Sex-specific foraging behaviour is affected by wind conditions in a sexually-size dimorphic seabird

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ABSTRACT

Flexibility in foraging behaviour is a key individual trait, promoting adaptive responses to changing environmental conditions. Such flexibility can be especially pronounced in marine predators that forage in highly dynamic environments and pursue ephemeral and patchily distributed prey. Individual characteristics, social interactions and resource availability may all promote behavioural flexibility, which in turn may foster divergence in foraging tactics within populations. The adoption of specific foraging tactics by individuals from the same population could be driven by a complex mixture of intrinsic and extrinsic factors. We GPS-tracked chick-rearing parents of a sexually-size dimorphic avian marine top-predator, the Scopoli's shearwater (*Calonectris diomedea*), across multiple foraging trips to investigate 1) intra-individual variation in foraging behaviour and 2) the effect of sex and wind conditions on the adoption of specific foraging tactics. Based on cluster analysis applied to GPS-derived behavioural patterns at the foraging trip scale, we identified variation in foraging tactics, from fine- to coarse-scale foraging (FF and CF, respectively). FF trips were characterised by lower flight activity, shorter travel distances and more intensive prey searching behaviour compared to CF trips. Individuals were not consistently performing FF or CF trips. Males were more prone to perform FF trips compared to females, but both sexes shifted towards CF trips with increasing wind intensity, likely to exploit the energetic advantages of dynamic soaring. We conclude that sex-specific foraging tactics reflect the interplay between sex-specific energetic optima, originating from differences in morphology, and a reduction of the niche overlap between the sexes. By adopting flexible, sex-specific foraging tactics, shearwaters likely optimize their energy expenditure during the energy-demanding chick-rearing stage. Our study outlines the importance of both intrinsic and extrinsic factors in shaping inter-individual variability in foraging behaviour.

INTRODUCTION

Foraging behaviour is a key individual trait that is tightly linked to fitness and thus to population processes (Pyke et al., 1977; Stephens & Krebs, 1986; Weimerskirch et al., 2012). To be successful, individuals should search for food in a way that minimizes energy expenditure and maximizes energy intake (Emlen, 1966; Krebs, 1978). However, the balance between costs and benefits depends on a range of different factors and constraints. Cognitive and physical capabilities of individuals, predation and competition pressures, resources abundance and distribution, predictability and luck can all affect foraging efficiency, making foraging behaviour an extremely plastic trait (Cook et al., 2006; Weimerskirch, 2007; Montevecchi et al., 2009; Torres & Read, 2009; Wilson et al., 2018). As a result of this plasticity, and to optimize individual foraging activity, different foraging tactics could arise within the same population (Heithaus & Dill, 2009; Boyd et al., 2014, Austin et al., 2019), where a specific tactic must have associated features that clearly distinguishes it from its alternative(s) (Gross, 1996). Here we define a foraging tactic as a distinguishable combination of behavioural patterns (i.e. multiple behaviours) shared by different individuals to search for food (similarly to Louzao et al., 2014; Cecere et al., in press).

The presence of different foraging tactics within the same population could be especially advantageous in marine central-place foragers, such as breeding seabirds, that target ephemeral resources in highly dynamic, three-dimensional environments, while rearing their altricial chicks (Weimerskirch, 2007). Moreover, these species commonly breed in large aggregations, resulting in strong intra-specific competition for resources (Ashmole, 1963; Wakefield et al., 2013), which should further promote the evolution and maintenance of a flexible foraging behaviour.

The adoption of specific foraging tactics by different individuals from the same population could be linked to individual characteristics (intrinsic drivers), such as social dominance, with competitive individuals forcing subordinate individuals to adopt alternative foraging tactics (Milligan et al., 2017). Similarly, different nutritional and energetic requirements, individual specialisation and personality can all affect the adoption of different foraging tactics (Patrick et al., 2013; Louzao et al., 2014; Patrick & Weimerskirch, 2014; Alarcón et al., 2017; Votier et al., 2017). Moreover, several intrinsic traits are tightly linked to sex. In seabirds, sexual size dimorphism can result in sex differences in flight efficiency and aerial agility, foraging areas and behaviour, provisioning rate and preferred preys, ultimately affecting foraging behaviour (Gonzalez-Solis et al., 2000; Weimerskirch & Lys, 2000; Lewis et al., 2005; Weimerskirch et al., 2006; Trefry & Diamond, 2017; Austin et al., 2019). Sex differences in foraging behaviour also occur in monomorphic seabirds (Gray et al., 2001), indicating that factors such as physiological requirements and parental roles may be important in shaping foraging tactics (Welcker et al., 2009; Alarcón et al., 2017). Intrinsic traits can also vary with age, leading individuals of different age classes to adopt divergent foraging tactics (e.g. Skórka & Wójcik, 2007). In general, older animals are more experienced, resulting in greater foraging efficiency and foraging site fidelity (Woo et al., 2008), while immature individuals tend to be more exploratory (Votier et al., 2017). However, senescent individuals could be less fit than younger ones, resulting in the adoption of less energy-demanding foraging tactics (Catry et al., 2011).

