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1 **Contrasting movement strategies among juvenile albatrosses and**
2 **petrels**

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5 **Sophie de Grissac*^{a,b}, Luca Börger^c, Audrey Guitteaud^a and Henri Weimerskirch^{a,b}**

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7 ^a Centre d'Etudes Biologiques de Chizé, UMR 7372 CNRS & Université de La Rochelle, Villiers
8 en Bois, France.

9 ^b UMR 9220 CNRS IRD ENTROPIE, Université de la Réunion, Saint Denis, France.

10 ^c Department of Biosciences, College of Science, University of Swansea, Swansea, UK.

11 * Corresponding author: sophie.degrissac@cebc.cnrs.fr

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14 **Short title:** Foraging strategies of juvenile seabirds

17 **Abstract**

18 Animal movement is a fundamental eco-evolutionary process yet the behaviour of juvenile
19 animals is largely unknown for many species, especially for soaring seabirds which can range
20 widely over the oceans at low cost. We present an unprecedented dataset of 98 juvenile
21 albatrosses and petrels (nine species), tracked for the first three months after independence.
22 There was a startling diversity within and among species in the type and scale of post-natal
23 movement strategies, ranging from area-restricted to nomadic patterns. Spatial scales were
24 clustered in three groups that ranged from <3000km to > 6000km from the natal nest. In seven of
25 the nine species, the orientation of flight paths and other movement statistics showed strong
26 similarities between juveniles and adults, providing evidence for innate orientation abilities. Our
27 results have implications for understanding the development of foraging behaviour in naïve
28 individuals and the evolution of life history traits such as survival, lifespan and breeding strategy.

29

30 **Key words**

31 Dispersal; ecology; foraging; migration; net squared displacement; Procellariiformes; seabirds

32 **Introduction**

33 Juvenile and immature individuals play a key role in the dynamics of animal populations ¹,
34 particularly in long-lived species for which they can represent up to 50% of the total population
35 ². It is therefore essential to account for the specific traits and strategy of juveniles when
36 modelling the fate of populations ³. However, for most species, the behaviour and fate of
37 juveniles remain almost unknown. In animals with parental care, the critical stage for juveniles is
38 when they start to move and forage independently. At this stage, juveniles generally suffer high
39 mortality, which is likely a result of low foraging efficiency or non-optimal morphology
40 compared to that of adults ^{4,5}. How such naïve individuals navigate in their environment,
41 especially for large scale dispersive movements such as migration or exploration, has been
42 identified as a priority for research ⁶.

43 The concept of dispersal, or natal dispersal, is often used to describe the movement of a juvenile
44 leaving its natal grounds to breed elsewhere ⁷. This therefore excludes the post-fledging
45 movements of highly philopatric species, which return to breed at their natal colonies. However,
46 as pointed out in recent studies ⁸, dispersal includes the “movement of new fledglings in all
47 directions with no inherent directional preferences”. These movements may, in time, lead to
48 ‘true’ dispersal, in the most commonly used sense ⁷, or to the birds’ return to their colony of
49 origin.

50 Substantial individual variability has been documented in the dispersal behaviour of terrestrial
51 animals ^{7,9}. Individuals move in heterogeneous environments, making their displacement
52 landscape-dependant. Indeed, non-flying terrestrial animals are severely constrained by
53 movement costs related to energy landscapes ^{10,11}. While birds are far less constrained, terrestrial
54 birds still generally follow topographic features and landmasses during their migration or

55 dispersal, and use specific sites for stop-overs ⁸. The case of seabirds is very different, as adults
56 have capacities for large scale movements over open, comparatively featureless oceans ^{12,13}. This
57 is particularly true for procellariiform species (albatrosses and petrels), which can undertake
58 extremely long migratory movements ^{14,15}. When juvenile petrels and albatrosses leave their
59 nests for the first time, they have ‘the world as their oyster’, in that they can potentially fly at low
60 metabolic costs, using winds to move in a vast, apparently homogenous, environment. These
61 naive birds face no topographic constraints on where and when to move. Whilst the oceanic
62 realm is certainly not a featureless environment for seabirds that are known to be sensitive to
63 oceanographic features such as bathymetry, currents, wind zonation, eddies, or odours such as
64 dimethyl sulphide ¹⁶, the spatial scales are larger than in terrestrial habitats by many orders of
65 magnitude ¹⁷. This adds further interest to the question of how these animals forage in the marine
66 environment.

67 In most seabird species, juveniles leave their natal breeding grounds independently from their
68 parents, and thus have to explore the environment and learn to forage entirely on their own.
69 Existing studies on land birds have shown that juveniles may follow an innate navigation
70 programme to some extent, while acquiring cues to improve their foraging proficiency ¹⁴. The
71 innate parts of juvenile movements can be similar to the movements of adults for some species
72 ¹⁸, while for others they may differ ^{19,20} with respect to the timing ^{21,22}, track characteristics (e.g.
73 sinuosity ²³) or route choice (e.g. less productive areas ^{4,22,24}). These differences in terrestrial
74 birds have generally been explained by the lack of experience in juveniles ²⁵ leading to
75 navigation errors. Though a lower competitiveness on foraging grounds in relation to adults ²⁶
76 may also have selected for endogenous post-fledging dispersal programmes that favour intra-
77 specific spatial segregation. However, very limited data exist to allow a general understanding of

78 the dispersal movements of juvenile seabirds within and across species. Without a strict
79 endogenous programme and highly constraining landscape features, we may expect juvenile
80 seabird movements to vary considerably within and between species.

81 Here we present the first cross-species study of post-fledging movements in juvenile seabirds,
82 comparing the large-scale movement strategies of juveniles from nine closely related
83 procellariiform species during their first months at sea. The nine species, i.e. two species of great
84 albatrosses, two species of mollymawk albatrosses, two species of sooty albatrosses, two species
85 of giant petrels and one species of petrel (Table 1), constitute an ideal study system as they breed
86 in the central Indian Ocean (Supplementary Fig.1) and face similar environmental conditions
87 when they leave their natal breeding sites. Adults of the nine species exhibit contrasting
88 movement patterns during the inter-breeding period, i.e. when they are not central place foragers.
89 They either show a typical migratory behaviour, i.e. moving regularly from breeding grounds to
90 winter quarters and back ²⁷, ranging widely in the Southern Ocean with no specific destination,
91 or remain near the breeding grounds throughout the year ^{20,28-30}. These species also show
92 contrasting life history strategies, with great albatrosses and sooty albatrosses being longer lived
93 than the other species, and juvenile survival being very different between species ³¹⁻³³. By
94 comparing movement types and characteristics, we can test whether juveniles of each species
95 follow a programmed route, whether their routes or destinations follow those of the adults or
96 whether they differ in timing, directionality, sinuosity or targeted habitat type ^{8,23,34}. For
97 example, rapid movement away from the natal breeding colony or use of different areas than
98 those used by adults may reduce intraspecific competition since it is generally assumed that
99 competition between immatures and older birds leads to spatial segregation between age-classes

100 ^{4,19,26}. Such competition may have consequences on individual fitness and population dynamics

101 ^{4,35}.

