

## Bird migration: when vagrants become pioneers

Alexander C. Lees<sup>1,2,\*</sup> and James J. Gilroy<sup>3</sup>

Vagrancy - the appearance of individuals far from their regular range - is a surprisingly common phenomenon in many bird species, often occurring in spatiotemporally predictable patterns [1,2]. The phenomenon has generated a large academic corpus – rich both in description of the patterns of vagrancy and in theories about the potential biological significance of this phenomenon, but typically short on empirical evidence [3,4]. For example, the regular appearance of dozens of ostensibly Asian songbirds in Europe, North Africa and the Middle East has been documented for several centuries; species that breed in Siberia and normally migrate to the Indian Subcontinent or South-east Asia for winter. Some species are so regular in Western Europe as to raise the possibility of an alternative hypothesis – that they represent small but viable populations performing regular migrations to wintering grounds half a hemisphere away from most conspecifics. We coined the term ‘pseudo-vagrants’ [5] to describe such populations, arguing that they may be of considerable biological significance, and not biological ‘dead-ends’ as commonly assumed. In this issue Dufour et al. [6] have finally provided firm evidence that the appearance in Europe of at least one regular Siberian ‘vagrant’ does indeed represent an apparently viable population, with a novel and idiosyncratic migration strategy. This discovery has considerable ramifications for our understanding of flexibility and constraint in avian migration systems [7] especially in the context of global change.

Ascertaining the origins and annual cycles of ‘vagrant’ birds is a challenge that has defied ornithologists for decades. Traditional migration monitoring methods like bird ringing have amassed very few meaningful recoveries of vagrants [3], and most of the species involved are too small to carry expensive satellite tags that would give real-time information on their position. All other forms of tracking technology necessitate that the individual be recaptured – difficult when we typically only encounter vagrants unpredictably on migration, heading to and from destinations unknown. Dufour et al. [6] resolved this problem by selecting a focal species – the Richard's Pipit (*Anthus richardi*) - that has a somewhat predictable pattern of occurrence in Europe, albeit still as a considerable rarity. This species has long been suspected of having a toehold as a regular migrant to Europe, despite breeding no nearer than the grasslands of the Eastern Palearctic and typically wintering only in south and south-east Asia. Intriguingly, the species was first described not from specimens obtained in Asia, but by Louis Vieillot from birds collected in eastern France by Charles Richard (1745–1835), the director of the postal service at Lunéville, whose name the species now bears [8]. Since then, Richard's Pipits have remained a rare but regular feature of Europe's avifauna, usually appearing along western coasts in autumn (and far more infrequently in spring). There is evidence of an increase through the latter half of the 20<sup>th</sup> century, albeit confounded by widening public interest in birdwatching and in our capacity to identify tricky ‘little brown jobs’ like pipits. From the 1980s onwards the species began to be found wintering around the Mediterranean basin, sometimes even in small flocks; circumstances suggestive of a ‘pseudo-vagrant’ population migrating annually along an unusual longitudinal axis between Europe and Asia [4]. However, alternative theories could also explain this regular overwintering – perhaps population increases were simply leading to a higher background rate of vagrancy [9], with the over-winterers ultimately destined never to return to their natal area in spring. A further alternative was that these

individuals were indeed performing a novel migration, but perhaps from an undiscovered population breeding far closer to Europe than the Central Asian Steppe.

Dufour et al. [6] adopted a three-fold approach to test the pseudo-vagrancy hypothesis, involving intensive fieldwork to determine demographic structure, return rates and track the migratory movements of individuals, followed by an interrogation of citizen science data to understand demographic trends and finally a modelling approach to compare the environmental conditions in these novel wintering areas to those of the species' regular range. The team were able to catch 81 individuals to colour-ring (colour-band) them and ascertain their ages – of which 34% were adults. Of 68 individuals ringed in their first two seasons, 11 were re-sighted in subsequent winters. To track the pipits, the team equipped seven individuals with Global-Location-Sensors (GLS) dataloggers during the winter of 2019/2020 and then crossed their fingers that the birds would return the next season. The following winter they managed to recapture three individuals, all of which had spent the previous summer 6000 km away in the Novosibirsk Oblast region of Russia, at the western edge of the pipits' known breeding range. This demonstration of winter site fidelity (and apparently strong migratory connectivity) provides convincing evidence in support of the migration rather than vagrancy hypothesis. This was further strengthened by their review of archived digital images, which also indicated that adult birds were regularly recorded in winter elsewhere in the Iberian Peninsula, Morocco, western France, and Italy.

