

JOURNAL OF AVIAN BIOLOGY

Research article

Could bi-axial orientation explain range expansion in a migratory songbird?

Joe Wynn¹, Guillermo Fandos², Kira Delmore³, Benjamin M. Van Doren^{4,5}, Thord Fransson⁶ and Miriam Liedvogel^{1,7,8}

¹Institut für Vogelforschung 'Vogelwarte Helgoland', Wilhelmshaven, Germany

²Department of Biodiversity, Ecology and Evolution, Faculty of Biological Sciences, Universidad Complutense de Madrid, Madrid, Spain

³Texas A&M University, College Station, TX, USA

⁴Cornell Lab of Ornithology, Cornell University, Ithaca, NY, USA

⁵Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana-Champaign, Urbana, IL, USA

⁶Department of Environmental Research and Monitoring, Swedish Museum of Natural History, Stockholm, Sweden

⁷MPRG Behavioural Genomics, Max Planck Institute for Evolutionary Biology, Plön, Germany

⁸Biology and Environmental Sciences Department, Carl von Ossietzky Universität Oldenburg, Oldenburg, Germany

Correspondence: Joe Wynn (joseph.wynn@ifv-vogelwarte.de), Miriam Liedvogel (miriam.liedvogel@ifv-vogelwarte.de)

Journal of Avian Biology

2024: e03196

doi: [10.1111/jav.03196](https://doi.org/10.1111/jav.03196)

Subject Editor: Martin Paeckert

Editor-in-Chief: Jan-Åke Nilsson

Accepted 23 April 2024



The likelihood of a new migratory route emerging is presumably a function of 1) the associated fitness payoff and 2) the probability that the route arises in the first place. It has been suggested that diametrically opposed 'reverse' migratory trajectories might be surprisingly common and, if such routes were heritable, it follows that they could underlie the rapid evolution of divergent migratory trajectories. Here, we used Eurasian blackcap (*Sylvia atricapilla*; 'blackcap') ringing recoveries and geolocator trajectories to investigate whether a recently evolved northwards autumn migratory route – and accompanying rapid northerly wintering range expansion – could be explained by the reversal of each individual's population-specific traditional southwards migratory direction. We found that northwards autumn migrants were recovered closer to the sites specified by an axis reversal than would be expected by chance, consistent with the rapid evolution of new migratory routes via bi-axial variation in orientation. We suggest that the surprisingly high probability of axis reversal might explain why birds expand their wintering ranges rapidly and divergently, and propose that understanding how migratory direction is encoded is crucial when characterising the genetic component underlying migration.

Keywords: behaviour, evolution, inheritance, migration, navigation

Introduction

The ontogeny of long-distance avian migration is a central question in modern bioscience, requiring that cognition, physiology, behaviour and biomechanics come together in order to orchestrate organised movement towards a specific



www.avianbiology.org

© 2024 The Authors. Journal of Avian Biology published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

goal. Long-distance movement can be guided by information from several sources, all of which will interact with the environment to produce the observed phenotype. The relative contributions of – and (possible) interactions between – these sources will necessarily dictate the extent to which individuals and populations react to changes in the distribution of resources through time. In turn, these information sources that guide migratory behaviour are likely species-specific, and optimised for a specific migratory strategy. In some flocking and day-migratory species, information inherited culturally (via social learning from experienced conspecifics) explains much of the variation in route selection (Chernetsov et al. 2004, Mueller et al. 2013, Byholm et al. 2022), whilst in dispersive migrants associative (trial-and-error) learning is seemingly also important (Guilford et al. 2011). Asocial learning is also thought to play an important role in return migration, with ‘imprinting’ (often to a spatially informative gradient cue) specifically thought to underpin return migration to a precise breeding location (‘philopatry’; Wynn et al. 2020a, b, 2022).

Another core component of the migratory system, at least in some night-migratory, asocial taxa, is the genetic inheritance of migratory information. Evidence gathered over the past half-century suggests that the contribution of genetic information to migratory direction, especially in songbirds, can be substantial, with this evidence stemming from five main sources: 1) a large heritable component to migratory behaviour, even in hand-raised birds that have been reared isolated from their parents (Berthold and Querner 1981, Biebach 1983, Pulido et al. 2001); 2) the endogenous control of migratory behaviour in the absence of seasonal-specific cues (such as changes in photoperiod; Gwinner 1986); 3) the innate orientation of naïve birds without prior experience in the absence of adult conspecifics (Gwinner 1986, Zolotareva et al. 2021, Wynn et al. 2023); 4) the divergent trajectories of some fledglings when compared to conspecific adults (and apparently all other sympatric migratory taxa; Handel and Gill 2010, Lindström et al. 2011, Yoda et al. 2017); and e) the inheritance patterns of migratory traits both in the lab and in the wild (Helbig 1991, Sokolovskis et al. 2023). Taken together, these lines of evidence provide strong support that – at least in some taxa, such as songbirds – migratory direction in part is genetically determined.

Inherited directional information in birds is typically, though not universally (Thorup et al. 2020), assumed to comprise ‘clock and compass’ vector orientation: a compass to determine direction, and a clock to determine when to start and when to end migration (Berthold et al. 2013). This hypothesis is supported by experimental and observational studies, with naïve birds on their first migratory journey not being able to compensate for displacement from the conventional migratory trajectory (Perdeck 1958, Thorup et al. 2007) and following straight-line courses that accumulate error over time, consistent with vector navigation (Mouritsen and Mouritsen 2000, Yoda et al. 2017, Wynn et al. 2021). Cross-breeding experiments between individuals with different migratory routes suggest that

additive genetic variance might inform migratory direction, with the crossbred progeny of birds with distinct migratory directions following trajectories that seemingly represent intermediate directions (Helbig 1991, Delmore and Irwin 2014). Recent studies have, however, implicated a system of dominance in migratory route inheritance, possibly to avoid intermediate phenotypes (Sokolovskis et al. 2023), suggesting that different encoding mechanisms might predominate in different species.

Neither system, however, apparently accounts for the occurrence of highly divergent migratory directions. For example, Eurasian blackcaps have been observed to migrate north in the autumn with increasing regularity since the 1960s, with this shift in migratory strategy linked to both a changing climate and the increased availability of artificially provided food (Berthold et al. 1992, Bearhop et al. 2005, Plummer et al. 2015, Van Doren et al. 2021). Blackcaps typically migrate either south-east or south-west to winter in North Africa/southern Europe (Delmore et al. 2020a, b). Some birds from northerly breeding populations also exhibit longer distance, trans-Saharan movements (Bakken et al. 2003, Hall-Karlsson and Fransson 2008), meaning that recent northwards migrations have led to the establishment of a new wintering ground in the British Isles (Fig. 1) that is apparently discontinuous with the species’ historic wintering sites utilised by individuals following other orientation strategies. North-migrating blackcaps seemingly breed in sympatry with south-migrating conspecifics (Delmore et al. 2020a, b), and hence it is difficult to reconcile such divergent migratory trajectories with classically considered Mendelian mechanisms (Tautz et al. 2020). Assortative mating based on migratory destination has been suggested (Bearhop et al. 2005), and whilst this might explain how divergent routes are maintained within a population, it would not necessarily explain how they evolve in the first place.