102 The specific questions we want to address in this study are **(1)** Do closely related seabird species
103 differ in their movements during the first months of independence at sea? **(2)** Do naïve juvenile
104 birds have similar movement patterns to those of their parents? **(3)** Do the movement trajectories
105 provide evidence of an innate navigation programme, implying unique fixed departure directions
106 or direct orientation towards specific foraging areas instead of random movements? We discuss
107 the implication that differences in movement behaviour may have on the evolution of life history
108 components such as juvenile survival.

109

110 **Results**

111

112 **Comparison between juveniles.**

113 **General movement patterns**

114 The Net Squared Displacement (NSD) method ³⁶ was used to model and identify typical large-
115 scale movement types (Supplementary Methods 2-Fig.1). We observed that juveniles showed
116 striking interspecific differences in displacement behaviour in the first three months after leaving
117 the natal colony. Movement types ranged from sedentary to nomadic patterns (Table 2, Fig.1),
118 and included migratory-like movements and a specific pattern that we named “large-scale
119 looping type” (Fig.1.c). The majority of northern (67%) and southern (100%) giant petrels
120 showed a typical nomadic-type movement with large dispersal distances (range at three months >
121 6000km, Table 2), and an eastward trajectory, with all individuals circumnavigating Antarctica

122 within the first three months after leaving the natal colony (Table 2, Fig.1.a). Some individuals
123 stopped for variable durations in specific areas before resuming their eastward movements and
124 four individuals, for which the tracking time exceeded six months, completed a circumpolar
125 movement and started a second one. In contrast, most juvenile mollymawks (100% of the
126 yellow-nosed albatrosses and 86% of the black-browed albatrosses) and white-chinned petrels
127 (100%) showed migratory-type movements fitted by the “half-migration” model. Specifically,
128 the migratory–like movements of these species included a transit phase of 10-30 days with rapid
129 directional movement, followed by a settling phase in a restricted area. Since these movements
130 lacked the return trip, typical of true complete migration, during the 3-6 month study period, we
131 named the corresponding model ‘half-migration model’ (e.g.: Fig.1.b). These movements were
132 carried out over medium spatial scales (the range at three months was shorter than 6000km but
133 longer than 3000km, Table 2, Fig. 1.b). Juvenile sooty albatrosses and Amsterdam albatrosses
134 showed more individual variability that included all displacement types on a small to medium
135 spatial scale (range at three months < 3000km). Overall, the displacement types of these three
136 latter species were not characterized by any clear prevalent displacement strategy, with most
137 individuals remaining within a limited range from the colony through looping movements. We
138 therefore grouped these individuals into a category named “large-scale looping type”
139 (Fig.1.c). Wandering albatrosses showed an even higher intraspecific variability with some
140 individuals moving over a small scale in the Indian Ocean and showing a looping behaviour
141 (Fig.1.d: white dots), whereas others (60%, Table 2) moved further toward the Australian coast
142 and/or into the Pacific Ocean (Fig.1.d: black and grey dots), adopting either migratory type
143 movements or large-scale nomadic type movements. These differences in displacement lead
144 juveniles of the nine species to relocate to three broad geographic areas, with small-scale

145 dispersers (most sooty and great albatrosses) remaining in the central Indian Ocean, medium
146 scale dispersers (mollymawk albatrosses, petrels and some wandering albatrosses) making some
147 excursions out of the Indian Ocean, and large scale dispersers (giant petrels and some wandering
148 albatrosses) leaving the Indian Ocean, with some birds undertaking entire circumpolar
149 navigations.

150 **Orientation at departure and further bearings**

151 Departure flight directions taken by juveniles from their natal colony (Fig.2: black points) had
152 two distinct patterns. **1:** An oriented trajectory with very little inter-individual variability in flight
153 directions (within species, departure headings range was $\leq \pi/4$, indicating little variation in
154 direction, Rayleigh test of uniformity: all $P < 0.01$). This was the case for nomadic (giant
155 petrels) and migratory type species (mollymawks and white-chinned petrel). These two groups of
156 species also showed a high consistency in orientation with time, since the directionality of their
157 position with respect to the colony at month 2 and 3 (Fig.2: grey and white points) was similar to
158 the direction taken at departure (bearings range $< \pi/4$) with a small shift toward east for white-
159 chinned petrels. **2:** A high variability in departure heading toward east, west and north for the
160 three species exhibiting large-scale looping movements, i.e. the two sooty albatrosses (heading
161 toward north, $\pi > \text{range} < \pi/2$, Rayleigh test: $P > 0.1$) and Amsterdam albatrosses (range $> \pi$,
162 Rayleigh test: $P = 0.73$). This group with non-oriented flights at departure showed no further
163 consistency in orientation since positions were similarly scattered after two and three months.
164 Finally, most wandering albatrosses had a restricted departure direction (direction range = 1.8
165 rad, just over $\pi/2$) toward NE, but the directionality of positions were not consistent beyond
166 departure.

167 **Sinuosity and daily distance travelled (DDT)**

168 First, the paths of nomadic-type species (giant petrels) were typified by a lower sinuosity ($S <$
169 0.5) than other species (linear mixed model & post-hoc Tukey test: $P < 0.05$ when compared to
170 all species except wandering albatross and yellow-nosed albatross, Fig.3.a & Supplementary
171 Results 1). They also had the highest DDT ($354 \pm 58.9\text{km (SD)}$) of all species when averaged
172 over the 3 months (linear mixed model & post-hoc Tukey test: $P < 0.05$ when compared to all
173 species except light-mantled sooty albatross ($P = 0.054$ when compared to northern giant petrel),
174 Fig.3.b and Supplementary Results 2). The DDT varied between individuals but showed no clear
175 trend over time (linear mixed model & post-hoc Tukey test p-values in Supplementary Table 2).
176 Second, migratory-type species performed trajectories that directly (low sinuosity < 0.5) and
177 rapidly (high DDT > 240 km) took them from their natal colony to a restricted foraging area
178 during the first month (i.e. during the transit phase). Once the destination was reached (during
179 the 1st (mollymawks) or 2nd month (white-chinned petrel)) there was an increase in sinuosity
180 (linear mixed model & post-hoc Tukey test: $P < 0.05$ except for yellow-nosed albatross,
181 Supplementary Table 2) and a decrease in DDT (linear mixed model & post-hoc Tukey test: all P
182 < 0.05 , Supplementary Table 2). This phase corresponds to the settlement time, when the NSD
183 curve reaches the asymptote. The reason why white-chinned petrels settled later than
184 mollymawks (i.e. with transits lasting 30 to 40 days compared to 14 to 26 days in mollymawks)
185 is that all individuals started heading north (Kerguelen colony) or north-east (Crozet colony)
186 until they reached latitudes of 30°S (around the 9th day), which corresponds to the latitude of
187 Trade winds, i.e. easterly winds. Following this, individuals adopted a westerly heading to reach
188 their final destination off the coasts of South Africa. Finally, the group with large-scale looping
189 movements (sooty and Amsterdam albatrosses) had high orientation variability, medium

190 sinuosity (close to 0.5 or higher) and medium DDT ($241 \pm 72\text{km}$ (SD)) right from the first
191 month, with no significant trend over the whole period (Fig. 3.a, Supplementary Tables 2).

