

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.

▶ To cite this version:

Jelena Kralj, Aurore Ponchon, Daniel Oro, Barbara Amadesi, Juan Arizaga, et al.. Active breeding seabirds prospect alternative breeding colonies. Oecologia, 2023, 201 (2), pp.341-354. 10.1007/s00442-023-05331-y . hal-04254328

HAL Id: hal-04254328 https://hal.science/hal-04254328

Submitted on 25 Oct 2023

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- 1 Title: Active breeding seabirds prospect alternative breeding colonies
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3 Author's names:

- 4 Jelena Kralj, Institute of Ornithology, CASA, Gundulićeva 24, 10000 Zagreb, Croatia
- 5 Aurore Ponchon, School of Biological Sciences, University of Aberdeen, Zoology building,
- 6 Tillydrone Avenue, Aberdeen, AB24 2TZ, UK
- 7 Daniel Oro, CEAB (CSIC), Acces Cala Sant Francesc 14, 17300 Blanes, Catalonia, Spain
- 8 Barbara Amadesi, Istituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA),
- 9 Ozzano dell'Emilia, Italy
- 10 Juan Arizaga, Department of Ornithology, Aranzadi Sciences Society, Zorroagagaina, 11,
- 11 20014 Donostia, Spain
- 12 Nicola Baccetti, Istituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA),
- 13 Ozzano dell'Emilia, Italy
- 14 Thierry Boulinier, CEFE UMR 5175, Univ Montpellier, CNRS, EPHE, IRD, Univ Paul
- 15 Valéry Montpellier 3, Montpellier, France
- 16 Jacopo G. Cecere, Istituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA),
- 17 Ozzano dell'Emilia, Italy
- 18 Robin M. Corcoran, U.S. Fish and Wildlife Service, Kodiak National Wildlife Refuge, 1390
- 19 Buskin River Rd., Kodiak, Alaska, USA
- 20 Anna-Marie Corman, Research and Technology Centre (FTZ), University of Kiel, Hafentörn
- 21 1, 25761 Büsum, Germany
- 22 Leonie Enners, Research and Technology Centre (FTZ), University of Kiel, Hafentörn 1,
- 23 25761 Büsum, Germany
- 24 Abram Fleishman, Conservation Metrics, Inc, UCSC Coastal Science Campus, Santa Cruz,
- 25 California, USA

- 26 Stefan Garthe, Research and Technology Centre (FTZ), University of Kiel, Hafentörn 1,
- 27 25761 Büsum, Germany
- 28 David Grémillet, CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France; Percy
- 29 FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, South

30 Africa

- Ann Harding, Auk Ecological Consulting, PO Box 2052, Cordova, AK 99574, USA
- 32 José Manuel Igual, Animal Demography and Ecology Unit, IMEDEA (CSI-UIB), c M
- 33 Marques 21, 07190 Esporles, Spain
- 34 Luka Jurinović, Croatian Veterinary Institute, Poultry Centre, Heinzelova 55, 10000 Zagreb,

35 Croatia

- 36 Ulrike Kubetzki, Research and Technology Centre (FTZ), University of Kiel, Hafentörn 1,
- 37 25761 Büsum, Germany
- 38 Donald E. Lyons, National Audubon Society, 12 Audubon Road, Bremen, ME 04551 and
- 39 Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA
- 40 Rachael Orben, Department of Fisheries, Wildlife, and Conservation Sciences, Oregon State
- 41 University, Hatfield Marine Science Center, Newport Oregon, 97365, USA
- 42 Rosana Paredes, Department of Fisheries and Wildlife, 104 Nash Hall, Oregon State
- 43 University, Corvallis, Oregon 97331-3803, USA
- 44 Simone Pirrello, Istituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA),
- 45 Ozzano dell'Emilia, Italy
- 46 Bernard Recorbet, Conservatoire des Espaces Naturels de Corse, Borgo, France
- 47 Scott Shaffer, Department of Biological Sciences, San José State University, San Jose, CA
- 48 95192-0100, USA
- 49 Philipp Schwemmer, Research and Technology Centre (FTZ), University of Kiel, Hafentörn
- 50 1, 25761 Büsum, Germany