It has been speculated that vagrant songbirds are disproportionately abundant in a direction precisely opposing the normal migratory direction, though such trends are difficult to verify beyond anecdote due to necessarily small sample sizes and/or biases in the distribution of observers (reviewed by Lees and Gilroy 2022). Specifically, birds of multiple taxa have been observed to orient in a ‘reverse’ migratory direction – a direction diametrically opposed to the population-expected migratory direction – using ringing recoveries (Busse 1992), via observations of free-flying birds (Busse 1992, Åkesson 1993, Åkesson et al. 1996), via radar traces (Komenda-Zehnder et al. 2002) and in laboratory experimentation (Thorup 1998, Ożarowska et al. 2013). These observations suggest that migratory orientation in a ‘reversed’ direction is surprisingly common, and that this seemingly occurs without routes intermediate between the conventional and reversed routes being especially common. Whilst it is unclear what would cause markedly bi-axial variation in migratory populations, and indeed whether such variation would be heritable, the concept of ‘reverse migration’ could nonetheless provide a mechanism by which highly divergent migratory routes evolve and persist within sympatric populations. It is, then,

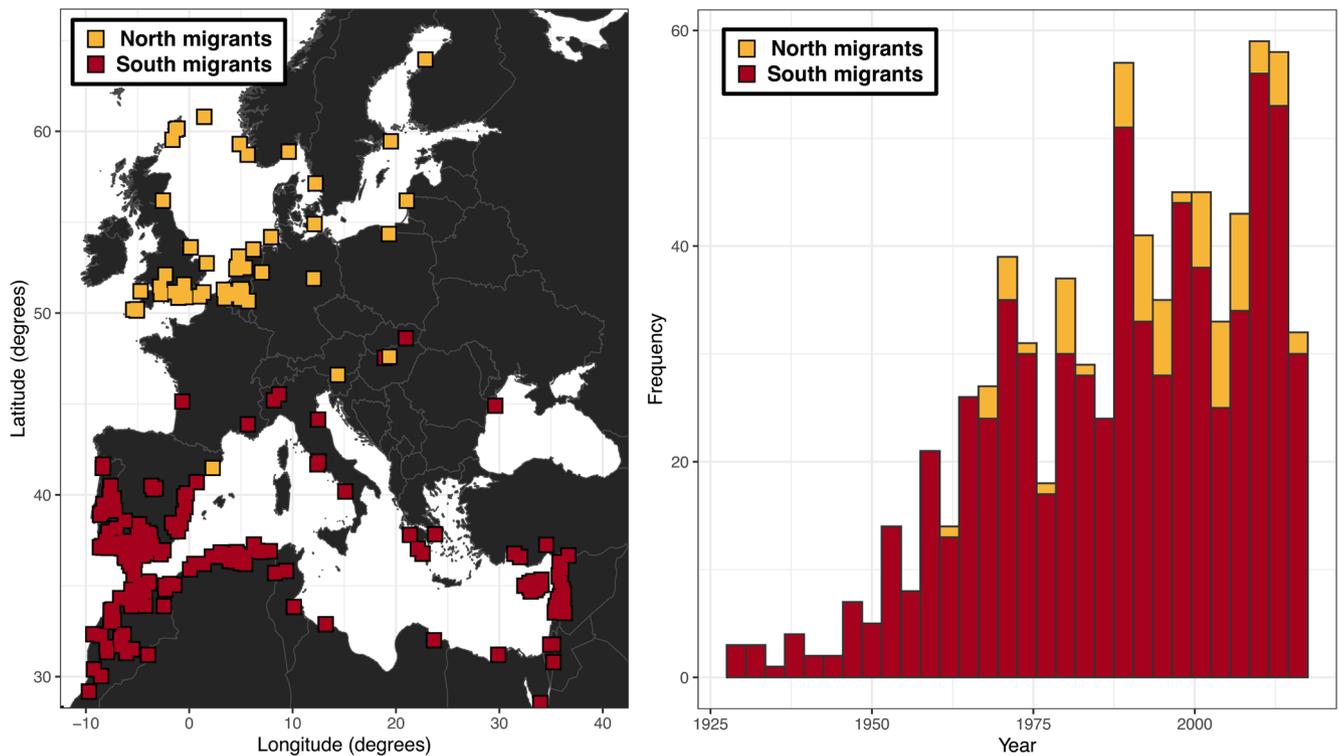


Figure 1. The wintering range expansion of the Eurasian blackcap. (left) The wintering position of blackcaps that have been caught on the breeding ground and subsequently recovered over the winter. Squares indicate wintering position and are coloured by migratory direction with northwards migrants highlighted in yellow and southwards migrants highlighted in red. (right) A histogram of blackcap ringing effort, coloured by migratory direction (as in left) in autumn. The y-axis refers to the frequency of birds ringed at the breeding site and recovered > 500 km away (see Methods for further detail). Whilst ringing effort has increased steadily over time, the occurrence of northwards movement is a relatively recent phenomenon.

of interest whether 1) divergent migratory routes are quantifiably consistent with bi-axial variation in orientation and 2) if so, what might explain such variation.

Reverse migration has been suggested to underlie recent changes in the wintering range of blackcaps (Busse 1992, Fransson and Stolt 1993, Bengtsson et al. 2009), though it is unclear whether northwards migration might instead represent the furthest extent of a surprisingly wide distribution of migratory directions during autumn (Berthold and Terrill 1988). Testing this requires a statistical approach that takes the heterogeneous distribution of suitable habitat and observers into account. Here, we used ringing recoveries collected over the last half-century (1962–2020; $n=78$) alongside geolocator positions gathered in the years 2016–2020 ($n=33$) to investigate whether northwards migration by Eurasian blackcaps is likely to represent a reversal of the population expected migratory direction. Blackcaps have two well-documented southwards migratory strategies, with birds from western Europe migrating south-west and birds breeding in eastern Europe migrating south-east in autumn (Delmore et al. 2020a, b). Therefore, under a theory of bi-axial orientation, we might expect that north-migrating birds from south-east Europe might migrate north-west and, conversely, north-migrating birds from south-west Europe might migrate north-east.

