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TITLE: The overlooked importance of vagrancy in ecology and evolution

ABSTRACT:

Vagrancy is the occurrences of individuals outside the normal geographic range of their species. These rare and unpredictable events have long been neglected by the scientific community, belying a growing body of evidence that vagrancy can have an important role in eco-evolutionary processes at both population and community scales.

MAIN TEXT:

Scientific neglect of an important phenomenon

Although vagrants have been enthusiastically cataloged by amateur naturalists for centuries, there has been relatively little research into their biological significance. While instances of **vagrancy** (see Glossary) are rare by nature, they may precipitate ecological or evolutionary outcomes, which would have been difficult to predict and are akin to ecological **'black swan' events** [1]. Similarly, little attention has been paid to the mechanisms underpinning vagrancy, despite their potential to illuminate heritability and developmental stability of movement programmes. Simultaneously, progress in the field has been hampered by inconsistent use of terminology, as well as inappropriate evolutionary concepts which have even verged on **group selection** arguments. In this forum, we argue that this poorly understood phenomenon deserves more attention from researchers, and needs a clarified framework grounded in robust evolutionary concepts to understand the eco-evolutionary consequences of extreme movements in the animal kingdom.

What is vagrancy?

We define vagrancy as the appearance of an individual outside the normal **geographic distribution** range of its species. While this definition is conceptually clear, delineating the normal distribution of a species is not always straightforward, except where distributions are constrained by clear biogeographic barriers such as water bodies or mountain ranges. In practice, range limits can routinely fluctuate over time, making it difficult to define areas where occurrence is rare enough to qualify as vagrancy. Even if vagrants are rare by definition, vagrants of abundant species can reach such high numbers locally that vagrancy may become hard to distinguish from regular movements. Yet, many instances of vagrancy involve occurrences in areas that are highly disjunct from the species' normal range, and even arbitrary threshold-based delimitation with respect to imperfectly known range limits can allow for valuable insights (see Figure 1).

The mechanisms that lead to vagrancy are variable and complex. Both **active** and **passive movements** can send individuals beyond the distribution of their species. Passive mechanisms include rafting, wind-borne movements, or displacement by water currents. Vagrancy by active movements can arise from outliers in distance and/or orientation during behavior initiated and actively controlled by animals, including **seasonal migration**, **dispersal**, **nomadism**, **irruptive movements**, **exploratory** or **foraging trips**.

While external drivers such as weather can intervene on both active and passive movements, a multitude of further external drivers (e.g., geomagnetic and solar anomalies) and internal mechanisms (e.g., plasticity and genetics) can contribute to vagrancy from active movements [2]. Our understanding of these causes, particularly internal ones, remains limited, though the spatial and temporal distribution of vagrant records suggest key processes include exaggeration of regular movements (seasonal migration, nomadism, erratic or foraging movement) or the malfunctioning of navigation systems [2]. These navigational errors are inferred based on occurrence patterns representing coherent but abnormal trajectories from those normally performed, hence suggesting that some vagrants are **misoriented** and not **disoriented**.

Vagrancy and dispersal are linked but not analogous

Vagrancy has recently been defined as a process by which organisms engage in long-distance dispersal movements outside of their known species range, or "the mechanism by which growing populations can colonize newly available habitats" [3]. While vagrancy *can* lead to dispersal and the colonization of new regions, it is important to recognize that not all vagrancy is dispersal (many cases of vagrancy are not followed by any reproduction attempt, others can end up with a return to the point of departure), and not all dispersal is vagrancy (most movements leading to dispersal do not go beyond the species' normal range).

Another source of confusion in the recent literature follows viewing the persistence of vagrancy as arising from benefits to the population as a whole [e.g., 3], implying group selection; no realistic mechanism predicts that some individuals sacrifice their fitness for the 'good of the species'. Some of the best examples of avian vagrancy involve young individuals migrating in a direction that does not lead them to the species' normal wintering range: most will not survive to reproduce, and they thus represent an evolutionary dead-end. New vagrants arise in every generation from the pool of normally migrating individuals. There is little doubt that these vagrancy movements are usually costly (and often lethal), as most movements outside a species' range bring the individuals to unsuitable habitats or far from any conspecifics. Vagrancy should thus be strongly counter-selected, and its contribution to changes in distribution is similar to those of mutations: most are deleterious but those that are favored fuel evolution and adaptation.

Vagrancy shines a light on movement ecology

Like many other biological phenomena, we need to study variation in orientation / navigation phenotypes to understand their biological bases. There are still many unanswered questions about the neurophysiological bases and heritability of animal navigation [4] and understanding why individuals engage in abnormal movements can help answer them.

