



# Active breeding seabirds prospect alternative breeding colonies

Jelena Kralj<sup>1</sup> · Aurore Ponchon<sup>2</sup> · Daniel Oro<sup>3</sup> · Barbara Amadesi<sup>4</sup> · Juan Arizaga<sup>5</sup> · Nicola Baccetti<sup>4</sup> · Thierry Boulonier<sup>6</sup> · Jacopo G. Cecere<sup>4</sup> · Robin M. Corcoran<sup>7</sup> · Anna-Marie Corman<sup>8</sup> · Leonie Enners<sup>8</sup> · Abram Fleishman<sup>9</sup> · Stefan Garthe<sup>8</sup> · David Grémillet<sup>10,11</sup> · Ann Harding<sup>12</sup> · José Manuel Igual<sup>13</sup> · Luka Jurinović<sup>14</sup> · Ulrike Kubetzki<sup>8</sup> · Donald E. Lyons<sup>15,16</sup> · Rachael Orben<sup>17</sup> · Rosana Paredes<sup>18</sup> · Simone Pirrello<sup>4</sup> · Bernard Recorbet<sup>19</sup> · Scott Shaffer<sup>20</sup> · Philipp Schwemmer<sup>8</sup> · Lorenzo Serra<sup>4</sup> · Anouk Spelt<sup>21</sup> · Giacomo Tavecchia<sup>13</sup> · Jill Tengeres<sup>16</sup> · Davorin Tome<sup>22</sup> · Cara Williamson<sup>21</sup> · Shane Windsor<sup>21</sup> · Hillary Young<sup>23</sup> · Marco Zenatello<sup>4</sup> · Ruben Fijn<sup>24</sup>

Received: 10 August 2022 / Accepted: 30 January 2023

© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2023

## Abstract

Compared to other animal movements, prospecting by adult individuals for a future breeding site is commonly overlooked. Prospecting influences the decision of where to breed and has consequences on fitness and lifetime reproductive success. By analysing movements of 31 satellite- and GPS-tracked gull and tern populations belonging to 14 species in Europe and North America, we examined the occurrence and factors explaining prospecting by actively 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 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 environments. More long-term tracking studies are needed to identify factors affecting patterns of prospecting in different environments and understand the consequences of prospecting on fitness at the individual and population level.

**Keywords** Tracking devices · Dispersal · Movements · Behavioural ecology · Gulls · Terns

## Introduction

Prospecting behaviour is present in migratory and non-migratory, solitary and colonial species and is defined as visits of individuals to potential alternative patches where they might breed in the future (Reed et al. 1999). During this process, individuals gather social and environmental information to assess the quality of potential breeding patches (Danchin et al. 2004; Dall et al. 2004). Prospectors have mainly been identified in non-breeding subadults or 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 Hanski 2010; Mares et al. 2014; Mayer et al. 2017), birds (Reed et al. 1999; Doligez et al. 2004; 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, individuals familiarize themselves with breeding patch size, local intraspecific competition, offspring quality and breeding success of conspecific or heterospecific individuals (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 (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). Prospecting before recruitment may affect age at first reproduction, and increase individual fitness and lifetime reproductive success (Schørring et al. 1999; Frederiksen and Bregnballe 2001; Genovart et al. 2020a).

Prospecting is a crucial component of informed dispersal and enables individuals to compare their current breeding patch with the neighbouring ones and make a decision on whether to stay or disperse (Boulonier and Danchin 1997; Reed et al. 1999). In general, philopatry has several advantages over dispersal, including the knowledge of the location

Communicated by Thomas Koert Lameris.

✉ Jelena Kralj  
jkralj@hazu.hr

Extended author information available on the last page of the article

of surrounding foraging grounds and social cohesion. The preference to breed in a familiar neighbourhood can enhance site fidelity. When emigration from a site is based on information use, dispersal is largely 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 decide about a future breeding patch, failed breeders prospect neighbouring patches (Fijn et al. 2014; Ponchon et al. 2017b). The degree of philopatry thus tends to be higher in stable and successful breeding patches (Palestis 2014). Should at some point dispersal occur, many individuals can leave their current breeding patch at once, which can result in significant 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).

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 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 selection is still understudied and the occurrence of prospecting in various species, including seabirds, is still not well understood (Grémillet and Boulinier 2009; Ponchon et al. 2013). Based on the collected evidence so far, prospecting in adults is commonly attributed to failed breeders (Fijn et al. 2014; Ponchon et al. 2015a, 2017b). Prospecting is energy-demanding, and birds occupied with reproductive duties are not expected to spend time visiting conspecific colonies (Reed et al. 1999). Yet, recently, a few tracking studies have revealed that some adults who are still actively breeding (i.e. successful in their current breeding attempt) may visit conspecific breeding patches (Martinović et al. 2019; Oro et al. 2021). Such prospecting during active breeding is largely understudied, despite its potential broad 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 an important component of habitat selection.

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 numerous theoretical works which stressed that prospecting is expected to evolve especially in temporally predictable environments (Boulinier and Danchin 1997; Doligez et al. 2004; Bocedi et al. 2012; Ponchon et al. 2021), we hypothesized that PAB was more likely to occur in populations that bred in relatively stable environments. Based on the optimal-timing hypothesis, according to which prospecting occurrence is the greatest during chick-rearing, 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 period.

## Materials and methods

### Data collection

We collated data from studies based on satellite- and GPS-tracking of adult breeding seabirds collected through different projects that mostly aimed to study foraging movements (Table 1). We restricted our study to gulls and terns from Europe and North America as the species of these families are known to vary in philopatry and life-history traits, and extensive tracking data during the breeding season is available (Schreiber and Burger 2002; Brooke 2018). We selected studies in areas where the position of conspecific breeding patches were known based on field research or surveying or monitoring programs. Colonies can be defined as aggregates 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 formation of clustered nests spatially separated by topographic features (single cliffs, islands, roofs, etc.).