To explore the climate suitability of the species' ancestral wintering range to the derived range Dufour et al. used citizen science records of the species and compared the climate suitability of southern Europe between 1961-1990 and 1990-2018. They found that the potential climate niche of the species had expanded northwards between these two periods – concurrent with the discovery of the species regularly wintering in southern Europe. They go on to provide a convincing case that this discovery is not simply the result of changes in observer awareness and activity. However, there remains the possibility that this disjunct wintering population may be more historically dynamic. The German ornithologist Heinrich Gätke was convinced as long ago as the 19<sup>th</sup> Century that Richard's Pipits performed regular return-migrations from Siberia to Europe, and recorded them on the North Sea migration outpost of Helgoland in considerable numbers, writing "*Nor must such individuals [of Richard's Pipits] be in any sense regarded as isolated rarities or 'stragglers,' for not only are they met with regularly every autumn, but they frequently attain to the comparatively large numbers of from ten to fifty, and in two or three instances of even a hundred individuals in a single day*" [1]. Gätke suspected the birds were migrating to Iberia, and 24 years previously Howard Saunders wrote in his treatise on the birds of Southern Spain that the species was not uncommon there in some winters [10].

Many questions remain – how ephemeral might these pseudo-vagrant populations be, at what point do such wintering populations become viable or self-sustaining, and what is the mechanistic basis for the emergence of an apparently novel migratory orientation entirely divergent from the population at large? The underlying causes of vagrancy in migratory birds are often assumed to be either wind drift or 'faulty' internal compass mechanisms that cause individuals to deviate from their normal routes [11]. In both cases, the long-term colonisation of new stop-over or wintering sites can only occur if the 'directions' for the novel migratory route can be passed on to subsequent generations. In the case of vagrancy arising from wind-drift, this could only realistically occur through cultural transmission (i.e. young birds following

adults that learned the novel route in previous years). Internal compass 'errors', by contrast, could also be transferred genetically, and there is some evidence for this being a driver of rapid migratory change [12]. One form of navigational 'error' that may cause extreme long-distance vagrancy akin to the pipits of Dufour et al. [6] is 'reverse migration' [4, 11]. Here, migrating individuals are thought to mistake north for south when reading their innate compass, and thus perform their 'intended' migration backwards [4]. This could explain the original arrival of Richard's Pipits in Western Europe, given that their normal migration route may involve an initial eastward trajectory to avoid crossing the Gobi Desert and Himalayan massif (Fig. 1). The potential for this form of navigation error to give rise to novel and heritable migratory programmes remains unknown.

An ebb and flow of small extralimital foothold wintering populations might be expected among abundant long-distance migrants that are inevitably prone to vagrancy through abmigration or wind-drift, but such footholds are likely to be easily extinguished by stochastic events such as cold winters. Nevertheless, their existence is powerful evidence that bird migration routes can be remarkably flexible despite the constraints imposed by energetics and navigatory systems [7]. Migratory species are among those most significantly affected by habitat loss and climate change, but species with higher migratory dispersion - i.e., those occupying larger non-breeding ranges relative to breeding, are less likely to be declining [13]. This reinforces the notion that although most vagrants are ultimately of little biological significance, a significant proportion may become the founders of new migratory routes and even populations [4, 14], which may mitigate impacts of global change and even lead to new populations establishing themselves on divergent evolutionary pathways [15].

## References

1. Gätke, H. (1895). Heligoland as an ornithological observatory: the result of fifty years' experience. D. Douglas.
2. Grinnell, J. (1922). The role of the 'accidental'. *Auk* 39, 373–380.
3. Newton, I. (2010). *The migration ecology of birds*. Elsevier.
4. Lees, A.C. and Gilroy, J.J. (2021). Vagrancy in Birds. Bloomsbury
5. Gilroy, J.J. and Lees, A.C. (2003). Vagrancy theories: are autumn vagrants really reverse migrants?. *Br. Birds* 96, 427–438.
6. Dufour, P., Franceschi, C., Doniol-Valcroze, P., Jiguet, F., Guéguen, M., Renaud, J., Lavergne, S., Crochet, P-A. (2021). Uncovering a new westward migration route in an Asian passerine bird. *Curr. Biol.* xxxxx
7. Sutherland, W.J. (1998). Evidence for flexibility and constraint in migration systems. *J. Avian Biol.* 29, 441–446.
8. Mearns, R., Gouraud, C. and Chevrier, L. (2015). The identity of Richard of Richard's pipit (*Anthus richardi* Vieillot, 1818). *Arch. Nat. Hist.* 42, 85–90.
9. Veit, R.R. (2000). Vagrants as the expanding fringe of a growing population. *Auk* 117, 242–246.
10. Saunders, H. (1871). A list of the birds of Southern Spain. *Ibis* 13, 205–225.
11. Thorup, K., Ortvad, T. E., Holland, R. A., Rabøl, J., Kristensen, M. W., & Wikelski, M. (2012). Orientation of vagrant birds on the Faroe Islands in the Atlantic Ocean. *J. Ornithol.* 153, 1261–1265.
12. Berthold, P., Helbig, A. J., Mohr, G., & Querner, U. (1992). Rapid microevolution of migratory behaviour in a wild bird species. *Nature* 360, 668–670.