Material and methods

Selecting ringing records

Ringing data were derived from the European Union for Bird Ringing (EURING, <https://euring.org/>) based on a query for all Eurasian blackcaps ringed and subsequently recovered. Given the spatiotemporal biases associated with ‘citizen science’ data, and the sensitivity of any analysis of migratory direction to these biases, it is key to subset ringing data to include only instances in which the same bird is caught during both the breeding and the non-breeding periods. From these birds, we can then select individuals where the non-breeding position is located north of the breeding site. In previous studies that utilise ringing records to study navigation, the problem of how to categorise birds as breeding was solved by exhaustively subsetting the data using different criteria to ensure that the method of subsetting did not drive the results (Paradis et al. 1998, Wynn et al. 2022). Here, however, we sought to improve upon this method further by including phenotypic markers of breeding and migration to ensure that birds recaptured on migration (rather than breeding/non-breeding ground) were effectively excluded from the analysis.

To remove migrating birds, we sought to ascertain the point in time at which breeding became far more likely than

migration. The onset of breeding in blackcaps is characterised by the development of both a brood patch in females and a cloacal protrusion in males, whilst very young blackcaps that have not completed post-juvenile moult prior to autumn migration (and hence have not left the breeding site) have a field-identifiable plumage (EURING code '3J'). Similarly, birds ringed as chicks in the nest are recorded as such in EURING. In contrast, migrating blackcaps typically have a higher fuel load than breeding birds (Svensson 1970), which manifests as subcutaneous fat. Since both the breeding and migratory phenotypes are distinctly recognisable at the point of ringing, we first sought to use ringing data to isolate the time of year at which breeding became more likely than migrating. We did this by comparing the probability of occurrence of breeding versus non-breeding phenotypes at different times of year, defining breeding birds as either birds ringed as chicks in the nest or free-flying birds with a cloacal protuberance, brood patch or juvenile plumage, and migrant birds as having a fat score of > 3 (meaning a high degree of visible subcutaneous fat) or the equivalent fuel load of 17.5% as calculated using mass and maximum wing chord based on established methods (Kelsey et al. 2019). Birds that satisfied the criteria of neither breeding nor migrating phenotype were not included in either distribution, since their life history stage when captured was unclear.

We divided the map of Europe into a $5^\circ \times 5^\circ$ grid, and for each grid point we subsetted the overall EURING database for every bird with a breeding phenotype within 5° of the grid point in question. We then repeated this process for both spring and autumn migratory phenotypes. If the sample size for each of spring migration, breeding and autumn migration was > 10 , we calculated a density curve (bandwidth = 10) of the recorded Julian dates for spring migration, breeding and autumn migration (Supporting information). The points at which spring migration density $<$ breeding density (i.e. the point at which a ringing event was more likely to represent a breeding bird than a migrant) and the point at which breeding density $<$ autumn migration density (i.e. the point at which a ringing event was more likely to represent a migrant bird than a breeding bird) were then isolated for each grid square. Based on this categorisation, we could identify the respective dates at which breeding was likely to commence and end (Supporting information) for all points in Europe where ringing data were available.

Whilst it would be possible to use the calculated start and end of breeding from each point in Europe where data exist to subset our data to include only birds likely to be breeding, we chose not to do this, since 1) this would lead to a paucity of data from ringing schemes where biometric information is not readily reported and 2) migration becoming less likely than breeding does not exclude migration occurring entirely. As such, we sought to define breeding in our analysis as either birds recorded with a breeding phenotype as defined above, or recorded from within a core breeding window of 15 June–15 July in our analysis. Within this time window birds from all over Europe were very unlikely to be on migration (Supporting information), and the window used

was consistent with the breeding phenology and migratory timings reported in previous studies (Delmore et al. 2020a, b). The position of this window relative to overall migratory and breeding phenology from across Europe is shown in Supporting information. Only birds that showed northwards autumn migratory direction and moved > 500 km between ringing and recovery ($n=78$) were retained in our main analysis (Supporting information), to ensure that all movements represented genuine migratory movements, and not dispersal. We chose 500 km as cut-off distance since almost all migratory birds tracked with a geolocator travelled more than 500 km, and including birds moving shorter distances ran the risk of falsely including birds that did not migrate but were instead showing dispersive movements in our analysis. Each individual was represented once, and no bird registered two trajectories that satisfied our inclusion criteria.

Several birds apparently ringed during the breeding season in Cyprus and the Middle East were retained by the above criteria. Whilst we have no reason to remove these birds from the analysis per se, such records do not tally with what is currently known about the breeding range of migratory blackcaps (Shirihai 1996, Hatzofe and Yom-Tov 2002, Komenda-Zehnder et al. 2002). This discrepancy might arise owing to a lack of data to parameterise migratory phenology in these regions, hence we ran our analyses twice – with and without these birds included – to ensure that including them did not bias any results. The results with these birds excluded is presented in the main text; see Supporting information for the results with them retained.

In our analysis we also included wintering/breeding positions as estimated from light-level geolocator (GLS) tracked blackcaps. When considering geolocator trajectories ($n=33$), breeding and wintering positions were ascertained using the 'geolight' package (Lisovski and Hahn 2012) using the methods outlined in Delmore et al. (2020a, b).

Randomisation analyses

For each north-migrating bird we attempted to quantify how close the bird was recovered to the site expected by an axis reversal. We did this via a three-stage process, designed to reduce taking biases in ringing effort into account. First, to estimate an expected southwards migratory direction for a population from which a given north-migrating bird originates, we calculated the (circular) mean southwards migratory direction taken by the 50 closest southwards breeding-to-wintering ringing records (see above) to the focal north-migrating bird (Fig. 2). By adding 180° to this direction (vector reversal), we could then estimate the northwards migratory trajectory expected under an axis-reversal. Second, by moving the observed distance along this mirrored trajectory, we could estimate the site at which a bird might be expected to be recovered. This we did by selecting the active ringing site closest to the site predicted by the axis reversal, so the hypothesised migratory direction took into account the patchy distribution of ringing effort and suitable habitat. Third, by measuring the angular deflection observed

