DISPATCH

Bird migration: When vagrants become pioneers

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Vagrant birds are frequently recorded outside of their regular geographic range. A new study documents how vagrancy, in this case in an Asian songbird can lead to establishment of a new migration route.

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 been documented intensely — describing patterns of vagrancy and developing 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 such as Olive-backed Pipits (*Anthus hodgsoni*), Yellow-browed (*Phylloscopus inornatus*) and Dusky Warblers (*P. fuscatus*) in Europe, North Africa and the Middle East has been demonstrated for several centuries; species that breed in Siberia and normally migrate to the Indian Subcontinent or South-east Asia for winter. Some of these species are so regular in Western Europe as to raise the possibility of an alternative hypothesis to vagrancy — that they are 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 often assumed. In this issue of *Current Biology*, Paul Dufour, Sébastien Lavergne, Pierre-André Crochet and colleagues[6] have finally provided firm evidence that the appearance in Europe of at least one regular Siberian 'vagrant' bird 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 bird migration[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, such as bird ringing, have amassed very few meaningful recoveries of vagrants[3], and many species involved are too small to carry expensive satellite tags that would give real-time information on their position. 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. In their study, Dufour and colleagues[6] have resolved this problem by selecting a focal species — Richard's Pipit (*Anthus richardi*; Figure 1) — that occurs somewhat predictably in Europe, while still being rare (Figure 2). Richard's Pipit 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 (Figure 2), usually appearing along western coasts in autumn (and far less often in spring). There is evidence of an increase through the latter half of the 20th century, albeit confounded by widening public interest in birdwatching and in our increased capacity to identify tricky 'little brown birds', such as pipits, with better optical equipment. From the 1980s onwards, the species began to be found wintering around the Mediterranean basin, sometimes even in small flocks, which suggested 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. Alternatively, these individuals might indeed perform a novel migration, but perhaps from an undiscovered population breeding far closer to Europe than the Central Asian Steppe.

Dufour and colleagues[6] adopted a three-fold approach to test the pseudo-vagrancy hypothesis, involving intensive fieldwork to determine demographic structure, return rates and migratory movements of individuals. They also relied on citizen-science data to understand demographic trends and finally used a modelling approach to compare the environmental conditions in these novel wintering areas to those of the species' regular range. The team was able to catch 81 individuals to colour-ring (colour-band) them and ascertain their ages (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 birds with Global-Location-Sensor 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) convincingly supports the hypothesis that this is a novel migration pattern rather than vagrancy. This notion was further strengthened by their review of archived digital images, which 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 new range, Dufour and colleagues[6] 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 provide a convincing case that this discovery is not simply the result of changes in observer awareness and activity. However, this disjunct wintering population may be more historically dynamic. In the 19th century, the German ornithologist Heinrich Gätke was convinced 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 and colleagues[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 (Figure 2).

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 particularly prone to vagrancy through ‘abmigration’ (where individuals establish pairs in the winter quarters and may accompany their mate on spring migration to a breeding area geographically disjunct from their natal one) 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 — 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].

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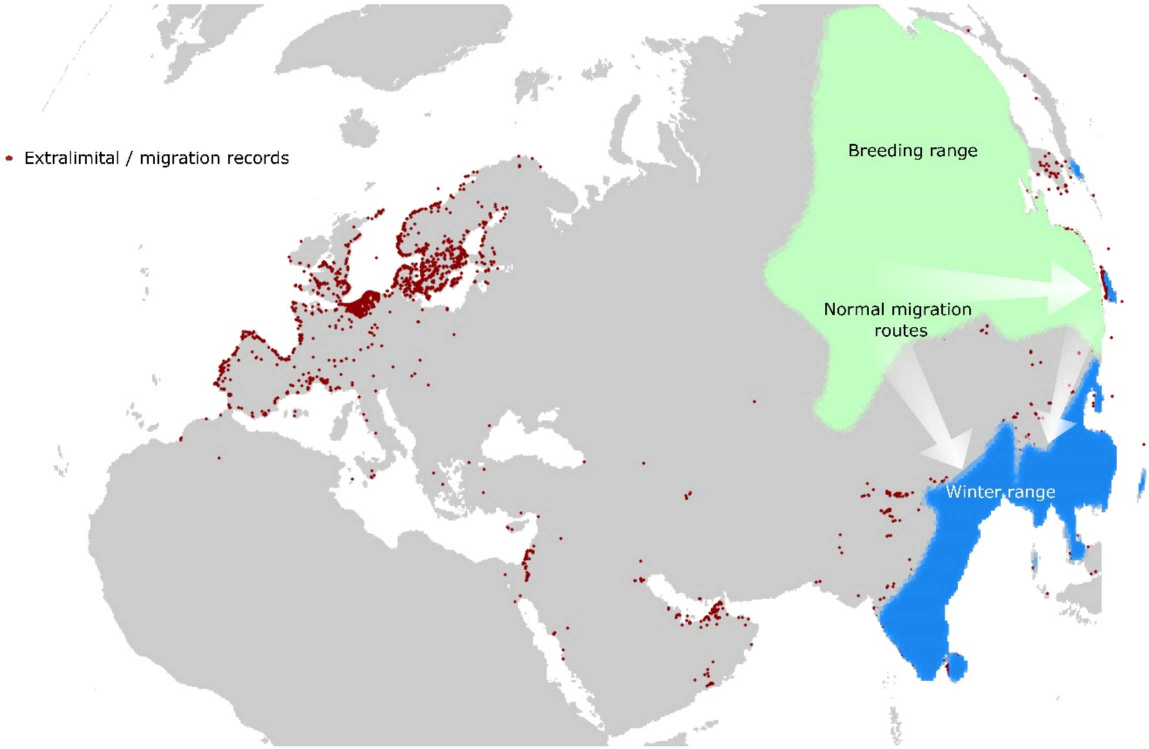
Figure 1. A first year Richard's Pipit (*Anthus richardi*).
Photo: Ayuwat Jearwattanakanok.

Figure 2. Geographic range of the Richard's Pipit *(Anthus richardi*)
Breeding range indicated in green, and non-breeding range in blue with recent extralimital records extracted from eBird (https://ebird.org/) as red dots.


Extralimital / migration records
Breeding range
Normal migration routes
Winter range