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## Active breeding seabirds prospect alternative breeding colonies

Jelena Kralj, Aurore Ponchon, Daniel Oro, Barbara Amadesi, Juan Arizaga, Nicola Baccetti, Thierry Boulinier, Jacopo Cecere, Robin Corcoran, Anna-Marie Corman, et al.

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77 **ABSTRACT**

78 Compared to other animal movements, prospecting by adult individuals for a future breeding  
79 site is commonly overlooked. Prospecting influences the decision of where to breed and has  
80 consequences on fitness and lifetime reproductive success. By analysing movements of 31  
81 satellite- and GPS-tracked gull and tern populations belonging to 14 species in Europe and  
82 North America, we examined the occurrence and factors explaining prospecting by actively  
83 breeding birds. Prospecting in active breeders occurred in 85.7% of studied species, across  
84 61.3% of sampled populations. Prospecting was more common in populations with frequent  
85 inter-annual changes of breeding sites and among females. These results contradict theoretical  
86 models which predict that prospecting is expected to evolve in relatively predictable and stable  
87 environments. More long-term tracking studies are needed to identify factors affecting patterns  
88 of prospecting in different environments and understand the consequences of prospecting on  
89 fitness at the individual and population level.

90

91 **KEYWORDS:** tracking devices, dispersal, movements, behavioural ecology, gulls, terns

92

93

94 **INTRODUCTION**

95

96 Prospecting behaviour is present in migratory and non-migratory, solitary and colonial species  
97 and is defined as visits of individuals to potential alternative patches where they might breed  
98 in the future (Reed et al. 1999). During this process, individuals gather social and  
99 environmental information to assess the quality of potential breeding patches (Danchin et al.  
100 2004; Dall et al 2005). Prospectors have mainly been identified in non-breeding subadults or  
101 adults, which are supposed to search for a new breeding patch (Reed et al. 1999). Several

102 empirical studies showed that prospecting occurs in many taxa such as mammals (Selonen and  
103 Hanski 2010; Mares et al. 2014; Mayer et al. 2017), birds (Reed et al. 1999; Doligez et al. 2004;  
104 Parejo et al. 2007, Calabuig et al. 2010; Ponchon et al. 2017b), reptiles (Cote and Clobert 2007),  
105 amphibians (Pizzatto et al. 2016), and insects (Seeley and Buhrman 2001). During prospecting,  
106 individuals familiarize themselves with breeding patch size, local intraspecific competition,  
107 offspring quality and breeding success of conspecific or heterospecific individuals  
108 (Mönkkönen et al. 1999; Cayuela et al. 2018). Individuals can use that information to make  
109 what are called ‘informed dispersal’ decisions about where they will breed in future years  
110 (Clobert et al. 2009). Prospecting is especially important for immatures, as they do not have  
111 previous experience with any breeding patch apart from their natal site (Reed et al. 1999).  
112 Prospecting before recruitment may affect age at first reproduction, and increase individual  
113 fitness and lifetime reproductive success (Schorring et al. 1999; Frederiksen and Bregnballe  
114 2001; Genovart et al. 2020a).

115 Prospecting is a crucial component of informed dispersal and enables individuals to compare  
116 their current breeding patch with the neighbouring ones and make a decision on whether to stay  
117 or disperse (Boulinier and Danchin 1997; Reed et al. 1999). In general, philopatry has several  
118 advantages over dispersal, including the knowledge of the location of surrounding foraging  
119 grounds and social cohesion. The preference to breed in a familiar neighbourhood can enhance  
120 site fidelity. When emigration from a site is based on information use, dispersal is largely  
121 related to individual breeding success with failed breeders being more likely to disperse than  
122 successful breeders, especially in an unsuccessful breeding patch (Boulinier et al. 2008). To  
123 decide about a future breeding patch, failed breeders prospect neighbouring patches (Fijn et al.  
124 2014; Ponchon et al. 2017b). The degree of philopatry thus tends to be higher in stable and  
125 successful breeding patches (Palestis 2014). Should at some point dispersal occur, many  
126 individuals can leave their current breeding patch at once, which can result in significant

127 population size fluctuations and even collapses (Palestis 2014; Ponchon et al. 2015b; Genovart  
128 et al. 2020b). In birds, adult prospecting is mainly documented in later stages of the breeding  
129 cycle, during chick-rearing, when breeding success is easy to assess and when failed breeders  
130 have spare time before moulting or migration (Boulinier and Lemel 1996; Doligez et al. 2004;  
131 Ward 2005). Prospecting may also occur before the breeding season, despite time constraints  
132 associated with seasonal nesting (Farrell et al. 2012; Spendelow and Eichenwald 2018).

133 Until recently, prospecting was mainly studied from marked individuals (e.g. Ward 2005;  
134 Dugger et al. 2010; Mares et al. 2014). Recent increases in the use of animal tracking  
135 technologies have begun to show how widespread prospecting behaviours can be in free-living  
136 populations. However, compared to the analysis of foraging habitat selection, breeding habitat  
137 selection is still understudied and the occurrence of prospecting in various species, including  
138 seabirds, is still not well understood (Grémillet and Boulinier 2009; Ponchon et al. 2013).

139 Based on the collected evidence so far, prospecting in adults is commonly attributed to failed  
140 breeders (Fijn et al. 2014; Ponchon et al. 2015a; Ponchon et al. 2017b). Prospecting is energy-  
141 demanding, and birds occupied with reproductive duties are not expected to spend time visiting  
142 conspecific colonies (Reed et al. 1999). Yet, recently, a few tracking studies have revealed that  
143 some adults who are still actively breeding (i.e. successful in their current breeding attempt)  
144 may visit conspecific breeding patches (Martinović et al. 2019; Oro et al. 2021). Such  
145 prospecting during active breeding is largely understudied, despite its potential broad  
146 occurrence. The fact that active breeders are devoting time and energy to prospect while also  
147 meeting the energy requirements of incubating and rearing young suggests that prospecting is  
148 an important component of habitat selection.

149 In this study, we collected satellite- and GPS-tracking data of 31 populations of 14 colonial  
150 gull and tern species during the breeding season to explore the occurrence of prospecting in  
151 active breeders (PAB) and assess the factors affecting that behaviour. We further analysed a

152 subset of prospecting trips to identify their temporal and spatial patterns. Based on the  
153 numerous theoretical works which stressed that prospecting is expected to evolve especially in  
154 temporally predictable environments (Boulinier and Danchin 1997; Doligez et al. 2004; Bocedi  
155 et al. 2012; Ponchon et al. 2021), we hypothesized that PAB was more likely to occur in  
156 populations that bred in relatively stable environments. Based on the optimal timing  
157 hypothesis, according to which prospecting occurrence is the greatest during chick-rearing,  
158 when the best quality information about conspecific reproductive success can be achieved  
159 (Boulinier et al. 1996), prospecting was expected to be more frequent during chick-rearing  
160 period.

161

## 162 **MATERIAL AND METHODS**

### 163 **Data collection**

164 We collated data from studies based on satellite- and GPS-tracking of adult breeding seabirds  
165 collected through different projects that mostly aimed to study foraging movements (Table 1).  
166 We restricted our study to gulls and terns from Europe and North America as the species of  
167 these families are known to vary in philopatry and life-history traits, and extensive tracking  
168 data during the breeding season is available (Schreiber & Burger 2002, Brooke 2018). We  
169 selected studies in areas where the position of conspecific breeding patches were known based  
170 on field research or surveying or monitoring programs. Colonies can be defined as aggregates  
171 of only-breeding territories (Danchin et al. 1998). Colony determination is often subjective and  
172 differs for each species (Jovani et al. 2008). In this paper, we define a “breeding patch” as a  
173 formation of clustered nests spatially separated by topographic features (single cliffs, islands,  
174 roofs, etc.).

175 We defined PAB (prospecting in active breeders) as the visit to other conspecific breeding  
176 patches by a breeding individual during the incubation or chick-rearing stage. Due to the



177 different temporal resolutions of GPS/satellite positions (between 5 and 30 minutes) in the  
178 different studies, prospecting was confirmed if two successive locations (with a null speed  
179 when available) were recorded at the visited patch, indicating at least a short resting period. In  
180 populations with frequent perturbations, where breeding patches might be abandoned for  
181 several years and then recolonised, visits to all known breeding patches were categorised as  
182 prospecting, even if the patch was not confirmed to be active in the respective year (Oro et al.  
183 2021).

184 We collected data from 1196 adult individuals belonging to 14 species. In general, birds were  
185 captured towards the end of the incubation stage to reduce the likeliness of clutch abandonment  
186 and maximize the capturability. The majority (90.8%) of birds were tracked during a single  
187 breeding season (from a few days to a few weeks), while 9.2% of birds were tracked during 2  
188 or more (maximum 5) successive breeding seasons, resulting in a total sample of 1392  
189 birds/seasons. The sex of birds was known in 1170 cases, with 587 females and 583 males.