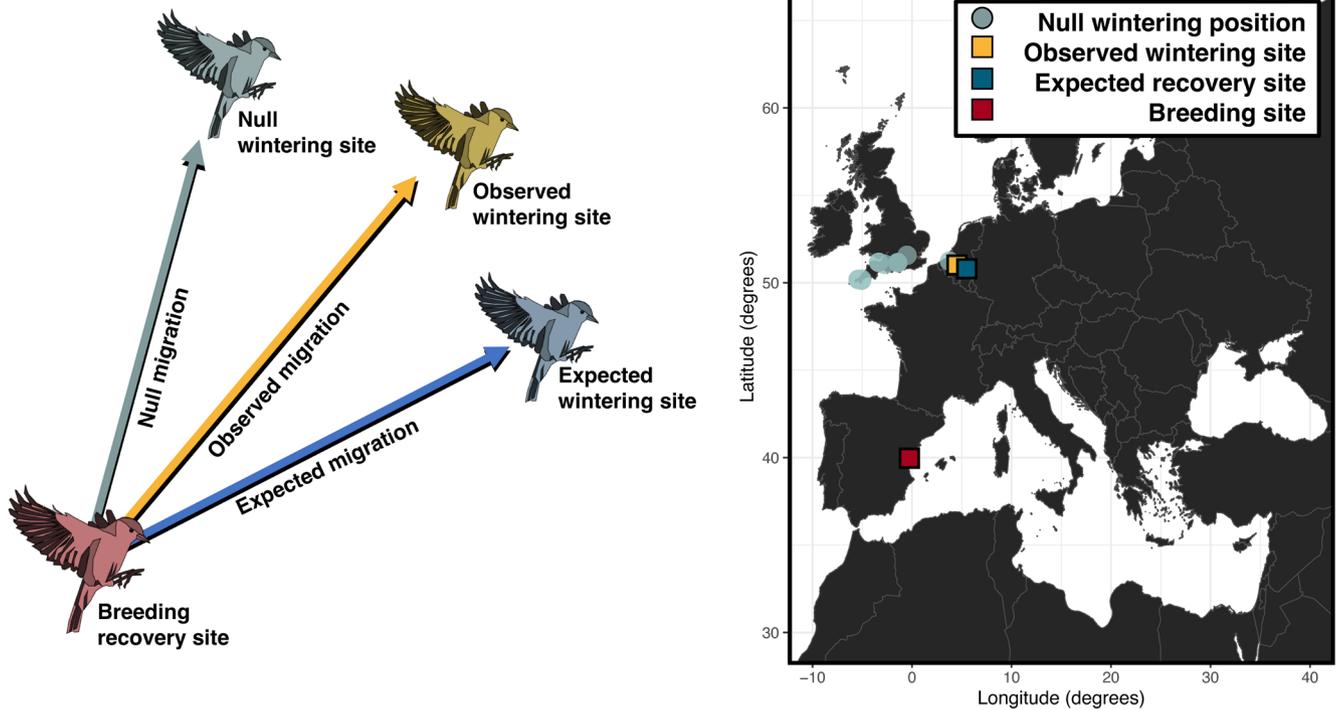


Figure 2. A null model of blackcap northwards migration. (left) An example of how the distances between the expected wintering site and the observed/null wintering positions vary for a blackcap breeding in south-west Spain (red). (right) Schematic outlining the quantities used in our statistical analysis: the null migrations generated in our randomisation (light blue, Methods), the observed recovery site (yellow) and the recovery site expected under a model of bi-axial directional variation (dark blue).

trajectory and this expected trajectory, we could estimate how well the observed trajectories fit our model/hypothesis. The smaller the angular deflection between the observed and expected trajectories, the better the fit of the model.

If bi-axial variation were the only contributing factor to the northwards movement of blackcaps, we might expect them to follow the path predicted by axis reversal perfectly. However, there are presumably other factors that are important to consider (habitat suitability, encounter probability, mortality probability, etc.) and hence we would instead expect them to be closer than expected by chance (rather than being perfectly aligned). As a consequence, it is key to establish a realistic null model of northwards migration that does not directly stem from axis reversal. In such a model we suggest that the northwards movements taken by birds at a given site should be equal to those actually observed – that is to say, they are in the same directions, travel the same distances and are constrained to be recovered at the same sites – but, ultimately, are random. If the observed birds are closer to the expected trajectory than the simulated null model birds are, this would support the idea that northwards movement of blackcaps is driven by variation in an inherited bi-axial migratory program.

To create realistic null wintering sites for each bird, we first assigned a northwards bearing selected at random (with replacement) from all recorded northwards bearings. Second, we isolated the site that was the same distance along

the randomly selected bearing as the observed bird moved. Finally, we then constrained the null recovery site to the nearest site where a bird was ringed/recovered, so as to ensure that the null model birds had the same distribution constraints as real birds. To ensure that differences in ringing effort through time did not induce biases in the null model that were unreflective of real ringing effort, null birds were constrained to ringing sites that were active within 10 years of the ringing record for which the null movement was being calculated. Importantly, ringed birds were also constrained to take randomly selected migratory directions and be recovered at wintering sites inherited from other ringed birds and, similarly, the null trajectories simulated for GLS-tracked birds were derived from other GLS-tracked birds. This ensured that the constraints on wintering sites seen in the observed birds were carried forward into the null model, and that the biases associated with a given tracking technology were maintained for the null model.

We ran our null model 100 000 times, each time calculating a mean and a median angular deflection from the expected trajectory. In turn, we compared these to our empirical mean and median deflection angles. We then calculated the number of times the null model had a smaller angular deflection than was observed empirically, and hence calculated a p-value for both the mean and median observed-versus-expected distances. All p-values were corrected for the 2-tailed tests performed by multiplying the p-value by 2.

Analysis of migratory destination

In order to assess whether north-migrating blackcaps ended their migratory trajectories at a different latitude to south-migrating conspecifics – consistent with previous studies (Delmore et al. 2020b) – we used a t-test to compare the wintering latitude of southerly migrants to the wintering latitude of northerly migrants.

Results

Using our randomisation, we found that blackcaps were recovered significantly closer to the site predicted by an axis reversal than would be expected owing to chance. This was true both when considering the mean (randomisation; $p < 0.001$) and median (randomisation; $p = 0.027$) angular deflections from the course predicted under bi-axial variation in orientation. The fact that both the mean and median angular deflections from the expected trajectories were smaller than would be expected by chance suggests that variation in migratory direction is consistent with bi-axial orientation, even when biases caused by ringing effort, habitat distribution and topography are taken into account (Fig. 3). We further found, consistent with previous studies, that this bi-axial tendency appears to underpin a marked difference in wintering latitude (t-test; $t = 35.9$, $p < 0.001$).

This would imply that 1) bi-axial orientational variance facilitates wintering range expansion in blackcaps and 2) given that the pattern is unlikely to reflect the constraints imposed on blackcaps by topography and habitat, this likely

reflects bi-axial orientation variation in the inherited migratory direction.

