than heading south. The pattern of spring occurrence of several New World warblers (family Parulidae) and other Nearctic migrants in southern South America is also potentially an example of this phenomenon.

◄ Citrine Wagtail *Motacilla citreola*, Strandfontein WTP, Western Cape, South Africa, 27 April 2015. This, the fourth record for South Africa, may be a spring 'reverse migrant' that has wintered further north in Africa and erroneously migrated south on its return migration (*Niall Perrins*).

This pattern raises an interesting conundrum: whilst reverse migration appears to be the cause of these spring vagrancy events, it must also be the case that these individuals were able to orientate correctly southwards in their first migration – and hence reach their correct winter ranges – only to lose their capacity to tell north from south in the return stage. Why would this occur? One possible explanation again relates to the use of the magnetic compass and how this compass operates with respect to the Equator. As previously mentioned, that the avian magnetic compass does not function in the same way as a human compass – it indicates only the difference between polewards and Equator-wards, and does not actually identify north or south *per se*. When a bird crosses the Equator from north to south, the magnetic compass will become temporarily unreadable as the lines of magnetic field are extremely slight at very low latitudes. Moving further into the Southern Hemisphere, however, when the compass becomes readable again, it would be 'flipped' such that the lines of inclination now point towards the South Pole. To account for this change, the bird must be aware of the fact that it has crossed the Equator and be able to adjust for the fact that its magnetic inclination compass now points towards south rather than north. Any individual that then winters the opposite side of the Equator from its breeding range, but fails to mentally account for the fact that its magnetic compass has flipped, would then automatically mistake south for north in subsequent attempts to orientate.



◄ **Figure 5.** Autumn vagrancy of Fork-tailed Flycatcher *Tyrannus savana* to North America by the migratory subspecies *savana* could be explained by reverse migration of the 'spring' leg of their austral migration (red arrow). This mechanism assumes that the birds in question navigate correctly on their first migration northwards but mistake north for south on the return journey – perhaps because they fail to compensate for the magnetic 'flip' that occurs when crossing the Equator. Abundance data from eBird Status and Trends provided by the Cornell Lab of Ornithology (Fink *et al*. 2020).

Clearly, birds could use other compass senses (Sun or star cues) to detect and adjust for this magnetic flip but, as previously described, these other mechanisms all require some degree of learning and are vulnerable to disruption by weather patterns. Many inexperienced juveniles might default to the magnetic compass during their first migration, and might therefore be vulnerable to navigating erroneously with a flipped magnetic compass after crossing the Equator. The same mechanism of spring reverse migration has been invoked as an explanation for the frequent occurrence of Fork-tailed Flycatcher *Tyrannus savana* and other South American austral migrants in North America (Howell *et al.* 2014). Occurrences of this species tend to peak in August–November, corresponding with 'spring' in the biological calendar of this austral migrant species. Reverse migration offers a convincing explanation for their occurrence, but again this relies on an assumption that these birds completed their first migration correctly, navigating from breeding areas in southern South America to spend their winter close to the Equator (Figure 5). In the austral spring (autumn in the Northern Hemisphere), birds that had crossed into the Northern Hemisphere would then need to correct for the fact that their magnetic compass now identifies north rather than south – any individuals that fail to recognise this change might perform a reverse spring migration to North America, if they were to rely solely on their magnetic compass.

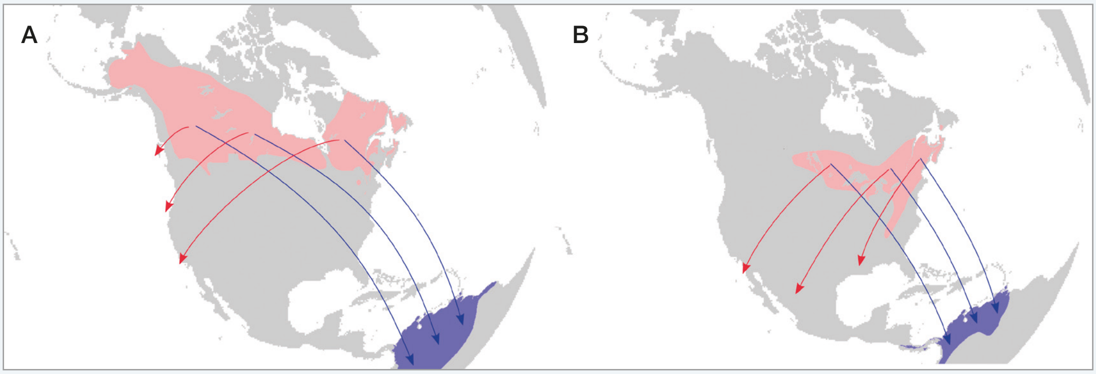
◄ Fork-tailed Flycatcher *Tyrannus savana*, Pointe-Lebel, Manicouagan, Quebec, Canada, 14 October 2017. Appearing in Canada in October, this individual may have wintered successfully in northern South America, but instead of heading back south it has ventured north and ended up at least 7,000km away from the breeding areas of the migratory nominate subspecies in central Brazil (*Ian Davies*).

Mirror-image misorientation

As noted above, in order to orientate correctly using its internal compass, a bird must complete two steps – the first being to identify a reference point (north), and the second to rotate itself to the correct angle with respect to this reference point. Mirror-image misorientation can theoretically arise when a bird gets the first step correct (i.e. it identifies north and south) but then mistakes left for right when pivoting its body with respect to this compass reference point.

This mechanism was first proposed as a cause of vagrancy by De Sante during his studies of the annual appearance of migrants from eastern North America at vagrant hotspots in coastal California (de Sante 1973). De Sante observed that the relative abundance of some species, most notably eastern boreal migrants that normally migrate south-east along the Atlantic seaboard in autumn, could not be explained by weather patterns alone. In particular, the relative abundance of different eastern vagrant species in California was not straight-

◄ Blackpoll Warbler *Setophaga striata*, Cordell Bank pelagic, California, United States, 9 September 2008. This individual, which boarded a boat well offshore, seems to be on an orientation destined to take it to a watery Pacific grave (*Steve Howell*).