190 Gulls and terns have semi-precocial chicks that leave the nest within 2-4 days (terns) or up to  
191 8 days (gulls) after hatching. The ledge-nesting kittiwakes are the exception with chicks staying  
192 in the nest for around 30 days (Lance and Roby 1998; Coulson 2011). We used monitored or  
193 presumed nest fate to assess whether tagged birds were actively breeding. Nest fate covered  
194 the period of incubation and early chick-rearing and was monitored using cameras or through  
195 visual monitoring of nests. Alternatively, it was presumed from the movements of tracked  
196 birds, where regular visits to their breeding patch (based on GPS positions) during the  
197 incubation and early chick-rearing period were considered as indication of active breeding (e.g.  
198 Ponchon et al. 2017a; Picardi et al. 2020). Incubating birds or birds with young chicks were  
199 considered to be active breeders, no matter the final fate of their offspring. Movements after  
200 presumed breeding failure were not analysed. Tracked birds that failed early during tracking  
201 were not included in the analysis.

## 202 **Selection of variables**

203 We tested how intrinsic and environmental factors affected the occurrence of PAB. We  
204 recorded variables related to the birds and variables describing their breeding patch. For each  
205 bird, its identification number, species, sex, species-specific duration of incubation and chick-  
206 rearing, and relative tracking duration for each breeding season were recorded. The categorical  
207 variables related to the breeding patch included in our model were patch identification number,  
208 occurrence of large breeding failure, frequent changes of breeding locations (CBL), habitat  
209 type and patch stability, whereas the continuous variables were distance to the closest  
210 conspecific breeding patch (DCC) and latitude. Additionally, for prospecting individuals,  
211 distances to the prospected patches were recorded.

212 Duration of incubation and chick-rearing stage until fledging is given as an average time in  
213 days, extracted from BWPi (2006) and Billerman et al. (2020) for European and North  
214 American species respectively. The relative tracking duration was provided in four categories,  
215 representing < 25%, 25-50%, 51-75% and > 75% of the breeding season duration (egg-laying  
216 to fledging). We assessed whether regular breeding failure (as the result of predation, adverse  
217 weather, flooding, or food shortage) occurred at the studied patches. Information whether  
218 groups of birds frequently changed their breeding locations was often based on long-term  
219 monitoring or data obtained by colour-ringing. The type of habitat where species evolved  
220 distinguished ephemeral habitats (such as dynamic marshes, salt pans and dunes) and stable  
221 habitats (rocky cliffs, rocky islands). For defining breeding patch stability, codes were used as  
222 follows: 1 - (one of) the biggest colonies in the study area; 2 - stable but smaller breeding patch,  
223 frequently used; 3 - new or infrequently used breeding patch (Supplementary Material Table  
224 1).

## 225 **Statistical analyses**

226 We built generalized linear mixed-effects models (GLMM) to assess the factors affecting the  
227 occurrence of PAB for each tracked individual as a binomial response variable, using  
228 categorical and continuous predictors with logit link. Relative tracking duration and breeding  
229 patch ID were included as random variables. We checked variables for collinearity and  
230 excluded the variable “species” from the models. Interactions among variables (CBL, DCC,  
231 stability, sex) were tested, but did not significantly influence the models. Model fit accounting  
232 for model complexity was evaluated using the Akaike information criterion corrected for small  
233 sample sizes (AICc, Burnham and Anderson 2002). Since the top three models (lowest AICc)  
234 had  $\Delta AICc$  less than two, these models were conditionally averaged using the `model.avg`  
235 function (Bartón 2020). Statistical analyses were conducted in R version 4.1.1 (R Core Team  
236 2021) using the `lme4` (Bates et al. 2015) and `MuMIn` (Bartón 2020) packages.

237 We further aimed at identifying temporal and spatial patterns of PAB based on 322 prospecting  
238 tracks from 113 individuals from 11 species. We used Yates corrected Chi-square test to  
239 analyse the difference in the occurrence of prospecting trips between sexes, breeding stages  
240 (incubation or chick-rearing) and time of the day (day vs. night). The correlation between the  
241 distance to the closest breeding patch and prospected patches were analysed by Pearson  
242 correlation.

243

## 244 **RESULTS**

### 245 **Factors affecting the occurrence of PAB**

246 From 31 populations of 14 gull and tern species analysed, prospecting in active breeders (PAB)  
247 was recorded in 19 populations of 12 species (Table 1): 2 out of 5 tern populations and 17 out  
248 of 27 gull populations. The percentage of prospecting individuals among all breeders ranged  
249 from 0.6 to 70%. Higher percentages (>25% prospecting individuals in studies with a minimum  
250 of 10 tagged birds) were recorded among five species: Mediterranean gull, *Larus*

251 *melanocephalus*, Audouin's gull *Larus audouinii*, yellow-legged gull *Larus michahellis*,  
252 sandwich tern *Thalasseus sandvicensis* and common tern *Sterna hirundo*.

253 The inter-annual change of breeding location and sex were shown to be the most important  
254 variables affecting the occurrence of PAB (Table 2). Conditionally averaged best three models  
255 (Figure 1) showed that probability for PAB was higher in populations showing frequent inter-  
256 annual change of breeding location (GLMM z value = 3.819,  $p < 0.001$ ) and among females  
257 (GLMM z value = 2.201,  $p < 0.01$ ).

### 258 **Analysis of prospecting trips**

259 From prospecting trips of birds with known sex (N = 185), 61.6% were undertaken by females  
260 (Figure 2). Females had higher median prospecting distances in six species and higher  
261 maximum distances to prospected colonies in six species, but due to the small sample size, the  
262 difference was significant only for one population of Audouin's gulls (Supplementary Material  
263 Table 2). From all prospecting trips with a known stage of the breeding cycle (N= 243), 63%  
264 were undertaken during the chick-rearing stage, with similar values (53.3-60.8%) obtained for  
265 individuals with longer relative tracking durations (>50% of the breeding season). Also, 40.8%  
266 of prospecting trips with a reported time of day (N=277) included nocturnal visits in prospected  
267 colonies. Nocturnal trips were more common during the incubation stage (51.1% of trips during  
268 that stage) than during the chick-rearing (29.4% of trips) (Yates corrected  $\chi^2 = 4.46$ ,  $p < 0.05$ ).

269 The majority of visited patches were < 100 km from the breeding patch (Figure 3, Figure 4)  
270 and distances to prospected patches (range 0.8-345 km) were highly correlated to the distances  
271 to the closest breeding patch (range 0.8-385 km) (Pearson correlation = 0.368,  $p < 0.01$ ).

272 The greatest number of prospecting tracks were collected for the sandwich tern from the  
273 Netherlands (41 individuals with a total of 133 prospecting trips). For that species, the median  
274 number of prospecting trips per bird was 2 (range 1-8), while the median distance was 8 km  
275 (range: 5-202). Most prospecting trips of the sandwich tern were undertaken only during the

276 daytime, but 39.1% of them also included nocturnal visits in prospected colonies. Also, 42.1%  
277 of trips were undertaken during the incubation stage. The percentage of trips that included  
278 nocturnal visits at the prospected colony was higher during the incubation stage (60.7%) than  
279 during chick-rearing (23.4%), the difference being significant (Yates corrected  $\chi^2= 7.20$ ,  $p <$   
280  $0.01$ ). More nocturnal visits during the incubation stage were also found in common tern (5  
281 during incubation versus 1 during the chick-rearing stage), but the total number of trips was  
282 low ( $N = 12$ ). A substantial percentage of nocturnal visits were undertaken by Audouin's and  
283 yellow-legged gulls (47.6% and 46.2% respectively), whereas Mediterranean gulls prospected  
284 only during daytime.

285

## 286 **DISCUSSION**

287

288 Contrary to our predictions, prospecting in active breeders (PAB), a behaviour largely  
289 unnoticed in the scientific literature, was recorded in 85.7% of studied gull and tern species  
290 and 61.3% of sampled populations. During the breeding period, central place foragers like  
291 seabirds are constrained in time and energy, as they must divide their time between foraging  
292 for themselves and investing in reproduction (Orians and Pearson 1979). The fact that  
293 prospecting frequently occurs during incubation and chick-rearing stresses its importance in  
294 the breeding habitat selection process and might be much more widespread than currently  
295 acknowledged.

