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19 **TITLE:** The overlooked importance of vagrancy in ecology and evolution

20
21 **ABSTRACT:**

22
23 Vagrancy is the occurrences of individuals outside the normal geographic range of their species.
24 These rare and unpredictable events have long been neglected by the scientific community,
25 belying a growing body of evidence that vagrancy can have an important role in eco-
26 evolutionary processes at both population and community scales.

27
28 **MAIN TEXT:**

29
30 *Scientific neglect of an important phenomenon*

31
32 Although vagrants have been enthusiastically cataloged by amateur naturalists for centuries,
33 there has been relatively little research into their biological significance. While instances of
34 **vagrancy** (see Glossary) are rare by nature, they may precipitate ecological or evolutionary
35 outcomes, which would have been difficult to predict and are akin to ecological ‘**black swan**’
36 **events** [1]. Similarly, little attention has been paid to the mechanisms underpinning vagrancy,
37 despite their potential to illuminate heritability and developmental stability of movement
38 programmes. Simultaneously, progress in the field has been hampered by inconsistent use of
39 terminology, as well as inappropriate evolutionary concepts which have even verged on **group**
40 **selection** arguments. In this forum, we argue that this poorly understood phenomenon deserves
41 more attention from researchers, and needs a clarified framework grounded in robust
42 evolutionary concepts to understand the eco-evolutionary consequences of extreme movements
43 in the animal kingdom.

44
45 *What is vagrancy?*

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

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

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

73
74 *Vagrancy and dispersal are linked but not analogous*

75
76 Vagrancy has recently been defined as a process by which organisms engage in long-distance
77 dispersal movements outside of their known species range, or “the mechanism by which
78 growing populations can colonize newly available habitats” [3]. While vagrancy *can* lead to
79 dispersal and the colonization of new regions, it is important to recognize that not all vagrancy
80 is dispersal (many cases of vagrancy are not followed by any reproduction attempt, others can
81 end up with a return to the point of departure), and not all dispersal is vagrancy (most
82 movements leading to dispersal do not go beyond the species' normal range).

83 Another source of confusion in the recent literature follows viewing the persistence of
84 vagrancy as arising from benefits to the population as a whole [e.g., 3], implying group
85 selection; no realistic mechanism predicts that some individuals sacrifice their fitness for the
86 ‘good of the species’. Some of the best examples of avian vagrancy involve young individuals
87 migrating in a direction that does not lead them to the species' normal wintering range: most
88 will not survive to reproduce, and they thus represent an evolutionary dead-end. New vagrants
89 arise in every generation from the pool of normally migrating individuals. There is little doubt

90 that these vagrancy movements are usually costly (and often lethal), as most movements outside
91 a species' range bring the individuals to unsuitable habitats or far from any conspecifics.
92 Vagrancy should thus be strongly counter-selected, and its contribution to changes in
93 distribution is similar to those of mutations: most are deleterious but those that are favored fuel
94 evolution and adaptation.

95 96 *Vagrancy shines a light on movement ecology*

97
98 Like many other biological phenomena, we need to study variation in orientation / navigation
99 phenotypes to understand their biological bases. There are still many unanswered questions
100 about the neurophysiological bases and heritability of animal navigation [4] and understanding
101 why individuals engage in abnormal movements can help answer them.

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

112 113 *Ecological and evolutionary consequences of vagrancy*

114
115 Most of the time, vagrancy has few consequences, as vagrants arriving in unsuitable habitats
116 far from conspecifics are likely to die before reproducing. Furthermore, some individuals that
117 engage in extreme exploratory movements might permanently return to their natal area,
118 resulting in no evolutionary impact. Yet many ecological and evolutionary consequences of
119 vagrancy have been reported in various regions and across diverse taxonomic groups.

120 Some of the most important ecological consequences of vagrancy (depicted in green in
121 Figure 2) involve the dispersal of pathogens or parasites through passive transport by vagrants
122 [5]. More generally, vagrancy is a key avenue for the colonization of new areas, sometimes far
123 from species' ancestral range and is thus an increasingly important process underpinning species
124 responses to rapid climate change and land-use [6]. Importantly, colonization may also involve
125 pest species which could represent new challenges for agriculture [7]. It might be assumed that
126 vagrancy promotes the colonization of new areas more frequently if it occurs before or during
127 the breeding season, but this has not been clearly tested. Even in the absence of colonization,
128 vagrants can have important impacts - for example novel predators reaching insular
129 environments can disrupt ecosystem stability and potentially threaten endemic species [8].

130 Vagrants may promote the evolution of new migration routes, whether they are encoded
131 genetically [9], or culturally ([10]; Figure 2), provided that the novel route is transferred to
132 offspring [11]. Vagrancy can also foster the evolution of new species after the colonization of
133 new regions, whether vagrancy originated from active movements (e.g., misoriented migrants)

134 or passive movements (e.g., rafting [12]). Finally, vagrancy can also promote the evolution of
135 new modes of reproduction, as illustrated by the emergence of exclusive parthenogenesis in an
136 otherwise sexually reproducing damselfly (citrine fork-tail *Ischnura hastata*) after it colonized
137 the Azores [13].

138

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

142

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174 FIGURE LEGENDS:

175

176 **Figure 1. How to identify individuals as vagrants?**

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

195

196 **Figure 2. Important ecological and evolutionary consequences of vagrancy across the**
197 **animal kingdom.**

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

209

210

211 **GLOSSARY:**

212

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

214

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

217

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

220

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

225

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

229

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

234

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

237

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

244

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

247

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

251

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

255

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

258

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

261

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

264

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