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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 ΔAICc 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
476 of animals were followed.

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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490 terns, JK and DT for common terns and RF for sandwich terns. All authors contributed
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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	Δ 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, Δ 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

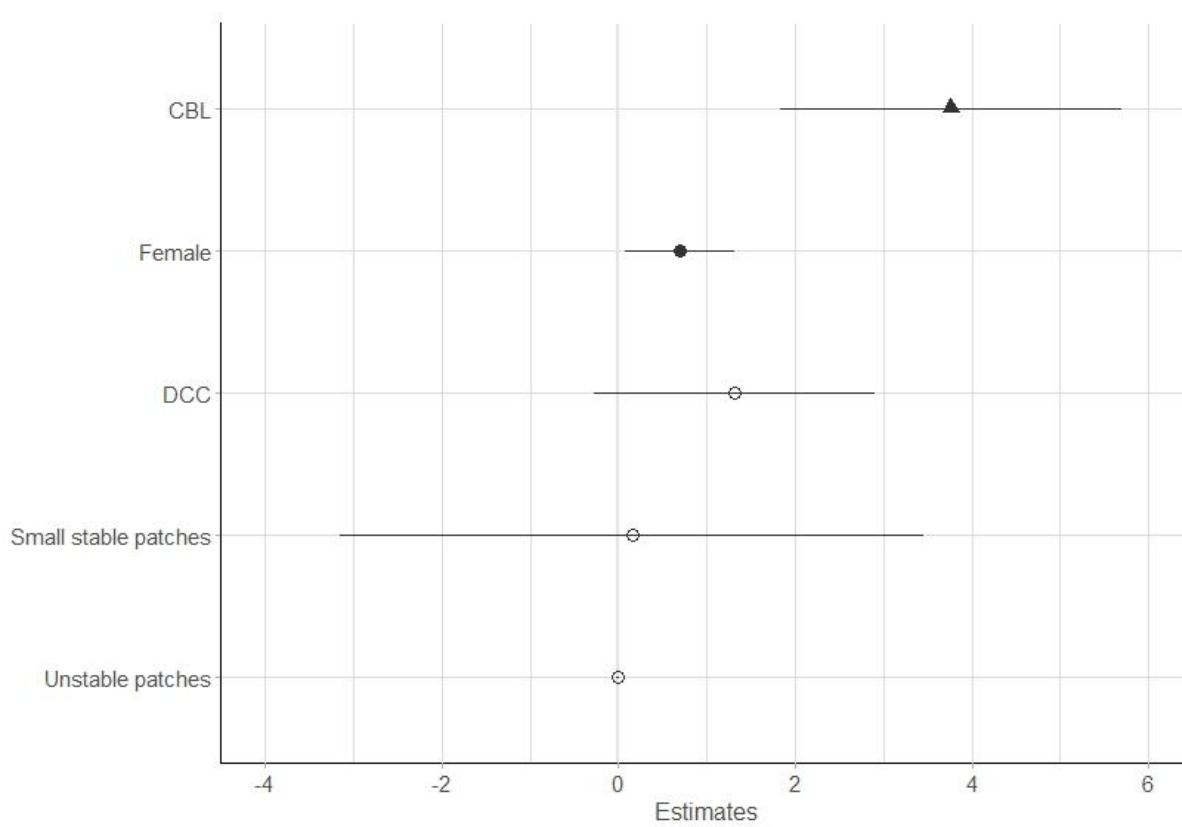
532 **Figure 3.** Distances to the prospected breeding patches by actively breeding birds. Data present
533 results from Audouin’s gull *Larus audouinii* in Spain (ES) and Croatia (HR), yellow-legged
534 gull *Larus michahellis* on the Balearic Islands, common tern *Sterna hirundo* in Croatia and
535 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