For example, many young migratory birds undertake their first seasonal migration alone using compass headings and information on distance/flight duration hardwired into their neural systems [4] but we still do not fully understand how environmental cues are deciphered to achieve this. In this context, misorientation patterns in vagrants failing to identify the reference point on the compass (e.g. either magnetic north or south in the case of **reverse migration**, depending on the hemisphere [2]) or failing to use the correct angle with respect to the north–south reference line (in the case of **mirror-image migration** [2]) can teach us a lot about how birds use a north-south reference for orientation. Similarly, exploring the role of magnetic anomalies in driving vagrancy could provide key insights into the use of magnetic cues in migration.

Ecological and evolutionary consequences of vagrancy

Most of the time, vagrancy has few consequences, as vagrants arriving in unsuitable habitats far from conspecifics are likely to die before reproducing. Furthermore, some individuals that engage in extreme exploratory movements might permanently return to their natal area, resulting in no evolutionary impact. Yet many ecological and evolutionary consequences of vagrancy have been reported in various regions and across diverse taxonomic groups.

Some of the most important ecological consequences of vagrancy (depicted in green in Figure 2) involve the dispersal of pathogens or parasites through passive transport by vagrants [5]. More generally, vagrancy is a key avenue for the colonization of new areas, sometimes far from species' ancestral range and is thus an increasingly important process underpinning species responses to rapid climate change and land-use [6]. Importantly, colonization may also involve pest species which could represent new challenges for agriculture [7]. It might be assumed that vagrancy promotes the colonization of new areas more frequently if it occurs before or during the breeding season, but this has not been clearly tested. Even in the absence of colonization, vagrants can have important impacts - for example novel predators reaching insular environments can disrupt ecosystem stability and potentially threaten endemic species [8].

Vagrants may promote the evolution of new migration routes, whether they are encoded genetically [9], or culturally ([10]; Figure 2), provided that the novel route is transferred to offspring [11]. Vagrancy can also foster the evolution of new species after the colonization of new regions, whether vagrancy originated from active movements (e.g., misoriented migrants) or passive movements (e.g., rafting [12]). Finally, vagrancy can also promote the evolution of new modes of reproduction, as illustrated by the emergence of exclusive parthenogenesis in an otherwise sexually reproducing damselfly (citrine forktail *Ischnura hastata*) after it colonized the Azores [13].

We contend that vagrancy research can play an important role in advancing our understanding of spatial ecology and evolution, with the potential to pay dividends in unlocking new insights into large-scale eco-evolutionary dynamics.

REFERENCES:

1. Anderson, S.C. et al. (2017) Black-swan events in animal populations. *Proceedings of the National Academy of Sciences* 114, 3252–3257
2. Lees, A.C. and Gilroy, J.J. (2021) *Vagrancy in Birds*, Christopher Helm
3. Veit, R.R. et al. (2022) Editorial: Vagrancy, exploratory behavior and colonization by birds: Escape from extinction? *Front Ecol Evol* 10: 960841. doi: 10.3389/fevo.2022.960841
4. Mouritsen, H. (2018) Long-distance navigation and magnetoreception in migratory animals. *Nature* 558, 50–59
5. Ellis, V.A. et al. (2023) Host shift and natural long-distance dispersal to an oceanic island of a host-specific parasite. *Biol Lett* 19: 1920220459. 20220459 doi: 10.1098/rsbl.2022.0459
6. Hill, L. (2018). Vagrant status of lucerne seed web moth, *Etiella behrii* (Zeller 1848) (Lepidoptera: Pyralidae) in Tasmania. *Crop Protection* 104, 65–71.
7. Kalwij, J.M. et al. (2019) Vagrant birds as a dispersal vector in transoceanic range expansion of vascular plants. *Sci Rep* 9, 4655
8. Jiguet, F. et al. (2007) Quantifying stochastic and deterministic threats to island seabirds: last endemic prions face extinction from falcon peregrinations. *Anim Conserv* 10, 245–253
9. Dufour, P. et al. (2021) A new westward migration route in an Asian passerine bird. *Current Biology* 31, 5590-5596.e4
10. Madsen, J. et al. (2023) Rapid formation of new migration route and breeding area by Arctic geese. *Current Biology* 33, 1162-1170.e4
11. Vickers, S. H., Franco, A. M., & Gilroy, J. J. (2023). Non-reproductive dispersal: an important driver of migratory range dynamics and connectivity. *Ecography* 5, e06201.
12. Ali, J.R. and Vences, M. (2019) Mammals and long-distance over-water colonization: The case for rafting dispersal; the case against phantom causeways. *Journal of Biogeography* 46: 2632–2636
13. Lorenzo-Carballa, M.O. et al. (2017) Parthenogenesis did not consistently evolve in insular populations of *Ischnura hastata* (Odonata, Coenagrionidae). *Ecol Entomol* 42, 67–76

FIGURE LEGENDS:

Figure 1. How to identify individuals as vagrants?