192 **Distance to colony and habitats**

193 During the first 15 days all species moved rapidly and directly away from the natal colony (mean
194 range at 15 days = $1323 \pm 786\text{km}$ (SD)). After one month, nomadic giant petrels had reached a
195 significantly longer range than the other species (linear mixed model and & post-hoc Tukey test:
196 $P < 0.05$, Supplementary Table 3) and tended to stay in oceanic waters (Bathymetry $< -3000\text{m}$,
197 Table 3 & Supplementary Fig.2). They encountered significantly cooler surface temperatures
198 than other species (linear mixed model and & post-hoc Tukey test: $P < 0.05$, Supplementary
199 Fig.2) mainly because of their passage into the Pacific Ocean. Some northern giant petrels
200 however, stopped for variable duration in neritic waters, for example in the productive Chilean
201 Patagonian shelf (where chlorophyll *a* values $> 3\text{mg.m}^3$). Migratory-type species rapidly
202 increased their distance to the colony until they reached slope edges off Australia (mollymawks,
203 mean bathymetry $> -2000\text{m}$ for both species, waters significantly shallower than that of other
204 species (linear mixed model and & post-hoc Tukey test: $P < 0.05$, Table 3 & Supplementary
205 Fig.2) or oceanic waters along eastern South-African coasts in the Agulhas current area (white-
206 chinned petrels, mean bathymetry = $-3493 \pm 391\text{m}$ (SD), Table 3, Supplementary Fig.2). White-
207 chinned petrels foraged at lower latitudes than other species (Fig.4) and encountered warmer
208 surface temperatures than other species (Supplementary Fig.2, significant difference only
209 compared to giant petrels, wandering, black-browed and light-mantled sooty albatross; linear
210 mixed model and post-hoc Tukey test: $P < 0.05$). The three looping species that remained within
211 a 3000km radius of their natal colony foraged almost exclusively in deep oceanic areas
212 (respectively 100, 90% and 89% of individuals of the two sooty species and Amsterdam

213 albatrosses, Table 3; mean bathymetry = $-3793 \pm 178\text{m}$ (SD), see Supplementary Fig.2).
214 Amsterdam albatrosses encountered warmer waters at lower latitudes than others (Fig.4,
215 Supplementary Fig.2). Finally, wandering albatrosses showed a strong individual variability with
216 respect to the distance from the colony (from small to large dispersal range) and the habitat
217 frequented, comprising both neritic (continental slopes or oceanic features like ridges) and
218 oceanic areas (Table 3, Supplementary Fig.2).

219 With respect to chlorophyll *a*, although there was a tendency for some species, such as northern
220 giant petrels, black-browed, yellow-nosed and wandering albatrosses, to favour waters with
221 higher chlorophyll *a* (Supplementary Fig.2), the differences were only significant between
222 northern giant petrels and three species: sooty albatrosses, Amsterdam albatrosses and white-
223 chinned petrel (linear mixed model and & post-hoc Tukey test: $P < 0.05$)

224 **Comparison with non-breeding adults.**

225 When the breeding season ended, adult birds left the colony for an extended period, during the
226 winter time for most species, returning to the colony 5-12 months later for a new breeding
227 season. By fitting the migratory model to their trajectories, the NSD method identified three
228 distinct at-sea dispersal scales for the adults of the nine species (Table 3). First, adult giant
229 petrels stayed all year round close to their colony with low variation around an asymptotic range
230 (Table 3). All the other species moved on average $> 3000\text{km}$ from the colony (Table 3). Adult
231 mollymawks moved to a distance of 5000-6000km (medium scale) with little variation around
232 the asymptotic range (Table 3). In other words, they moved rapidly to a specific zone, the
233 wintering area, where they remained, with only small scale movements. This wintering area was
234 the same for all individuals of the species and was located over neritic waters; nearby and over
235 the Australian continental shelf. The two species of Sooty albatrosses and Amsterdam

236 albatrosses had medium to long inter-breeding dispersal distances with higher range variations
237 (larger wintering area scale) and a high variability within species (Table 3). These three species
238 foraged mainly in oceanic habitats. White-chinned petrels were intermediate between the two
239 latter groups and wandering albatrosses showed strong inter-individual variability with
240 individuals belonging to the three groups and foraging both in neritic and oceanic waters (Table
241 3).

242 Finally, adults foraged at significantly higher latitudes than juveniles for six of the nine species
243 (Wilcoxon test: $P < 0.05$ for northern giant petrel, black-browed, Amsterdam, wandering and
244 both sooty albatrosses, Fig. 4). Adult and juvenile white-chinned petrels foraged at similar
245 latitudes but different longitudes with adults foraging west of South-Africa (mean longitude =
246 $14.72 \pm 2.17^\circ\text{E}$ (SD)) and juveniles foraging mostly east of South-Africa (mean longitude =
247 $40.83 \pm 1.11^\circ\text{E}$ (SD)). There was no significant difference in latitude for southern giant petrels,
248 but, as for white-chinned petrels, there was a longitudinal segregation between juveniles and
249 adults caused by their different strategies (nomadic *vs* resident movement type).

250

251 **Discussion**

252

253 Our study is the first to provide a comprehensive examination of juvenile movement strategies
254 among seabirds. It shows clearly that (1) although species are closely related, the juveniles of the
255 nine species differ extensively in their movement patterns when they leave their colony of origin,
256 and (2) that for each species the movement types of juveniles in the first three months following
257 independence are generally similar to those of wintering adults, except for the two species of

258 giant petrel. In addition, movement patterns appear to be similar within most species, but show
259 high variability for some species with individuals showing mixed strategies.

260

261 **Interspecific variability in movement strategies and comparison with adults**

262 Overall, the juveniles of the nine species showed very large-scale post-fledging movements from
263 basin-wide movements to circumpolar trips. A common behaviour found in all species is the
264 preliminary rapid movement that takes all individuals away from the vicinity of their colony of
265 origin. This behaviour may allow a reduction of competition with breeding adults present around
266 the colony at this time, especially in the large albatrosses where breeding adults are present
267 throughout the year. After this first transit phase, individuals used three very different main types
268 of large-scale movement patterns.

269 Juveniles of the two species of mollymawks and white-chinned petrels all exhibited the same
270 migratory strategy as the adults. Their trajectory parameters during the settlement phase are
271 typical of foraging in a restricted area – suggesting an Area Restricted Search³⁷. In mollymawks,
272 destinations of juveniles partly overlapped with wintering zones of adults over the continental
273 shelf or shelf-break. These species appear as ‘typical’ migratory species as the route to the
274 wintering grounds corresponds to a narrow corridor used by all age groups, similar to that seen in
275 certain land birds^{8,18,38}. Analyses at finer scales may help to determine how juveniles and adults
276 interact in specific overlapping winter feeding areas, e.g. in black-browed and yellow-nosed
277 albatrosses, and how this affects juvenile survival and/or foraging skill acquisition.

278 Conversely, juvenile white-chinned petrels head north to exploit favourable Trade winds at low
279 latitudes that allowed them to reach eastern Africa at low cost. In contrast, adults directly moved

280 to the west to their over-winter site. This leads to segregation between adults and juveniles, at
281 least during the first part of winter. Adults use mainly neritic productive waters of the Benguela
282 current off western South-Africa, whereas juveniles use more oceanic features like oceanic
283 ridges in sub-tropical relatively warm waters (Fig. 4 and Supplementary Fig.2).