### 296 **Drivers of prospecting: breeding patch, sex and distance**

297 The relation between prospecting and inter-annual change of breeding locations is consistent  
298 with the well-supported hypothesis that prospecting helps individuals select their future  
299 breeding site (Reed et al. 1999). Changing a breeding location might be preceded by sabbatical  
300 year(s), during which individuals prospect potential breeding sites (Munilla et al. 2016; Oro et

301 al. 2021); however, our results show that currently breeding birds also engage in PAB.  
302 Prospecting during different stages of the breeding cycle also allows breeding individuals to  
303 compare the quality of their current breeding patch to other localities over a wider area,  
304 informing the decision of whether to disperse or not. This information could be used for the  
305 current or future breeding seasons. As <10% of individual birds in our study were tracked over  
306 multiple consecutive breeding seasons, we could not examine whether prospecting birds  
307 actually used gathered information to disperse to a prospected patch the following season.  
308 However, Oro et al. (2021) found no prospecting in successfully breeding Audouin's gulls that  
309 were philopatric in the following year, and intensive prospecting in both successful and  
310 unsuccessful breeders that dispersed in the following year, highlighting the crucial role of  
311 prospecting in dispersal decision. Prospecting patterns might thus potentially reflect  
312 individuals' intentions to disperse. However, this tight link between prospecting and  
313 subsequent dispersal is still challenging to record in the field, as individuals must be tracked  
314 over long periods and large spatial scales.

315 We considered relative breeding patch size and frequency of its use as a proxy for the stability  
316 of the patch but also as an indicator of environmental quality. However, patch stability in our  
317 study did not have a significant effect on PAB. This contradicts previous theoretical models  
318 that showed that prospecting may only evolve in a relatively predictable and stable environment  
319 (Boulinier and Danchin 1997; Doligez et al. 2003; Bocedi et al. 2012). Nevertheless, those  
320 models mostly addressed prospecting where dispersal occurred the following year, not during  
321 the same breeding season. The difference in timing of information use might be crucial in an  
322 unstable environment, since in this case, information gathered during prospecting might be  
323 used immediately, such as for reneating purposes. As replacement clutches are more likely to  
324 be laid after failure in earlier stages of the breeding season (Pakanen et al. 2014), prospecting  
325 during the incubation suggests that PAB may also be used to identify suitable patches for

326 renesting elsewhere within the same season (Ward 2005; Martinović et al. 2019). At the same  
327 time, PAB was more common during the early chick-rearing stage than during incubation,  
328 which is consistent with the “optimal-timing hypothesis” (Boulinier et al. 1996).

329 Prospecting was more common in breeding females than in males, as already observed in adult  
330 breeding yellow-headed blackbirds *Xanthocephalus xanthocephalus* (Ward 2005). In general,  
331 females have higher dispersal probabilities in most bird species (Greenwood 1980), which may  
332 explain higher prospecting rates. Similarly, in six species females travelled greater maximum  
333 distances to prospected colonies than males. It has been shown that in several seabird species,  
334 the smaller sex undertakes longer foraging trips during the breeding season (Phillips et al.  
335 2017). In the current study, females were the smaller and lighter sex in all seabirds examined.  
336 Therefore, they may use less energy for flying, which might be the underlying reason for their  
337 longer prospecting flights (Wearmouth and Sims 2008). In general, parental care in studied  
338 gulls and terns is shared between sexes (Leclaire et al 2010; Kavelaars et al 2021) with some  
339 differences among species. For example, females often perform more incubation and chick-  
340 rearing, whereas males perform most territory attendance in gulls and more provisioning in  
341 terns and some gulls (Pierotti, 1981; Fasola and Saino 1995).

342 Distances to the prospected colonies were highly correlated with distances to the closest  
343 breeding patch. In our study, birds usually visited patches close to their current breeding patch,  
344 but on five occasions, visits to the nearest breeding patch (ranging 10-24 km) were not  
345 recorded. Whether active breeders visit all available patches or only some of them might  
346 depend on the number and distances to potential breeding patches, but also on the previous  
347 experience of individuals. As breeding seabirds must return frequently to their breeding patch  
348 to undertake reproductive duties, maximal prospecting distances of active breeders were  
349 expected to be lower than in failed breeders. This was confirmed in Audouin’s gulls where the  
350 maximum distance to prospected patches was 164 km in active and 360 km in failed breeders

351 (Oro et al. 2021), and in sandwich terns, where maximal distances in active breeders (202 km)  
352 were lower than in failed breeders from the same colonies (850 km; Fijn et al. 2014).  
353 Nocturnal visits were recorded in 40.8% of prospecting trips and were more frequent during  
354 incubation. Frequent prospecting or longer visits to prospected colonies decrease nest  
355 attendance, creating a trade-off between nest attendance and prospecting. Peak numbers of  
356 Audouin's gulls prospecting at night were also reported by Oro et al. (2021). Nocturnal visits  
357 might decrease negative interactions with conspecifics and predators while enabling the  
358 assessment of population density and breeding success.

### 359 **Intra- and inter-specific differences in PAB**

360 Kittiwakes were the exception among studied seabirds, as almost no PAB was recorded.  
361 Previous tracking studies on breeding black-legged kittiwakes showed that prospecting only  
362 occurred in failed breeders (Ponchon et al. 2015b; Ponchon et al. 2017b). In our study, only  
363 one bird from 324 black-legged kittiwakes and two from 94 red-legged kittiwakes *Rissa*  
364 *brevirostris* prospected while actively breeding. Furthermore, the occurrence of PAB differed  
365 between populations of the same species: PAB occurred in Oregon, but was not observed in  
366 Californian populations of the western gull *Larus occidentalis*, whereas in yellow-legged gull,  
367 PAB was common in the Balearic population, but not in the Atlantic one (Delgado et al. 2021,  
368 Table 1). Overall, inter- and intra- species variability calls for more detailed studies of PAB in  
369 different populations of the same species but also in species with different life-history  
370 strategies. Possible factors that could affect prospecting are differences in physical  
371 environments (e.g. populations at the core/edge of species range, number of conspecific  
372 colonies), density-dependence at both inter- and intra-specific level, a regime of perturbation,  
373 age-distribution, laying synchrony and habitat suitability (including foraging opportunities and  
374 predator density; Oro et al. 1996; Tavecchia et al. 2008; Sanz-Aguilar et al. 2009).



375 Other factors that might influence prospecting are animal personality shown to affect dispersal  
376 (Cote et al. 2010; Schuett et al. 2012) and individual experience or age (Oro et al. 1999; Payo-  
377 Payo et al. 2017). Older immatures individuals generally prospect less, with increased fidelity  
378 to a selected site before attempting breeding for the first time (Cadiou et al. 1994, Dittmann et  
379 al. 2005; Campioni et al. 2017). In contrast, older adults may be more likely to prospect, such  
380 as in meerkats *Suricata suricatta* (Mares et al. 2014). Knowing the age of tracked individuals  
381 may provide greater clarity on whether individuals of different age and experience display  
382 different prospecting patterns.

### 383 **The effect of data quality**

384 In the present study, we assumed that any visit to a conspecific colony was for prospecting.  
385 Even if we cannot rule out the possibility that some individuals visited breeding patches for  
386 other purposes than prospecting for a future breeding site (see Ponchon et al 2015a), being  
387 present in another breeding patch with other conspecifics may still provide information that  
388 could be used for dispersal and settlement decisions. Accordingly, we believe our assumption  
389 did not significantly affect our results. On the contrary, PAB evidence might still be  
390 underestimated, especially in studies involving a small number of tracked individuals or short  
391 tracking periods, or if not all conspecific breeding patches were identified and visits to these  
392 sites were not recorded as prospecting. Moreover, in our study, adults were mostly tracked  
393 from the mid-incubation stage onwards, so visits to other colonies at the beginning of the  
394 incubation stage were not recorded. Similarly, visits towards the end of the rearing stage were  
395 not included, as it was not possible to identify if breeding was over for individuals (by fledging  
396 or chick loss).

397 A few studies showed long-distance movements and prospecting in birds (Boulinier et al. 2016;  
398 Cooper and Marra 2020), highlighting the underestimation of the frequency and spatial scale  
399 at which animals move outside of their territories. Understanding the purpose and scale of

400 prospecting movements and being able to relate them to actual dispersal would have important  
401 implications for the ecology, evolution, and conservation of species, especially in the current  
402 context of environmental change (Dugger et al. 2010; Ponchon et al. 2015b). The number of  
403 tracking studies is increasing, especially in the marine environment. Although many of them  
404 aimed to identify foraging behaviour or migration routes, they might also be a source of other  
405 information (Hays et al. 2016). Regardless of the goal of tracking studies, more attention should  
406 be given to the movements of individuals that differ from usual foraging patterns. In species  
407 that often disperse, tracking prospecting in breeding adults as well as tracking their visits to  
408 potential, but empty patches might provide insights into their intentions in terms of current and  
409 future breeding habitat selection and colonisation of new breeding patches (Oro 2020; Oro et  
410 al. 2021). It would also help to identify already existing breeding patches and be an important  
411 tool for planning the monitoring of breeding populations, assessing population borders and  
412 designing conservation measures.