In addition to intrinsic drivers, extrinsic ones could affect the adoption of different foraging tactics. For example, wind condition is a key component of the marine environment influencing seabird ability to both reach profitable foraging grounds and to locate and catch prey (Daunt et al., 2006, Lewis et al., 2015; Tarroux et al., 2016). The flying behaviour of dynamic soarers, in particular, is strongly affected by wind (Weimerskirch et al., 2000; Richardson et al., 2018). For instance, Murphy's petrels (*Pterodroma ultima*) exploit favourable tailwinds to perform long-distance foraging trips (Clay et al., 2019), allowing large areas to be covered with a low energetic investment. Ultimately, extrinsic factors could affect individuals differently according to their intrinsic characteristics. It has been argued that sex differences in wing-loading between males/females and juvenile/adults drive variation in the at-sea distributions of wandering albatrosses (*Diomedea exulans*) (Shaffer & Costa, 2001). Despite many previous studies focused on individual variation and specialization in seabird foraging behaviour (e.g. Patrick et al., 2014; Ceia & Ramos, 2015), the characterization of intra-population variation in foraging tactics and the analysis of their drivers are still poorly explored (Lewis et al., 2015).

We investigated whether foraging tactics consistently differed among individuals and whether tactic adoption was predicted by sex and wind conditions in a seabird species. We focused on the Scopoli's shearwater (*Calonectris diomedea*), a large (ca. 550 g) procellariform breeding in the central Mediterranean Sea. Like other procellariforms, the Scopoli's shearwater is a dynamic soarer, taking advantage of winds for travelling over long distances at reduced energetic costs (Paiva et al., 2010a). Furthermore, it shows sexual size dimorphism, males being ca. 20% heavier than females and having a higher wing loading (see Results). Analysing GPS tracks over multiple foraging trips performed during the early chick-rearing stage, we first characterized foraging tactics at the trip level according to behavioural modes derived from the analysis of movement patterns. Secondly, we investigated whether the adoption of a given foraging tactic affected spatio-temporal trip characteristics and the exploitation of different environments. Thirdly, we investigated individual consistency in foraging tactics and whether sex and wind conditions at trip onset affected their adoption. We predicted that females should more frequently perform foraging trips that led them to search for food far from the colony site, as they are likely to both be outcompeted by males due to smaller size and experience lower energy costs of flight. Secondly, we expected both sexes to perform foraging trips that involve reaching farther areas under strong winds at departure, exploiting the energetic benefits of dynamic soaring.

MATERIAL AND METHODS

Target species and study site

The Scopoli's shearwater is a colonial seabird endemic to the Mediterranean Sea (Sangster et al., 2012). It breeds from April to October in rocky islands and sea-facing cliffs, where it lays eggs in burrows that are mostly located in rock crevices and under large stones (Cramp & Simmons, 1977). It feeds mainly on small pelagic fish and planktonic organisms (Grémillet et al., 2014), but it can exploit fishery discards (Cecere et al., 2015; Cianchetti-Benedetti et al., 2018). Males are significantly heavier than females, with larger skeletal size and higher wing loading (Appendix, Table A1).

We carried out the study on two small islets between Sardinia (Italy) and Corse (France), located ca. 7 km apart (Barrettini: 41°17'3.59"N, 9°24'5.96"E; Spargiotto: 41°14'59.83"N, 9°19'25.01"E), belonging to the Parco Nazionale dell'Arcipelago di La Maddalena (Italy). The area hosts a population of 400-1000 breeding pairs (Baccetti et al., 2009).

GPS deployment and foraging trip identification

During the early chick-rearing stage (July/August 2018), we equipped 55 individuals (27 males, 28 females) with archival GPS devices (modified i-gotU GT-120, Mobile Action, Hong Kong). We attached devices to the back feathers using Tesa® tape (Tesa SE, Hamburg, Germany) and retrieved them after ca. 10 days. The total mass of deployed devices was 19.5 g (including tape) and on average did not exceed 3.5% of body mass (mean ± SD; females: 3.5 ± 0.27%, males: 2.9 ± 0.16%). We set GPS loggers to record locations at 10-min intervals. Upon capture, we recorded body mass using a spring balance (± 10 g) and standard morphometric measures (see Appendix, Table A1) with a dial calliper (± 0.1 mm) and a steel ruler (± 1 mm). For a subsample of individuals, we photographed the stretched right wing on a panel with a scale bar. We calculated upper wing area using ImageJ software (Schneider et al., 2012) and derived wing loading by dividing body mass for twice the value of wing area. Birds were sexed using individual or partner vocalizations (Cure et al., 2009). Three individuals could not be recaptured, and GPS loggers were not retrieved. Eight loggers did not contain any data due to device failure or to device being waterlogged. Overall, we obtained data from 44 out of 55 individuals recruited for the study.