284 Circumpolar nomadism, i.e. flying with dominant winds toward East, allowed juvenile giant
285 petrels to rapidly reach areas very distant from their colony and from resident wintering adults,
286 resulting in an extreme case of segregation whereby juveniles do not overlap at all with adults²⁰.

287 Spatial segregation between age classes during all or part of the breeding cycle occurs in many
288 species (e.g. ^{22,23,40-42}). It has been described for other procellariiform species like black-footed
289 albatross²⁴ or Manx shearwater³⁹ and is generally explained by competitive exclusion of
290 juveniles by experienced adults⁴ in the closest favourable foraging areas around the colonies.

291 Whereas in many taxa segregation arises from size differences between young and adult^{40,42}, it
292 has been suggested that in monomorphic species with deferred sexual maturity, like seabirds,
293 experience rather than size may drive segregation³⁹. Competition between age classes may have
294 important consequences for the dynamics of the population²⁶ since it may affect the reproductive
295 success and survival of individuals^{8,43}. Naïve young individuals excluded actively from the best
296 foraging places by adults can be forced to use suboptimal feeding areas^{4,39}. Giant petrels are
297 known for being particularly aggressive competitors⁴⁴, mainly scavenging when around the
298 colony. Thus we can assume that juveniles may not be competitive enough to access on land the
299 seal and penguin carcasses or even fisheries waste used by adults. Juveniles may feed more on
300 pelagic resources until they are able to compete with experienced birds. This creates ontogenic
301 niche divergence and will probably result in a progressive shift in diet during the immaturity
302 period. A similar pattern of spatial segregation was found between adult and juvenile giant

303 petrels in the Southern Atlantic⁴⁵, where juveniles moved out of the adult' range after 30 days,
304 to forage in productive upwelling areas that sustained many seabird species. In contrast to giant
305 petrels from Crozet and Kerguelen, Southern Atlantic juvenile giant petrels, while spatially
306 segregated, feed in a similar oceanic system as adults (shelf and shelf break)⁴⁵.

307 The third strategy that involved large-scale looping movements at the scale of the Southern
308 Indian Ocean was used by juvenile sooty albatrosses, Amsterdam albatrosses and some
309 wandering albatrosses. Overlap between adult and juvenile of these species is probably reduced
310 by the extensive size of the sector used in the large looping movements, and by differences in
311 latitudes.

312 Although strategies differ extensively among albatrosses and petrels, they are consistent within
313 genus. Each genus presents particular anatomic characteristics; different wing loading and wing
314 shape that affect flight speed, manoeuvrability and energetic requirements at take-off or landing
315⁴⁶. These differences are likely to affect dispersive abilities as well as foraging ecology⁴⁷, an
316 interesting aspect to investigate in further detail in future research. Albatrosses and petrels are
317 known to make extensive use of wind to reduce energetic costs while flying^{46,48}. In our study,
318 fifty five percent of the individuals/species flew mainly with dominant winds, the Westerlies, at
319 the beginning of their trip, and later on for giant petrels. Wind is probably a major factor
320 affecting seabird dispersal and in some species it has been shown that young birds are also
321 affected by other environmental conditions^{18,25} such as resource distribution⁴⁹, e.g. signalled by
322 dimethyl sulphide gradients (phytoplankton related odour)¹⁶.

323 **Individual variability**

324 There were striking differences in individual variability within species, ranging from strongly
325 consistent juvenile displacement types to species with a high degree of intra-specific variability.

326 Most species belonged to the former category, whereas wandering albatrosses belonged to the
327 latter, showing a mix of the three movement strategies with a very high individual variability in
328 all parameters. Considering that all individuals encountered the same conditions at departure
329 with essentially no movement constraints in an entirely unexplored environment, the low
330 individual variability within long-range species that visit neritic waters (mollymawks, petrels) is
331 particularly striking. Conversely, more oceanic species with shorter dispersal ranges tended to
332 show more individual variability. This is particularly true for wandering albatross where
333 individual variability is the highest. Those individual differences may be in part sex-specific^{7,50}.
334 However adults were similarly variable in migratory behaviour^{51, 7}, suggesting that variability
335 in movement strategy is driven not only by external conditions but also by the traits and internal
336 state of individuals (morphology, physiology, behaviour). In a relatively homogeneous landscape
337 with few external movement constraints, internal factors may have a more pronounced effect on
338 the large-scale movement patterns of juveniles and lead to higher individual variability than in
339 coastal waters where a higher probability of interactions (due to topography, high bird density,
340 fisheries) may affect movement costs and foraging decisions. Accordingly, despite high within-
341 population variability, individual Atlantic puffins (*Fratercula arctica*) show high consistency
342 among years in their own migratory routes⁵². The authors suggested that juvenile puffins may
343 make long exploratory trips to different areas acquiring the experience needed to navigate their
344 environment and find appropriate foraging zones. Since juvenile wandering albatrosses travelled
345 across the whole Indian Ocean or further during their first year at sea, using mixed movement
346 strategies, one might wonder if this could correspond to an exploratory behaviour. Individuals
347 might acquire knowledge and progressively reduce the range of areas they visit and associated

348 movement patterns until they adopt a foraging strategy that is consistent from year to year, as the
349 adults do during sabbatical years throughout their life ⁵¹.

350 **Innate navigation programme**

351 While anatomy, physiology, competition and environmental conditions may strongly affect
352 seabird post-fledging movement strategies ⁵³, our findings suggest that juveniles may also partly
353 use an innate navigation programme when leaving their natal colony ⁵⁴. Unlike species for which
354 juvenile migratory capacities are enhanced by the presence of adults ³⁸, juvenile
355 procellariiformes are left by their parents before they fledge. However, we found that juvenile
356 strategies were consistent from the start within species, and were similar to those of adults
357 outside of the breeding season in most species. This suggests that juveniles first follow internal
358 cues, especially for the timing and direction of departure, but also for their destination in the case
359 of mollymawks and white-chinned petrels. The latter are striking examples since, in order to
360 reach the targeted foraging ground west of their colony, all individuals first flew northwards to
361 find favourable winds instead of following the Westerly flow or flying against it to reach directly
362 the destination. This likely genetically encoded behaviour might have been selected to use the
363 less expensive route in terms of energetics and cause the dispersion of juveniles to more distant
364 feeding grounds ^{50,55}. In contrast to this innate behaviour, it has been suggested that young
365 Atlantic puffins may rely more on a true learning process ³⁹. Overall, juvenile seabirds probably
366 depend on both innate and acquired skills in different proportion depending on the species. For
367 example, young Cory's shearwaters innately follow the same general strategy as older birds, but
368 progressively improve their migratory route with age ²². Orientating in the apparently featureless
369 environment of the pelagic ocean seems challenging, and the navigation cues, innate or acquired
370 by experience and memory, are far from being clear ^{16,56-58}. This innate programme that drives

371 juveniles on very specific routes may be a disadvantage in a context of rapid global change when
372 birds may need to adapt to a shift in resources distribution, with unconditional fixed strategies
373 probably being inferior to condition-dependent strategies ³⁵. In migrating birds several
374 populations have retained their original route that has become sub-optimal in the context of
375 climate change ⁵⁹. Interestingly, all these cases refer to species where the juveniles migrate
376 independently from the adults and rely on their genetic programme for the first migration, such
377 as most of our study species. There seems to be no such case of apparently sub-optimal routes
378 among species where the juveniles accompany the adults on migration ⁵⁹. Thus, populations with
379 independent juveniles may be less flexible in terms of migration or movement strategy, for
380 example when facing long-term changes that need strategy adjustments.