## 413 **CONCLUSION**

414 By reviewing the occurrence of PAB among different gull and tern species, we highlighted the  
415 importance of prospecting in adult breeding seabirds. We showed that PAB is more common  
416 in populations with frequent breeding dispersal and among females. Informed dispersal may  
417 help populations to recover faster in response to environmental change by tracking better  
418 environmental conditions, notably through extinction-recolonization dynamics (Ponchon et al.  
419 2015b). Still, little is known about the drivers that influence prospecting and subsequent  
420 settlement in a new breeding patch, including the effect of various environmental factors (Payo-  
421 Payo et al. 2017; Oro et al. 2021). Our results call for more long-term tracking studies  
422 simultaneously monitoring the breeding success not only of individuals but also of whole  
423 breeding patches to identify factors affecting spatial and temporal patterns of prospecting in

424 different stages of populations and different environments This would ultimately allow us to  
425 better predict species response to environmental change.

426

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430

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475 **Ethical approval:** All applicable institutional and/or national guidelines for the care and use  
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477 **Consent to participate:** NA

478 **Consent for publication:** NA

479 **Availability of data and material:** The datasets analysed during the current study are  
480 available from the corresponding author upon reasonable request.

481 **Code availability:** NA

482 **Authors' contributions:** JK collected and analysed the data and wrote the first draft of the  
483 manuscript. JK, AP, DO and RF wrote the manuscript. SP prepared the map with prospecting  
484 tracks. All authors contributed with published or unpublished data: AP, DG, TB, RP, AH and  
485 RO for black-legged kittiwakes, RP, RO, SS and AF for red-legged kittiwakes, LS, SP and  
486 JGC for Mediterranean gulls and gull-billed terns, LJ, BR, NB, MZ, BA and DO for Audouin's  
487 gulls, SG and UK for mew gulls, SS, HY and RO for western gulls, SG, A-MC, AS, CW and  
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491 critically to the manuscript and gave final approval for publication.

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497 **Table 1.** Tracking studies of seabird movements included in the analysis of prospecting in active  
498 breeders. The number of prospecting individuals refers to birds prospecting during the active breeding.  
499 References based on tracking data included in this study are provided. References related to study of  
500 prospecting movements are given in bold.  
501

Species	Country	Year	No. of tracked individuals	No. of prospecting individuals	Percentage of prospecting individuals	Data owners
<i>Rissa tridactyla</i>	France	2014	36	0	0	Ponchon, A., Grémillet, D.
<i>Rissa tridactyla</i>	Norway	2010-2015	136	0	0	Ponchon, A., Boulinier, T.
<i>Rissa tridactyla</i>	USA	2008-2010	152	1	0.7	Paredes, R., Harding, A., Orben, R.,
<i>Rissa brevirostris</i>	USA	2010	23	0	0	Paredes, R., Irons, D., Roby, D.
<i>Rissa brevirostris</i>	USA	2015-2017	71	2	2.8	Orben, R., Fleishman, A., Kitaysky, A. Shaffer, S., Paredes, R.
<i>Larus melanocephalus</i>	Italy	2016	10	7	70	Serra, L., Pirrello, S., Cecere, J.G.
<i>Larus audouinii</i>	Croatia	2017-2021	28	12	42.9	Jurinović, L.
<i>Larus audouinii</i>	France	2014-2016	8	0	0	Recorbet, B.
<i>Larus audouinii</i>	Italy	2013-2020	30	3	10	Baccetti, N., Zenatello, M., Amadesi, B.

<i>Larus audouinii</i>	Spain	2006- 2011	38	16	42.1	Oro, D.
<i>Larus canus</i>	Germany	2018- 2020	19	0	0	Garthe, S., Kubetzki U.
<i>Larus canus</i>	Germany	2019- 2020	11	2	18.2	Garthe, S.
<i>Larus occidentalis</i>	USA	2013- 2020	177	0	0	Shaffer, S., Young, H., Warzybok, P., Jahncke, J.
<i>Larus occidentalis</i>	USA	2013- 2020	51	0	0	Young, H., Shaffer, S.,
<i>Larus occidentalis</i>	USA	2013- 2020	39	4	10.3	Orben, R.
<i>Larus fuscus</i>	Germany	2009- 2012, 2017- 2020	30	2	6.7	Garthe, S., Corman A-M.
<i>Larus fuscus</i>	Germany	2013- 2014	25	1	4	Garthe, S., Corman A-M.
<i>Larus fuscus</i>	United Kingdom	2016- 2020	12	1	8.3	Spelt, A., Williamson, C., Windsor, S.
<i>Larus argentatus</i>	Germany	2017- 2020	17	1	5.9	Garthe, S.
<i>Larus argentatus</i>	Germany	2019- 2020	7	0	0	Garthe, S.

<i>Larus argentatus</i>	Germany	2016-2020	30	2	6.7	Garthe, S., Schwemmer, P.
<i>Larus argentatus</i>	Germany	2012-2015	15	2	13.3	Garthe, S., Enners, L.
<i>Larus michahellis</i>	Croatia	2019-2021	10	1	10	Jurinović, L.
<i>Larus michahellis</i>	Spain	2018-2019	30	0	0	Arizaga, J.
<i>Larus michahellis</i>	Spain	2016-2021	20	7	35	Tavecchia, G., Igual, J.M.
<i>Larus marinus</i>	Germany	2016-2020	22	2	9.1	Garthe, S., Schwemmer, P.
<i>Onychoprion aleuticus</i>	USA	2019	10	0	0	Tengeres, J., Corcoran, R., Lyons, D.
<i>Gelochelidon nilotica</i>	Italy	2019-2020	15	0	0	Serra, L., Pirrello, S., Cecere, J.G.
<i>Sterna hirundo</i>	Croatia	2018	16	6	37.5	Kralj, J.
<i>Sterna hirundo</i>	Slovenia	2018-2019	7	0	0	Tome, D.
<i>Thalasseus sandvicensis</i>	Netherlands	2012-2020	101	41	40.6	Fijn, R.

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506 **Table 2.** Generalized linear mixed-effects models testing factors affecting the occurrence of prospecting  
 507 in active breeding gulls and terns with relative tracking duration and breeding patch ID as random  
 508 variables. The bottom model is the full model. The first three models were conditionally averaged.

Variables in the model	np	Dev	AICc	$\Delta$ AICc	Wi
CBL + sex	5	407.6	417.68	0	0.443
CBL + sex + stability	7	404.7	418.78	1.10	0.256
CBL + sex + DCC	6	407.2	419.31	1.63	0.197
habitat + sex	5	411.2	421.23	3.55	0.075
CBL + sex + stability + DCC + RBF + latitude + habitat + IF	12	398.9	423.14	5.46	0.029

509 Variables: CBL – frequent change of breeding location, stability - breeding patch stability, DCC –  
 510 distance to the closest colony, habitat – habitat where species evolved, RBF – regular breeding failure,  
 511 IF – duration of incubation and fledging (for details, see Material and Methods); np - number of  
 512 estimable parameters, Dev - relative deviance, AICc - Akaike’s information criterion corrected for  
 513 small sample sizes,  $\Delta$ AICc - difference between the current model and the model with the lowest  
 514 AICc, Wi – Akaike model weight.

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522 **Figure captions:**

523 **Figure 1.** Marginal effects of model variables on the occurrence of prospecting in actively  
524 breeding seabirds. CBL - frequent change of breeding location, DCC - distance to the closest  
525 colony, “Small stable patches” refers to category 2 of the variable “stability” and “Unstable  
526 patches” to category 3 of the variable “stability” (for details, see Material and Methods). Error  
527 bars show 95% confidence interval. Significance: filled triangle < 0.01, filled circle < 0.05,  
528 open circle - non significant.

529

530 **Figure 2.** Number of prospecting trips (all studied species pooled) per sex and breeding stage.