▲ **Figure 6.** Mirror-image routes (red) and normal migration routes (blue) of Blackpoll Warbler *Setophaga striata* (left) and Blackburnian Warbler *Setophaga fusca* (right). The higher relative frequency of the former as an autumn vagrant to California could be explained by mirror-image misorientation, although many other factors are also likely to be at play.

forward to explain in simple terms of population size, and it appeared to be related to migration routes. For example, one of the most frequent autumn vagrants to the region is Blackpoll Warbler *Setophaga striata*, a species that breeds abundantly in boreal forests across North America but migrates almost exclusively along the eastern North American coast in autumn. Populations at the western extreme of the breeding range must therefore initially follow an eastward orientation, a mirror image of which would bring birds directly to California (and other points along the Pacific coastline) (Figure 6). It is interesting to contrast this with another abundant boreal breeder – Blackburnian Warbler *Setophaga fusca* – a species with a similar migration but a breeding range that does not extend so far west across the North American continent. A mirror image of the autumn orientation for westernmost populations of Blackburnian Warbler would only take vagrant individuals as far west as New Mexico (Figure 6), with a low likelihood of bringing them to California. As predicted by the theory, Blackburnian Warbler is one of the rarer autumn vagrants in the state, outnumbered by Blackpoll Warblers more than 20 to 1 (although it is important to recognise that Blackpoll Warbler also has a far larger population size and breeds much closer to California than Blackburnian Warbler).

Further tentative support for the mirror-image orientation hypothesis came from tests carried out on vagrant Blackpoll Warblers trapped for ringing in California. Measurements of their overnight migratory orientation showed a mix of individuals showing both the 'normal' south-eastward orientation and its mirror image (De Sante 1973) – suggesting that at least some individuals were indeed fitting the expected pattern of misorientation. It is difficult to know how much to read into the apparent mixture of orientations shown by these tested birds, as the sample size was small. One possible explanation, however, is that individuals may not make the mirror image error consistently every time they attempt to orientate. In other words, their compass is not

► Tree Pipit *Anthus trivialis*, Hegurajima Island, Ishikawa, Japan, 23 April 2019. This vagrant to Japan might conceivably fit the pattern of mirror image misorientation (*Yann Muzika*).

inherently 'flipped', but when attempting to orientate ahead of any given flight, they may sometimes pivot the correct way, and at other times get it wrong. Such a mixture of mirror-image and correct orientations over the course of a migration could carry birds on a wide variety of possible route deviations, and hence give rise to a plethora of different vagrancy outcomes.

Compass errors and the axis of migration

A statistical analysis by Thorup (2004) found strong evidence that the frequency of vagrants within 'reverse migration shadows' in Northern Europe was far greater among species that migrate in an easterly or south-easterly direction in autumn (e.g. from Eastern Europe to South Asia) relative to species that migrate primarily north–south (e.g. from southern Europe to Africa). The seminal example of reverse migration described above, involving Red-breasted and Collared Flycatchers, also illustrates this pattern quite neatly – the west–east migrating Red-breasted Flycatcher is a common autumn vagrant within its reverse migration shadow in Western Europe, but the north–south migrating Collared Flycatcher remains extremely rare even in the zone covered by a reversal of its migration in Scandinavia (Figure 4).

What might explain this link between east–west migration and the likelihood of individuals making significant compass errors on their first migration? One possible explanation is that this simply reflects the relative difficulty of making orientation decisions when the desired direction deviates significantly from either north or south. If we recall our model of how a bird uses its compass to orientate, this involves locating north and then pivoting by a certain amount to ensure the bird is pointing in the correct direction. It is possible that the further a bird has to pivot from its north–south reference, the greater the likelihood it will become confused and/or unable to keep track of where north is. This seems particularly likely in the case of birds orientating using the magnetic compass, which as described above requires birds to evaluate the angle of dip in the lines of magnetic field visible in the sky above them. When a bird has to orientate itself horizontally with respect to these lines (which is the case when moving east or west), evaluating which way they dip may be more difficult than for when a bird's desired orientation is closer to the angle of the lines themselves.

Another possible explanation for the link between east–west migration and misorientation relates to the pattern of variation in magnetic fields across regions – and in particular the region of Siberia where many vagrants to Europe originate. Across Siberia there is a strong gradient in the pattern of magnetic declination – i.e. how different the apparent direction of magnetic north is from true north. A juvenile bird traversing the steepest part of this gradient from west to east would see marked shifts in the apparent direction of magnetic north from one day to the next. One possibility is that these frequent shifts could cause confusion and disorientation, increasing the chances that individuals will make a significant error like mistaking north for south. Furthermore, if the bird was attempting to calibrate its magnetic compass using other compass cues, such as the pattern of polarised light at sunset (as has been shown in some species), the angle of calibration would have to change significantly from day to day as the lines of the magnetic field shift. Potentially, this further increases the chances of confusion. Given that huge numbers of birds successfully complete these east–west migrations each year, it is clear that most individuals have the capacity to navigate these shifting fields in one way or another. Nevertheless, the apparent predisposition towards misorientation in some Siberian species could well be related to the significant variability in magnetic fields across the east–west gradient in that region.

Magnetic anomalies

The reverse migration and mirror-image hypotheses both involve large-scale errors made when individuals 'read' their internal compass – i.e. mistaking north for south, or left for right. As such, both hypotheses assume that the bird in question possesses some form of 'working' compass (i.e. a mechanism for consistently identifying north from south) but that they 'read' this compass incorrectly. Another possible explanation for navigational errors is that some individuals may lack the capacity to correctly discern any compass heading at all – in other words, they entirely lack a functioning compass. In the case of the magnetic compass, this could plausibly arise due to local-scale anomalies in the magnetic field associated with the properties of underlying bedrock.

As described in the previous section, three of the four avian compass mechanisms require some degree of learning during early life in order to be used effectively – a high-precision clock sense is needed to use the Sun or polarisation compasses, and the patterns of stars around the point of polar rotation must be learned in order to use the celestial compass. Particularly among long-distance migrants, it is easy to imagine a scenario where a late-fledged individual might have insufficient time – and in particular insufficient windows of clear weather – to

► Siberian Accentor *Prunella montanella*, Mossy Hill, Shetland, Scotland, 10 October 2016, the first British record of an unprecedented westward incursion by this species in 2016 (*Stuart Piner*).

properly develop the use of these compasses prior to embarking on migration. Such an individual would likely rely almost entirely on their magnetic compass to navigate, as this is generally assumed to function without any need for learning, or any set of weather conditions. It may not function correctly, however, in areas of significant magnetic anomaly (Winklhofer *et al.* 2013).