381 **Link between dispersal strategies and life histories**

382 The three main strategies used by juvenile albatrosses and petrels were found in three distinct
383 groups: mollymawks and white chinned petrels, great and sooty albatrosses and giant petrels
384 respectively. The first two groups have contrasting life history strategies independent of their
385 size: mollymawks and white chinned petrels are shorter-lived species than the others, with
386 annual breeding and high mortalities during the juvenile-immature stages, whereas great
387 albatrosses and sooty albatrosses are longer lived biennial species with high survival during
388 juvenile and immature phase ^{31-33,60}. Thus, the migratory strategy where juveniles and adults
389 share the same winter zones over shelf areas may result in higher costs in terms of survival than
390 the large looping strategy over oceanic waters. Moreover, oceanic species are generally longer
391 lived than neritic species ⁶¹. Giant petrels are particular in their dispersal strategies, they are
392 shorter lived for their size but demographic data about the survival of juveniles is lacking ⁶².
393 Although future research with higher numbers of loggers is necessary to estimate the survival of

394 juveniles during these first months, our results suggest a more general link between movement
395 strategies, juvenile survival and life history strategies.

396 The findings of this study may have major implications for understanding the evolutionary
397 mechanisms underlying the foraging behaviours of naïve individuals, and the link with the
398 characteristics of energy and spatial landscapes. Similarly, our results emphasize the importance
399 of linking movement strategies and population dynamics^{1,35}. Thanks to the rapid development of
400 new tagging technology, it is now possible to track multiple life history stages to study marine
401 predator ecology but also to better understand why juveniles suffer higher costs during the early
402 stage of their life.

403

404 **Methods**

405

406 **Field work and telemetry.**

407 Field studies were carried out on the Crozet (46.2°S, 52.4° E), Kerguelen (49.4°S, 70.1°E) and
408 Amsterdam (38.4°S, 77.3°E) islands, south western Indian Ocean (see map in Supplementary
409 Fig.1). All field procedures were approved by The Ethics Committee of IPEV and Comité de
410 l'Environnement Polaire and were carried out in accordance with the approved guidelines. We
411 tracked nine species of albatrosses and petrels belonging to different taxa: two species of great
412 albatrosses (Amsterdam albatross *Diomedea amsterdamensis*, wandering albatross *D. exulans*),
413 two species of Mollymawks albatrosses (Indian yellow-nosed albatross *Thalassarche carteri* and
414 black-browed albatross *T. melanophris*), two species of sooty albatrosses (sooty albatross
415 *Phoebastria fusca* and light-mantled sooty albatross *P. palpebrata*), two species of giant petrels

416 (northern giant petrel *Macronectes halli* and southern giant petrel *M. giganteus*), and one species
417 of petrel (white-chinned petrel *Procellaria aequinoctialis*) (Table 1). Instead of complete species
418 names, species codes are used in tables and figures, as detailed in Table 1.

419 **Juveniles.** Between 2001 and 2014, 98 chicks (Table 1) were fitted with Argos satellite
420 transmitters (Platform Terminal Transmitter, PTT 100, Microwave Telemetry, Columbia, USA)
421 just before fledging. Units were fixed on the birds' back feathers using adhesive tape and glue.
422 The mass of devices (20-50g) was always below the 3% of the body mass limit recommended for
423 flying birds (Phillips et al. 2003). Transmitters were powered with solar panels and worked with
424 duty cycle mode, 10hON-24hOFF, 18hON- 54OFF or 12hON-60hOFF. Some of the juveniles
425 were sexed using a molecular sexing method, others are of unknown sex. After data filtering and
426 homogenization (Supplementary Methods 1) we obtained a total of 83 tracks, with 53 lasting at
427 least 3 months and with an average of 0.65 ± 0.12 (SD) locations per day.

428 **Adults.** Adults from the same nine species and same sites were tracked during the non-breeding
429 season, when they are no longer central place foragers. Birds were fitted with light-recording
430 geolocators (GLS) weighting less than 3g and attached to a leg band, beginning in 2000. GLS
431 give positions twice per day with a low accuracy (median error of 180 km)⁶³. To compare the
432 overall large-scale movement patterns of juveniles and adults we randomly chose 10 complete
433 adult tracks per species starting at the end of a breeding season and ending at the beginning of
434 the next one. To compensate for the low accuracy of locations given by the GLS system we
435 smoothed the trajectories by averaging locations on a 3-days' time scale. Due to the low
436 accuracy and low frequency of sampling we used adult data only for the comparative analysis of
437 overall displacements and a global assessment of habitats used but not for the detailed trajectory
438 analysis.

439

440 **Movement Analysis.**

441 We used two types of approach for analysing the movement data, both implemented using the R
442 Software Environment ⁶⁴. **1:** The squared displacement method was used to identify and compare
443 movement types within and between age classes and species ³⁶. **2:** Movement statistics
444 commonly used for animal trajectory analysis were calculated to quantify detailed juvenile
445 movement parameters and test the innate navigation hypothesis ⁶⁵.

446 **Comparative analysis of displacement.**

447 To identify and compare movement types within and between age classes and species, we used
448 the squared displacement method ³⁶. The net squared displacement distance (NSD) is the squared
449 beeline distance (calculated using Haversine formula) between the starting point (here, the natal
450 colony of the birds) and each location of the trajectory. It is a fundamental statistic for movement
451 studies ^{66,67}. We used the NSD method ³⁶ to identify and compare different broad movement
452 types such as sedentary (“home range”), migratory and nomadic movement modes
453 (Supplementary Methods 2-Fig.1), and concurrently estimate general movement statistics such as
454 distance covered (Supplementary Table 1). The approach is continuous time based and allows for
455 the efficient analysis of unequally and irregularly sampled movement trajectories. Following ³⁶
456 we fitted the movement mode models (Supplementary Methods 2-Equation 1) using nonlinear
457 mixed effects models (nlme in ‘nlme’ R library) and evaluated the support from the data for the
458 different movement modes using the concordance criterion ⁶⁸. Before applying the goodness-of-
459 fit measure we also checked that the estimated parameters (e.g. timing or distance of dispersal)
460 were consistent with the spatio-temporal scales of the trajectory and discarded models that were
461 inconsistent (Supplementary Table 1).

462 **Juveniles.** We applied NSD models to juvenile movement data covering the first 3 months after
463 departure from the natal colony (see details in Supplementary Methods 2.1). Fig.1 shows typical
464 juvenile trajectories along with the corresponding NSD curve and model fit. We identified a new
465 movement type that we named “large-scale looping” (Fig.1.c, details in Supplementary Methods
466 2.2). To complete the information given by the NSD method, we calculated the distance from the
467 colony reached at 3 months for an index of dispersion distance and classified species as follows:
468 (1) small scale movements – birds which remained in the Indian Ocean, at a range shorter than
469 3000 km from the colony; (2) medium scale movements - birds which dispersed to the
470 Australian or South-African coasts, i.e. between 3000 and 6000km; and (3) large scale
471 movements - birds which left the Indian Ocean and ranged farther than 6000km.