We defined PAB (prospecting in active breeders) as the visit to other conspecific breeding patches 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 min) 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

**Table 1** Tracking studies of seabird movements included in the analysis of prospecting in active breeders

Species	Country	Year	No. of tracked individuals	No. of prospecting individuals	Percentage of prospecting individuals	Data owners	References
<i>Rissa tridactyla</i>	France	2014	36	0	0	Ponchon, A., Grémillet, D	<b>Ponchon et al. (2017a)</b>
<i>Rissa tridactyla</i>	Norway	2010–2015	136	0	0	Ponchon, A., Boulinier, T	<b>Ponchon et al. (2015a, b, 2017b)</b>
<i>Rissa tridactyla</i>	USA	2008–2010	152	1	0.7	Paredes, R., Harding, A., Orben, R.,	Paredes et al. (2012, 2014)
<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	Jurinović et al. (2019)
<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	<b>Baccetti et al. (2014)</b>
<i>Larus audouinii</i>	Spain	2006–2011	38	16	42.1	Oro, D	<b>Oro et al. (2021)</b>
<i>Larus canus</i>	Germany	2018–2020	19	0	0	Garthe, S., Kubetzki U	Kubetzki et al. (2020)
<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.,	Shaffer et al. (2017) and Clatterbuck et al. (2021)
<i>Larus occidentalis</i>	USA	2013–2020	51	0	0	Young, H., Shaffer, S.,	Guerra et al. (2022)
<i>Larus occidentalis</i>	USA	2013–2020	39	4	10.3	Orben, R	Clatterbuck et al. (2021)
<i>Larus fuscus</i>	Germany	2009–2012, 2017–2020	30	2	6.7	Garthe, S., Corman A-M	Corman et al. (2016)
<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	Spelt et al. (2019, 2021) Williamson et al. (2020, 2021)
<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	Garthe et al. (2016) and Schwemmer et al (2019)
<i>Larus argentatus</i>	Germany	2012–2015	15	2	13.3	Garthe, S., Enners, L	Enners et al. (2018)
<i>Larus michahellis</i>	Croatia	2019–2021	10	1	10	Jurinović, L	
<i>Larus michahellis</i>	Spain	2018–2019	30	0	0	Arizaga, J	Arizaga et al. (2017, 2018) and Zorrozueta et al. (2020)

**Table 1** (continued)

Species	Country	Year	No. of tracked individuals	No. of prospecting individuals	Percentage of prospecting individuals	Data owners	References
<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	Borrmann et al. (2019)
<i>Onychoprion aleuticus</i>	USA	2019	10	0	0	Tengeres, J., Corcoran, R., Lyons, D	Tengeres and Corcoran (2020)
<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	<b>Martinović et al. (2019)</b>
<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	<b>Fijn et al. (2014)</b>

The number of prospecting individuals refers to birds prospecting during the active breeding. References based on tracking data included in this study are provided. References related to study of prospecting movements are given in bold

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 8 days (gulls) after hatching. The ledge-nesting kittiwakes are the exception with chicks staying in the nest for around 30 days (Lance and Roby 1998; Coulson 2011). We used monitored or presumed nest fate to assess whether tagged birds were actively breeding. Nest fate covered the period of incubation and early chick-rearing and was monitored using cameras or through visual monitoring of nests. Alternatively, it was presumed from the movements of tracked 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. Ponchon et al. 2017a; Picardi et al. 2020). Incubating birds or birds with young chicks were considered to be active breeders, no matter the final fate of their offspring. Movements after presumed breeding failure were not analysed. Tracked birds that failed early during tracking were not included in the analysis.

### Selection of variables

We tested how intrinsic and environmental factors affected the occurrence of PAB. We recorded variables related to the birds and variables describing their breeding patch. For each bird, its identification number, species, sex, species-specific duration of incubation and chick-rearing, and relative tracking duration for each breeding season were recorded. The categorical variables related to the breeding patch included

in our model were patch identification number, 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 conspecific breeding patch (DCC) and latitude. Additionally, for prospecting individuals, distances to the prospected patches were recorded.

Duration of incubation and chick-rearing stage until fledging is given as an average time in days, extracted from BWPi (2006) and Billerman et al. (2020) for European and North American species, respectively. The relative tracking duration was provided in four categories, representing < 25%, 25–50%, 51–75% and > 75% of the breeding season duration (egg-laying to fledging). We assessed whether regular breeding failure (as the result of predation, adverse weather, flooding, or food shortage) occurred at the studied patches. Information whether groups of birds frequently changed their breeding locations was often based on long-term monitoring or data obtained by colour-ringing. The type of habitat where species evolved distinguished ephemeral habitats (such as dynamic marshes, salt pans and dunes) and stable 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, frequently used; 3—new or infrequently used breeding patch (Supplementary Material Table 1).

### Statistical analyses

We built generalized linear mixed-effects models (GLMM) to assess the factors affecting the occurrence of PAB for each tracked individual as a binomial response variable, using

categorical and continuous predictors with logit link. Relative tracking duration and breeding patch ID were included as random variables. We checked variables for collinearity and excluded the variable “species” from the models. Interactions among variables (CBL, DCC, stability, sex) were tested, but did not significantly influence the models. Model fit accounting 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) had  $\Delta$ 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 2021) using the lme4 (Bates et al. 2015) and MuMIn (Bartón 2020) packages.

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.

## Results

### 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 (Fig. 1) showed that probability for PAB was higher in populations showing frequent inter-annual change of breeding location (GLMM  $z$  value = 3.819,  $p < 0.001$ ) and among females (GLMM  $z$  value = 2.201,  $p < 0.01$ ).