We identified foraging trips following Lascelles et al. (2016). Foraging trips were identified when an individual moved ≥ 5 km from the colony for ≥ 5 h. We considered only complete trips and removed GPS locations at the colony (< 5 km from the colony). We then plotted and visually inspected each foraging trip in QGIS v.2.18 (QGIS Development Team, 2009) to check they were correctly identified. The tracking dataset is available in the BirdLife Seabird Tracking Database (http://www.seabirdtracking.org/).

Ethical note

Capture, handling and tagging procedures were conducted by the Italian Institute for Environmental Protection and Research (ISPRA), under the authorization of Law 157/1992 [Art.4(1) and Art 7(5)], which regulates research on wild bird species. Permission to work at the study site was granted from Parco Nazionale dell'Arcipelago di La Maddalena, within the framework of the agreement prot. 38675 between ISPRA and the National Park (dated June 26, 2018). Birds were caught by hand at their nest burrows and released back into them within 10 min to minimize stress. They were handled by experienced staff only and no bird was injured by the capturing/handling procedure. We visited the colony in early October to check the breeding success of tracked birds. All of them successfully fledged chicks, except for three pairs whose chick was likely predated by a peregrine falcon (*Falco peregrinus*).

Identification and characterization of foraging tactics

We inferred behavioural modes from GPS data using the Expectation-Maximization binary Clustering (EMbC) algorithm, an unsupervised, highly efficient clustering method based on maximum likelihood to identify behavioural patterns from movement data (Garriga et al., 2016). We relied on the EMbC as it requires few prior assumptions and it has been successfully applied to derive ecologically meaningful behaviours from movement data for many seabird species, including procellariforms (Louzao et al., 2014; de Grissac et al., 2017; Bennison et al., 2018; Soldatini et al., 2019; Weimerskirch et al., 2020). The algorithm exploits flight speed and turning angle values between consecutive locations to assign locations to one of four behavioural modes (low speed/low turning angle - LL, low speed/high turning angle - LH, high speed/low turning angle - HL, high speed/high turning angle - HH) according to the distribution of the data (Garriga et al., 2016) (Appendix, Fig. A1). The algorithm was applied using the R package "EMbC" (Garriga et al., 2016). The four behavioural modes were described as four typical behaviours of the species (Louzao et al. 2014), namely floating (LL), intensive search (LH), relocation (HL) and extensive search (HH). To minimize incorrect labelling of single locations, we applied a post-processing smoothing procedure (implemented in the package) based on temporal state correlation. We used the default value of the maximum likelihood difference to accept a relabelling ($\delta w = 1$; i.e. "accept all changes"). Due to some incorrect behavioural assignment from EMbC algorithm, we applied two additional corrections. Single locations labelled as "intensive search" at the beginning or end of a series of locations that were classified as "floating" were re-labelled as "floating". Similarly, whenever we detected a single location or pair of locations labelled as "intensive search" interspersed within a series of consecutive locations that had been classified as "floating behaviour", we re-labelled them as "floating". These corrections led to re-labelling of 1582 GPS locations (out of 48208) (Appendix, Fig. A2).

To investigate foraging behaviour, we calculated the percentage (%) of each behaviour for each foraging trip (Louzao et al., 2014). We excluded from the calculation of percentages 1) those locations occurring during night-time (between sunset and sunrise, determined using the *crepuscule* function from R package “maptools”; Bivand & Lewin-Koh, 2018); and 2) all locations occurring on the final day of a trip that were later than 18:00 and within a 10-km buffer from the colony site. Night-time data were excluded because foraging events during night-time are rare (Rubolini et al., 2015), and birds spend the night either flying or floating on the sea surface. Hence, any behaviour performed during night-time is unrelated to the actual foraging tactic. Data for the last day of the trip were excluded because they were mostly ‘rafting behaviour’, not related to foraging. Rafting occurs when shearwaters gather in large groups at sea in the surrounding of the colony site before sunset, as they wait to enter their burrows with complete darkness (Brooke & Cox, 2004).

To describe foraging tactics, we relied on a clustering approach of the percentage of the four behaviours occurring in each trip, according to the framework of analysis proposed by Louzao et al. (2014). Cluster analysis was performed with a K-means procedure on the percentage of the four behaviour for each trip using the R package “stats” (R Core Team, 2018). We chose a K-means approach because of its simplicity, efficiency and empirical success (Jain, 2010). We assessed the optimal number of clusters using the *NbClust* procedure from the “NbClust” R package (Charrad et al., 2015), which computes 30 indexes for determining the optimal number of clusters. It then suggests the best number of clusters based on the majority consensus rule. The potential absence of clustering in the data was considered. As the *NbClust* procedure identified two clusters as the best number, we applied the K-means algorithm with K = 2 (i.e. two clusters) over a maximum of 500 iterations. We considered these two clusters of foraging trips (trip types) as illustrating two main foraging tactics, i.e. distinguishable combinations of behavioural patterns occurring within foraging trips.