472 **Adults.** For adult birds we applied the NSD method on the whole inter-breeding period, i.e. 5 to
473 12 months depending on the species. All adult trajectories were best fitted by the migratory
474 model as adults always returned to the colony to breed. As for juveniles, we compared inter-
475 breeding migration distances and displacements scale in the wintering areas along with the type
476 of habitat used (neritic or oceanic) as detailed in Supplementary Methods 2.3.

477 **Trajectory parameters analyses.**

478 To quantify detailed juvenile movement parameters and test the innate navigation hypothesis, we
479 calculated movement statistics commonly used for animal trajectory analysis⁶⁵, i.e. orientation,
480 daily distance travelled, sinuosity and range. For consistency, all parameters were averaged over
481 15 day time periods for the three first months of the trips for each individual. To aid
482 visualization, however, we present only the first 15 days of each month in our figures, i.e. values
483 for three periods of 15 days. Circular statistics for orientation analyses were computed with the R
484 package “circular”⁶⁹. For other parameters, we used linear mixed effect models (lme within

485 ‘nlme’ R package ⁷⁰) with individual as random factor to take into account individual variability,
486 followed by post-hoc Tukey tests (‘multcomp’ R package ⁷¹) to test for temporal and
487 interspecific differences (see lme & Tukey test results in Supplementary Results 1 & 2 and
488 Supplementary Table 2). Differences between time periods or between species were considered
489 significant at the $P < 0.05$ level in Tukey pair-wise comparison tests. For all models we visually
490 checked that model assumptions were met. For Yellow-nosed albatrosses and other species after
491 a certain amount of time, small sample sizes lead to unsatisfactory residual distribution and thus
492 the tests for these species are to be considered with care (see supplementary Method 3 for
493 details). Parameters calculated for each track were: the bearing taken at departure, the
494 directionality of the bird with respect to the colony after two and three months, the sinuosity of
495 tracks, the daily distance travelled and the mean latitude attained. Details for parameter
496 calculations and statistics can be found in Supplementary Methods 3.

497 **Habitats used**

498 To determine the conditions where juveniles settled in specific areas we examined the
499 bathymetric characteristics of their last locations (neritic waters when depth $> -3000\text{m}$, i.e. from
500 lower continental slope to continental shelf, or oceanic area when over deeper waters), and
501 compared this with adults’ broad habitat types (Supplementary Methods 2.3). Although it was
502 not possible here to obtain accurate information on adult habitat, we extracted bathymetry, daily
503 sea surface temperature (SST) and monthly chlorophyll *a* (CHL*a*) values for all juveniles’
504 trajectories. Environmental data were downloaded from the NOAA coast watch website
505 (<http://coastwatch.pfeg.noaa.gov/erddap/index.html>). To allow comparison between species,
506 bathymetry, SST and CHL*a* values have been summarised in Supplementary Fig.2. As for
507 trajectory parameters, differences between species have been tested with linear mixed models

508 and Tukey post-hoc tests in order to take individual variability into account. We used all
509 locations with environmental data available and took autocorrelation into account in the models.
510 Conversely, the large inaccuracy of GLS locations did not permit to reach any conclusions about
511 adult habitat characteristics.

512

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697

698 **Author contributions**

699 H.W. designed research and corrected the manuscript; S.d.G. collected field data, analysed data
700 and wrote the manuscript; L.B helped for NSD analyses and manuscript writing, A.G. did
701 preliminary statistical analyses. *All authors gave final approval for publication.*

702 **Competing interests**

703 *We have no competing interests.*

Table 1

Dataset information. Abbreviation used, mass, colony of origin and number of birds equipped with tracking duration (mean \pm standard deviation (minimum – maximum)) by species, for juveniles and adults. Masses are only indicative for species and obtained from literature ⁷². A, C and K are respectively Amsterdam, Crozet and Kerguelen Islands.

Taxa	Species	Scientific name	Species code	Mass (kg)	Colony	Juveniles		Adults	
						N	Tracking time	N	Tracking time
Great albatrosses	Amsterdam albatross	<i>Diomedea amsterdamensis</i>	AMAL	8.0	A	11	123 \pm 91 (21 – 280)	8	329 \pm 48 (252 – 369)
	Wandering albatross	<i>Diomedea exulans</i>	WAAL	10.9	C, K	23	159 \pm 89 (26 – 379)	10	222.3 \pm 13 (330-366)
Mollymawks	Yellow-nosed albatross	<i>Thalassarche carteri</i>	YNAL	2.6	A	4	48 \pm 40 (3.0 – 94)	10	320 \pm 31.6 (198-297)
	Black-browed albatross	<i>Thalassarche melanophris</i>	BBAL	3	K	12	69 \pm 30 (15 – 96)	10	373 \pm 26 (165-249)
Sooty albatrosses	Sooty albatross	<i>Phoebastria fusca</i>	SOAL	2.8	A, C	13	107 \pm 79 (2 – 254)	10	310 \pm 52 (174-375)
	Light mantled sooty albatross	<i>Phoebastria palpebrata</i>	LMSA	3.3	C, K	7	90 \pm 60 (8 – 186)	10	136 \pm 28 (273-366)
Giant petrels	Northern giant petrel	<i>Macronectes halli</i>	NOGP	5	C, K	10	118 \pm 61 (44 – 227)	10	346 \pm 15 (351-387)
	Southern giant petrel	<i>Macronectes giganteus</i>	SOGP	5	C	5	96 \pm 65 (43 – 190)	10	322 \pm 8 (120-144)
Petrel	White-chinned petrel	<i>Procellaria aequinoctialis</i>	WCPE	1.2	C, K	13	48 \pm 42 (15 – 109)	10	271 \pm 14 (303-336)
Total						98	96 \pm 37	88	292 \pm 73

1 **Table 2**

2 **Prevalence of different movement modes for juveniles of nine procellariiform species**
 3 **identified using the NSD method and movement scale at 3 months.**

Taxa	Species	NSD models				Range at 3 months	Movement Scale
		Home-range	Nomad	Half migration	Migration		
Giant petrels	NOGP	0	66%	33%	0	17350 ± 2565	large
	SOGP	0	100%	0	0	23859 ± 2299	large
Mollymawks	YNAL	0	0	100%	0	4869	medium
	BBAL	0	14%	86%	0	5971 ± 1648	medium
Petrels	WCPE	0	0	100%	0	4117 ± 510	medium
Sooty albatrosses	LMSA	0	0	50%	50%	2221 ± 1421	small
	SOAL	57%	43%	0	0	1730 ± 702	small
Great albatrosses	AMAL	0	43%	57%	0	2943 ± 1525	small
	WAAL	0	33%	66%	0	4233 ± 2285	medium