### Analysis of prospecting trips

From prospecting trips of birds with known sex ( $N = 185$ ), 61.6% were undertaken by females (Fig. 2). Females had higher median prospecting distances in six species and

**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

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

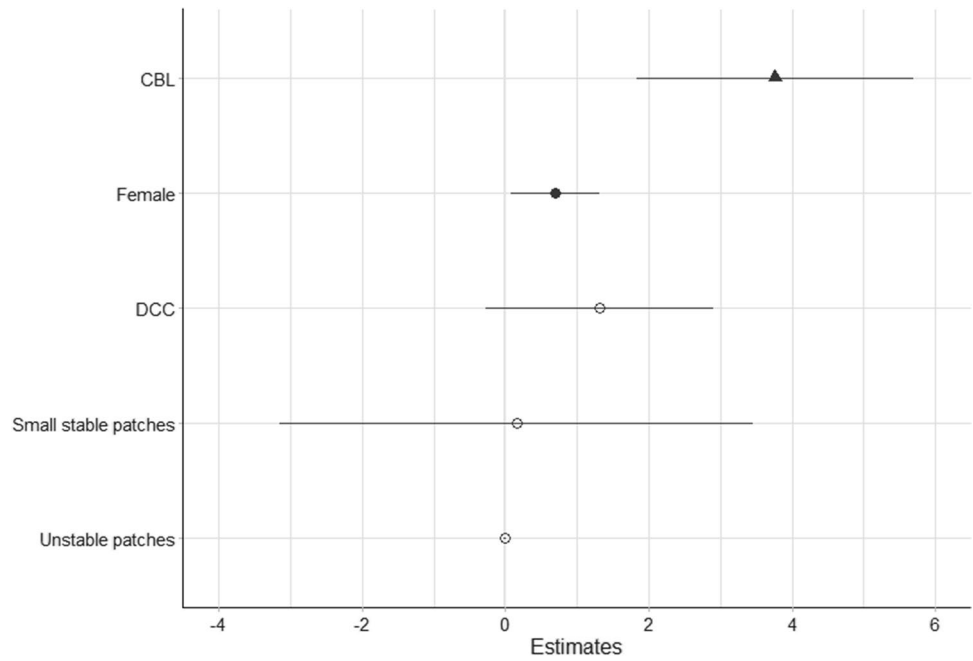
The bottom model is the full model. The first three models were conditionally averaged

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

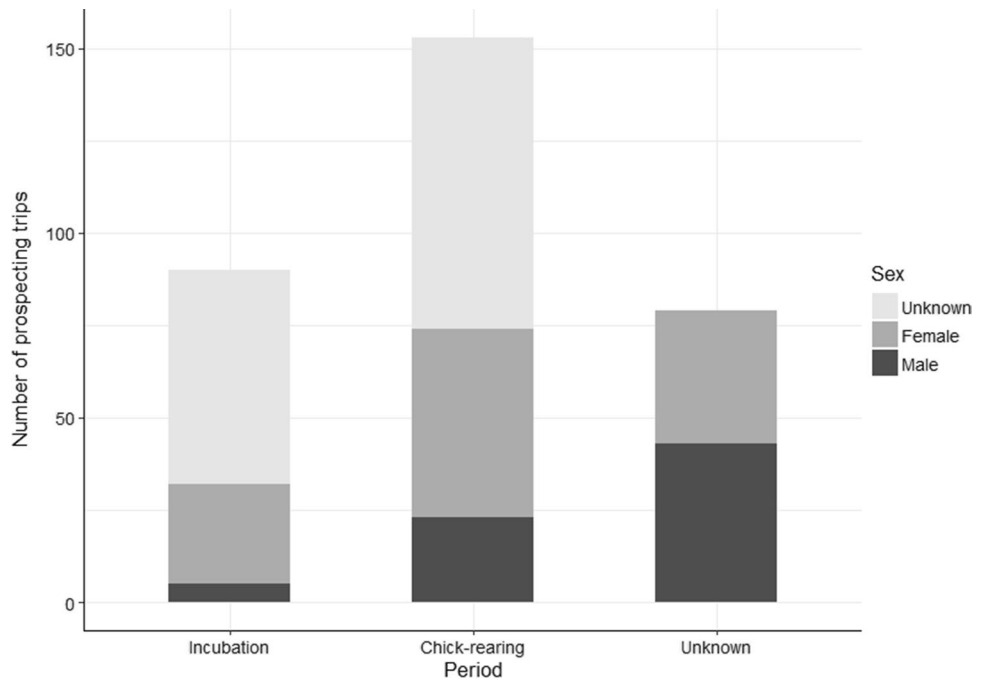
higher maximum distances to prospected colonies in six species, but due to the small sample size, the difference was significant only for one population of Audouin’s gulls (Supplementary Material Table 2). From all prospecting trips with a known stage of the breeding cycle ( $N = 243$ ), 63% were undertaken during the chick-rearing stage, with similar values (53.3–60.8%) obtained for individuals with longer relative tracking durations (> 50% of the breeding season). Also, 40.8% of prospecting trips with a reported time of day ( $N = 277$ ) included nocturnal visits in prospected 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  $\chi^2 = 4.46$ ,  $p < 0.05$ ). The majority of visited patches were < 100 km from the breeding patch (Figs. 3, 4) and distances to prospected patches (range 0.8–345 km) were highly correlated to the distances to the closest breeding patch (range 0.8–385 km) (Pearson correlation = 0.368,  $p < 0.01$ ).

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% of trips were undertaken during the incubation stage. The percentage of trips that included nocturnal visits at the prospected colony was higher during the incubation stage (60.7%) than during chick-rearing (23.4%), the difference being significant (Yates corrected  $\chi^2 = 7.20$ ,

**Fig. 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 <math>p < 0.01</math>, filled circle <math>p < 0.05</math>, open circle—non significant