Discussion

Using randomisation analyses, we found that north-migrating blackcaps took migratory bearings closer to those predicted by a complete axis reversal than would be expected by chance. Whilst our analyses aim to take into account biases in the spatial and temporal distribution of ringing effort, we cannot exclude that our results arise because an unconsidered factor is skewing blackcap migratory directions towards bimodality. Nonetheless, given an apparent paucity of unconsidered a priori factors that might skew ringing records bi-modally – and the fact our null model was entirely parameterised using real data – we suggest that genuine bi-modal variation in orientation is the best explanation of the trend at hand. This would suggest that a surprisingly high probability of bi-axial orientation may underpin recent migratory responses to a rapid anthropogenic environmental alteration.

Any facet of animal behaviour can be questioned both on its mechanistic basis – ‘how’ has the behaviour occurred – and also for its adaptive underpinning – ‘why’ it occurs (Tinbergen 1963, Wynn and Liedvogel 2023). Changes in migratory behaviour must, therefore, reflect both a change in the adaptive benefit associated with a given route – in this instance changes in the climate and in food availability (Plummer et al. 2015) – but likely also a change in the information input into the mechanism that drives migratory

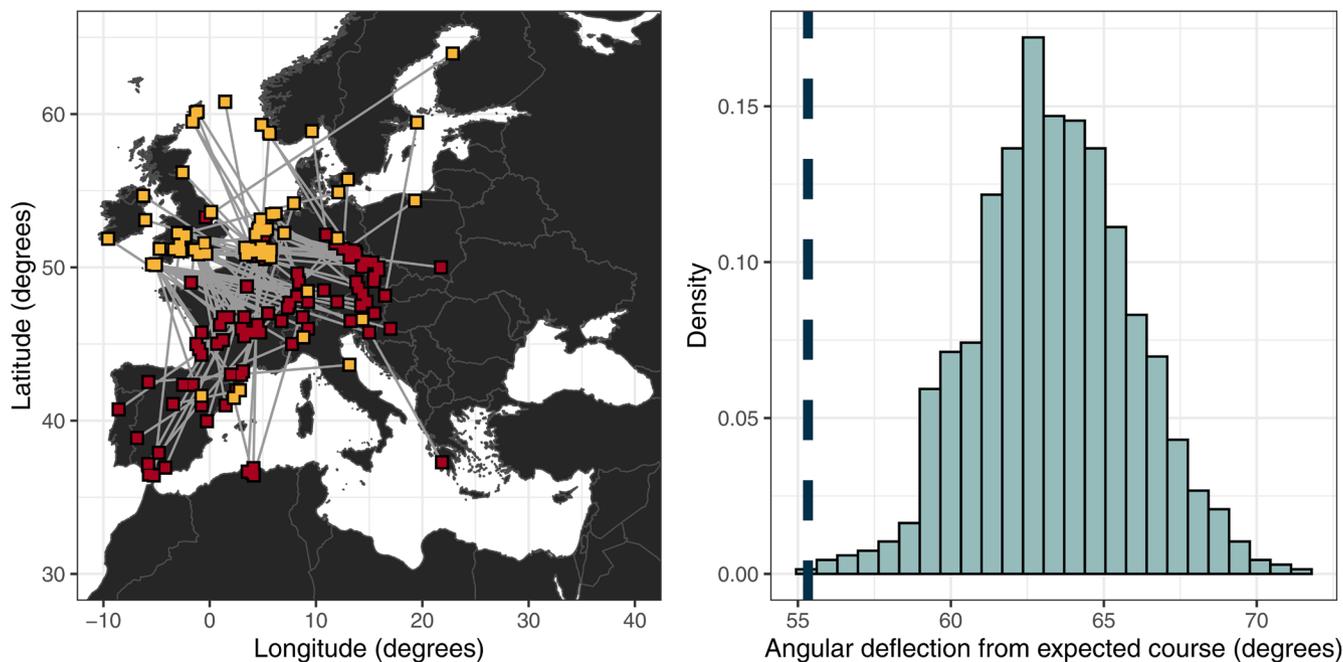


Figure 3. Axial variation in the migratory routes of Eurasian blackcaps. (left) The breeding (red) and wintering (yellow) sites of north-migrating blackcaps used in this analysis, with each recovery linked by a grey line between the breeding and non-breeding sites. (right) A histogram showing the mean angular deflection between null recovery sites and the expected recovery site, with the true observed-to-expected distance shown as a darker dashed line.

movement in a given direction (Wynn and Liedvogel 2023). The exception to this would be exclusively environmental factors – for example, pure wind drift – though such explanations seem unlikely. This is because a purely environmental factor-driven explanation would suggest birds act without agency and float ‘balloon-like’ through their environment, which we know is not the case given that birds express migratory preferences that can be quantified both in the field and in the laboratory. Hence, we suggest that changes in migratory behaviour must be explained by a combination of non-proximal change in the adaptive advantages of different migratory strategies – here, provided by anthropic environmental alteration – and also the mechanisms of migration.

As discussed above, the primary information inputs into the migratory phenotypes are typically considered to be cultural inheritance (Byholm et al. 2022), asocial learning (Guilford et al. 2011, Wynn et al. 2020a, b) and genetic inheritance (Sokolovskis et al. 2023). Consequentially, one (or multiple) of these sources could in principle drive bi-axial orientation to be disproportionately common. Over the course of several studies, blackcaps have been shown to have a major heritable component to their migratory orientation behaviour (Helbig 1991, Pulido et al. 2001, Delmore et al. 2020a, b), which supports the idea that the trend reported here likely reflects genetic evolution. This is further supported by details of the blackcap life history – they are short-lived, nocturnal migrants thought to migrate independent of conspecifics – which makes learning (either from experienced conspecifics or via trial-and-error) less likely. Further, there is no clear mechanism by which learning would lead to a precisely bi-modal pattern of migratory directions. Therefore, whilst the results presented here do not rule out a change in migratory destination underpinned by learnt information, and other hypotheses are undoubtedly possible, we believe that the trend at hand most conclusively reflects idiosyncrasies in the process by which migratory information is genetically encoded and inherited. We consequently discuss this concept further below.