4

5

6

7 **Table 3**

8 **Dispersion distances and habitats visited by juveniles and adults.**

Taxa	Species	Juveniles			Adults		
		Movement scale	Habitat (%individuals)		Dispersion distance	Variation at asymptote	Habitat
Giant petrels	NOGP	large	O	(70%)	836 ± 143	357 ± 65	N/O
	SOGP	large	O	(80%)	1291 ± 186	364 ± 110	N/O
Mollymawks	YNAL	medium	N	(100%)	5004 ± 476	488 ± 265	N
	BBAL	medium	N	(81%)	3985 ± 328	291 ± 88	N
Petrels	WCPE	medium	N/O	(57% / 43%)	5415 ± 328	605 ± 174	N
Sooty albatrosses	LMSA	small	O	(100%)	3862 ± 438	1084 ± 241	O
	SOAL	small	O	(90%)	4817 ± 1124	759 ± 430	O
Great albatrosses	AMAL	small	O	(89%)	3078 ± 966	712 ± 147	O
	WAAL	medium	O/N	(77% / 23%)	5456 ± 457	1018 ± 847	N/O

9

10 All adults' trajectories fitted by the migratory type NSD model, the dispersion distance is the
 11 distance to colony of the migratory model asymptote and the variation around the asymptote is
 12 calculated with the residuals of the model. Habitats are oceanic (O) and neritic (N).

13

14

15 **Legends to figures**

16 **Fig.1. Typical juvenile trajectory patterns (left) and corresponding NSD curves** (right, red
17 lines are best NSD model fits) illustrated by **a)** Northern giant petrel (nomadic type), **b)** Black-
18 browed albatross (half-migration type), **c)** Sooty albatross (large-scale looping type best fitted
19 here by a home-range NSD model). Panel **d)** shows 3 different trajectory types of juvenile
20 wandering albatross and NSD fits corresponding (red line) with nomadic type movement (black
21 dots, full red line), half-migratory type movement (grey dots, dashed red line) and large-scale
22 looping movement (white dots, dash-dot red line). White star and diamond are respectively
23 Crozet and Kerguelen colonies. Maps have been generated with R⁶⁴ and the “ggplot2” library⁷³
24 and free-access coastline data (from *naturalearthdata.com*).

25

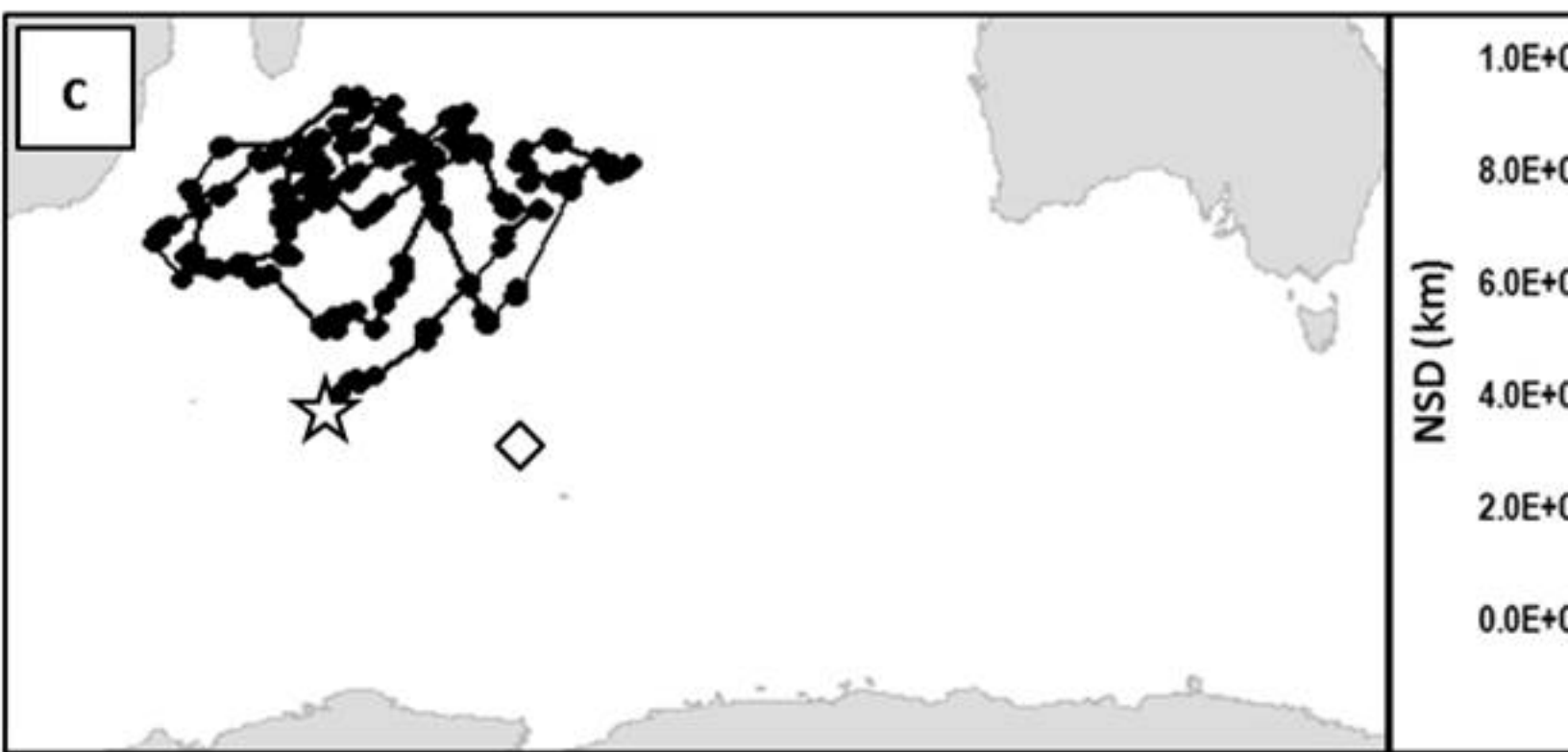
26 **Fig.2. Orientations.** Departure directions (black dots) and rhumb bearing of the position at 2
27 months (grey dots) and 3 months (white) with respect to the departure point, i.e. the birth colony.

28

29 **Fig.3. Sinuosity and daily distance travelled.** **a)** Average sinuosity of the trajectory during the
30 first 15 days at sea of month 1 (black dots), month 2 (grey dots) and month 3 (white dots). **b)**
31 Average daily distance travelled (DDT) \pm one standard error (bars) during the 15 first days of
32 months 1 (black), 2 (grey) and 3 (white).

33

34 **Fig.4. Latitudes.** Mean latitude \pm one standard error (bars) attained during the third month at sea
35 by juveniles (white circles) and by adults during inter-breeding season (black circles). Significant
36 differences between juveniles and adults are **: $P < 0.05$ and ***: $P < 0.01$ (Wilcoxon test).