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

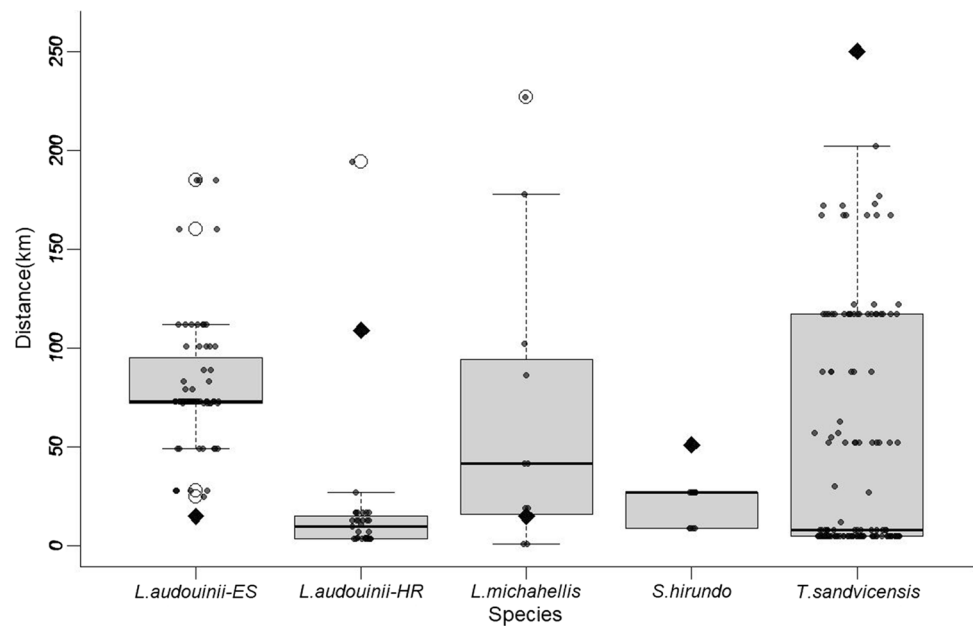


$p < 0.01$ ). More nocturnal visits during the incubation stage were also found in common tern (5 during incubation versus 1 during the chick-rearing stage), but the total number of trips was low ( $N = 12$ ). A substantial percentage of nocturnal visits were undertaken by Audouin’s and yellow-legged gulls (47.6% and 46.2%, respectively), whereas Mediterranean gulls prospected only during daytime.

### Discussion

Contrary to our predictions, prospecting in active breeders (PAB), a behaviour largely unnoticed in the scientific literature, was recorded in 85.7% of studied gull and tern species and 61.3% of sampled populations. During

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



the breeding period, central place foragers like seabirds are constrained in time and energy, as they must divide their time between foraging for themselves and investing in reproduction (Orians and Pearson 1979). The fact that prospecting frequently occurs during incubation and chick-rearing stresses its importance in the breeding habitat selection process and might be much more widespread than currently acknowledged.

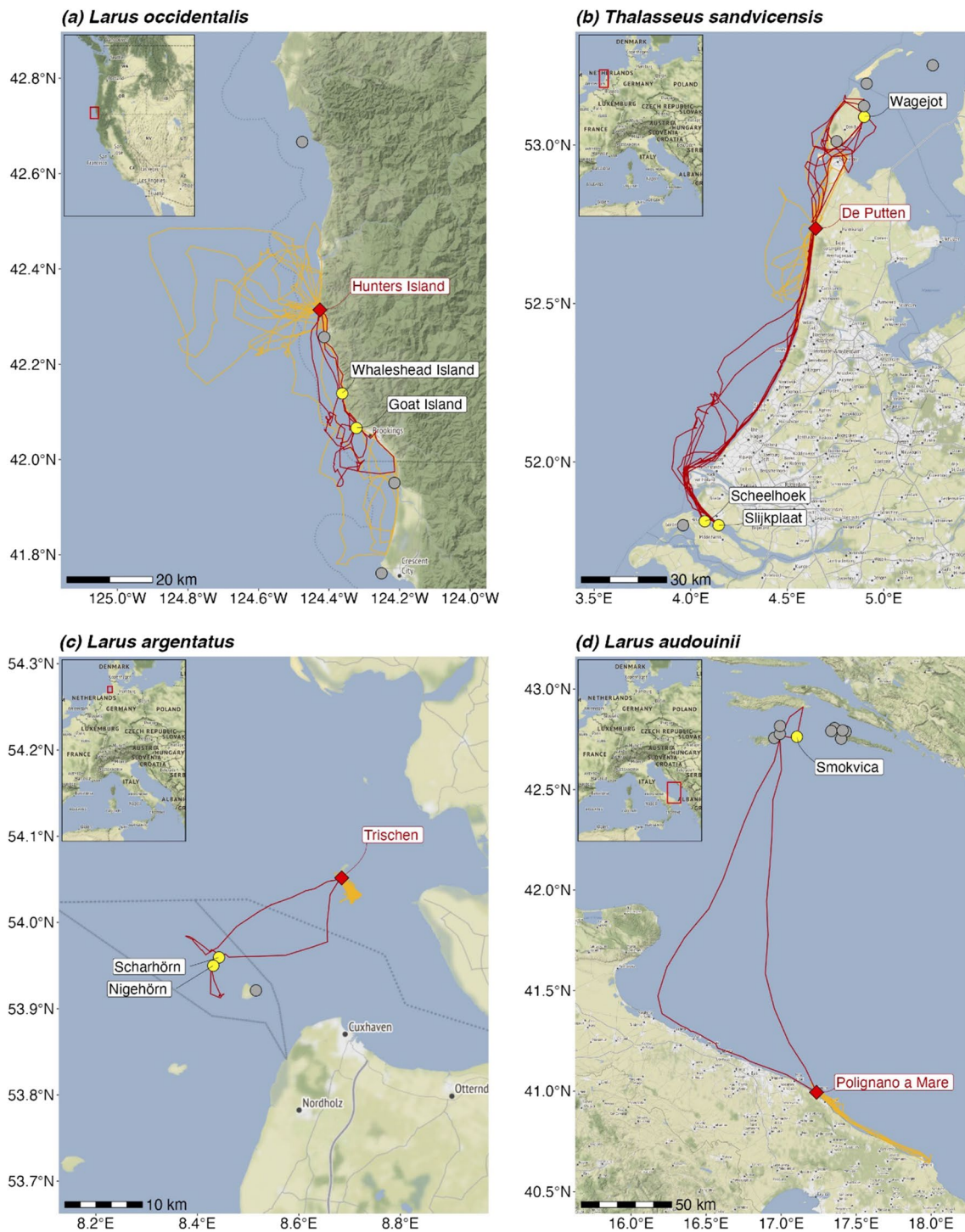
### Drivers of prospecting: breeding patch, sex and distance

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. Prospecting during different stages of the breeding cycle also allows breeding individuals to compare the quality of their current breeding patch to other localities over a wider area, informing the decision of whether to disperse or not. This information could be used for the current or future breeding seasons. As < 10% of individual birds in our study were tracked over multiple consecutive breeding seasons, we could not examine whether prospecting birds 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 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 prospecting in dispersal decision. Prospecting patterns might thus potentially reflect 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 over long periods and large spatial scales.