531

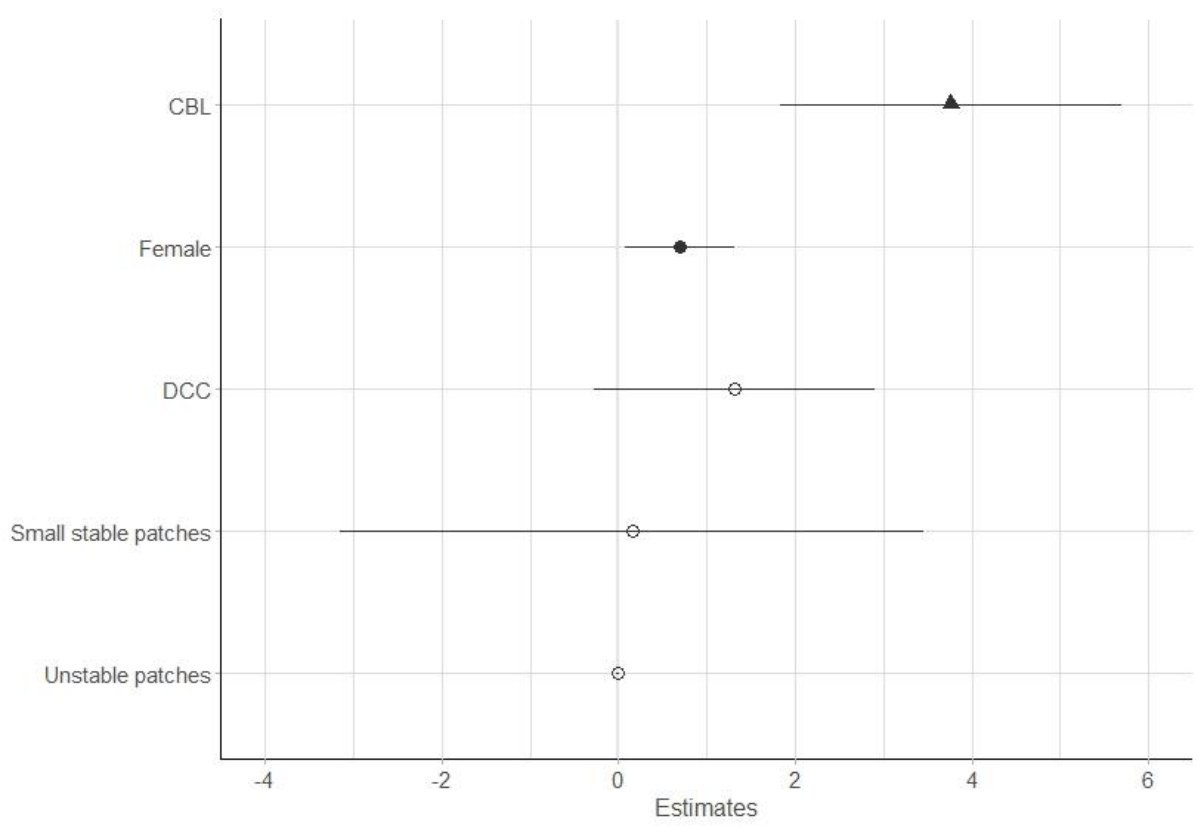
532 **Figure 3.** Distances to the prospected breeding patches by actively breeding birds. Data present  
533 results from Audouin’s gull *Larus audouinii* in Spain (ES) and Croatia (HR), yellow-legged  
534 gull *Larus michahellis* on the Balearic Islands, common tern *Sterna hirundo* in Croatia and  
535 sandwich tern *Thalasseus sandvicensis* in The Netherlands. Boxplots show the median, and the  
536 upper (Q3) and lower (Q1) quartiles, whiskers extending up to 1.5 times the interquartile range  
537 from the median, empty dots are outliers. Points represent individual prospecting trips. Black  
538 diamonds indicate the distance to the closest breeding patch that was not visited during  
539 tracking.

540

541 **Figure 4.** Examples of prospecting trips of four individuals: a) western gull *Larus*  
542 *occidentalis* ID 117639606, b) sandwich tern *Thalasseus sandvicensis* ID B-H65, c) herring  
543 gull *Larus argentatus* ID N105787 and d) Audouin’s gull *Larus audouinii* ID CROG01.  
544 Symbol used: red square - breeding colony, yellow dots - prospected conspecific breeding  
545 patches, grey dots - non-prospected conspecific breeding patches, red lines - prospecting

546 trips, orange line - foraging trips during 10 days (5 days before and 5 days after prospecting  
547 trips).

548 Figure 1



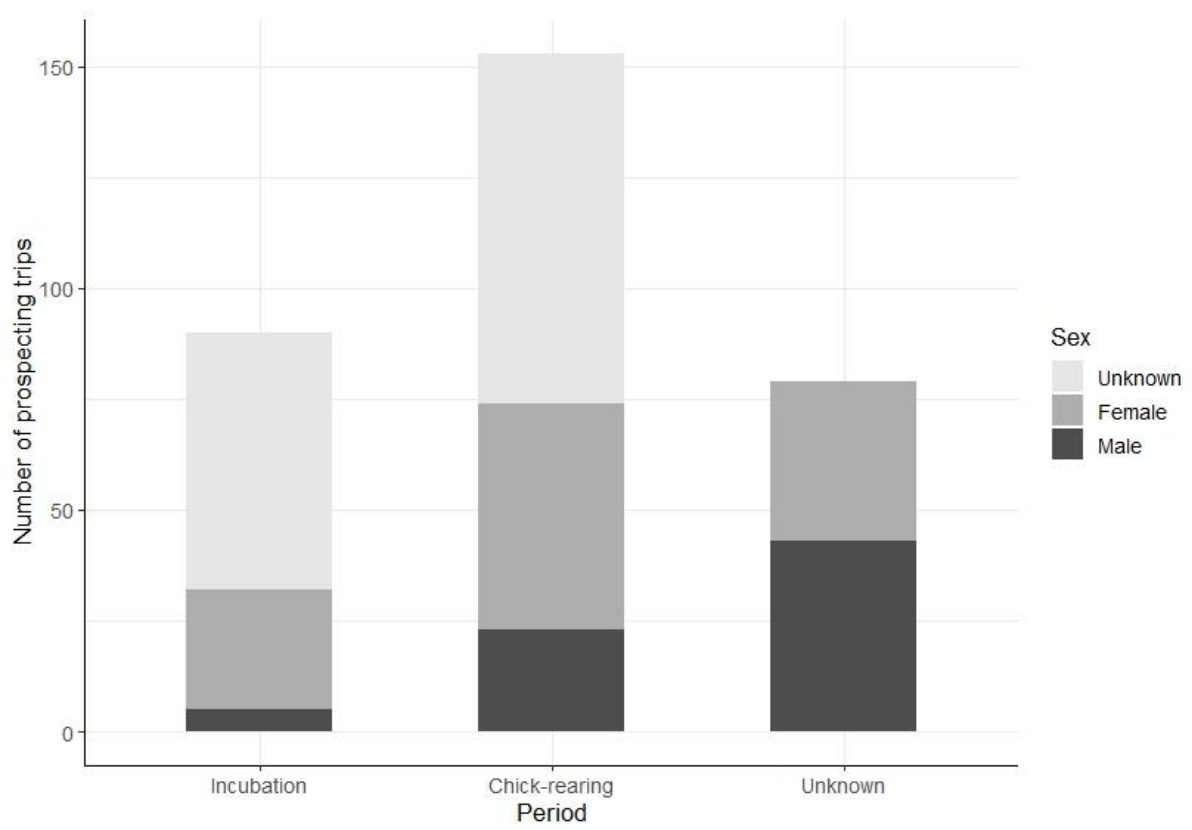
549

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551 Figure 2

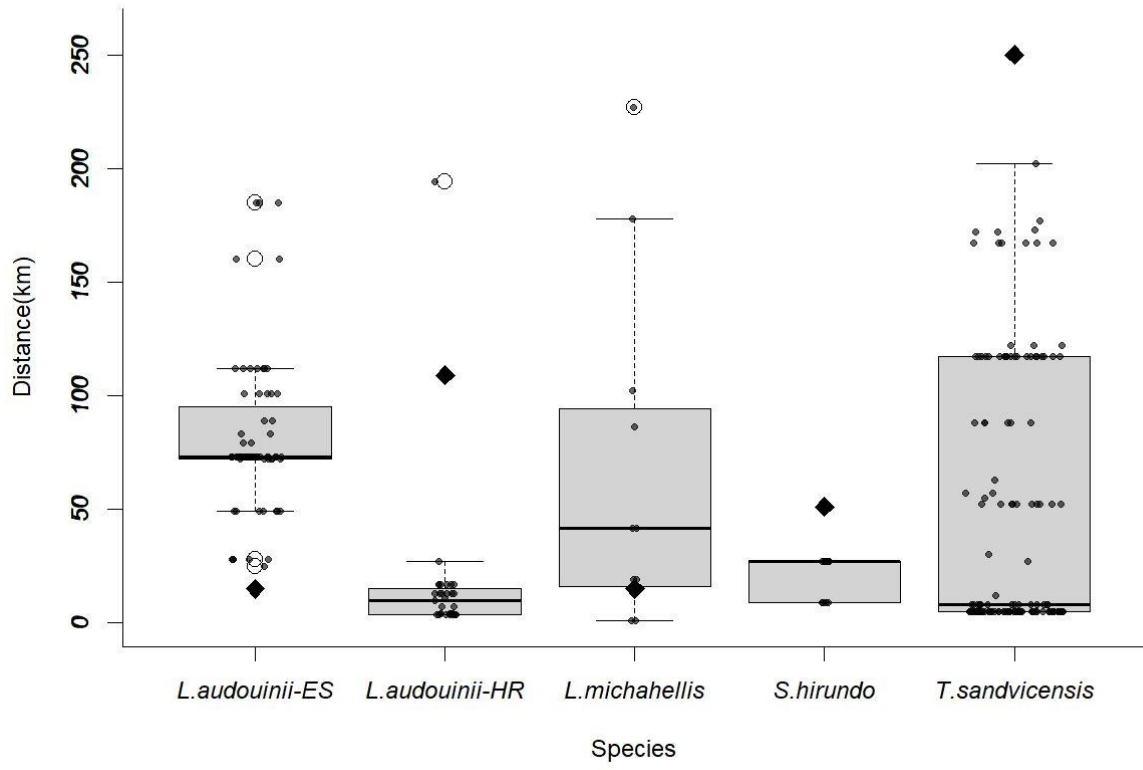
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555 Figure 3