- Lorenzo Serra, Istituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA), Ozzano
 dell'Emilia, Italy
- 53 Anouk Spelt, Department of Aerospace Engineering, University of Bristol, United Kingdom
- 54 Giacomo Tavecchia, Animal Demography and Ecology Unit, IMEDEA (CSI-UIB), c M
- 55 Marques 21, 07190 Esporles, Spain
- 56 Jill Tengeres, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA
- 57 Davorin Tome, Department of Organisms and Ecosystems Research, National Institute of
- 58 Biology, 1000 Ljubljana, Slovenia
- 59 Cara Williamson, Department of Aerospace Engineering, University of Bristol, United
- 60 Kingdom, cara.williamson@bristol.ac.uk
- 61 Shane Windsor, Department of Aerospace Engineering, University of Bristol, United
- 62 Kingdom
- 63 Hillary Young, University of California Santa Barbra, Department of Ecology, Evolution and
- 64 Marine Biology
- 65 Marco Zenatello, Istituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA),
- 66 Ozzano dell'Emilia, Italy
- 67 Ruben Fijn, Bureau Waardenburg bv, Consultants for Environment & Ecology,
- 68 Varkensmarkt 9, 4101 CK Culemborg, the Netherlands
- 69
- 70 Correspondence: Jelena Kralj, Institute of Ornithology, CASA, Gundulićeva 24, 10000
- 71 Zagreb, Croatia, jkralj@hazu.hr, phone ++385 1 4825 401
- 72
- 73
- 74
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77 ABSTRACT

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

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- 91 KEYWORDS: tracking devices, dispersal, movements, behavioural ecology, gulls, terns
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- 94 INTRODUCTION
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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

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

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

population size fluctuations and even collapses (Palestis 2014; Ponchon et al. 2015b; Genovart
et al. 2020b). In birds, adult prospecting is mainly documented in later stages of the breeding
cycle, during chick-rearing, when breeding success is easy to assess and when failed breeders
have spare time before moulting or migration (Boulinier and Lemel 1996; Doligez et al. 2004;
Ward 2005). Prospecting may also occur before the breeding season, despite time constraints
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; Dugger et al. 2010; Mares et al. 2014). Recent increases in the use of animal tracking 134 135 technologies have begun to show how widespread prospecting behaviours can be in free-living populations. However, compared to the analysis of foraging habitat selection, breeding habitat 136 selection is still understudied and the occurrence of prospecting in various species, including 137 seabirds, is still not well understood (Grémillet and Boulinier 2009; Ponchon et al. 2013). 138 Based on the collected evidence so far, prospecting in adults is commonly attributed to failed 139 breeders (Fijn et al. 2014; Ponchon et al. 2015a; Ponchon et al. 2017b). Prospecting is energy-140 demanding, and birds occupied with reproductive duties are not expected to spend time visiting 141 conspecific colonies (Reed et al. 1999). Yet, recently, a few tracking studies have revealed that 142 some adults who are still actively breeding (i.e. successful in their current breeding attempt) 143 may visit conspecific breeding patches (Martinović et al. 2019; Oro et al. 2021). Such 144 prospecting during active breeding is largely understudied, despite its potential broad 145 146 occurrence. The fact that active breeders are devoting time and energy to prospect while also meeting the energy requirements of incubating and rearing young suggests that prospecting is 147 an important component of habitat selection. 148

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

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

161

162 MATERIAL AND METHODS

163 **Data collection**

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

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

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

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

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

202 Selection of variables

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

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

225 Statistical analyses

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

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

243

244 **RESULTS**

245 Factors affecting the occurrence of PAB

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

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

The inter-annual change of breeding location and sex were shown to be the most important variables affecting the occurrence of PAB (Table 2). Conditionally averaged best three models (Figure 1) showed that probability for PAB was higher in populations showing frequent interannual change of breeding location (GLMM z value =3.819, p < 0.001) and among females (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 (Figure 2). Females had higher median prospecting distances in six species and higher 260 maximum distances to prospected colonies in six species, but due to the small sample size, the 261 262 difference was significant only for one population of Audouin's gulls (Supplementary Material Table 2). From all prospecting trips with a known stage of the breeding cycle (N=243), 63% 263 were undertaken during the chick-rearing stage, with similar values (53.3-60.8%) obtained for 264 individuals with longer relative tracking durations (>50% of the breeding season). Also, 40.8% 265 of prospecting trips with a reported time of day (N=277) included nocturnal visits in prospected 266 267 colonies. Nocturnal trips were more common during the incubation stage (51.1% of trips during that stage) than during the chick-rearing (29.4% of trips) (Yates corrected $\chi^2 = 4.46$, p < 0.05). 268 The majority of visited patches were < 100 km from the breeding patch (Figure 3, Figure 4) 269 and distances to prospected patches (range 0.8-345 km) were highly correlated to the distances 270 to the closest breeding patch (range 0.8-385 km) (Pearson correlation = 0.368, p<0.01). 271