We calculated, for each trip, three spatio-temporal trip metrics (trip duration, total trip length and maximum distance from the colony). We defined total trip length as the sum of linear distances (km) between each subsequent location in the foraging trip and the maximum distance from the colony as the maximum linear distance (km) from the colony reached during a foraging trip. We defined trip duration as the time interval (h) between the start and the end of a foraging trip.

To describe the different habitat features encountered during foraging trips, we calculated the mean value of environmental variables along the entire trip (considering all four behaviours and GPS locations). The environmental variables considered were selected according to the species' marine habitat preferences (Cecere et al., 2013; Cecere et al., 2014; Péron et al., 2018), namely bathymetry, slope, chlorophyll *a* concentration, sea-surface temperature (SST) and mixed layer depth. We obtained bathymetry from NOAA using the R package "Marmap" (Pante et al., 2018) and we calculated the slope from bathymetry using R package "Raster" (Hijmans, 2018). Other environmental variables were accessed through the EU Copernicus Marine Service Information (http://marine.copernicus.eu/about-us/about-eu-copernicus). Further details on environmental variables are shown in Appendix, Table A2.

The effect of performing different trip types on spatio-temporal trip metrics and environmental features encountered were tested by means of linear mixed models (LMMs) with trip type as a binary predictor and bird identity as a random intercept effect to account for repeated trips performed by the same individual. Trip metrics and environmental were $\log_{10}$-transformed to improve normality of residuals. Mixed models were fitted using the R package "lme4" (Bates et al., 2014).

Extrinsic and intrinsic drivers of foraging behaviour

To assess the effect of wind on the likelihood of performing different trip types, we calculated, for each trip, wind intensity at colony at the time of departure. We accessed wind data through Global Forecast System (GFS) of the USA's National Weather Service (NWS) using the "rWind" R package (Fernández-López & Schliep, 2018) (Appendix, Table A2). Trip departures were approximated to the nearest 3-hour block, to match the temporal resolution of the wind data. We obtained the U (zonal or east/west) and V (meridional or north/south) flow components from wind direction and intensity using the R package "RNCEP" (Kemp et al., 2012). For the first location of each trip outside a 10-km buffer from the colony, we calculated sidewind (flow component perpendicular to the direction of movement) and tailwind (flow parallel along the direction of movement) intensity according to equations in Kemp et al. (2012b). We used the absolute value of sidewind and hereafter we refer to sidewind and tailwind intensity as “sidewind” and “tailwind” respectively. We modelled the probability of performing a given trip type by means of a binomial GLMM, with trip type as the binary dependent variable, bird identity as a random intercept effect, and sex, islet, wind intensity, tailwind and sidewind as fixed effects. Wind intensity at colony, tailwind and sidewind were weakly correlated (wind intensity-tailwind: $r = 0.05$; wind intensity-sidewind: $r = - 0.02$; sidewind-tailwind: $r = - 0.37$) and could therefore be included simultaneously in the model. The initial model included all 2-way interactions with sex, which were removed from the final model in a single step if not significant ($P > 0.05$). To assess individual consistency in performing a specific trip type, we calculated the proportion of variance explained by the random intercept effect, accounting for variance explained by fixed effects (i.e. the adjusted repeatability, R_{adj}), of the probability of performing FF trips, using the observation-level variance obtained via the delta method (Nakagawa et al., 2017). Significance of R_{adj} was assessed by a likelihood ratio test (Zuur et al., 2009).

RESULTS

Identification and characterization of foraging tactics

We obtained 265 foraging trips from 44 individuals (21 males, 23 females) tracked during the chick-rearing stage (Fig. 1, S1 Video). Trips lasted on average 33 hours (± 33 SD), spanning between one and 11 days. Overall, we obtained a mean of 6 foraging trips per individual (± 3 SD). Nine out of 30 indexes suggested the presence of two clusters in the dataset, while different numbers of clusters were suggested by a maximum of five indexes, resulting in two as the optimal number. The clusters of trips identified by the K-means clustering (between sum of squares / total sum of squares = 34%) represented two trip types, which we named "coarse-scale foraging" (CF) trips and "fine-scale foraging" (FF) trips, respectively, based on the different proportions of the four behaviours in each trip (Fig. 2). CF trips showed more extensive search, less intensive search, more relocation and less floating compared to FF trips (Fig. 2) (mean ± SD percentages of GPS locations assigned to different behaviours per trip, CF vs. FF: extensive search, 35.2% ± 12.4 vs. 24.1% ± 8.0; intensive search, 14.3% ± 7.0 vs. 23.1% ± 11.1; relocation, 34.8% ± 12.1 vs. 18.6% ± 8.0; floating, 15.5% ± 7.8 vs. 34.1% ± 11.7). These two trip types likely represented two main foraging tactics occurring in our study population. More details on the clustering procedure are shown in Appendix (Fig. A3).