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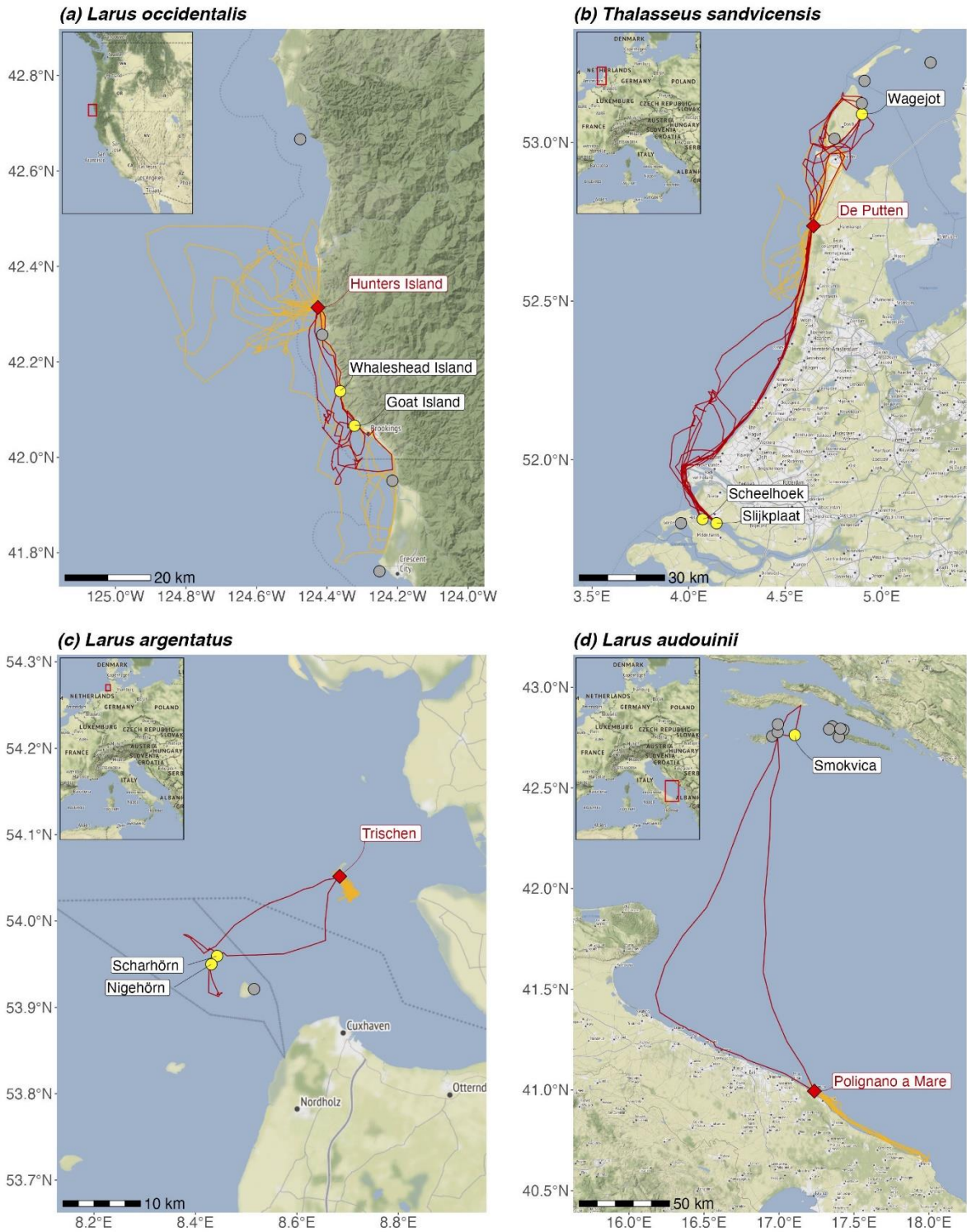
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561 Figure 4

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566 **REFERENCES**

- 567 Arizaga J, Zorrozuza N, Egunez A (2018) Between the land and sea: how Yellow-legged Gulls  
568 have changed their dependence on marine food in relation to landfill management. In: Mikkola  
569 H (ed) Seabirds ed., InTech, London; pp 67–78
- 570 Arizaga J, Laso M, Zorrozuza N, Delgado S, Aldalur A, Herrero A (2017) Uso del espacio por  
571 adultos de gaviota patiamarilla *Larus michahellis* Naumann, 1840 durante el periodo  
572 reproductor: resultados preliminares en relación al uso de vertederos. Munibe Cienc. nat.  
573 65:67–80
- 574 Baccetti N, Nissardi S, Zenatello M (2014) GPS-tags reveal strong links to North Africa *Larus*  
575 *audouinii* breeding in Sardinia. Mediter Waterbirds Bull 2:24–26
- 576 Bartoń K (2020) MuMIn: Multi-Model Inference. R package version 1.43.17. [https://CRAN.R-](https://CRAN.R-project.org/package=MuMIn)  
577 [project.org/package=MuMIn](https://CRAN.R-project.org/package=MuMIn)
- 578 Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using  
579 lme4. J Stat Soft 67:1-48. doi: 10.18637/jss.v067.i01
- 580 Billerman SM, Keeney BK, Rodewald PG, Schulenberg TS (eds.) (2020) Birds of the World.  
581 Cornell Laboratory of Ornithology, Ithaca, NY, USA. <https://birdsoftheworld.org/bow/home>
- 582 Bocedi G, Heinonen J, Travis JMJ (2012) Uncertainty and the role of information acquisition  
583 in the evolution of context-dependent emigration. Am Nat 179:606–620
- 584 Borrmann RM, Phillips RA, Clay T, Garthe S (2019) High foraging site fidelity and spatial  
585 segregation among individual great black-backed gulls. J Avian Biol 50:1–10
- 586 Boulinier T, Danchin E (1997) The use of conspecific reproductive success for breeding patch  
587 selection in terrestrial migratory species. Evol Ecol 11:505–517
- 588 Boulinier T, Danchin E, Monnat JY, Doutrelant C, Cadiou B (1996) Timing of prospecting and  
589 the value of information in a colonial breeding bird. J Avian Biol 27:252–256



590 Boulinier T, Lemel JY (1996) Spatial and temporal variations of factors affecting breeding  
591 habitat quality in colonial birds: some consequences for dispersal and habitat selection. *Acta*  
592 *Oecol* 17:531–552

593 Boulinier T, McCoy KD, Yoccoz NG, Gasparini J, Tveraa T (2008) Public information affects  
594 breeding dispersal in a colonial bird: kittiwakes cue on neighbours. *Biol Lett* 4 :538–540

595 Boulinier T, Kada S, Ponchon A, Dupraz M, Dietrich M, Gamble A et al. (2016) Migration,  
596 Prospecting, Dispersal? What Host Movement Matters for Infectious Agent Circulation? *Integr*  
597 *Comp Biol* 56:330–342

598 Brooke M (2018) *Far from land. The mysterious lives of seabirds.* Princeton University Press,  
599 New Jersey

600 Burnham KP, Anderson DR (2002) *Model Selection and Multimodel Inference: A Practical*  
601 *Information-Theoretic Approach*, 2nd edn. Springer-Verlag, New York, NY, USA.

602 BWPi (2006) BWPi 2.0.1. *Birds of the Western Palearctic Interactive DVD ROM*, Oxford  
603 University Press & BirdGuides Ltd.

604 Cadiou B, Monnat J-Y, Danchin E (1994) Prospecting in the kittiwake, *Rissa tridactyla*:  
605 different behavioural patterns and the role of squatting in recruitment. *Anim Behav* 47:847–  
606 856

607 Calabuig, G., Ortego J., Aparicio JM, Cordero PJ (2010) Intercolony movements and  
608 prospecting behaviour in the colonial lesser kestrel. *Anim Behav* 79:811–817

609 Campioni L, Granadeiro JP, Catry P (2017) Albatrosses prospect before choosing a home:  
610 intrinsic and extrinsic sources of variability in visit rates. *Anim Behav* 128:85–93

611 Cayuela H, Grolet O, Joly P (2018) Context-dependent dispersal, public information, and  
612 heterospecific attraction in newts. *Oecologia* 188: 1069–1080.