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

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

285

286 **DISCUSSION**

287

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

296 Drivers of prospecting: breeding patch, sex and distance

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

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

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

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

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

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

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).

Nocturnal visits were recorded in 40.8% of prospecting trips and were more frequent during incubation. Frequent prospecting or longer visits to prospected colonies decrease nest attendance, creating a trade-off between nest attendance and prospecting. Peak numbers of Audouin's gulls prospecting at night were also reported by Oro et al. (2021). Nocturnal visits might decrease negative interactions with conspecifics and predators while enabling the assessment of population density and breeding success.

359 Intra- and inter-specific differences in PAB

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

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

383 The effect of data quality

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

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

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

413 CONCLUSION

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

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

426

427 Acknowledgements: All authors would like to thank all colleagues and site staff / managers
428 that helped during field work and data analyses. We appreciate the comments from anonymous
429 reviewers who helped us to improve the paper.

430

431 Declarations

432 Funding: The study on black-legged kittiwakes in Norway was funded by the French Polar Institute (IPEV, programme no. 333 PARASITOARCTIQUE and OSU-OREME) and in 433 France by Eoliennes Offshores du Calvados, Eoliennes Offshores des Hautes Falaises and the 434 French Agency for Marine Protected Areas. Tracking of black-legged and red-legged 435 kittiwakes in Alaska was supported by the North Pacific Research Board. The studies on 436 Mediterranean gulls and gull-billed terns in Italy were funded by agreements between ISPRA 437 and the Italian Ministry for the Ecological Transition (MiTE), formerly Ministry for 438 Environment, Land and Sea Protection (MATTM); Decreti Min. Prot. 0004799 - 04/03/2016 439 and Prot. 34751 - 30/12/2019. The study of Audouin's gull in Spain was funded by the Spanish 440 Ministry of Science, AEI/FEDER and UE (grants re. CGL2016-80963-R and CGL2017-441 85210-P), Project LIFE + INDEMARES (2009-2014; LIFE07NAT/E/000732), and was 442 443 conducted by SEO/BirdLife. The study of Audouin's gull in Corse was founded by French Ministry of the Environment and CEN de Corse and in Italy by the Arcipelago Toscano 444 National Park ('The BIG FIVE' project), under the LIFE project 'Resto con Life' (LIFE13 445 NAT/IT/0000471) and by ISPRA. Tagging of Audouin's and yellow-legged gulls in Croatia 446 was funded under LIFE Artina project (LIFE17 NAT/HR/000594). Tracking of western gulls 447 in Oregon was funded by the Bureau of Ocean Energy Management M14AC00026 and in 448

California by several sources including SJSU RSCA and CSU COAST. Funds to monitor 449 vellow-legged gull movements in the Balearic Islands were provided by Agencia Estatal de 450 Investigación (AEI) and the EU found for regional development (FEDER), project n. 451 CGL2017-85210-P. The survey of the yellow-legged gull in the province of Gipuzkoa (Basque 452 Country, Spain) was funded by the Gipuzkoa Deputation. Tracking of gulls in Germany was 453 funded mainly by the projects WINDBIRD (grant no. 0325281, German Federal Ministry for 454 455 Economic Affairs and Energy according to a decision of the German Bundestag), STopP (grant no. 03F672B, German Federal Ministry of Research and Education), and BIRDMOVE and 456 457 TRACKBIRD (grant nos. 3515822100 and 3519861400), Federal Agency for Nature Conservation, with funds from the German Federal Ministry for the Environment, Nature 458 Conservation and Nuclear Safety. The study on lesser black-backed gulls in Bristol, United 459 Kingdom, was funded by European Research Council under the European Union's Horizon 460 2020 research and innovation programme (grant number 679355), the University Research 461 Committee (URC)/Institute for Advanced Studies (IAS) Interdisciplinary Research Internship 462 Scheme (IRIS) 2018, and the EPSRC Centre for Doctoral Training in Future Autonomous and 463 Robotic Systems (FARSCOPE) at the Bristol Robotics Laboratory. Tagging of common terns 464 in Croatia and Slovenia was founded by the Cooperation Programme Interreg V-A Slovenia -465 Croatia (grant SLO-HR347). Tracking sandwich terns in the Netherlands was part of PMR-466 NCV, a program to study the effects of the extension of Rotterdam Harbour, and WOZEP, a 467 program to study the effects of offshore wind farm developments in the Dutch coastal zone. 468 Both programs were commissioned by Rijkswaterstaat WVL. The study of Aleutian terns in 469 Alaska was funded by the National Fish and Wildlife Foundation Pacific Seabird Program 470 (Grant ID 61777), the U.S. Fish and Wildlife Service Kodiak National Wildlife Refuge, the 471 Alaska Department of Fish and Game, and Oregon State University Department of Fisheries, 472 Wildlife, & Conservation Sciences. 473