Performing CF trips resulted in longer travel distances and greater maximum distances from the colony (Table 1; Appendix, Fig. A4) and led birds to explore areas with higher chlorophyll *a* concentration, higher sea-surface temperature (SST), deeper waters and steeper slopes compared to the other tactic (Table 1). On the contrary, performing FF trips resulted in shorter maximum distances from the colony and travel distances (Table 1; Appendix, Fig. A4). FF trips led birds to explore areas with lower chlorophyll *a* concentrations, lower SST, and shallower waters and slopes compared to CF trips (Table 1). Trip duration and mixed layer depth did not differ significantly between trip types (Table 1). The observed differences in the environmental variables characterizing the two trip types correspond to 0.11-0.55 SD units of the range of environmental conditions experienced by shearwaters in the exploited area (see Appendix, Table A3).

Extrinsic and intrinsic drivers of foraging behaviour

Most birds performed both types of foraging trips (Fig. 3), resulting in no variance explained by individual identity ($R_{\mathrm{adj}} = 0$, $\chi^2 = 0$, $df = 1$, $P = 1$), indicating a high behavioural plasticity. Sex, sidewind and wind intensity at colony significantly predicted the probability of performing FF trips (Table 2). Males were more likely to perform FF trips (61% of trips) than females (34%) (Table 2).

With increasing wind intensity at the colony and sidewind, birds of both sexes were more likely to perform CF trips (Table 2, Fig. 4). Both sexes responded to wind conditions at trip departure in a similar way, as shown by the lack of statistically significant two-way interactions between wind effects and sex (all *P*-values > 0.1). No significant tailwind nor islet effects were detected (Table 2).

DISCUSSION

We investigated intra- and inter-individual variability in the foraging behaviour of a sexually-size dimorphic seabird. Based on behavioural annotation of movement data and subsequent clustering of behaviours at the trip level, we identified different types of foraging trips. These trip types, which we defined as coarse-scale (CF) and fine-scale (FF) foraging trips, likely represented different foraging tactics shared by birds of our study population. CF trips were characterized by high frequency of extensive search and relocation, while FF trips by high frequency of intensive search and floating on the sea surface. When performing CF trips, birds reached farther foraging grounds and covered greater distances compared to FF trips. However, trip duration did not differ among trip types, indicating that birds performing foraging trips to farther foraging grounds stayed away from the nest the same amount of time as those remaining around the colony (e.g. Appendix, Fig. A1). Different trip types led individuals to explore areas characterized by different environmental features. Although males were more likely to perform FF trips than females, most birds performed both trip types, suggesting highly flexible foraging behaviour. Both sexes were more likely to perform CF trips with increasing wind intensity at departure.

Trip types were defined according to a two-step clustering procedure, which may have forced a dichotomy along a continuous behavioral gradient. Nonetheless, behavioural differences among trip types were substantial and resulted in huge differences in spatio-temporal trip metrics and exploited environments. We thus believe that different trip types may represent different foraging tactics, and that they reflected a biologically meaningful distinction of foraging modes shared by individuals of our study population.

Overall, birds exploited areas characterized by favourable environmental features. Scopoli's shearwaters are known to prefer areas characterized by high chlorophyll *a* concentration, low sea-surface temperature and shallow waters (Cecere et al., 2013; Péron et al., 2018). On the one hand, CF trips led birds to areas with higher chlorophyll *a* concentrations and steeper slopes, known to bring prey close to surface (Piatt et al., 2006). On the other hand, with FF trips birds frequented on average shallower and cooler waters. Shearwater colony sites located between Sardinia and Corse are surrounded by productive waters providing abundant food resources (Cecere et al., 2014). Therefore, birds from our study colony may experience relatively weak parent-offspring conflict (Navarro & González-Solís, 2009; Cecere et al., 2014), resulting in a reduced need to alternate long-lasting foraging trips, aimed at self-provisioning, with short-lasting trips aimed at chick-provisioning. Although the latter phenomenon has been observed in several procellariform populations (Chaurand & Weimerskirch, 1994; Weimerskirch et al., 1994; Granadeiro et al., 1998), the proportion of long trips (> 4 days) was very low in our dataset (1.9%), most birds performing short trips only. This may contribute to explain the lack of differences in trip duration between CF and FF trips, despite the fact that, on average, CF trips led birds to distant foraging grounds.