Experiments with homing pigeons and other species have repeatedly shown that they can become disorientated when passing over magnetic anomalies – and in particular zones with significantly higher or lower magnetic intensity than their surroundings (Wiltschko & Wiltschko 2005). Such anomalous zones tend to be quite concentrated in space – perhaps a few kilometres in diameter – and therefore a bird passing over such an area during migration should become disorientated only briefly, before subsequently re-finding its correct heading after moving away. A juvenile migratory bird that is hatched within such an anomaly, however, could plausibly develop a very different magnetic compass sense than birds fledging in surrounding areas. Importantly, experimental evidence from pigeons suggests that the magnetic sense is ‘tuned’ to a narrow band of magnetic intensity around that experienced by a bird in early life (Winklhofer *et al.* 2013). This means that a bird fledged within a magnetic anomaly zone may struggle to orientate correctly once it moves out into areas with more normal magnetic conditions, as its compass is tuned to the unusual pattern of intensity of its natal area. Experiments suggest that birds can re-tune their compass to new intensities, but this takes many days to achieve, and may not be possible if the differences are very stark (Winklhofer *et al.* 2013).

► Pechora Pipit *Anthus gustavi*, Gambell, Nome, Alaska, United States, 26 August 2004, a predictable species at vagrant traps in northern Europe and the Bering Sea region; it breeds at high northern latitudes overlapping areas with magnetic anomalies (*Brian Sullivan*).

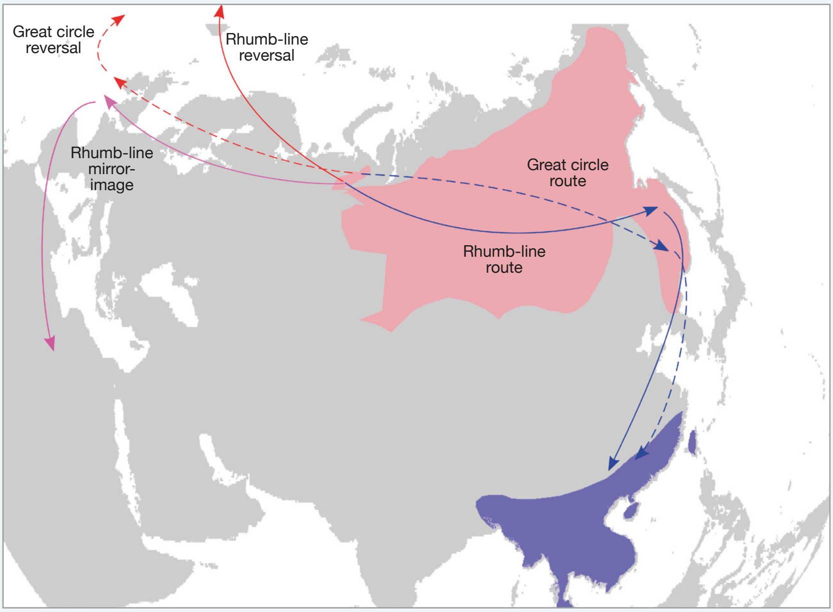
It is possible to consider a set of 'perfect storm' circumstances for a juvenile bird originating from within such an anomaly. If such a bird fledged late in the season, it may not have had sufficient opportunities to properly learn its star map or Sun compass and would therefore need to rely solely on its magnetic compass. Upon commencing migration, however, the bird would move out of the anomalous zone and immediately lose its ability to correctly orientate using its one fully functional compass. Such a bird might become completely disorientated, and potentially follow a random heading on its subsequent migratory flights – potentially ending up almost anywhere within the plausible flight range of the species. Such a scenario may seem unlikely, but when we consider the tens of millions of migratory birds that fledge each year, it is likely that circumstances such as these happen quite frequently. Perhaps most tellingly, one of the regions known to have some of the strongest local magnetic anomalies worldwide is western Siberia (Alerstam 1990), a region supporting a suite of species that are well-known for long-distance vagrancy to both Europe and North America.

Limitations to the reverse migration and mirror-image hypotheses

Although the reverse migration and mirror-image hypotheses can apparently explain some broad patterns of vagrant occurrence around the world, many other patterns are hard to reconcile with either model. Consider the example of an archetypal Siberian vagrant to Europe, and one that is often seen as a classic example of a reverse migrant – Yellow-browed Warbler *Phylloscopus inornatus* (Cottridge & Vinicombe 1996, Thorup 2004). This species breeds across Siberia, reaching its western limit in the Ural mountain range, and it winters in South-east Asia. Numbers of vagrant individuals in Western Europe have increased markedly in recent years, and the species is now a relatively frequent sight in late autumn at migration hotspots along the Atlantic seaboard.

Interestingly, tests of the migratory orientation of vagrant Yellow-browed Warblers trapped on the Faroe Islands suggested that these birds were predominantly migrating along west or south-westerly headings, on a route that would likely see them either reach Iberia or perish in the Atlantic (Thorup *et al.* 2012). Thorup *et al.* (2012) hypothesised that these patterns could be explained by Yellow-browed Warblers following a 'great circle' route in reverse and failing to make the expected switch in orientation that would normally happen when birds reach the Pacific Coast – a reversal of the southward switch normally made would carry reverse-migrating birds northwards towards the pole (Figure 7). However, there is scant evidence that juveniles of any species are capable of navigating along great circles, as this is a complex feat requiring constant adjustments of orientation to maintain the correct course (Åkesson & Hedenström 2007). Rather, evidence suggests that migrants usually follow a single directional bearing for each leg of the journey (Åkesson & Hedenström 2007), resulting in a 'rhumb line' rather than a great circle route. Interestingly, reversal of a rhumb-line route does not carry Yellow-browed Warblers as far as the British Isles but rather tracks much further north towards the Arctic (Figure 7).