13. Gilroy, J.J., Gill, J.A., Butchart, S.H., Jones, V.R. and Franco, A.M. (2016). Migratory diversity predicts population declines in birds. *Ecol. Lett.* 19, 308–317.
14. Davis, R.A. and Watson, D.M. (2018). Vagrants as vanguards of range shifts in a dynamic world. *Biol. Conserv.* 224, 238–241.
15. Rolshausen, G., Segelbacher, G., Hobson, K.A. and Schaefer, H.M. (2009) Contemporary evolution of reproductive isolation and phenotypic divergence in sympatry along a migratory divide. *Curr. Biol.* 19, 2097–2101.

<sup>1</sup>Department of Natural Sciences, Manchester Metropolitan University, Manchester, M1 5GD, UK

<sup>2</sup>Cornell Lab of Ornithology, Cornell University, Ithaca, NY 14850, USA

<sup>3</sup>School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, UK

\*Email: [alexander.lees@mmu.ac.uk](mailto:alexander.lees@mmu.ac.uk)



Figure 1. an [age] Richard's Pipit (*Anthus richardi*) taken on novel wintering grounds in (location, date] {photographer]

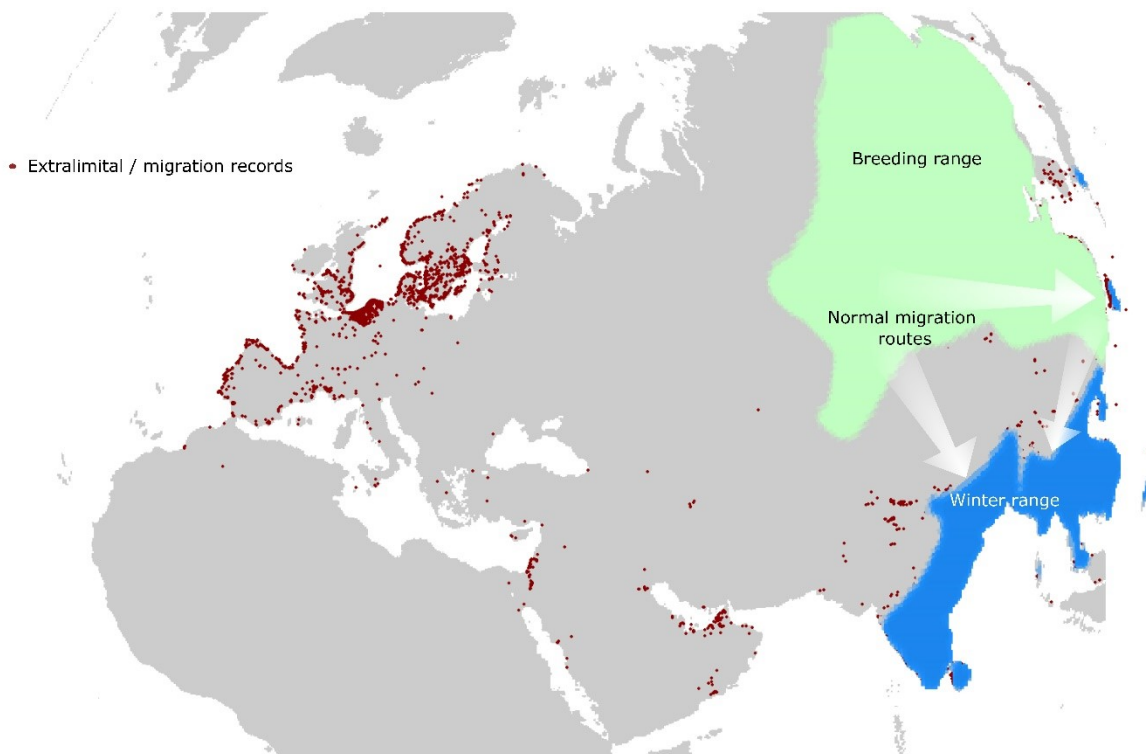


Figure 2. Breeding (green) and non-breeding (blue) range of the Richard's Pipit (*Anthus richardi*) with recent extralimital records extracted from eBird (<https://ebird.org/>)