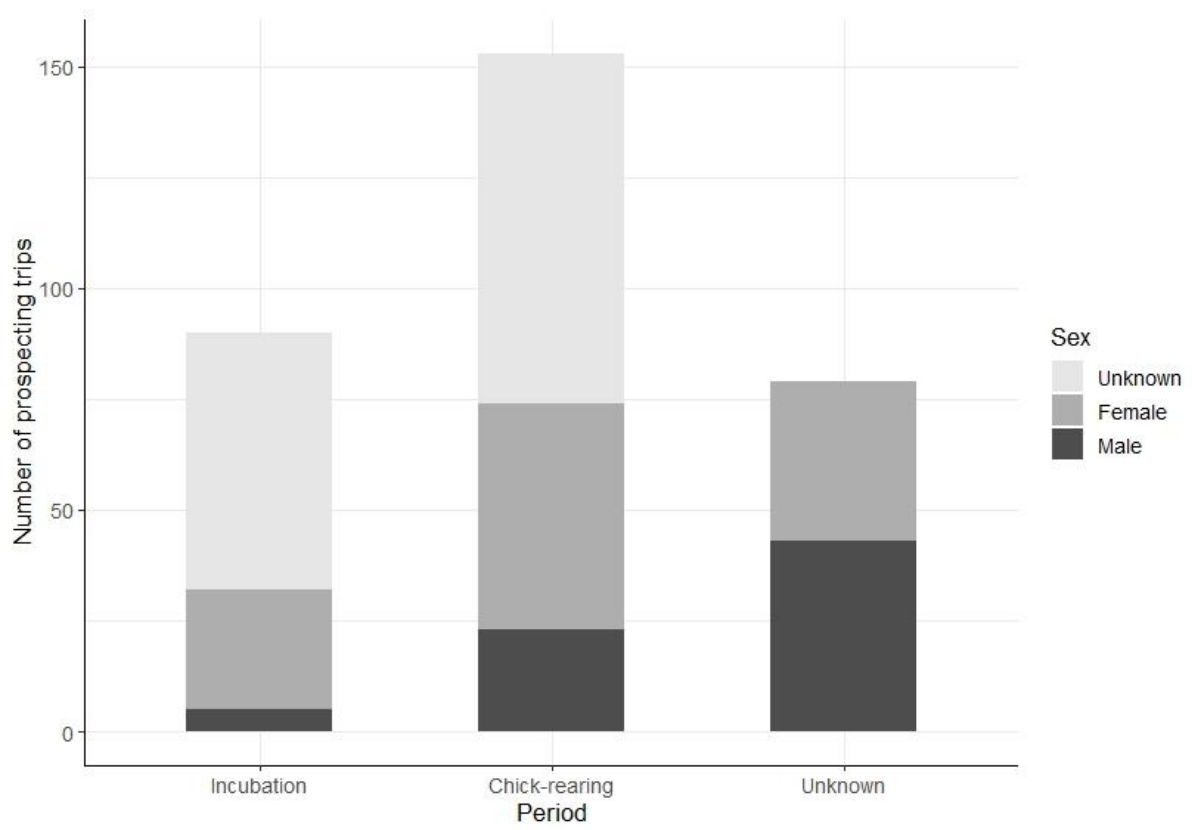
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551 Figure 2

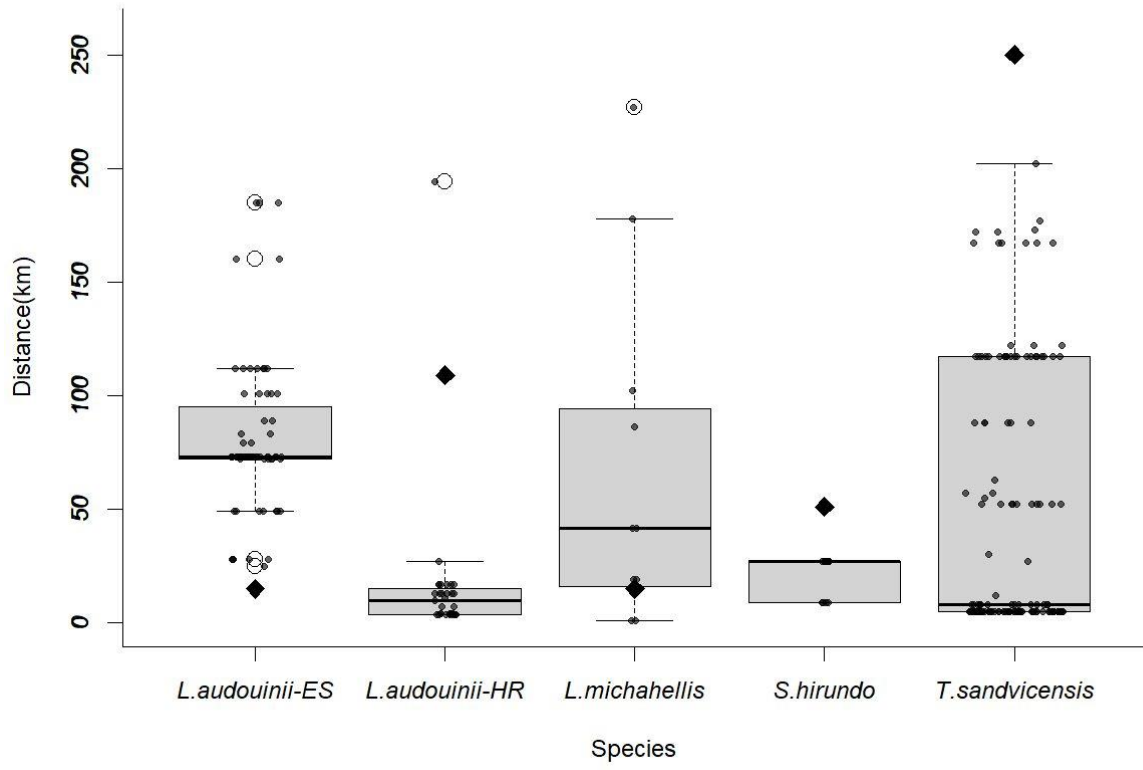
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555 Figure 3