NOGP

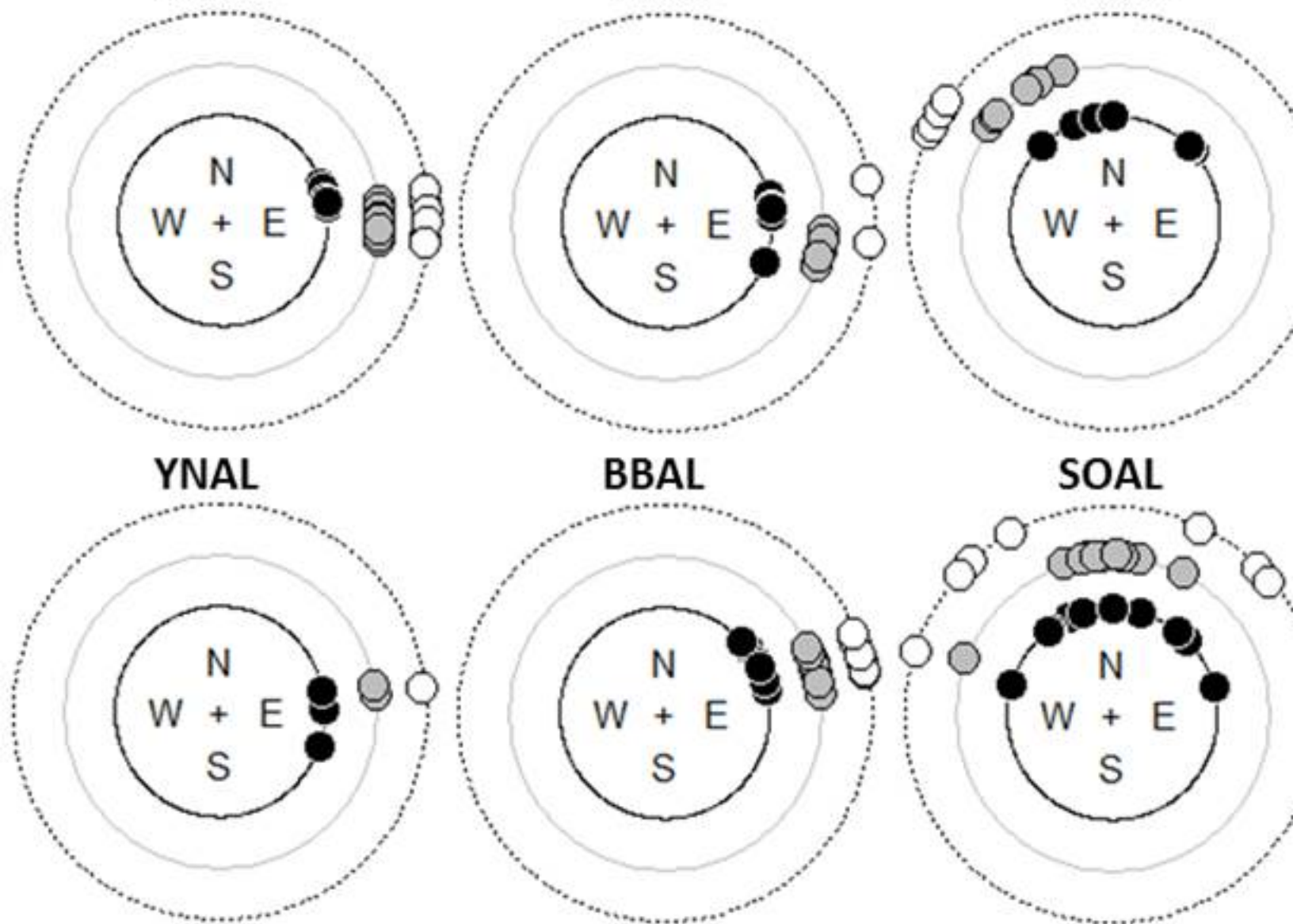
SOGP

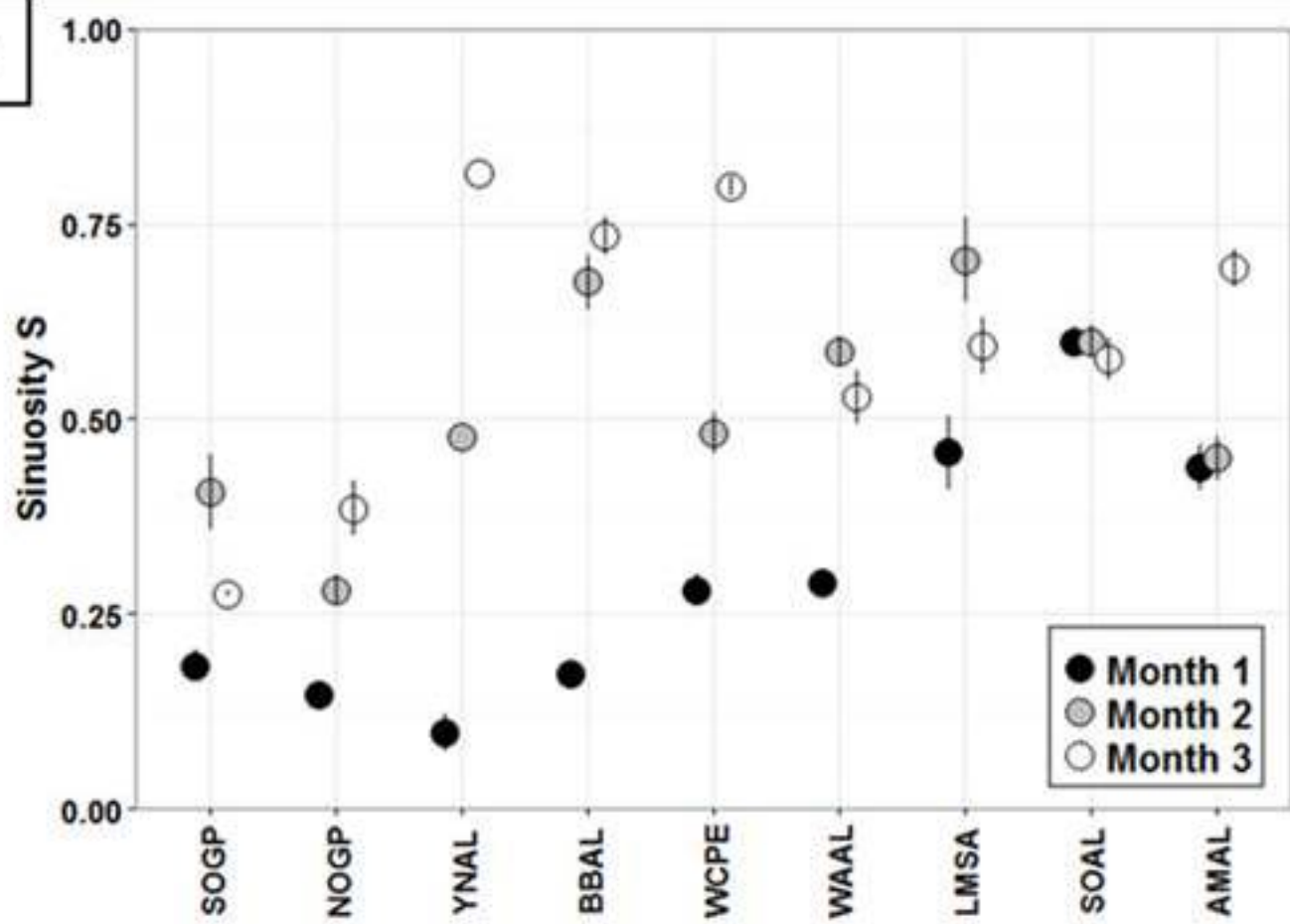
WCPE

YNAL

BBAL

SOAL



a**b**