We considered relative breeding patch size and frequency of its use as a proxy for the stability of the patch but also as an indicator of environmental quality. However, patch stability in our study did not have a significant effect on PAB. This contradicts previous theoretical models that showed that prospecting may only evolve in a relatively predictable and stable environment (Boulinier and Danchin 1997; Doligez et al. 2003; Bocedi et al. 2012). Nevertheless, those 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 unstable environment, since in this case, information gathered during prospecting might be used immediately, such as for reneating purposes. As replacement clutches are more likely to be laid after failure in earlier stages of the breeding season (Pakanen et al. 2014), prospecting during the incubation suggests that PAB may also be used to identify suitable patches for reneating 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 breeding yellow-headed blackbirds *Xanthocephalus xanthocephalus* (Ward



**Fig. 4** Examples of prospecting trips of four individuals: **a** western gull *Larus occidentalis* ID 117,639,606, **b** sandwich tern *Thalasseus sandvicensis* ID B-H65, **c** herring gull *Larus argentatus* ID N105787 and **d** Audouin’s gull *Larus audouinii* ID CROG01. Symbol used: red

square—breeding colony, yellow dots—prospected conspecific breeding 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 trips)

2005). In general, females have higher dispersal probabilities in most bird species (Greenwood 1980), which may 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, 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. Therefore, they may use less energy for flying, which might be the underlying reason for their longer prospecting flights (Wearmouth and Sims 2008). In general, parental care in studied gulls and terns is shared between sexes (Leclaire et al 2010; Kavelaars et al 2021) with some differences among species. For example, females often perform more incubation and chick-rearing, whereas males perform most territory attendance in gulls and more provisioning in terns and some gulls (Pierotti 1981; Fasola and Saino 1995).

Distances to the prospected colonies were highly correlated with distances to the closest breeding patch. In our study, birds usually visited patches close to their current breeding patch, but on five occasions, visits to the nearest breeding patch (ranging 10–24 km) were not recorded. Whether active breeders visit all available patches or only some of them might depend on the number and distances to potential breeding patches, but also on the previous experience of individuals. As breeding seabirds must return frequently to their breeding patch to undertake reproductive duties, maximal prospecting distances of active breeders were expected to be lower than in failed breeders. This was confirmed in Audouin's gulls where the maximum distance to prospected patches was 164 km in active and 360 km in failed breeders (Oro et al. 2021), and in sandwich terns, where maximal distances in active breeders (202 km) 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.

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

Kittiwakes were the exception among studied seabirds, as almost no PAB was recorded. Previous tracking studies on breeding black-legged kittiwakes showed that prospecting only occurred in failed breeders (Ponchon et al. 2015b, 2017b). In our study, only one bird from 324 black-legged kittiwakes and two from 94 red-legged kittiwakes *Rissa brevirostris* prospected while actively breeding. Furthermore, the occurrence of PAB differed between populations of the same species: PAB occurred in Oregon, but was not observed in Californian populations of the western gull *Larus occidentalis*, whereas in yellow-legged gull, PAB was

common in the Balearic population, but not in the Atlantic one (Delgado et al. 2021, Table 1). Overall, inter- and intra-species variability calls for more detailed studies of PAB in different populations of the same species but also in species with different life-history 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 colonies), density-dependence at both inter- and intraspecific level, a regime of perturbation, age-distribution, laying synchrony and habitat suitability (including foraging opportunities and predator density; Oro et al. 1996; Tavecchia et al. 2008; Sanz-Aguilar et al. 2009).

Other factors that might influence prospecting are animal personality shown to affect dispersal (Cote et al. 2010; Schuett et al. 2012) and individual experience or age (Oro et al. 1999; Payo-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 al. 2005; Campioni et al. 2017). In contrast, older adults may be more likely to prospect, such as in meerkats *Suricata suricatta* (Mares et al. 2014). Knowing the age of tracked individuals may provide greater clarity on whether individuals of different age and experience display different prospecting patterns.

### The effect of data quality

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

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 implications for the ecology,

evolution, and conservation of species, especially in the current 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 aimed to identify foraging behaviour or migration routes, they might also be a source of other information (Hays et al. 2016). Regardless of the goal of tracking studies, more attention should 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 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 al. 2021). It would also help to identify already existing breeding patches and be an important tool for planning the monitoring of breeding populations, assessing population borders and designing conservation measures.

## Conclusion

By reviewing the occurrence of PAB among different gull and tern species, we highlighted the importance of prospecting in adult breeding seabirds. We showed that PAB is more common in populations with frequent breeding dispersal and among females. Informed dispersal may help populations to recover faster in response to environmental change by tracking better environmental conditions, notably through extinction-recolonization dynamics (Ponchon et al. 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 (Payo-Payo et al. 2017; Oro et al. 2021). Our results call for more long-term tracking studies simultaneously monitoring the breeding success not only of individuals but also of whole breeding patches to identify factors affecting spatial and temporal patterns of prospecting in different stages of populations and different environments. This would ultimately allow us to better predict species response to environmental change.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00442-023-05331-y>.

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

**Author contribution statement** JK collected and analysed the data and wrote the first draft of the 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 RO for black-legged kittiwakes, RP, RO, SS and AF for red-legged kittiwakes, LS, SP and 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 SW for lesser black-backed gulls, SG, PS and LE for herring gulls, LJ, JA, GT and JMI for yellow-legged gulls, SG and PS for the great black-backed gulls, JT, RC and DL for Aleutian terns, JK and DT for common terns and RF for sandwich terns. All authors contributed critically to the manuscript and gave final approval for publication.