◄ Red-flanked Bluetail *Tarsiger cyanurus*, North Ronaldsay, Orkney, Scotland, 26 September 2008, now a routine autumn vagrant to Western Europe, which seems to be associated with its concurrent westward range expansion (*Alexander Lees*).



► **Figure 7.** Reversal and mirror-image migration trajectories of Yellow-browed Warblers *Phylloscopus inornatus* from the western range extent. Reverse migration (red) along a great circle route (dashed line) could explain the frequency of the species in western Europe, but there is scant evidence that any young birds are capable of great circle navigation. Rhumb-line navigation is more likely, but reversal of this would send birds north of the British Isles. Mirror-image misorientation of a rhumb-line heading is perhaps more plausible, but we would expect then to see more birds reorienting through the eastern Mediterranean in late autumn.

However, thousands of Yellow-browed Warblers are now recorded annually in the British Isles in autumn, with a clear seasonal pattern of initial arrivals in the north and a gradual filtering south-west (de Juana 2008). The species also appears in considerable numbers in Iberia during late autumn, some weeks after the peak of abundance in the British Isles and Scandinavia, again suggesting the birds are largely travelling on a south-west heading after arrival in northern Europe (de Juana 2008).

Mirror-image misorientation is somewhat more plausible as an explanation for vagrancy in this species, as mirrored routes would bring larger numbers of birds into northwestern Europe, in line with the normal pattern of observation (Figure 7). The south-west and westerly orientation of birds on the Faroe Islands observed by Thorup *et al.* (2012) would also fit well with the mirror-image hypothesis. However, a direct mirror route would then see birds reorienting back towards the eastern Mediterranean, reflecting the dog-leg nature of the normal route (Figure 7). In reality, there are far more records in the western Mediterranean than in the east, suggesting that a simple mirror mechanism does not perfectly explain the observed pattern either (de Juana 2008).

It is also worth noting that Yellow-browed Warbler's breeding range stretches eastwards almost as far as Kamchatka (Figure 7). Both reverse migration and mirror-image misorientation at the eastern end of the breeding range would see vagrants heading across the Bering Sea towards the Pribilof and Aleutian Islands in Alaska. There are indeed multiple autumn records of Yellow-browed Warblers from these vagrant hotspots, and numbers seem to be increasing (Howell *et al.* 2014). However, this species is still an extremely rare vagrant

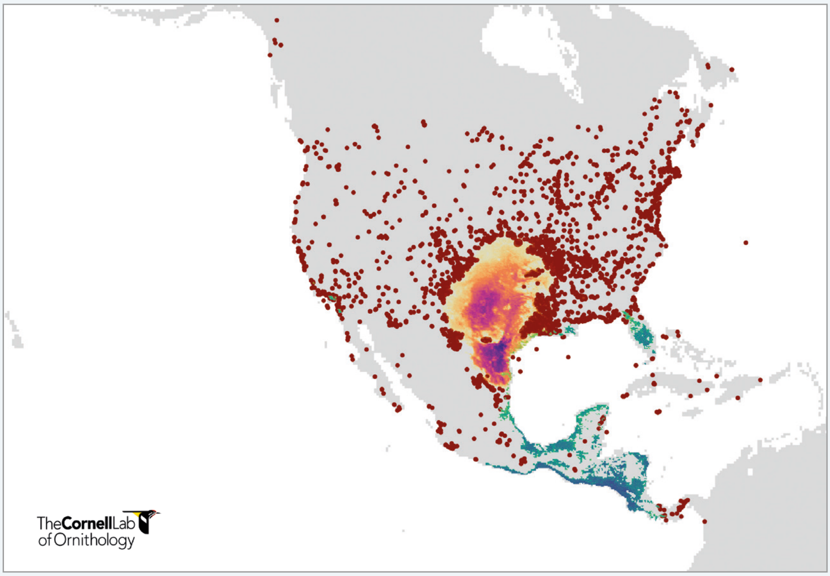
► Yellow-browed Warbler *Phylloscopus inornatus*, Melrakkaslétta, Norðurland eystra, Iceland, 7 Oct 2014. This bird is an increasingly common feature of autumn, not just in Iceland but across western Europe (*Yann Kolbeinsson*).

in Alaska, despite there being multiple well-watched sites located firmly within the 'reverse migration shadow' at the eastern end of the range. If reverse migration was the primary mechanism driving the movement of thousands of Yellow-browed Warblers into Europe each autumn, why is the same thing not happening at the other end of the range?

One possibility is that Yellow-browed Warblers have established a new and self-sustaining migration route through Europe to unknown wintering areas in Western Africa (Gilroy & Lees 2003). Individuals using this route could therefore be 'correctly' following their internal compass, tracing a migratory program they inherited from their parents – they would thus not be vagrants at all but members of a viable subpopulation that was initially founded by vagrant individuals (perhaps under mirror-image misorientation). We have previously termed such cases 'pseudo-vagrants' (Gilroy & Lees 2003), as the individuals involved do not truly meet our definition of vagrants (birds outside their 'normal' range). In the case of Yellow-browed Warbler, the relative paucity of observations in possible African wintering areas, as well as the limited spring passage through Europe, perhaps suggests that this 'pseudo-vagrant' explanation may be unsatisfactory (de Juana 2008). However, wintering site fidelity has been confirmed for a Yellow-browed Warbler trapped and ringed in January 2018 near Tarifa in Andalucía, Spain, which was refound in November of the same year (Tonkin & Gonzalez 2019). Recent work with stable isotopes (deuterium-to-hydrogen ratios) suggests that birds passing through Scandinavia had their origins in the west of the species' range in the Ural Mountains (de Jong *et al.* 2019), but it is difficult to say whether these individuals are following a viable new migration route or are simply victims of a common (and as yet unidentified) navigation error.

Reverse migration and mirror-image misorientation both involve basic compass errors that probably arise commonly in nature, and there is little doubt that they are major causes of vagrancy in migratory species. However, they are likely just two of many factors that can cause navigation errors. Vagrants frequently appear in areas well outside their 'reverse migration shadows' (Cottridge & Vinicombe 2004), indicating that these simple models cannot offer a blanket explanation for all vagrancy. Indeed, for many species patterns of vagrancy do not correspond with reverse migration shadows at all – for example, Blyth's Pipit *Anthus godlewskii* and Richard's Pipit *Anthus richardi* are both regular vagrants to Western Europe, but this region lies completely outside the reverse shadow of their normal migration, which traverses broadly north–south across Central Asia. Indeed, reverse migration would predict both species to occur more frequently in the Bering Sea region, where neither has ever occured (Lees & VanderWerf 2011).