613 Clatterbuck CA, Lewison RL, Orben RA, Ackerman JT, Torres LG, Suryan RM, Warzybok P,  
614 Jahncke J, Shaffer SA (2021) Foraging in marine habitats increases mercury concentrations in  
615 a generalist seabird. *Chemosphere* 279:130470

616 Clobert J, Le Galliard JF, Cote J, Meylan S, Massot M (2009) Informed dispersal, heterogeneity  
617 in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol Lett*  
618 12:197–209

619 Coulson JC (2011) *The kittiwake*. T & AD Poyser, London, UK.

620 Cooper NW, Marra PP (2020) Hidden long-distance movements by a migratory bird. *Curr Biol*  
621 30(20):4056–4062.e3, doi: [10.1016/j.cub.2020.07.056](https://doi.org/10.1016/j.cub.2020.07.056)

622 Corman A-M, Mendel B, Voigt CC, Garthe S. (2016) Varying foraging patterns in response to  
623 competition? A multicolony approach in a generalist seabird. *Ecol Evol* 6:974–986.

624 Cote J, Clobert J (2007): Social information and emigration: Lessons from immigrants. *Ecol.*  
625 *Lett* 10:411–417 doi: 10.1111/j.1461-0248.2007.01032.x

626 Cote J, Clobert J, Brodin T, Fogarty S, Sih A (2010) Personality-dependent dispersal:  
627 Characterization, ontogeny and consequences for spatially structured populations. *Philos Trans*  
628 *R Soc B Biol Sci* 365:4065–4076

629 Dall SRX, Giraldeau, Olsson O, McNamara JM, Stephens DW (2004) Information and its use  
630 by animals in evolutionary ecology. *Trends Ecol Evol* 20:187–193

631 Danchin É, Boulinier T, Massot M. (1998) Conspecific reproductive success and breeding  
632 habitat selection: implications for the study of coloniality. *Ecology* 79:2415–2428

633 Danchin É, Giraldeau, L-A, Valone, TJ, Wagner RH (2004) Public information: from nosy  
634 neighbors to cultural evolution. *Science* 305:487–491

635 Delgado S, Herrero A, Aldalur A, Arizaga J (2021) High philopatry rates of Yellow-legged  
636 Gulls in the southeastern part of the Bay of Biscay. *Avian Res* 12:36

637 Dittmann T, Zinsmeister D, Becker PH (2005) Dispersal decisions: common Terns, *Sterna*  
638 *hirundo*, choose between colonies during prospecting. *Anim Behav* 70:13–20

639 Doligez B, Cadet C, Danchin E, Boulinier T (2003) When to use public information for  
640 breeding habitat selection? The role of environmental predictability and density dependence.  
641 *Anim Behav* 66:973–988

642 Doligez B, Pärt T, Danchin E (2004) Prospecting in the collared flycatcher: gathering public  
643 information for future breeding habitat selection? *Anim Behav* 67:457–466

644 Dugger KM, Ainley DG, Lyver PO, Barton K, Ballard G. (2010) Survival differences and the  
645 effect of environmental instability on breeding dispersal in an Adelie penguin meta-population.  
646 *Proc Natl Acad Sci USA* 107:12375–12380

647 Enners L, Schwemmer P, Corman A-M, Voigt CC, Garthe S (2018) Intercolony variations in  
648 movement patterns and foraging behaviors among herring gulls (*Larus argentatus*) breeding in  
649 the eastern Wadden Sea. *Ecol Evol* 8:7529–7542

650 Farrell SL, Morrison ML, Campomizzi AJ, Wilkins RN (2012) Conspecific cues and breeding  
651 habitat selection in an endangered woodland warbler. *J Anim Ecol* 81:1056–1064

652 Fasola M., Canova L. (1992) Nest habitat selection by eight syntopic species of Mediterranean  
653 gulls and terns. *Colon Waterbird* 15:169-291

654 Fasola M, Saino N (1995) Sex-biased parental-care allocation in three tern species (Laridae,  
655 Aves). *Can J Zool* 73:1461–1467

656 Fijn RC, Wolf P, Courtens W, Verstraete H, Stienen EW, Iliszko L, Poot MJ (2014) Post-  
657 breeding prospecting trips of adult Sandwich Terns *Thalasseus sandvicensis*. *Bird Study*  
658 61:566–571

659 Frederiksen M, Bregnballe T (2001) Conspecific reproductive success affects age of  
660 recruitment in a great cormorant, *Phalacrocorax carbo sinensis*, colony. *P R Soc B* 268:1519–  
661 1526

662 Garthe S, Schwemmer P, Paiva VH, Corman A-M, Fock H, Voigt CC, Adler S (2016)  
663 Terrestrial and marine foraging strategies of an opportunistic seabird species breeding in the  
664 Wadden Sea. *PLoS One* 11:e0159630

665 Genovart M, Oro D, Choquet R, Pradel R (2020a) Informed recruitment or the importance of  
666 taking stock. *bioRxiv*. arXiv: 2005. 06248

667 Genovart M, Gimenez O, Bertolero A, Choquet R, Oro D, Pradel R (2020b) Decrease in social  
668 cohesion in a colonial seabird under a perturbation regime. *Sci Rep* 10:18720

669 Greenwood PJ 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim*  
670 *Behav* 28:1140–1162

671 Grémillet D, Boulinier T (2009) Spatial ecology and conservation of seabirds facing global  
672 climate change: a review. *Mar Eco Prog Ser* 391:121–137

673 Guerra AS, Bui A, Klope M, Orr DA, Shaffer SA, Young HS (2022) Leaving more than  
674 footprints: anthropogenic nutrient subsidies to a protected area. *Ecosphere*, in press.

675 Harrison XA, Donaldson L, Correa-Cano ME, Evans J, Fisher DN, Goodwin C et al. (2018) A  
676 brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ*  
677 6:e4794, doi: 10.7717/peerj.4794

678 Hays GC, Ferreira LC, Sequeira AMM, Meekan MG, Duarte CM, Bailey H. et al. (2016) Key  
679 questions in marine megafauna movement ecology. *Trends Ecol Evol* 31:463–475

680 Jovani R, Mavor R, Oro D (2008) Hidden patterns of colony size variation in seabirds: a  
681 logarithmic point of view. *Oikos* 117:1774-1781 doi: 10.1111/j.1600-0706.2008.17065.x

682 Jurinović L, Zec M, Dumbović Mazal V, Kralj J (2019) Explorative GPS-tracking of foraging  
683 movements by Audouin’s Gulls reveals no association with fishing vessels in Croatia. *Ardea*  
684 107:213–221

685 Kavelaars MM, Baert JM, Van Malderen J, Stienen EWM, Shamoun-Baranes J, Lens L, Müller  
686 W. (2021) Simultaneous GPS-tracking of parents reveals a similar parental investment within

687 pairs, but no immediate co-adjustment on a trip-to-trip basis. *Mov Ecol.* 9:42. doi:  
688 10.1186/s40462-021-00279-1.

689 Kubetzki U, Garthe S, Schwemmer P, Heinze B (2020) Sturmmöwe an der Ostsee: Küsten-  
690 oder Agrarvogel? *Falke* 67(8):8–13

691 Lance BK, Roby DD (1998) Diet and Postnatal Growth in Red-Legged and Black-Legged  
692 Kittiwakes: An Interspecies Comparison. *Colon Waterbird* 21: 375–387 doi:10.2307/1521650

693 Leclaire S, Helfenstein F, Degeorges A, Wagner RH, Danchin É (2010) Family size and sex-  
694 specific parental effort in black-legged kittiwakes. *Behav* 147:1841–1862

695 Mares R, Bateman AW, English S, Clutton-Brock TH, Young AJ (2014) Timing of  
696 predispersal prospecting is influenced by environmental, social and state-dependent factors in  
697 meerkats. *Anim Behav* 88:185–193

698 Martinović M, Galov A, Svetličić I, Tome D, Jurinović L, Ječmenica B et al. (2019)  
699 Prospecting of breeding adult Common terns in an unstable environment, *Ethol Ecol Evol*  
700 31:457–468

701 Mayer M, Zedrosser A, Rosell F (2017) Extra-territorial movements differ between territory  
702 holders and subordinates in a large, monogamous rodent. *Sci Rep* 7:15261

703 Mönkkönen M, Härdling R, Forsman JT, Tuomi J (1999) Evolution of heterospecific attraction:  
704 using other species as cues in habitat selection. *Evol Ecol* 13:93–106

705 Munilla I, Genovart M, Paiva VH, Velando A (2016) Colony Foundation in an Oceanic  
706 Seabird. *PLoS One* 11: e0147222

707 Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Mitchell  
708 RD, Stairs GR (eds) *Analysis of Ecological Systems*. Ohio State University Press, Columbus,  
709 OH, USA. pp 154–177

710 Oro D (2020) *Perturbation, social feedbacks, and population dynamics in social animals*.  
711 Oxford University Press, Oxford.