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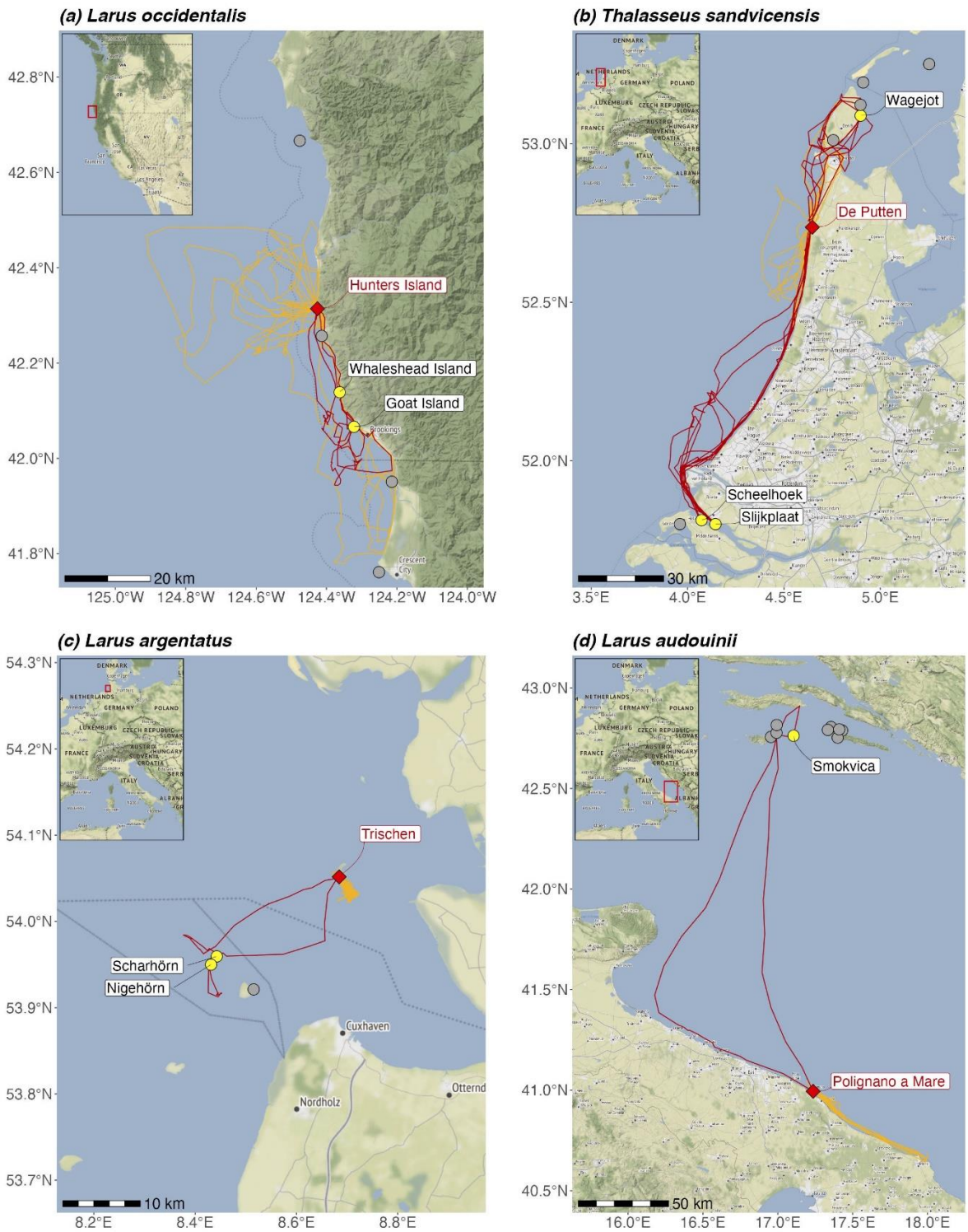
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561 Figure 4

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