Here we illustrate vagrancy records of different species: two migratory birds (the elegant tern in A and the scissor-tailed flycatcher in D), a migratory or nomadic dragonfly (the keyhole glider in B) and one marine mammal (the subantarctic fur seal in C). The first three examples illustrate trans-oceanic movements or records of vagrants hundreds or thousands of kilometers from their regular range. In such cases, it is easy to identify vagrants by examining the distribution of these occurrences compared to the species' range limits. In the last example (D), the limit is more difficult to define, as cases of vagrancy become progressively rarer as the distance from the species' distribution limits increases but may also depend on observation bias (coastal and observer effects: the second peak mainly corresponds to data from Florida, USA). Distribution ranges have been mapped using the IUCN distribution data (2022, https://www.iucnredlist.org). Occurrences data have been downloaded from GBIF (GBIF.org - doi: 10.15468/dl.wn2vxg; 10.15468/dl.n67prw; 10.15468/dl.wemabz; 10.15468/dl.ywmnhd) and were thinned and intersected with distribution data. Some occurrences have been added after reviewing the literature. Note that the y-axis (frequency) is not the same for the four species. Image credits: (A) elegant tern (*Thalasseus elegans*) by Sloalan (CC0 1.0), (B) keyhole glider (*Tramea basilaris*) by Hopeland (CC BY 4.0), (C) subantarctic fur seal (*Arctocephalus tropicalis*) by Antoine Lamielle (CC BY-SA 4.0) and (D) scissor-tailed flycatcher (*Tyrannus forficatu*s) by PEHart (CC BY-SA 2.0).

Figure 2. Important ecological and evolutionary consequences of vagrancy across the animal kingdom.
Key consequences, discussed in the text, are shown in colored, bold text. Ecological consequences are in green and evolutionary consequences are in red. Although vagrancy can affect all organisms, we list here examples of animal movements. Image credits: (A) São Tomé shrew (*Crocidura thomensis*) by Ricardo Lima, lowland streaked tenrec (*Hemicentetes semispinosus*) by Frank Vassen (CC BY 2.0), (B) citrine forktail (*Ischnura hastata*) by Judy Gallagher (CC BY 2.0), (C) pink-footed goose (*Anser brachyrhynchus)* by Christoph Moning (CC BY 4.0), (D) Richard's pipit (*Anthus richardi*) by Daniel-Lopez Velasco, (E) monarch butterfly (*Danaus plexippus*) by Bernard Spragg (CC0 1.0), (F) small flowering shrub (*Ochetophila trinervis*) by Guillermo Debandi (CC BY 4.0), (G) parasites (*Haemoproteus*) by Andrés Ramirez-Barrera (CC BY 4.0), (H) lucerne seed web moth (*Etiella behrii*) by dhorben (CC BY 2.0) and (I) peregrine falcon (*Falco peregrinus*) by Fyn Kynd (CC BY 2.9).

GLOSSARY:

Active movements: movements that are initiated and actively controlled by the animal itself.

Black swan events: improbable events that nonetheless occur, often with profound consequences.

Disorientation: the condition in which the animals exhibit a loss of orientation. The animal has lost its sense of direction entirely and is unable to determine its position or navigate accurately.

Dispersal: any movement that has the potential to lead to gene flow. It refers to the movement of individuals from their birth site to the site of their first breeding attempt ('natal dispersal') or the movement from one breeding site to another ('breeding dispersal'). Reproduction need not be successful for such movements to constitute dispersal.

Exploratory trips: exploratory movements usually performed by young animals prior to their first reproduction where they learn to navigate and explore their environment, find food, and establish territories.

Foraging movements: movements undertaken by an animal to search for, locate, and acquire food resources in its environment. Many seabirds can engage in extremely long foraging movements starting from and returning to their nest to feed during various stages of their breeding cycles.

Geographic distribution: the range of geographical locations in which a species is usually found, sometimes only during certain periods of the annual cycle.

Group-selection: a controversial concept that posits natural selection acts not only on individuals within a population but also on whole groups or social units. The idea is that certain traits or behaviors can evolve and be favored because they enhance the fitness of the group as a whole, even if they may not directly benefit the individual organisms within the group. Theoretical population genetics work has demonstrated that group selection can only occur under very restrictive conditions that are not normally met in nature.

Passive movements: movements that occur without direct active effort or control by the animal, mostly driven by external forces or factors in the environment.

Mirror-image migration: phenomenon described in bird migration where individuals follow a mirror image of their normal migration path by taking the correct angle with respect to the north-south axis but choosing a wrong east-west sense of that angle.

Misorientation: the condition in which animals become incorrectly oriented or lose their sense of direction. The animal can be facing a certain direction or following a particular path but its orientation or directional perception is inaccurate or mistaken.

Nomadism: movements of populations driven by spatio-temporal resource heterogeneity, not seasonally predictable

Reverse migration: phenomenon described in bird migration where an individual flies in the opposite direction of what is typical of its species during the spring or autumn migration.

Seasonal migration: regularly timed movements of organisms between breeding and non-breeding locations occupied at different points throughout the year.

Vagrancy: the appearance of an individual outside the normal distribution range of its species. Such individuals are defined as vagrants.