**Funding** The study on black-legged kittiwakes in Norway was funded by the French Polar Institute (IPEV, programme no. 333 PARASITO-ARCTIQUE and OSU-OREME) and in France by Eoliennes Offshores du Calvados, Eoliennes Offshores des Hautes Falaises and the French Agency for Marine Protected Areas. Tracking of black-legged and red-legged kittiwakes in Alaska was supported by the North Pacific Research Board. The studies on Mediterranean gulls and gull-billed terns in Italy were funded by agreements between ISPRA and the Italian Ministry for the Ecological Transition (MiTE), formerly Ministry for Environment, Land and Sea Protection (MATTM); Decreti Min. Prot. 0004799-04/03/2016 and Prot. 34751-30/12/2019. The study of Audouin's gull in Spain was funded by the Spanish Ministry of Science, AEI/FEDER and UE (grants re. CGL2016-80963-R and CGL2017-85210-P), Project LIFE + INDEMARES (2009–2014; LIFE07NAT/E/000732), and was 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 National Park ('The BIG FIVE' project), under the LIFE project 'Resto con Life' (LIFE13 NAT/IT/0000471) and by ISPRA. Tagging of Audouin's and yellow-legged gulls in Croatia was funded under LIFE Artina project (LIFE17 NAT/HR/000594). Tracking of western gulls in Oregon was funded by the Bureau of Ocean Energy Management M14AC00026 and in California by several sources including SJSU RSCA and CSU COAST. Funds to monitor yellow-legged gull movements in the Balearic Islands were provided by Agencia Estatal de Investigación (AEI) and the EU found for regional development (FEDER), project n. CGL2017-85210-P. The survey of the yellow-legged gull in the province of Gipuzkoa (Basque Country, Spain) was funded by the Gipuzkoa Deputation. Tracking of gulls in Germany was funded mainly by the projects WINDBIRD (Grant no. 0325281, German Federal Ministry for 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 TRACKBIRD (Grant nos. 3515822100 and 3519861400), Federal Agency for Nature Conservation, with funds from the German Federal Ministry for the Environment, Nature Conservation and Nuclear Safety. The study on lesser black-backed gulls in Bristol, United Kingdom, was funded by European Research Council under the European Union's Horizon 2020 research and innovation programme (Grant number 679355), the University Research Committee (URC)/Institute for Advanced Studies (IAS) Interdisciplinary Research Internship Scheme (IRIS) 2018, and the EPSRC Centre for Doctoral Training in Future Autonomous and Robotic Systems (FARSCOPE) at the Bristol Robotics Laboratory. Tagging of common terns in Croatia and Slovenia was funded by the Cooperation Programme Interreg V-A Slovenia – Croatia (Grant SLO-HR347). Tracking sandwich terns in the Netherlands was part of PMR-NCV, a program to study the effects of the extension of Rotterdam Harbour, and WOZEP, a program to study the effects of offshore wind farm developments in the Dutch coastal zone. Both programs were commissioned by Rijkswaterstaat WVL. The study of Aleutian terns in Alaska was funded by the National Fish and Wildlife Foundation Pacific Seabird Program (Grant ID 61777), the U.S. Fish and Wildlife Service Kodiak National Wildlife Refuge, the Alaska Department of Fish and Game, and Oregon State University Department of Fisheries, Wildlife, & Conservation Sciences.

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

**Code availability** Not applicable.

## Declarations

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

**Ethical approval** All applicable institutional and/or national guidelines for the care and use of animals were followed.

**Consent to participate** Not applicable.

**Consent for publication** Not applicable.

## References


- Arizaga J, Laso M, Zorrozuza N, Delgado S, Aldalur A, Herrero A (2017) Uso del espacio por adultos de gaviota patiamarilla *Larus michahellis* Naumann, 1840 durante el periodo reproductor: resultados preliminares en relación al uso de vertederos. *Munibe Cienc Nat* 65:67–80
- Arizaga J, Zorrozuza N, Egunez A (2018) Between the land and sea: how Yellow-legged Gulls have changed their dependence on marine food in relation to landfill management. In: Mikkola H (ed) *Seabirds* ed. InTech, London, pp 67–78
- Baccetti N, Nissardi S, Zenatello M (2014) GPS-tags reveal strong links to North Africa *Larus audouinii* breeding in Sardinia. *Mediterr Waterbirds Bull* 2:24–26
- Bartón K (2020) MuMIn: multi-model inference. R package version 1.43.17. <https://CRAN.R-project.org/package=MuMIn>
- Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Soft* 67:1–48. <https://doi.org/10.18637/jss.v067.i01>
- Billerman SM, Keeney BK, Rodewald PG, Schulenberg TS (eds.) (2020) *Birds of the World*. Cornell Laboratory of Ornithology, Ithaca, NY, USA. <https://birdsoftheworld.org/bow/home>
- 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
- 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
- Boulinier T, Danchin E (1997) The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. *Evol Ecol* 11:505–517
- 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
- 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, McCoy KD, Yoccoz NG, Gasparini J, Tveraa T (2008) Public information affects 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, prospecting, dispersal? What host movement matters for infectious agent circulation? *Integr 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
- BWPi, (2006) BWPi 2.0.1. *Birds of the western palearctic interactive DVD ROM*. Oxford University Press & BirdGuides Ltd.
- 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
- Campioni L, Granadeiro JP, Catry P (2017) Albatrosses prospect before choosing a home: intrinsic and extrinsic sources of variability in visit rates. *Anim Behav* 128:85–93
- Cayuela H, Grolet O, Joly P (2018) Context-dependent dispersal, public information, and heterospecific attraction in newts. *Oecologia* 188:1069–1080
- 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
- Clobert J, Le Galliard JF, Cote J, Meylan S, Massot M (2009) Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol Lett* 12:197–209
- Cooper NW, Marra PP (2020) Hidden long-distance movements by a migratory bird. *Curr Biol* 30(20):4056–4062. <https://doi.org/10.1016/j.cub.2020.07.056>. (e3)
- Corman A-M, Mendel B, Voigt CC, Garthe S (2016) Varying foraging patterns in response to competition? A multicolony approach in a generalist seabird. *Ecol Evol* 6:974–986
- Cote J, Clobert J (2007) Social information and emigration: lessons from immigrants. *Ecol Lett* 10:411–417. <https://doi.org/10.1111/j.1461-0248.2007.01032.x>
- Cote J, Clobert J, Brodin T, Fogarty S, Sih A (2010) Personality-dependent dispersal: Characterization, ontogeny and consequences for spatially structured populations. *Philos Trans R Soc B Biol Sci* 365:4065–4076
- Coulson JC (2011) *The kittiwake*. T & AD Poyser, London
- Dall SRX, Giraldeau OO, McNamara JM, Stephens DW (2004) Information and its use by animals in evolutionary ecology. *Trends Ecol Evol* 20:187–193
- Danchin É, Boulinier T, Massot M (1998) Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. *Ecology* 79:2415–2428
- Danchin É, Giraldeau L-A, Valone TJ, Wagner RH (2004) Public information: from nosy neighbors to cultural evolution. *Science* 305:487–491
- 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
- 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 dependence. *Anim Behav* 66:973–988
- Doligez B, Pärt T, Danchin E (2004) Prospecting in the collared flycatcher: gathering public information for future breeding habitat selection? *Anim Behav* 67:457–466
- Dugger KM, Ainley DG, Lyver PO, Barton K, Ballard G (2010) Survival differences and the effect of environmental instability on breeding dispersal in an Adelle penguin meta-population. *Proc Natl Acad Sci USA* 107:12375–12380