If migratory direction were heritable, it would follow that the patterns of variance observed must somehow reflect the way in which migratory information is encoded. A dominant pattern of inheritance at a single genetic locus has recently been shown to apparently explain departures from the classically considered additive model of genetic variation in migratory trajectory (Helbig 1991, Sokolovskis et al. 2023). However, neither model of inheritance explains the bi-axial pattern at hand. Whilst examples of epistasis – interactions between genes at different loci to produce deviant phenotypes – are rare in animal behaviour (Godoy-Herrera et al. 2004, Yamamoto et al. 2009), it is possible that epistatic interactions produce a rare but predictable ‘reverse’ orientation direction that has become increasingly common in recent years. Indeed, a polygenic basis and/or epistatic interactions between genes at different loci could explain how extremely divergent migratory directions might arise extremely rapidly, since this would allow for divergent phenotypes to not depend on novel mutations/genetic

variants, but arise instead from standing genomic variation (Barrett and Schluter 2008). Epistatic interactions could involve the ‘clock’ used to determine migratory timing – as has been speculated to underpin the remarkable reversal of migratory direction/phenology described in cliff swallows *Petrochelidon pyrrhonota* and barn swallows *Hirundo rustica* in the Americas (Winkler et al. 2017, Areta et al. 2021, Helm and Muheim 2021) – though if this were the case in blackcaps, we might expect a reversal of breeding phenology also. Hence, it is perhaps more likely that axis reversal or bi-axial orientation instead reflects the mechanism by which orientation information is encoded.

To discuss precisely how directional information might be encoded such that bi-axial directional variation occurs is speculative. Nonetheless, it is possible that these divergent migratory routes reflect the axial encoding of direction, with birds storing the autumn migratory route as an axis of direction alongside a preference for a given pole of that axis (Wynn et al. 2022). This is an idea supported by the fact that songbirds apparently inherit both an autumn and a spring migratory direction (Zolotareva et al. 2021, Wynn et al. 2023). We might even suggest that the sensory and cognitive basis of avian compass orientation – where magnetic and star compass orientation is conducted relative to the pole/equator (and thus is symmetrical in both directions) rather than north/south (i.e. directional) – makes this two-step process (and in turn bi-axial orientation more generally) surprisingly plausible (Emlen 1967a, b, Wiltschko and Wiltschko 1972, Helm and Muheim 2021).

Irrespective of the underlying mechanism, understanding that migratory variance might vary bi-axially has two implications for our understanding of migratory ecology going forward. First, understanding the causes of bi-axiality in migratory direction is of some importance when investigating which gene(s) or regulatory region(s) is/are responsible for determining migratory direction. Recent advances in the affordability and resolution of biologging and genetic sequencing technology make genome-wide associations with migratory phenotype possible (Delmore et al. 2016, 2020a, b, 2023, Toews et al. 2019, Sokolovskis et al. 2023), and if such techniques were applied to migratory direction it is key that the mechanism by which directional information is encoded is understood fully. Without a complete understanding of how direction varies, and is in turn encoded, such analyses might fail to capture variance in migratory direction correctly, and hence lead to the erroneous association/dissociation of loci with directional traits.

Second, understanding the probability with which a given migratory route in one particular species is generated is key to understanding how and why migratory routes evolve in response to environmental change. If certain migratory phenotypes are unexpectedly common, then it would follow that – should conditions on these routes change – then increases in their use might be expected. This could in turn explain why birds from the eastern Palearctic – with a typical south-easterly migratory autumn direction – are becoming increasingly common in north-west Europe (Perea 2019,

Dufour et al. 2021). Understanding the interaction between ecological change and the mechanisms of migratory inheritance is, therefore, key to understanding some perhaps unanticipated consequences of global anthropic change.

Whilst it is necessarily difficult to draw conclusions based solely upon correlative analyses, we nonetheless believe our results inform upon both 1) the mechanisms by which migratory directions are encoded and 2) how future studies into the genetic correlates of migration direction might be conducted. Further, our results might be of utility when considered within the context of recent environmental shifts (e.g. changes in land use, climate and human activity). Therefore, we suggest that further studies utilising historic ringing recoveries or tracking data could be of considerable interest when considering how long-term ecological changes might interact with the mechanisms governing migratory direction to produce novel migratory routes.

Acknowledgements – We would like to thank both the European Union for Bird Ringing (EURING) data bank for compiling the data used in this study and everyone in Europe who has ringed a blackcap, without whom studies like this are not possible. We would also like to thank Oliver Padget, Tim Guilford, Paris Jagers, Joe Morford and Katrina Siddiqi-Davies for comments on an early version of this concept. An earlier version of this work is presented as a pre-print (Wynn et al. 2022).

Funding – This work was supported through funding from the Max Planck Society (MFFALIMN0001) and the DFG (SFB 1372 – Magnetoreception and Navigation in Vertebrates).

Author contributions

Joe Wynn: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Software (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Guillermo Fandos:** Formal analysis (supporting); Methodology (supporting); Writing – review and editing (supporting). **Kira Delmore:** Formal analysis (supporting); Investigation (supporting); Writing – review and editing (supporting). **Benjamin M. Van Doren:** Formal analysis (supporting); Writing – review and editing (supporting). **Thord Fransson:** Formal analysis (supporting); Writing – review and editing (supporting). **Miriam Liedvogel:** Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Project administration (equal); Resources (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/jav.03196>.