An element of randomness is inherent in vagrancy, as it is in any species trait. The migratory program that birds inherit genetically is likely to be a key source of this random variation – many vagrants may in fact therefore be reading their internal compasses correctly but following an errant heading. Such errors are likely to arise commonly due to mutations or transcription errors during the process by which migratory orientations are inherited. Such directional variability is likely to generate a universal degree of 'scatter' in migratory



◀ **Figure 8.** Vagrant occurrences of Scissor-tailed Flycatcher *Tyrannus forficatus* (red dots) around the normal breeding (orange–purple) and winter (blue–green) ranges of the species. Vagrant records extracted from eBird (Sullivan *et al*. 2014) and abundance data from eBird Status and Trends provided by the Cornell Lab of Ornithology (Fink *et al*. 2020).

orientations, with the possibilities for vagrancy being limited only by the physiological capabilities of birds setting out in those directions. The scatter of Scissor-tailed Flycatcher *Tyrannus forficatus* occurrences across North America illustrates this random pattern very clearly (Figure 8). This species is perhaps an ideal model for understanding vagrancy – its central United States distribution means there is good observer coverage in all directions where vagrants might move, so patterns are unlikely to be biased by variation in detection rates. Correspondingly, vagrants have been found in all possible directions around the breeding range, with no particular bias towards reverse or mirror-image migration shadows (Figure 8, Gilroy & Lees 2003).

In reality, understanding the exact causes of vagrancy in any given species or region will always be difficult, due to the plethora of likely mechanisms at play, as well as the imperfect nature of the data at our disposal. Observer effort is hugely variable across most regions, particularly in Eurasia, potentially creating patterns in the data that are actually little more than artefacts of where people are looking (Gilroy & Lees 2003). Whilst simple forms of compass misorientation do offer compelling explanations for many vagrancy patterns, the reality is undoubtedly more complex and multifaceted than any simple models might suggest.

Vagrancy in social migrants

Thus far, we have focussed on the difficulties migrants face when navigating using their own sensory instincts, and the mechanisms by which these instincts can lead to vagrancy. It is important to recognise, however, that relatively few birds undertake their migrations entirely in isolation from other individuals. Even among nominally 'solitary' species (a category that includes many nocturnal passerine migrants), individuals usually have a tendency to associate with others when embarking on long flights. Some species migrate almost exclusively in flocks, with some even sticking to close-knit family groups while on the move. Socialising during migration provides a clear benefit in terms of safety in numbers, allowing individuals to reduce their exposure to predation risk during flights and stopovers (Lindström 1989). A potentially more important advantage, however, is that migrating in groups can reduce the likelihood of making navigational errors.

We have already explored how navigation is an acute and complex challenge for inexperienced birds. It stands to reason, therefore, that there may be advantages to individuals 'double-checking' their navigation decisions by comparing them against others around them. Migrating in groups, either closely or loosely, can provide migrants with this opportunity – effectively representing a fail-safe against making directional errors

▲ A pair of Tufted Ducks *Aythya fuligula* with a single drake Greater Scaup *Aythya marila* and a pair of Lesser Scaup *Aythya affinis*, Kuilima Wastewater Treatment Plant, Honolulu, Hawaii, United States, 19 February 2011, an eclectic small flock of diving ducks in the middle of the Pacific. On returning to breeding areas they may well travel together and this may lead to further vagrancy events given that Tufted Duck does not breed in sympatry with Lesser Scaup and vice versa (*Eric Vanderwerf*).

(Simons 2004). The vast synchronous departures that occur during peak migration may also help serve this purpose – the contact calls that fill the sky on such nights may in part serve to allow individuals to keep track of the flight direction of other individuals, providing a continuous error-checking service for inexperienced juveniles (Farnsworth 2005).

For species that migrate within single-species flocks, the social component of navigation may be even more direct. Evidence suggests that some species defer navigation decisions to a subset of experienced (usually older) individuals, with younger birds following behind and perhaps learning a trail of visual beacons along the way (Flack *et al.* 2012). Some flocking species also navigate collectively, with decisions apparently being made through some mechanism of group consensus building (Biro *et al.* 2006). Both Skylarks *Alauda arvensis* and White Storks *Ciconia ciconia* have been shown to make more accurate navigation decisions when flying in large groups, suggesting that more brains can mean better decisions – effectively suggesting that birds can 'crowd-source' a good migratory orientation (Rabøl & Noer 1973, Chernetsov *et al.* 2004).

Given that flocking improves navigation accuracy, we might predict that flock-migrating species should be less vulnerable to vagrancy than solitary migrants. However, heavy reliance on social navigation becomes extremely problematic for individuals that somehow become detached from their flock. For obligate social navigators such as cranes and geese, the cultural component of migration may be so strong that juveniles become completely disorientated and unable to navigate if they detach from their flocks (Mueller *et al.* 2013). Long-range vagrancy in immatures of these species is therefore quite common (Wolfson *et al.* 2020) and is counterintuitively even more frequent in rarer species that tend to have sparse and fragmented populations. An immature Siberian Crane *Leucogeranus leucogeranus* that arrived in Taiwan in December 2014 vividly illustrated this – having become detached from its family group during migration, the disorientated bird wandered far out of range, eventually being found in the car park of a subway station in Taipei. After being captured and released at a nearby marsh, the bird became a national celebrity and was even appointed its own bodyguard by the Taiwanese government, before eventually migrating to an unknown destination the following spring (Ramzy 2016).

A common outcome for lost juvenile cranes or geese is to join up with flocks of other species – sometimes entirely different genera – and migrate with them. These flocks can become 'carrier species' that often lead the stray individuals into long-range vagrancy. Each year, birders across the Holarctic avidly search through

▲ Pink-footed Goose *Anser brachyrhynchus* with Canada Geese *Branta canadensis*, Arthur J. Hendrickson Park, Nassau, New York, United States, 30 December 2016. The former is an increasing visitor to the north-east United States (*Jay McGowan*).