Both intrinsic (i.e. sex) and extrinsic (i.e. wind) factors were involved in modulating foraging behaviour. Sex was a strong intrinsic driver of trip type, males being more likely to adopt behaviours compatible with the FF tactic compared to females. Sex differences in foraging behaviour have been observed in several procellariform seabirds (Weimerskirch & Lys, 2000; Paiva et al., 2017) and can originate from the interplay between different energetic constraints linked to size and inter-sexual competition for resources (Pinet et al., 2012). However, some previous studies on the foraging behaviour of *Calonectris* shearwaters failed to document sex differences (Navarro & González-Solís, 2009; Ramos et al., 2009; Paiva et al., 2010b; Paiva et al., 2010c; Cecere et al., 2013). This could be partly due to the fact that sex differences in foraging behaviour may emerge under specific environmental conditions only (Paiva et al., 2017). Moreover, relatively high resource predictability in our study area may play a role in shaping sex-specific foraging behaviours, as it has been suggested that unpredictability of prey could reduce intersexual behavioural differences (Courbin et al., 2018). Compared to females, male Scopoli's shearwaters should experience a higher cost of flight, since it positively covaries with wing loading (Hertel & Ballance, 1999; Shaffer & Costa, 2001). This may explain why males mainly performed foraging trips characterized by lower time spent on the wing. Males may have buffered frequent energy-demanding intensive search bouts by spending more time floating on the sea surface compared to females. While floating, individuals could be either resting and/or foraging by using the sit-and-wait prey searching technique (Pianka, 1966; Cianchetti-Benedetti et al., 2018). In contrast, females mainly performed trips characterized by a greater proportion of relocation and extensive search, implying that they mainly foraged on the wing.

It has been shown that male and female Scopoli's shearwaters do not differ in foraging areas selection neither during the incubation nor during the chick-rearing stage, even when exploiting different seascapes (Cecere et al., 2015). Moreover, at our study colony, the lack of significant sex difference in N^{15} isotopic signature of feathers grown during chick-rearing stage (L. Campioni et al., unpublished data) may suggest that males and females target the same prey items, sharing the same trophic niche and implying that some amount of intersexual competition may occur. Males are heavier and larger and therefore possibly more competitive than females in feeding interactions. Therefore, it is likely that they meet their energetic optimum spending less time on the wing and remaining in the proximity of the colony, where they might outcompete females.

On top of such sexual difference in foraging behaviour, the likelihood of performing CF trips increased in both sexes as wind intensity and sidewind at trip departure increased. CF trips allowed birds to reach farther foraging areas, likely exploiting the energetic advantages of dynamic soaring. Indeed, with sidewind, dynamic soaring birds may travel with small energetic costs using an S-shaped dynamic soaring manoeuvre (Weimerskirch et al., 2000; Wakefield et al., 2009; Paiva, et al., 2010a; Spivey et al., 2014; Richardson et al., 2018). At the same time, it is also likely that strong winds hampered sit-and-wait foraging due to sea wave surge. Moreover, under strong winds, intensive search could be more costly than extensive search, forcing individuals to switch flight and foraging mode. Indeed, the observed differences in the proportion of extensive/intensive search between trip types could be due to wind effects on flight mode, including speed and/or turning angle (Gibb et al., 2017; Ventura et al., 2020). Overall, our results suggest that Scopoli's shearwaters can flexibly adapt their foraging behaviour according to windscapes, minimizing energy expenditure by exploiting variation in weather conditions, similarly to other dynamic soaring species (Elliott et al., 2014; Ventura et al., 2020).

Ultimately, different tactics could represent alternative means of achieving, on average, the same energetic outcome (Clay et al*.*, 2019). Inter-sexual differences in foraging behaviour could be a way of expanding the ecological niche of breeding pairs and reducing inter-sexual competition for access to resources. This, in turn, may allow optimal chick provisioning rates under fluctuating environmental conditions, buffering the risk of offspring starvation. In the long-term, a high flexibility in foraging behaviour, both within-individuals and between the sexes, might be a useful asset in environments exposed to rapid and dramatic changes, such as those seas and oceans are currently undergoing (Halpern et al., 2008).

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Table 1. Effects of trip type (coarse-scale, CF, vs. fine-scale, FF, trips) on spatio-temporal trip metrics and environmental variables.

Variables	**CF trips ($N = 136$)**	**FF trips ($N = 129$)**	χ^2	*df*	*P*	**Marginal R^2**	**Conditional R^2**
Spatio-temporal							
Trip duration (h)	34.4 ± 29.4	32.4 ± 36.1	2.09	1	0.15	0.01	0.04
Total trip length (km)	370.0 ± 318.9	240.6 ± 263.7	20.04	1	< 0.001	0.07	0.15
Maximum distance (km)	115.0 ± 93.9	67.8 ± 56.8	19.88	1	< 0.001	0.07	0.19
Environmental							
Bathymetry (m)	-251.5 ± 252.1	-157.4 ± 253.1	12.16	1	< 0.001	0.04	0.34
Slope (°)	1.26 ± 0.84	1.06 ± 1.00	7.56	1	0.006	0.03	0.22
Chl a (mg m^{-3})	0.045 ± 0.005	0.043 ± 0.003	9.13	1	0.002	0.04	0.12
SST (°C)	26.03 ± 0.84	25.79 ± 0.68	4.41	1	0.036	0.02	0.09
Mixed layer depth (m)	12.19 ± 0.66	12.10 ± 0.50	3.38	1	0.06	0.01	0.01

The effect of trip type on mean spatio-temporal trip metrics and environmental features encountered was assessed by means of linear mixed models with bird identity as a random intercept effect. Significance was tested by likelihood ratio tests. Marginal (proportion of variance explained by fixed effects) and conditional (proportion of variance explained including both fixed and random effects) R^2 were estimated by means of the R package “performance” (Nakagawa and Schielzeth 2013). Values are mean ± SD.