474 **Conflict of interest:** The authors declare that they have no conflict of interest.

475 Ethical approval: All applicable institutional and/or national guidelines for the care and use476 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 are480 available from the corresponding author upon reasonable request.

481 Code availability: NA

Authors' contributions: JK collected and analysed the data and wrote the first draft of the 482 483 manuscript. JK, AP, DO and RF wrote the manuscript. SP prepared the map with prospecting tracks. All authors contributed with published or unpublished data: AP, DG, TB, RP, AH and 484 RO for black-legged kittiwakes, RP, RO, SS and AF for red-legged kittiwakes, LS, SP and 485 486 JGC for Mediterranean gulls and gull-billed terns, LJ, BR, NB, MZ, BA and DO for Audouin's gulls, SG and UK for mew gulls, SS, HY and RO for western gulls, SG, A-MC, AS, CW and 487 SW for lesser black-backed gulls, SG, PS and LE for herring gulls, LJ, JA, GT and JMI for 488 yellow-legged gulls, SG and PS for the great black-backed gulls, JT, RC and DL for Aleutian 489 terns, JK and DT for common terns and RF for sandwich terns. All authors contributed 490 critically to the manuscript and gave final approval for publication. 491

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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.

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

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

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

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

Variables in the model	np	Dev	AICc	ΔAICc	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	12	398.9	423 14	5 46	0.029
+ lattitude + habitat + IF	12	570.7	123.11	5.10	0.02)

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:**

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

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

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

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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

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











561 Figure 4





33.0°N-32.0°N-32.0°N-32.0°N-32.0°N-32.0°N-

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4.0°E

5.0°E

(b) Thalasseus sandvicensis



3.5°E



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566 **REFERENCES**

- 567 Arizaga J, Zorrozua 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, Zorrozua 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-
- 577 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
- 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
- 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
- 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
- the value of information in a colonial breeding bird. J Avian Biol 27:252–256

- Boulinier T, Lemel JY (1996) Spatial and temporal variations of factors affecting breeding
 habitat quality in colonial birds: some consequences for dispersal and habitat selection. Acta
 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
- 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
- Brooke M (2018) Far from land. The mysterious lives of seabirds. Princeton University Press,
 New Jersey
- Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: A Practical
 Information-Theoretic Approach, 2nd edn. Springer-Verlag, New York, NY, USA.
- BWPi (2006) BWPi 2.0.1. Birds of the Western Paleartic Interactive DVD ROM, Oxford
 University Press & BirdGuides Ltd.
- 604 Cadiou B, Monnat J-Y, Danchin E (1994) Prospecting in the kittiwake, Rissa tridactyla:
- different behavioural patterns and the role of squatting in recruitment. Anim Behav 47:847–
 856
- Calabuig, G., Ortego J., Aparicio JM, Cordero PJ (2010) Intercolony movements and
 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
- heterospecific attraction in newts. Oecologia 188: 1069–1080.