▲ Terek Sandpiper *Xenus cinereus*, migrating north with Common Ringed Plover *Charadrius hiaticula* and Dunlin *Calidris alpina*, Alkborough, Lincolnshire, England, 18 May 2020 (*Graham Catley*).

wintering flocks of Arctic-breeding geese and cranes in search of stray vagrants that have fallen foul of this mechanism. Some individuals will then continue to migrate back to the Arctic with their adopted species year after year, producing hybrid offspring in some cases (Ottenburghs *et al.* 2016). Species that migrate in family flocks such as geese may also be unusually prone to vagrancy from their second year onwards, when they finally leave the family group after completing their first migration as juveniles. Such birds must eventually leave the guidance of their parents and strike out on their own, at which point they may risk becoming lost or entrained in carrier groups of other migrating species.

Vagrancy arising through individuals following carrier flocks of other species is likely to be common in many flock-forming species. Arctic-breeding waders have some of the highest rates of global vagrancy among any species, driven in part by the extreme difficulty of compass navigation at high latitudes. The fact that they commonly migrate in flocks is likely to be another key factor, especially as it is common for waders in the Arctic to breed side-by-side with species that winter in completely different parts of the world. Many Nearctic-breeding wader species are surprisingly frequent vagrants to Europe, and they often appear in the company of Ringed Plovers *Charadrius hiaticula* of the *tundrae* subspecies, which breeds as far west as the Canadian Arctic. These westernmost populations migrate across the North Atlantic to winter in Europe and West Africa (Flegg 2004), and it seems likely that juveniles of Nearctic species regularly tag along with these flocks and follow them to the wrong side of the Atlantic.

Social navigation clearly plays an important role in explaining patterns of vagrancy in many species, both as a direct driver via carrier flocks, and as an indirect factor allowing inexperienced individuals to minimise their risk of vagrancy by error-checking their own orientation decisions. The true extent to which birds 'crowd-source' their navigation decisions is still unknown, particularly amongst nocturnal migrants, and much is still to be learned about the mechanisms that underpin the collective decision-making of birds during migration. Nevertheless, it is clear that social navigation can commonly lead to birds going astray during migration, and searching through flocks of migrants remains one of the most reliable strategies for birders intent on finding vagrants.

WIND DRIFT AND VAGRANCY

In the preceding sections we have explored how navigation errors can cause vagrancy in the absence of any external environmental influences. This 'endogenous' component is expected to generate a fairly constant baseline level of vagrancy among migratory birds in any given area and season, regardless of weather patterns or any other exogenous factors. However, any birder with an interest in vagrant-hunting knows that the chances of encountering rare birds can be a matter of feast or famine (and usually the latter), and that this variation can be largely attributed to the weather. The link between vagrancy and weather patterns is so strong that birders often become obsessive students of isometric charts and forecast models, trying to identify wind patterns that might bring flights of interesting birds in their direction. Such forecasting is a fickle business, however, and disappointment is usually the outcome of any attempt to predict the timing and location of arrivals of vagrant birds.

Whilst the association between winds and vagrant occurrence is often quite obvious, it can be difficult to say whether the wind itself is the fundamental driver of birds going astray in a given circumstance, or simply a secondary factor that acts to concentrate individuals with errant navigational instincts. In some cases, there can be little doubt that winds are the sole cause of vagrancy – particularly when large numbers are simultaneously displaced outside their normal ranges by storm events (Elkins 1979). Exploring the circumstances surrounding mass displacements can shed light on how birds respond to weather patterns and the conditions that might be expected to cause significant weather-driven vagrancy around the world.

◄ Hermit Thrush *Catharus guttatus*, Cape Clear, Cork, Ireland, 20 October 2006, the second record for Ireland of this Nearctic vagrant (*Chris Batty*).

To understand the role of the weather in driving vagrancy, a good starting point is to explore the ways in which migrating birds interact with winds from the bird's perspective. Most birds are utterly at home in the air. The sky is the main habitat for many species that have evolved complex behaviours to allow them to use winds to their advantage, helping them save energy, find food or escape predators. The ways that migrating birds interact with winds have been subject to intensive scientific study, and many insights have recently been gained from detailed examinations of the tracks of satellite-tagged birds, as well as the movements that can be inferred from radar images. These discoveries are gradually allowing us to build up a detailed understanding of the complex ways in which migratory birds are influenced by winds, and the circumstances in which wind patterns can switch from highly beneficial to potentially fatal.

The sky as a complex habitat

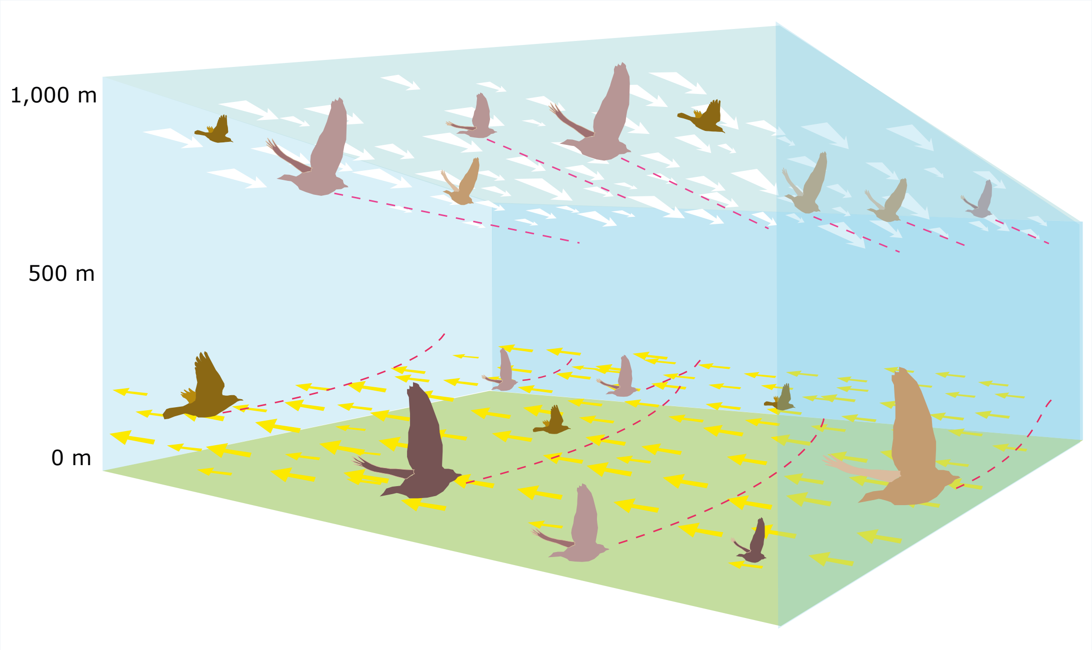
An important starting point in understanding the role of winds as a driver of vagrancy is to recognise that we, as humans, have very little intuitive grasp of the conditions that birds experience in the airspace above us. From our narrow perspective on the ground, we tend to think of the wind as a one-dimensional phenomenon – a movement of air that has a direction and strength, corresponding with the conditions we experience at ground level. Studying weather maps only serves to reinforce this perception, representing the wind as a one-dimensional flow across the planet, that can be easily described by simple sets of arrows or isobars. In reality, the windscape experienced by a bird is far more complex – a three-dimensional 'habitat' comprising an ever-changing maze of jets, boundaries and eddies, invisible to the eye, but keenly felt by any bird ascending through the atmosphere (Davy *et al.* 2017).