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.xsj3tx9px> (Wynn et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Åkesson, S. 1993. Coastal migration and wind drift compensation in nocturnal passerine migrants. – *Ornis Scand.* 24: 87–94.
- Åkesson, S., Karlsson, L., Walinder, G. and Alerstam, T. 1996. Bimodal orientation and the occurrence of temporary reverse bird migration during autumn in south Scandinavia. – *Behav. Ecol. Sociobiol.* 38: 293–302.
- Areta, J. I., Salvador, S. A., Gandoy, F. A., Bridge, E. S., Gorleri, F. C., Pegan, T. M., Gulson-Castillo, E. R., Hobson, K. A. and Winkler, D. W. 2021. Rapid adjustments of migration and life history in hemisphere-switching cliff swallows. – *Curr. Biol.* 31: 2914.
- Bakken, V., Runde, O. J., Tjørve, E. and Koblik, E. A. 2003. Norsk ringmerkjingsatlas, vol. 1. – Stavanger Museum.
- Barrett, R. D. H. and Schluter, D. 2008. Adaptation from standing genetic variation. – *Trends Ecol. Evol.* 23: 38–44.
- Bearhop, S., Fiedler, W., Furness, R. W., Votier, S. C., Waldron, S., Newton, J., Bowen, G. J., and Farnsworth, K., Berthold, P. and Farnsworth, K. 2005. Assortative mating as a mechanism for rapid evolution of a migratory divide. – *Science* 310: 502–504.
- Bengtsson, D., Fransson, T. and Roer, J. E. 2009. Occurrence of continental blackcaps *Sylvia atricapilla* in northern Europe. – *Ornis Svecica* 19: 41–49.
- Berthold, P. and Querner, U. 1981. Genetic-basis of migratory behavior in European warblers. – *Science* 212: 77–79.
- Berthold, P. and Terrill, S. B. 1988. Migratory behaviour and population growth of blackcaps wintering in Britain and Ireland: some hypotheses. – *Ring. Migr.* 9: 153–159.
- Berthold, P., Helbig, A. J., Mohr, G. and Querner, U. 1992. Rapid microevolution of migratory behavior in a wild bird species. – *Nature* 360: 668–670.
- Berthold, P., Gwinner, E. and Sonnenschein, E. 2013. Avian migration. – Springer.
- Biebach, H. 1983. Genetic determination of partial migration in the European robin (*Erithacus rubecula*). – *Auk* 100: 601–606.
- Busse, P. 1992. Migratory behaviour of blackcaps (*Sylvia atricapilla*) wintering in Britain and Ireland: contradictory hypotheses. – *Ring* 14: 51–75.
- Byholm, P., Beal, M., Isaksson, N., Lötberg, U. and Åkesson, S. 2022. Paternal transmission of migration knowledge in a long-distance bird migrant. – *Nat. Commun.* 13: 1–7.
- Chernetsov, N., Berthold, P. and Querner, U. 2004. Migratory orientation of first-year white storks (*Ciconia ciconia*): inherited information and social interactions. – *J. Exp. Biol.* 207: 937–943.
- Delmore, K. E. and Irwin, D. E. 2014. Hybrid songbirds employ intermediate routes in a migratory divide. – *Ecol. Lett.* 17: 1211–1218.
- Delmore, K. E., Toews, D. P. L., Germain, R. R., Owens, G. L. and Irwin, D. E. 2016. The genetics of seasonal migration and plumage color. – *Curr. Biol.* 26: 2167–2173.
- Delmore, K. E., Van Doren, B. M., Conway, G. J., Curk, T., Garrido-Garduno, T., Germain, R. R., Hasselmann, T., Hiemer, D., van der Jeugd, H. P., Justen, H., Lugo Ramos, J. S.,

- Maggini, I., Meyer, B. S., Phillips, R. J., Remisiewicz, M., Roberts, G. C. M., Sheldon, B. C., Vogl, W. and Liedvogel, M. 2020a. Individual variability and versatility in an eco-evolutionary model of avian migration. – *Proc. R. Soc. B* 287: 20201339.
- Delmore, K., Illera, J. C., Perez-Tris, J., Segelbacher, G., Ramos, J. S. L., Durieux, G., Ishigohoka, J. and Liedvogel, M. 2020b. The evolutionary history and genomics of European blackcap migration. – *eLife* 9: e54462.
- Delmore, K. E., Van Doren, B. M., Ullrich, K., Curk, T., van der Jeugd, H. P. and Liedvogel, M. 2023. Structural genomic variation and migratory behavior in a wild songbird. – *Evol. Lett.* 7: 401–412.
- Dufour, P., de Franceschi, C., Doniol-Valcroze, P., Jiguet, F., Guéguen, M., Renaud, J., Lavergne, S. and Crochet, P.-A. 2021. A new westward migration route in an Asian passerine bird. – *Curr. Biol.* 31: 5590–5596.e4.
- Emlen, S. T. 1967a. Migratory orientation in the indigo bunting, *Passerina cyanea*. Part II: mechanism of celestial orientation. – *Auk* 84: 463–489.
- Emlen, S. T. 1967b. Migratory orientation in the indigo bunting, *Passerina cyanea*. Part I: evidence for use of celestial cues. – *Auk* 84: 309–342.
- Fransson, T. and Stolt, B.-O. 1993. Is there an autumn migration of continental blackcaps (*Sylvia atricapilla*) into northern Europe. – *Vogelwarte* 37: 89–95.
- Godoy-Herrera, R., Burnet, B. and Connolly, K. 2004. Conservation and divergence of the genetic structure of larval foraging behaviour in two species of the *Drosophila simulans* clade. – *Heredity* 92: 14–19.
- Guilford, T., Freeman, R., Boyle, D., Dean, B., Kirk, H., Phillips, R. and Perrins, C. 2011. A dispersive migration in the Atlantic puffin and its implications for migratory navigation. – *PLoS One* 6: article e21336.
- Gwinner, E. 1986. Circannual rhythms in the control of avian migrations. – In: Rosenblatt, J. S. (ed.), *Advances in the study of behavior*, vol. 16. Elsevier, pp. 191–228.
- Hall-Karlsson, K. S. S. and Fransson, T. 2008. How far do birds fly during one migratory flight stage? – *Ring. Migr.* 24: 95–100.
- Handel, C. M. and Gill, R. E. 2010. Wayward youth: trans-Berlingian movement and differential southward migration by juvenile sharp-tailed sandpipers. – *Arctic* 63: 273–288.
- Hatzofe, O. and Yom-Tov, Y. 2002. Global warming and recent changes in Israel's avifauna note. – *Isr. J. Zool.* 48: 351–357.
- Helbig, A. J. 1991. Inheritance of migratory direction in a bird species: a cross-breeding experiment with SE- and SW-migrating blackcaps (*Sylvia atricapilla*). – *Behav. Ecol. Sociobiol.* 28: 9–12.
- Helm, B. and Muheim, R. 2021. Bird migration: clock and compass facilitate hemisphere switching. – *Curr. Biol.* 31: R1058–R1061.
- Kelsey, N. A., Schmaljohann, H. and Bairlein, F. 2019. A handy way to estimate lean body mass and fuel load from wing length: a quantitative approach using magnetic resonance data. – *Ring. Migr.* 34: 8–24.
- Komenda-Zehnder, S., Liechti, F. and Bruderer, B. 2002. Is reverse migration a common feature of nocturnal bird migration? – an analysis of radar data from Israel. – *Ardea* 90: 325–334.
- Lees, A. and Gilroy, J. 2022. *Vagrancy in birds*. – Princeton Univ. Press.
- Lindström, Å., Gill, R. E. Jr, Jamieson, S. E., McCaffery, B., Wernberg, L., Wikelski, M. and Klaassen, M. 2011. A puzzling migratory detour: are fueling conditions in Alaska driving the movement of juvenile sharp-tailed sandpipers? – *Condor* 113: 129–139.
- Lisovski, S. and Hahn, S. 2012. GeoLight-processing and analysing light-based geolocator data in R. – *Methods Ecol. Evol.* 3: 1055–1059.
- Mouritsen, H. and Mouritsen, O. 2000. A mathematical expectation model for bird navigation based on the clock-and-compass strategy. – *J. Theor. Biol.* 207: 283–291.
- Mueller, T., O'Hara, R. B., Converse, S. J., Urbanek, R. P. and Fagan, W. F. 2013. Social learning of migratory performance. – *Science* 341: 999–1002.
- Ożarowska, A., Ilieva, M., Zehtindjiev, P., Åkesson, S. and Muš, K. 2013. A new approach to evaluate multimodal orientation behaviour of migratory passerine birds recorded in circular orientation cages. – *J. Exp. Biol.* 216: 4038–4046.
- Paradis, E., Baillie, S. R., Sutherland, W. J. and Gregory, R. D. 1998. Patterns of natal and breeding dispersal in birds. – *J. Anim. Ecol.* 67: 518–536.
- Perdeck, A. 1958. Two types of orientation in migrating starlings, *Sturnus vulgaris* L., and chaffinches, *Fringilla coelebs* L., as revealed by displacement experiments. – *Ardea* 55: 1–3.
- Perea, J. M. G. 2019. Ringing recovery of yellow-browed warbler in Andalucía confirms overwintering in consecutive winters. – *Br. Birds* 112: 683–687.
- Plummer, K. E., Siriwardena, G. M., Conway, G. J., Risely, K. and Toms, M. P. 2015. Is supplementary feeding in gardens a driver of evolutionary change in a migratory bird species? – *Global Change Biol.* 21: 4353–4363.
- Pulido, F., Berthold, P., Mohr, G. and Querner, U. 2001. Heritability of the timing of autumn migration in a natural bird population. – *Proc. R. Soc. B* 268: 953–959.
- Shirihai, H. 1996. *The birds of Israel*. – Academic Press.
- Sokolovskis, K., Lundberg, M., Åkesson, S., Willemoes, M., Zhao, T., Caballero-Lopez, V. and Bensch, S. 2023. Migration direction in a songbird explained by two loci. – *Nat. Commun.* 14: 165.
- Svensson, L. 1970. *Identification guide to European passerines*. – Naturhistoriska Riksmuseet.
- Tautz, D., Reeves, G. and Pallares, L. F. 2020. New experimental support for long standing concepts of polygenic genetics implies that the Mendelian genetic paradigm needs to be revised: the new (old) genetics, ver. 1.0. – *NAL-live*. 2020: 1–15.
- Thorup, K. 1998. Vagrancy of yellow-browed warbler *Phylloscopus inornatus* and Pallas's warbler *Ph. proregulus* in north-west Europe: misorientation on great circles? – *Ring. Migr.* 19: 7–12.
- Thorup, K., Bisson, I. A., Bowlin, M. S., Holland, R. A., Wingfield, J. C., Ramenofsky, M. and Wikelski, M. 2007. Evidence for a navigational map stretching across the continental US in a migratory songbird. – *Proc. Natl Acad. Sci. USA* 104: 18115–18119.
- Thorup, K., Vega, M. L., Snell, K. R. S., Lubkovskaia, R., Willemoes, M., Sjöberg, S., Elbe-Bürger, A. and Bulyuk, V. 2020. Flying on their own wings: young and adult cuckoos respond similarly to long-distance displacement during migration. – *Sci. Rep.* 10: 1.
- Tinbergen, N. 1963. On aims and methods of ethology. – *Z. Tierpsychol.* 20: 410–433.
- Toews, D. P. L., Taylor, S. A., Streby, H. M., Kramer, G. R. and Lovette, I. J. 2019. Selection on VPS13A linked to migration in a songbird. – *Proc. Natl Acad. Sci. USA* 116: 18272–18274.