Table 2. Binomial generalized linear mixed model testing the effect of intrinsic and extrinsic factors on the likelihood of performing fine-scale (FF) foraging trips.

Predictors	**β ± SE**	χ^2	***df***	***P***	**Effect size *r***
Sex	1.02 ± 0.27	14.75	1	< 0.001	0.24
Sidewind	-0.34 ± 0.10	12.67	1	< 0.001	0.24
Tailwind	0.01 ± 0.05	0.01	1	0.98	0.01
Wind intensity at colony	-0.13 ± 0.06	4.60	1	0.030	0.14
Islet	0.38 ± 0.28	1.79	1	0.18	0.08

The binomial dependent variable (trip type) was coded as 0 for CF and 1 for FF trips. Sex and islet were coded as 0 for female, 1 for male and 1 for Barrettini, 2 for Spargiotto, respectively. The model included individual identity as random intercept effect. Significance of fixed effect terms was tested by likelihood ratio tests. The model was not overdispersed ($\Phi = 1.1$).). Model R^2 was 0.17 (marginal) and 0.17 (conditional), while R_{adj} was 0.00 (all values estimated according to Nakagawa et al., 2017). Effect size was calculated as the absolute value of Pearson's *r* obtained from the "r2glmm" R package (Jaeger, 2017).

Table A1. Morphometrics of GPS-tagged female and male Scopoli's shearwaters.

Measure	**Females ($N = 28$)**	**Males ($N = 27$)**	t	P
Wing (mm)	342 ± 9	353 ± 6	5.40	< 0.001
Tarsus (mm)	52 ± 2	54 ± 2	5.15	< 0.001
Keel (mm)	61 ± 3	65 ± 3	5.29	< 0.001
Bill length (mm)	48 ± 2	52 ± 1	8.42	< 0.001
Bill height (mm)	13 ± 0.6	14 ± 0.5	8.35	< 0.001
Body mass (g)	563.9 ± 43.9	674.1 ± 38.0	9.94	< 0.001
Wing loading (g/cm^2)[a]	0.45 ± 0.03	0.52 ± 0.04	3.84	0.002

a: wing loading was measured for a subsample of individuals only (6 females, 11 males). Mean ± SD values are reported. Sex differences were assessed by a Student's *t*-test.

Table A2. Details on the environmental variables considered for this study

Variable	**Unit**	**Spatial resolution**	**Temporal resolution**	**Dataset details**
Bathymetry	M	1 km	/	ETOPO1
Slope	°	1 km	/	ETOPO1
Chl-a	mg/m^3	4 km	1 day	MEDSEA_ANALYSIS_FORECAST_BIO_006_014
Sea Surface Temperature (SST)	°C	4 km	1 day	MEDSEA_ANALYSIS_FORECAST_PHY_006_013
Mixed Layer Thickness (MLT)	M	4 km	1 day	MEDSEA_ANALYSIS_FORECAST_PHY_006_013
Wind intensity (10 m)	m/s	50 km	3 hours	NOAA/NCEP (GFS) Atmospheric Model collection
Wind direction (10 m)	°	50 km	3 hours	NOAA/NCEP (GFS) Atmospheric Model collection

Datasets were downloaded from the Copernicus website (http://marine.copernicus.eu/services-portfolio/access-to-products/).

Table A3. Variability of six environmental features used to describe habitats frequented during coarse-scale (CF) or fine-scale (FF) foraging trips across the study area.

Variable	**Mean ± SD**	**Mean difference (SD units)**
Bathymetry (m)	-304.0 ± 480.0	0.19
Slope (°)	1.42 ± 1.82	0.11
Chl a (mg m^{-3})	0.046 ± 0.016	0.13
SST (°C)	26.17 ± 0.89	0.27
Mixed layer depth	12.05 ± 0.80	0.11

Mean ± SD were calculated for each variable based on all GPS locations (N = 49790) collected from all individuals (N = 44), describing the variation in the overall habitat used by birds from La Maddalena Archipelago during the chick-rearing stage. The mean difference between CF and FF trips is expressed in SD units of the available habitat.

Figure 1. Maps of coarse-scale (CF) and fine-scale (FF) trips. The sample size is 136 CF trips and 129 FF trips. The colony location is shown as a star (picture of GPS-tagged Scopoli's shearwater by M. Ugo).