- Enners L, Schwemmer P, Corman A-M, Voigt CC, Garthe S (2018) Intercolony variations in movement patterns and foraging behaviors among herring gulls (*Larus argentatus*) breeding in the eastern Wadden Sea. *Ecol Evol* 8:7529–7542
- 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 species 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
- Fijn RC, Wolf P, Courtenis W, Verstraete H, Stienen EW, Iliszko L, Poot MJ (2014) Post-breeding prospecting trips of adult Sandwich Terns *Thalasseus sandvicensis*. *Bird Study* 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
- Garthe S, Schwemmer P, Paiva VH, Corman A-M, Fock H, Voigt CC, Adler S (2016) Terrestrial and marine foraging strategies of an opportunistic seabird species breeding in the Wadden Sea. *PLoS One* 11:e0159630
- 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
- Genovart M, Oro D, Choquet R, Pradel R (2020a) Informed recruitment or the importance of taking stock. *bioRxiv*. <http://arxiv.org/2005.06248>
- Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. *Anim Behav* 28:1140–1162
- Grémillet D, Boulunier 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* 13(12):e4371. <https://doi.org/10.1002/ecs2.4371>
- 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* 6:e4794. <https://doi.org/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
- Jovani R, Mavor R, Oro D (2008) Hidden patterns of colony size variation in seabirds: a logarithmic point of view. *Oikos* 117:1774–1781. <https://doi.org/10.1111/j.1600-0706.2008.17065.x>
- Jurinović L, Zec M, Dumbović Mazal V, Kralj J (2019) Explorative GPS-tracking of foraging movements by Audouin's Gulls reveals no association with fishing vessels in Croatia. *Ardea* 107:213–221
- Kavelaars MM, Baert JM, Van Malderen J, Stienen EWM, Shamoun-Baranes J, Lens L, Müller 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. <https://doi.org/10.1186/s40462-021-00279-1>
- Kubetzki U, Garthe S, Schwemmer P, Heinze B (2020) Sturm Möwe an der Ostsee: Küsten- oder Agrarvogel? *Falke* 67(8):8–13
- Lance BK, Roby DD (1998) Diet and postnatal growth in red-legged and black-legged kittiwakes: an interspecies comparison. *Colon Waterbird* 21:375–387. <https://doi.org/10.2307/1521650>
- 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 meerkats. *Anim Behav* 88:185–193
- Martinović M, Galov A, Svetličić I, Tome D, Jurinović L, Ječmenica B et al (2019) Prospecting of breeding adult Common terns in an unstable environment. *Ethol Ecol Evol* 31:457–468
- 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: using 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
- 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, Columbus, pp 154–177
- Oro D (2020) Perturbation, social feedbacks, and population dynamics in social animals. Oxford University Press, Oxford
- Oro D, Genovart X, Ruiz X, Jimenez J, Garcia-Gans J (1996) Differences in diet, population 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
- 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
- Oro D, Bécarea 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. <https://doi.org/10.1007/s00442-021-05040-4>
- Pakanen V-M, Rönkä N, Thomson R, Koivula K (2014) Informed reneesting decisions: the effect of nest predation risk. *Oecologia* 174:1159–1167
- Palestis BG (2014) The role of behavior in tern conservation. *Curr Zool* 60:500–514
- Paredes R, Harding AMA, Irons DB, Roby DD, Suryan R, Orben RA, Renner H, Young R, Kitaysky A (2012) Proximity to multiple foraging habitats enhances seabirds' resilience to 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-Bird KJ, Ladd C, Renner H, Heppe S, Phillips RA, Kitaysky AS (2014) Foraging Responses of Black-Legged Kittiwakes to Prolonged Food-Shortages around Colonies on the Bering Sea Shelf. *PLoS One* 9:e92520
- Parejo D, White J, Clobert J, Dreiss A, Danchin E (2007) Blue tits use fledgling quantity and quality as public information in breeding site choice. *Ecology* 88:2373–2382
- Payo-Payo A, Genovart M, Sanz-Aguilar A, Greño JL, García-Tarrasón M, Bertolero A et al (2017) Colonisation in social species: the importance of breeding experience for dispersal in overcoming information barriers. *Sci Rep* 7:42866. <https://doi.org/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 Ser* 578:117–150
- 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 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