The ground-level winds that we experience represent the basement of a high-rise complex, with each 'floor' comprising a band of airflow that may differ in speed and direction from levels above and below it. To make matters more complicated, these floors are prone to shift unpredictably in space and time, creating a turbulent environment that must be perilous and confusing for inexperienced or exhausted birds (Dokter *et al.* 2011). This high-rise complex is referred to by meteorologists as the 'boundary layer' – the lower part of the troposphere where the air mass is heavily influenced by the shape of Earth's surface. It is within this layer – typically the first 2–3km above the ground – that the vast majority of bird flight and migration takes place. A brief snapshot of life in this environment can be gained during the take-off and landing phases of aeroplane flight, as we pass through what can feel like 'pockets' of turbulent air that buffet aircraft, sometimes causing surprising vertical lurches that can leave your stomach in your mouth. Given that these forces are strong enough to shake the metal hull of an aeroplane, it is easy to imagine just how disruptive the winds could be to an airborne bird.

► European Honey-buzzard *Pernis apivorus* Skaw, Unst, Shetland, Scotland, 23 May 2009. Wind drift, or perhaps a navigational failure, took this migrant far west over the Atlantic – an error that proved fatal, the bird probably having been killed and eaten by Great Skuas *Stercorarius skua* (*Rik Addison*).

We have previously discussed how challenging it must be for migratory birds to orient themselves in their desired migratory heading, given that it involves the mastery of multiple internal compass senses that each require different sensory inputs. Now, we must extend this thinking to acknowledge that birds must attempt to do this whilst also finding their way through the complex and potentially hostile aerial environment – a challenge that must make navigation even more difficult. Not only must birds constantly keep track of their various compass senses, they must do this whilst also seeking safe passage through the three-dimensional airspace, avoiding disruption and trying to locate bands of airflow that will help rather than hinder their onward passage.

Until recently, we knew very little about the behaviour of individual birds during the course of a single migratory flight. Recent advances in tracking have allowed researchers to follow individual birds in precise detail, revealing their routes, speeds and flight heights on a minute-by-minute basis. One of the first studies to track the flight of a passerine on migration was carried out by Bowlin *et al.* (2015), who attached tiny radio



▲ **Figure 9.** Winds may simultaneously flow in multiple directions at different heights within the air column. In some circumstances, tailwinds (white arrows) may only be present at upper elevations, and birds migrating at ground level may be exposed to sidewinds (and thus drifted) unless they are able to gain enough elevation to reach the zone of optimal wind conditions above.

transmitters to nine Swainson's Thrushes *Catharus ustulatus* in Illinois; they were subsequently able to follow each of them for the duration of a single nocturnal migration flight, using a tracking antenna fitted to a vehicle on the ground. As is typical for nocturnal migrants, the thrushes all set off soon after dusk and rapidly gained height, with all birds showing a similar pattern of behaviour at the very start of their flights, climbing to an elevation of around 1km very soon after take-off (Figure 9).

After this initial ascent, however, the flight paths of the individual birds began to diverge, with each one exhibiting its own unique flight pattern. Some continued to climb throughout the night, others gradually descended, and some made continual ascents and descents of hundreds of metres as they continued on their journey. This variation surprised the researchers, as theoretical models of bird flight suggest that to maximise energy conservation, birds with flapping flight should seek to maintain a single elevation if possible. Bowlin and colleagues hypothesised that the thrushes were having to continually adjust their flight height in response to changing conditions within the atmosphere – perhaps moving up and down in search of tailwinds, trying to escape turbulent pockets of air, or moving above or below clouds to maintain a clear view of the stars above. It is easy to imagine circumstances whereby inexperienced migrants would become confused or disorientated within this ever-changing environment, potentially leading to frequent errors in navigation.

Similar patterns of complex vertical movement during migration have also been observed from radar stations. Intriguingly, radar signals often indicate that migrating birds form 'layered' patterns within the air column, with multiple narrow bands of intense migration at different levels above the ground. Dokter *et al.* (2013) showed that this happens frequently in Europe around high pressure systems in spring, where migrating birds appear to group into two distinct bands – one close to ground level and another at a considerable height (1–2km). They found that these patterns were almost always associated with a set of conditions where wind directions were unfavourable at ground level, but tailwinds could be found at greater altitudes within low-level jet streams about 1km above ground. This pattern of layered winds is a common feature of high pressure systems, and it is thus possible that birds have evolved to recognise barometric conditions where they can find ideal tailwinds at altitude, even when ground-level wind directions are unsuitable. This observation gives us an important insight into how winds might cause vagrancy. It is notable that of the two layers of migrating birds, only one was within the zone of optimal winds – the other, at ground level, concerns large numbers of birds flying in sidewinds that may cause them to drift (Dokter *et al.* 2013). Many birds are seemingly unable to escape this band by climbing to the better, higher zone, apparently becoming ‘trapped’ in sidewinds at ground level. These individuals have perhaps failed in their attempts to ascend into the jet stream, and instead find themselves vulnerable to drifting off course unless they are able to compensate by battling against the wind.