- Van Doren, B. M., Conway, G. J., Phillips, R. J., Evans, G. C., Roberts, G. C. M., Liedvogel, M. and Sheldon, B. 2021. Human activity shapes the wintering ecology of a migratory bird. – *Global Change Biol.* 27: 2715–2727.
- Wiltschko, W. and Wiltschko, R. 1972. Magnetic compass of European robins. – *Science* 176: 62–64.
- Winkler, D. W., Gandoy, F. A., Areta, J. I., Iliif, M. J., Rakhimberdiev, E., Kardynal, K. J. and Hobson, K. A. 2017. Long-distance range expansion and rapid adjustment of migration in a newly established population of barn swallows breeding in Argentina. – *Curr. Biol.* 27: 1080–1084.
- Wynn, J. and Liedvogel, M. 2023. Lost: on what level should we aim to understand animal navigation? – *J. Exp. Biol.* 226: jeb245441.
- Wynn, J., Collet, J., Prudor, A., Corbeau, A., Padget, O., Guilford, T. and Weimerskirch, H. 2020a. Young frigatebirds learn how to compensate for wind drift. – *Proc. R. Soc. B* 287: article 20201970.
- Wynn, J., Padget, O., Mouritsen, H., Perrins, C. and Guilford, T. 2020b. Natal imprinting to the Earth's magnetic field in a pelagic seabird. – *Curr. Biol.* 30: 2869–2873.e2.
- Wynn, J., Guilford, T., Padget, O., Perrins, C. M., McKee, N., Gillies, N., Tyson, C., Dean, B., Kirk, H. and Fayet, A. L. 2022. Early-life development of contrasting outbound and return migration routes in a long-lived seabird. – *Ibis* 164: 596–602.
- Wynn, J., Padget, O., Mouritsen, H., Morford, J., Jagers, P. and Guilford, T. 2022. Magnetic stop signs signal a European songbird's arrival at the breeding site after migration. – *Science* 375: 446–449.
- Wynn, J., Leberecht, B., Liedvogel, M., Burnus, L., Chetverikova, R., Döge, S., Karwinkel, T., Kobylkov, D., Xu, J. and Mouritsen, H. 2023. Naive songbirds show seasonally appropriate spring orientation in the laboratory despite having never completed first migration. – *Biol. Lett.* 19: 20220478.
- Wynn, J., Fandos, G., Delmore, K., Van Doren, B. M., Fransson, T. and Liedvogel, M. 2024. Data from: Could bi-axial orientation explain range expansion in a migratory songbird?. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.xsj3tx9px>.
- Yamamoto, A., Anholt, R. R. H. and Mackay, T. F. C. 2009. Epistatic interactions attenuate mutations affecting startle behaviour in *Drosophila melanogaster*. – *Genet. Res.* 91: 373–382.
- Yoda, K., Yamamoto, T., Suzuki, H., Matsumoto, S., Müller, M. and Yamamoto, M. 2017. Compass orientation drives naive pelagic seabirds to cross mountain ranges. – *Curr. Biol.* 27: R1152–R1153.
- Zolotareva, A., Utvenko, G., Romanova, N., Pakhomov, A. and Chernetsov, N. 2021. Ontogeny of the star compass in birds: pied flycatchers (*Ficedula hypoleuca*) can establish the star compass in spring. – *J. Exp. Biol.* 224: jeb237875.