712 Oro D, Pradel R, Lebreton JD (1999) Food availability and nest predation influence life history  
713 traits in Audouin's gull, *Larus audouinii*. *Oecologia* 118:438–445

714 Oro D, Bécarea J, Bartumeus F, Arcos JM (2021) High frequency of prospecting for informed  
715 dispersal and colonisation in a social species at large spatial scale. *Oecologia* 197:395–409 doi:  
716 10.1007/s00442-021-05040-4

717 Oro D, Genovart X, Ruiz X, Jimenez J, Garcia-Gans J (1996) Differences in diet, population  
718 increase and breeding performance between two colonies of Audouin's Gulls *Larus audouinii*  
719 during breeding seasons affected by a trawling moratorium. *J Avian Biol* 27:245–251

720 Pakanen V-M, Rönkä N, Thomson R, Koivula K (2014) Informed reneating decisions: the  
721 effect of nest predation risk. *Oecologia* 174:1159–1167

722 Palestis BG (2014) The role of behavior in tern conservation. *Curr Zool* 60: 500–514

723 Paredes R, Harding AMA, Irons DB, Roby DD, Suryan R, Orben RA, Renner H, Young R,  
724 Kitaysky A (2012) Proximity to multiple foraging habitats enhances seabirds' resilience to  
725 local food shortages. *Mar Ecol Prog Ser* 471:253–269

726 Paredes R, Orben RA, Suryan RM, Irons DB, Roby DD, Harding AMA, Young RC, Benoit-  
727 Bird KJ, Ladd C, Renner H, Heppell S, Phillips RA, Kitaysky AS (2014) Foraging Responses  
728 of Black-Legged Kittiwakes to Prolonged Food-Shortages around Colonies on the Bering Sea  
729 Shelf. *PLoS One* 9: e92520

730 Parejo D, White J, Clobert J, Dreiss A, Danchin E (2007) Blue tits use fledgling quantity and  
731 quality as public information in breeding site choice. *Ecology* 88:2373–2382

732 Payo-Payo A, Genovart M, Sanz-Aguilar A, Greño JL, García-Tarrasón M, Bertolero A et al.  
733 (2017) Colonisation in social species: the importance of breeding experience for dispersal in  
734 overcoming information barriers. *Sci Rep* 7: 42866 doi:10.1038/srep42866

735 Phillips RA, Lewis S, González-Solís J, Daunt F (2017) Causes and consequences of individual  
736 variability and specialization in foraging and migration strategies of seabirds. *Mar Ecol Prog*  
737 *Ser* 578: 117–150

738 Picardi S, Smith BJ, Boone ME, Frederick PC, Cecere JG, Rubolini D et al. (2020) Analysis  
739 of movement recursions to detect reproductive events and estimate their fate in central place  
740 foragers. *Movement Ecol* 8:24

741 Pierotti, R (1981) Male and female parental roles in the Western Gull under different  
742 environmental conditions. *Auk* 98:532-549

743 Pizzatto L, Stockwell M, Clulow S, Clulow J, Mahony M (2016) Finding a place to live:  
744 conspecific attraction affects habitat selection in juvenile green and golden bell frogs. *Acta*  
745 *Etholog* 19:1–8

746 Ponchon A, Grémillet D, Doligez B, Chambert T, Tveraa T, González-Solís J, Boulinier T  
747 (2013) Tracking prospecting movements involved in breeding habitat selection: insights,  
748 pitfalls and perspectives. *Methods Ecol Evol* 4:143–150

749 Ponchon A, Chambert T, Lobato E, Tveraa T, Grémillet D, Boulinier T (2015a). Breeding  
750 failure induces large scale prospecting movements in the black-legged kittiwake. *J Exp Mar*  
751 *Biol Ecol* 473:138–145

752 Ponchon A, Garnier R, Grémillet D, Boulinier T (2015b) Predicting population responses to  
753 environmental change: the importance of considering informed dispersal strategies in spatially  
754 structured population models. *Divers Distrib* 21:88–100

755 Ponchon A, Aulert C, Le Guillou G, Gallien F, Péron C, Grémillet D (2017a) Spatial overlaps  
756 of foraging and resting areas of black-legged kittiwakes breeding in the English Channel with  
757 existing marine protected areas. *Mar Biol* 164:119

758 Ponchon A, Iliszko L, Grémillet D, Tveraa T, Boulinier T (2017b) Intense prospecting  
759 movements of failed breeders nesting in an unsuccessful breeding subcolony. *Anim Behav*  
760 124:183–191

761 Ponchon A, Scarpa A, Bocedi G, Palmer SCF, Travis MJJ (2021) Prospecting and informed  
762 dispersal: Understanding and predicting their joint eco-evolutionary dynamics. *Ecol Evol*  
763 11:15289–15302

764 R Core Team (2021) R: A language and environment for statistical computing. R Foundation  
765 for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>

766 Reed JM, Boulinier T, Danchin E, Oring LW (1999) Informed dispersal: prospecting by birds  
767 for breeding sites. *Curr Ornithol* 15:189–259

768 Sanz-Aguilar A, Massa B, Lo Valvo F, Oro D, Minguéz E, Tavecchia G (2009) Contrasting  
769 age-specific recruitment and survival in three colonies of storm petrels: which combination is  
770 best? *Ecography* 32:637–646

771 Schørring S, Gregersen J, Bregnballe T (1999) Prospecting enhances breeding success of first-  
772 time breeders in the great cormorant, *Phalacrocorax carbo sinensis*. *Anim Behav* 57: 647–654

773 Schreiber EA, Burger J (2002) *Marine Birds*. CRC Press, Boca Raton.

774 Schuett W, Laaksonen J, Laaksonen T (2012) Prospecting at conspecific nests and exploration  
775 in a novel environment are associated with reproductive success in the jackdaw. *Behav Ecol*  
776 *Sociobiol* 66:1341–1350. doi: 10.1007/s00265-012-1389-1

777 Shaffer SA, Cockerham S, Warzybok P, Bradley RW, Jahncke J, Clatterbuck CA, Lucia M,  
778 Jelincic JA, Cassell AL, Kelsey EC, Adams J (2017) Population-level plasticity in foraging  
779 behavior of western gulls (*Larus occidentalis*). *Mov Ecol* 5:1–13

780 Schwemmer P, Corman A-M, Koch D, Borrmann RM, Koschorreck J, Voigt CC, Garthe S  
781 (2019) Charakterisierung der Habitatwahl von Silbermöwen *Larus argentatus* durch GPS-



782 Datenlogger zur Einschätzung der Schadstoffbelastung an der deutschen Nordseeküste.  
783 Vogelwarte 57:13–30

784 Seeley TD, Buhrman SC (2001) Nest-site selection in honey bees: how well do swarms  
785 implement the "best-of-N" decision rule? Behav Ecol Sociobiol 49:416–427

786 Selonen V, Hanski IK (2010) Decision making in dispersing Siberian flying squirrels. Behav  
787 Ecol 21:219–225

788 Spelt A, Williamson C, Shamoun-Baranes J, Shepard E, Rock P, Windsor S (2019) Habitat use  
789 of urban-nesting lesser black-backed gulls during the breeding season. Sci Rep 9:1–11

790 Spelt A, Soutar O, Williamson C, Memmott J, Shamoun-Baranes J, Rock P, Windsor S (2021)  
791 Urban gulls adapt foraging schedule to human-activity patterns. Ibis 163:274–282

792 Spendelow JA, Eichenwald AJ (2018) Post-Spring Migration Colony-site Prospecting by  
793 Roseate Terns (*Sterna dougallii*). N Am Bird Bander 43:1–6

794 Tavecchia G, Minguéz E, de León A, Louzao M, Oro D. (2008) Living close, doing differently:  
795 small-scale asynchrony in demographic parameters in two species of seabirds. Ecology 89:77–  
796 85

797 Tengeres JE, Corcoran RM (2020) Aleutian Tern Satellite Tracking, Kodiak Archipelago,  
798 2019. Refuge report 2020.2, Kodiak National Wildlife Refuge, U.S. Fish and Wildlife Service,  
799 Kodiak, AK.

800 Ward MP (2005) Habitat selection by dispersing yellow-headed blackbirds: evidence of  
801 prospecting and the use of public information. Oecologia 145:650–657

802 Wearmouth VJ, Sims DW (2008) Sexual segregation in marine fish, reptiles, birds and  
803 mammals: behaviour patterns, mechanisms and conservation implications. Adv Mar Biol  
804 54:107–170

805 Williamson CJ, Spelt A, Windsor SP (2020) Bird-inspired velocity optimization for UAVs in  
806 the urban environment. AIAA Scitech 2020 Forum p. 1948.

807 Williamson CJ, Spelt A, Windsor SP (2021) Bird velocity optimization as inspiration for  
808 unmanned aerial vehicles in urban environments. *AIAA Journal* 59:2503–2516

809 Westerberg K, Brown R, Eagle G, Votier SC (2019) Intra-population variation in the diet of an  
810 avian top predator: generalist and specialist foraging in Great Black-backed Gulls *Larus*  
811 *marinus*, *Bird Study* 66:390–397, doi: 10.1080/00063657.2019.1693961

812 Zorrozua N, Delgado S, Aldalur A, Arizaga J (2020) Adverse weather reduces the spatial use  
813 of an opportunistic gull. *Behav* 157:667–681