One obvious way that migratory birds can avoid drifting in sidewinds is to simply stop flying. Radar studies indicate that birds are indeed highly selective about when they depart, with little movement taking place during periods of strong adverse winds, followed by radar screens lighting up with thousands of departing birds when winds finally become suitable for onward passage (van Doren *et al.* 2018). Of course, departing when the wind is helpful does not necessarily guarantee an easy onward flight – birds do not have the luxury of a five-day weather forecast to help plan their movements. To some extent, they may be able to ‘forecast’ wind patterns if they have evolved to recognise weather patterns that are likely to mean conditions will be suitable for onward flight for at least the next few hours. In eastern North America, for example, it has long been known that flights of nocturnal passerine migrants in autumn often follow the passage of a cold front, these commonly being followed by light winds from the north that provide ideal tailwinds for southbound migrants.

The strategy of avoiding migration when winds are not ideal has one major drawback – migrants may end up waiting for days or even weeks for a window of perfect conditions, severely slowing their progress. Waiting around is a risky strategy for a migrant, as the bird might end up running out of food or being hit by colder conditions than it is physiologically capable of surviving. As the migration season progresses, migrants may become more and more likely to depart even if wind conditions are not suitable. This may be one of the reasons why vagrant occurrences tend to peak later in migration seasons, both in spring and autumn, when lagging individuals become increasingly willing to run the risk of wind drift. Juvenile birds in particular tend to migrate later in the year than adults and may therefore not have the luxury of waiting around for the perfect wind conditions before moving.

▲ Swainson’s Thrush *Catharus ustulatus*, Cape May, New Jersey, United States, 30 September 2018. Radio transmitters fitted to this species revealed that they regularly make abrupt changes in flight altitude during migration, perhaps in search of zones with suitable tailwinds (*Michael O’Brien*).

How do birds respond to wind drift?

The extent to which sidewinds influence a bird's ultimate destination depends in part on the strength and direction of the wind relative to the bird's chosen direction, and also the bird's behavioural response to drift. In turn, this depends on whether birds are actually able to recognise the drift happening in the first place – and this may not be as simple as it first seems. As we discussed in the orientation section (page 9), most juvenile birds are likely to migrate using a simple 'clock-and-compass' approach, following a desired heading using an internal compass ('reading' the stars, Sun or magnetic field) for a given period of time. Such birds may struggle to detect wind drift during flight, as their only source of positional information comes from their innate compass sense – and the internal 'needle' of this will not change no matter how much the bird is drifted (Perdeck 1958). This may help explain why juvenile birds on their first autumn migration appear to be particularly prone to wind-driven vagrancy – in some cases they may simply be unaware that the drift is even happening.

One way that migratory species have solved this problem is by combining their innate compass sense with a set of 'beacons' – fixed features of the landscape below that are visible during flight and fall along the line of their desired heading; these are often referred to as 'leading lines' (Alerstam 1978). After deciding on a flight orientation initially using their internal compass cues (stars, Sun or magnetic field), birds may then be able to fix on visible features below them – perhaps mountain ranges, rivers or coastlines – and measure their progress towards these beacons during flight (Kullberg *et al.* 2007, see page 19). Unlike the internal compass, the position of these beacons will change whenever the bird is drifted sideways off its initial course. This will allow birds to 'see' drift as it happens, enabling them to compensate by changing their flight angle to maintain a net movement towards their desired heading. This may be one of the reasons why mass wind-drift events often correspond with low cloud or foggy conditions, leading to poor visibility, which prevents migrants from using their visual beacons to keep track of their course.

Whilst we might expect that birds will attempt to compensate for wind drift wherever possible, recent radar studies suggest that this might not always be the case, at least among nocturnal passerine migrants (Thorup *et al.* 2012). Horton *et al.* (2016) took advantage of recent advances in Doppler radar technology to measure not only the flight path of birds aloft, but also the direction they were facing, providing some remarkable new insights into how birds adjust their flight behaviour in response to drift. They found that large nocturnal flights often took place despite considerable sidewinds, and that in many cases birds showed little attempt to compensate for drift during the course of the night – rather, they simply continued to orientate themselves towards their desired heading and allowed the sidewinds to steadily drift them longitudinally. Interestingly, birds were far more likely to adjust their heading to account for wind drift when flying close to the Atlantic coast, relative to birds flying 200km inland.

There are two possible explanations for this, both of which are highly relevant to our understanding of wind-driven vagrancy. One relates to the use of 'leading lines' described above – it is possible that birds migrating along the coast are more aware of being drifted as they can use the coast as a leading line. Further inland, birds may lack such obvious landscape features upon which to fix, potentially making it more difficult to keep track of whether they are being drifted off course. Another possibility raised by Horton *et al.* (2016) is that birds may simply be less inclined to compensate for drift when flying further inland, because this compensation is energetically costly – the bird must pivot the axis of its body during flight to face further into the wind, such that the combination of its forward movement and the sidewind will cause it to move in the correct direction. This requires a much more forceful flight pattern, reducing the distance that the bird could fly before needing to refuel. Energy-conscious birds may therefore opt to maintain their normal axis of orientation and allow themselves to be drifted steadily off this course by the sidewind.

These observations indicate that vagrancy is perhaps most likely to arise when persistent sidewind conditions hit major inland migration routes, as birds on these flyways may be less inclined to battle against drift. This could in part explain a pattern that is very familiar to birders in Western Europe, where the presence of high pressure systems over Scandinavia or western Siberia in autumn can lead to a veritable glut of Eastern Palearctic vagrants arriving at coastal hotspots (Elkins 1988). These weather systems are usually associated with light easterly airflows and clear weather across Eurasia, potentially causing steady westward drift among migrants making overland movements south out of Siberia. If uncompensated, such drift could potentially accumulate over consecutive nights during stable anticyclonic conditions, gradually displacing large numbers of birds towards Western Europe (particularly those already following errant navigational instincts).