- 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
- Ponchon A, Grémillet D, Doligez B, Chambert T, Tveraa T, González-Solís J, Boulinier T (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 failure induces large scale prospecting movements in the black-legged kittiwake. *J Exp Mar Biol Ecol* 473:138–145
- Ponchon A, Garnier R, Grémillet D, Boulinier T (2015b) Predicting population responses to 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
- Ponchon A, Scarpa A, Bocedi G, Palmer SCF, Travis MJM (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. <https://www.R-project.org/>
- Reed JM, Boulinier T, Danchin E, Oring LW (1999) Informed dispersal: prospecting by birds for breeding sites. *Curr Ornithol* 15:189–259
- Sanz-Aguilar A, Massa B, Lo Valvo F, Oro D, Minguéz E, Tavecchia G (2009) Contrasting age-specific recruitment and survival in three colonies of storm petrels: which combination is best? *Ecography* 32:637–646
- 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 Sociobiol* 66:1341–1350. <https://doi.org/10.1007/s00265-012-1389-1>
- Schwemmer P, Corman A-M, Koch D, Borrmann RM, Koschorreck J, Voigt CC, Garthe S (2019) Charakterisierung der Habitatwahl von Silbermöwen *Larus argentatus* durch GPS-Datenlogger zur Einschätzung der Schadstoffbelastung an der deutschen Nordseeküste. *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
- Selonen V, Hanski IK (2010) Decision making in dispersing Siberian flying squirrels. *Behav Ecol* 21:219–225
- 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
- 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) Urban gulls adapt foraging schedule to human-activity patterns. *Ibis* 163:274–282
- Spendelov JA, Eichenwald AJ (2018) Post-spring migration colony-site prospecting by roseate terns (*Sterna dougallii*). *N Am Bird Bander* 43:1–6
- Tavecchia G, Minguéz 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
- Tengeres JE, Corcoran RM (2020) Aleutian tern satellite tracking, Kodiak archipelago 2019. Refuge report 2020.2. Kodiak National Wildlife Refuge, U.S. Fish and Wildlife Service, Kodiak
- 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
- Westerberg K, Brown R, Eagle G, Votier SC (2019) Intra-population variation in the diet of an avian top predator: generalist and specialist foraging in Great Black-backed Gulls *Larus marinus*. *Bird Study* 66:390–397. <https://doi.org/10.1080/00063657.2019.1693961>
- Williamson CJ, Spelt A, Windsor SP (2021) Bird velocity optimization as inspiration for unmanned aerial vehicles in urban environments. *AIAA J* 59:2503–2516
- Williamson CJ, Spelt A, Windsor SP (2020) Bird-inspired velocity optimization for UAVs in the urban environment. *AIAA Scitech 2020 Forum* p. 1948.
- Zorrozuza N, Delgado S, Aldalur A, Arizaga J (2020) Adverse weather reduces the spatial use of an opportunistic gull. *Behav* 157:667–681

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.

## Authors and Affiliations

Jelena Kralj<sup>1</sup>  · Aureore Ponchon<sup>2</sup> · Daniel Oro<sup>3</sup> · Barbara Amadesi<sup>4</sup> · Juan Arizaga<sup>5</sup> · Nicola Baccetti<sup>4</sup> · Thierry Boulinier<sup>6</sup> · Jacopo G. Cecere<sup>4</sup> · Robin M. Corcoran<sup>7</sup> · Anna-Marie Corman<sup>8</sup> · Leonie Enners<sup>8</sup> · Abram Fleishman<sup>9</sup> · Stefan Garthe<sup>8</sup> · David Grémillet<sup>10,11</sup> · Ann Harding<sup>12</sup> · José Manuel Igual<sup>13</sup> · Luka Jurinovic<sup>14</sup> · Ulrike Kubetzki<sup>8</sup> · Donald E. Lyons<sup>15,16</sup> · Rachael Orben<sup>17</sup> · Rosana Paredes<sup>18</sup> · Simone Pirrello<sup>4</sup> · Bernard Recorbet<sup>19</sup> · Scott Shaffer<sup>20</sup> · Philipp Schwemmer<sup>8</sup> · Lorenzo Serra<sup>4</sup> · Anouk Spelt<sup>21</sup> · Giacomo Tavecchia<sup>13</sup> · Jill Tengeres<sup>16</sup> · Davorin Tome<sup>22</sup> · Cara Williamson<sup>21</sup> · Shane Windsor<sup>21</sup> · Hillary Young<sup>23</sup> · Marco Zenatello<sup>4</sup> · Ruben Fijn<sup>24</sup>

<sup>1</sup> Institute of Ornithology, CASA, Gundulićeva 24, 10000 Zagreb, Croatia

<sup>2</sup> School of Biological Sciences, University of Aberdeen, Zoology Building, Tillydrone Avenue, Aberdeen AB24 2TZ, UK

- <sup>3</sup> CEAB (CSIC), Acces Cala Sant Francesc 14, 17300 Blanes, Catalonia, Spain
- <sup>4</sup> Istituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA), Ozzano Dell'Emilia, Italy
- <sup>5</sup> Department of Ornithology, Aranzadi Sciences Society, Zorroagaina, 11, 20014 Donostia, Spain
- <sup>6</sup> CEFE UMR 5175, Univ Montpellier, CNRS, EPHE, IRD, Univ Paul Valéry Montpellier 3, Montpellier, France
- <sup>7</sup> U.S. Fish and Wildlife Service, Kodiak National Wildlife Refuge, 1390 Buskin River Rd., Kodiak, AK, USA
- <sup>8</sup> Research and Technology Centre (FTZ), University of Kiel, Hafentörn 1, 25761 Büsum, Germany
- <sup>9</sup> Conservation Metrics, Inc, UCSC Coastal Science Campus, Santa Cruz, CA, USA
- <sup>10</sup> CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France
- <sup>11</sup> Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, South Africa
- <sup>12</sup> Auk Ecological Consulting, PO Box 2052, Cordova, AK 99574, USA
- <sup>13</sup> Animal Demography and Ecology Unit, IMEDEA (CSIC-UIB), M Marques 21, 07190 Esporles, Spain
- <sup>14</sup> Croatian Veterinary Institute, Poultry Centre, Heinzelova 55, 10000 Zagreb, Croatia
- <sup>15</sup> National Audubon Society, 12 Audubon Road, Bremen, ME 04551, USA
- <sup>16</sup> Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA
- <sup>17</sup> Department of Fisheries, Wildlife, and Conservation Sciences, Oregon State University, Hatfield Marine Science Center, Newport Oregon 97365, USA
- <sup>18</sup> Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331-3803, USA
- <sup>19</sup> Conservatoire des Espaces Naturels de Corse, Borgo, France
- <sup>20</sup> Department of Biological Sciences, San José State University, San Jose, CA 95192-0100, USA
- <sup>21</sup> Department of Aerospace Engineering, University of Bristol, Bristol, UK
- <sup>22</sup> Department of Organisms and Ecosystems Research, National Institute of Biology, 1000 Ljubljana, Slovenia
- <sup>23</sup> Department of Ecology, Evolution and Marine Biology, University of California Santa Barbara, Santa Barbara, USA
- <sup>24</sup> Bureau Waardenburg bv, Consultants for Environment and Ecology, Varkensmarkt 9, 4101 CK Culemborg, The Netherlands