- 613 Clatterbuck CA, Lewison RL, Orben RA, Ackerman JT, Torres LG, Suryan RM, Warzybok P,
- Jahncke J, Shaffer SA (2021) Foraging in marine habitats increases mercury concentrations in
- 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 Let
- 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: <u>10.1016/j.cub.2020.07.056</u>
- 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
- 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
- neighbors to cultural evolution. Science 305:487-491
- 635 Delgado S, Herrero A, Aldalur A, Arizaga J (2021) High philopatry rates of Yellow-legged
- Gulls in the southeastern part of the Bay of Biscay. Avian Res 12:36

- Dittmann T, Zinsmeister D, Becker PH (2005) Dispersal decisions: common Terns, *Sterna 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
- breeding habitat selection? The role of environmental predictability and density dependance.
- 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
- effect of environmental instability on breeding dispersal in an Adelie penguin meta-population.
- 646 Proc Natl Acad Sci USA 107:12375–12380
- 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
- the eastern Wadden Sea. Ecol Evol 8:7529–7542
- 650 Farrell SL, Morrison ML, Campomizzi AJ, Wilkins RN (2012) Conspecific cues and breeding
- habitat selection in an endangered woodland warbler. J Anim Ecol 81:1056–1064
- Fasola M., Canova L. (1992) Nest habitat selection by eight syntopic cpecies of Mediterranean
- gulls and terns. Colon Waterbird 15:169-291
- Fasola M, Saino N (1995) Sex-biased parental-care allocation in three tern species (Laridae,
 Aves). Can J Zool 73:1461–1467
- 656 Fijn RC, Wolf P, Courtens W, Verstraete H, Stienen EW, Iliszko L, Poot MJ (2014) Post-
- breeding prospecting trips of adult Sandwich Terns *Thalasseus sandvicensis*. Bird Study658 61:566–571
- Frederiksen M, Bregnballe T (2001) Conspecific reproductive success affects age of
 recruitment in a great cormorant, *Phalacrocorax carbo sinensis*, colony. P R Soc B 268:1519–
 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
- Genovart M, Oro D, Choquet R, Pradel R (2020a) Informed recruitment or the importance of
 taking stock. bioRxiv. arXiv: 2005. 06248
- 667 Genovart M, Gimenez O, Bertolero A, Choquet R, Oro D, Pradel R (2020b) Decrease in social
- cohesion in a colonial seabird under a perturbation regime. Sci Rep 10:18720
- Greenwood PJ 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim
 Behav 28:1140–1162
- 671 Grémillet D, Boulinier T (2009) Spatial ecology and conservation of seabirds facing global
- climate change: a review. Mar Eco Prog Ser 391:121–137
- Guerra AS, Bui A, Klope M, Orr DA, Shaffer SA, Young HS (2022) Leaving more than
 footprints: anthropogenic nutrient subsidies to a protected area. Ecosphere, in press.
- Harrison XA, Donaldson L, Correa-Cano ME, Evans J, Fisher DN, Goodwin C et al. (2018) A
- brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ
- 677 6;e4794, doi: 10.7717/peerj.4794
- Hays GC, Ferreira LC, Sequeira AMM, Meekan MG, Duarte CM, Bailey H. et al. (2016) Key
- 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
- 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

- pairs, but no immediate co-adjustment on a trip-to-trip basis. Mov Ecol. 9:42. doi:
 10.1186/s40462-021-00279-1.
- Kubetzki U, Garthe S, Schwemmer P, Heinze B (2020) Sturmmöwe an der Ostsee: Küstenoder Agrarvogel? Falke 67(8):8–13
- 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-
- specific parental effort in black-legged kittiwakes. Behav 147:1841–1862
- Mares R, Bateman AW, English S, Clutton-Brock TH, Young AJ (2014) Timing of
 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 Evol700 31:457–468
- 701 Mayer M, Zedrosser A, Rosell F (2017) Extra-territorial movements differ between territory
- holders and subordinates in a large, monogamous rodent. Sci Rep 7:15261
- Mönkkönen M, Härdling R, Forsman JT, Tuomi J (1999) Evolution of heterospecific attraction:
- vising other species as cues in habitat selection. Evol Ecol 13:93–106
- Munilla I, Genovart M, Paiva VH, Velando A (2016) Colony Foundation in an Oceanic
 Seabird. PLoS One 11: e0147222
- 707 Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Mitchell
- RD, Stairs GR (eds) Analysis of Ecological Systems. Ohio State University Press, Colombus,
- 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
- traits in Audouin's gull, *Larus audouinii*. Oecologia 118:438–445
- 714 Oro D, Bécares J, Bartumeus F, Arcos JM (2021) High frequency of prospecting for informed
- 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*
- 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 renesting decisions: the
- reffect 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
- 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
- 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
- overcoming information barriers. Sci Rep 7: 42866 doi:10.1038/srep42866

- Phillips RA, Lewis S, González-Solís J, Daunt F (2017) Causes and consequences of individual
 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
- of movement recursions to detect reproductive events and estimate their fate in central place
- 740 foragers. Movement Ecol 8:24
- Pierotti, R (1981) Male and female parental roles in the Western Gull under different
 environmental conditions. Auk 98:532-549
- 743 Pizzatto L, Stockwell M, Clulow S, Clulow J, Mahony M (2016) Finding a place to live:
- conspecific attraction affects habitat selection in juvenile green and golden bell frogs. Acta
 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,
- pitfalls and perspectives. Methods Ecol Evol 4:143–150
- 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
- r53 environmental change: the importance of considering informed dispersal strategies in spatially
- structured population models. Divers Distrib 21:88–100
- Ponchon A, Aulert C, Le Guillou G, Gallien F, Péron C, Grémillet D (2017a) Spatial overlaps
- of foraging and resting areas of black-legged kittiwakes breeding in the English Channel with
- existing marine protected areas. Mar Biol 164:119

- Ponchon A, Iliszko L, Grémillet D, Tveraa T, Boulinier T (2017b) Intense prospecting
 movements of failed breeders nesting in an unsuccessful breeding subcolony. Anim Behav
 124:183–191
- 761 Ponchon A, Scarpa A, Bocedi G, Palmer SCF, Travis JMJ (2021) Prospecting and informed
- dispersal: Understanding and predicting their joint eco-evolutionary dynamics. Ecol Evol
 11:15289–15302
- R Core Team (2021) R: A language and environment for statistical computing. R Foundation
 for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/
- Reed JM, Boulinier T, Danchin E, Oring LW (1999) Informed dispersal: prospecting by birds
- 767 for breeding sites. Curr Ornithol 15:189–259
- Sanz-Aguilar A, Massa B, Lo Valvo F, Oro D, Minguez E, Tavecchia G (2009) Contrasting
- 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-
- time breeders in the great cormorant, *Phalacrocorax carbo sinensis*. Anim Behav 57: 647–654
- Schreiber EA, Burger J (2002) Marine Birds. CRC Press, Boca Raton.
- Schuett W, Laaksonen J, Laaksonen T (2012) Prospecting at conspecific nests and exploration
- 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
- 577 Shaffer SA, Cockerham S, Warzybok P, Bradley RW, Jahncke J, Clatterbuck CA, Lucia M,
- Jelincic JA, Cassell AL, Kelsey EC, Adams J (2017) Population-level plasticity in foraging
- 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
- Seeley TD, Buhrman SC (2001) Nest-site selection in honey bees: how well do swarms
 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
- of urban-nesting lesser black-backed gulls during the breeding season. Sci Rep 9:1–11
- 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
- Tavecchia G, Minguez E, de León A, Louzao M, Oro D. (2008) Living close, doing differently:
- small-scale asynchrony in demographic parameters in two species of seabirds. Ecology 89:77–
 85
- 797 Tengeres JE, Corcoran RM (2020) Aleutian Tern Satellite Tracking, Kodiak Archipelago,
- 7982019. Refuge report 2020.2, Kodiak National Wildlife Refuge, U.S. Fish and Wildlife Service,
- 799 Kodiak, AK.
- Ward MP (2005) Habitat selection by dispersing yellow-headed blackbirds: evidence of
 prospecting and the use of public information. Oecologia 145:650–657
- Wearmouth VJ, Sims DW (2008) Sexual segregation in marine fish, reptiles, birds and
 mammals: behaviour patterns, mechanisms and conservation implications. Adv Mar Biol
 54:107–170
- 805 Williamson CJ, Spelt A, Windsor SP (2020) Bird-inspired velocity optimization for UAVs in
- the urban environment. AIAA Scitech 2020 Forum p. 1948.

- Williamson CJ, Spelt A, Windsor SP (2021) Bird velocity optimization as inspiration for
 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
- of an opportunistic gull. Behav 157:667–681