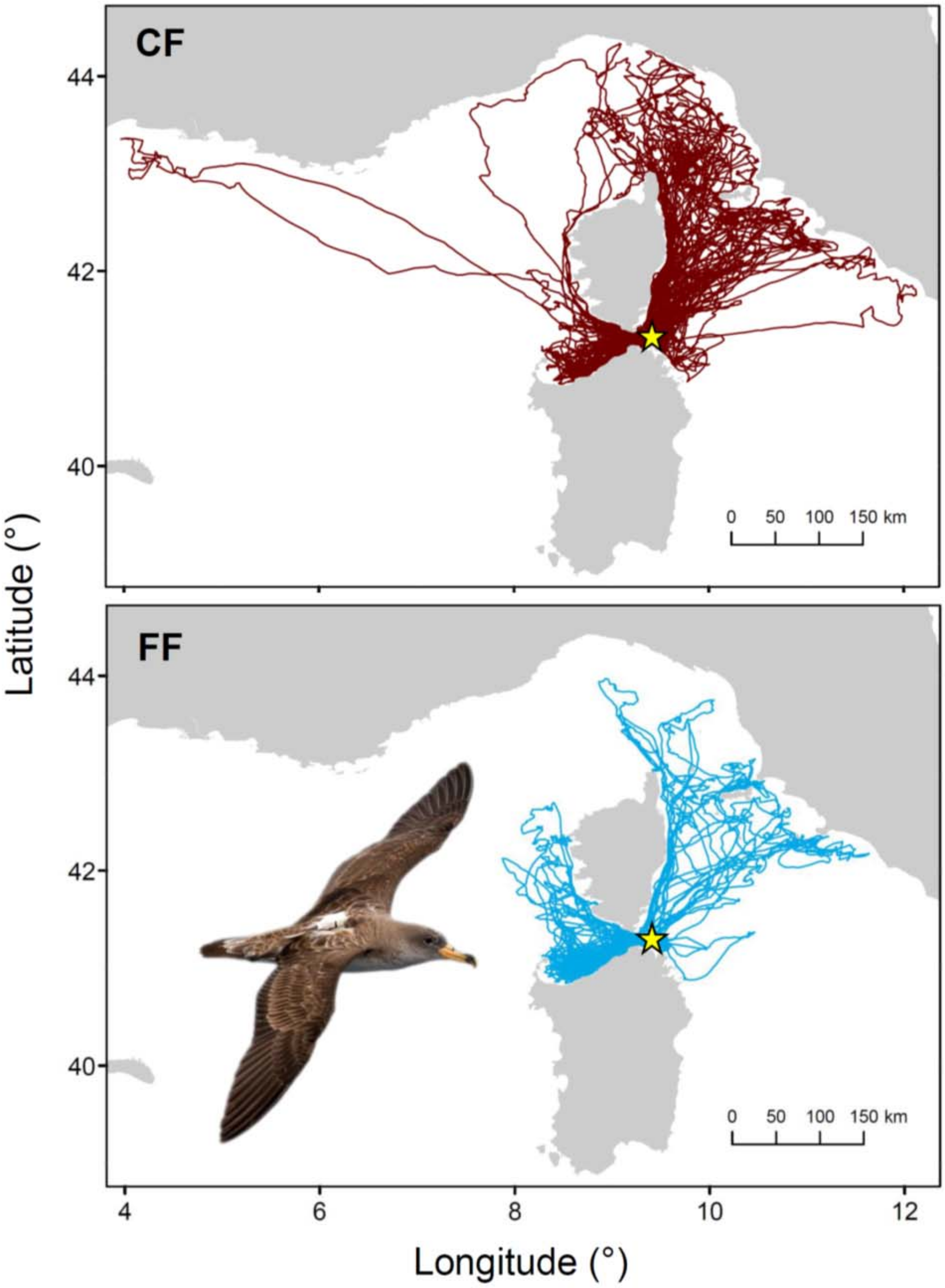


Figure 2. Scatterplot of GPS locations in relation to turning angle and speed from EMbC algorithm, and percentage of estimated behaviours for each foraging trip. Behavioural modes (different colours) identified by the EMbC algorithm before (a) and after (b) the post-smoothing procedure are shown. Solid grey lines show the binary delimiters (set of parameters dividing data into high/low values and defining the binary regions of the input space). LL (low speed and low turning angle, “floating”); LH (low speed and high turning angle, “intensive search”); HL (high speed and low turning angle, “relocation”); HH (high speed and high turning angle, “extensive search”); NC (non-classified data points; e.g. the last point of a trajectory). Panel (c) shows the percentage (%) of GPS locations assigned to each behaviour per trip ($N = 265$), according to the two identified clusters of trips (coarse-scale foraging, CF, and fine-scale foraging, FF, trips).

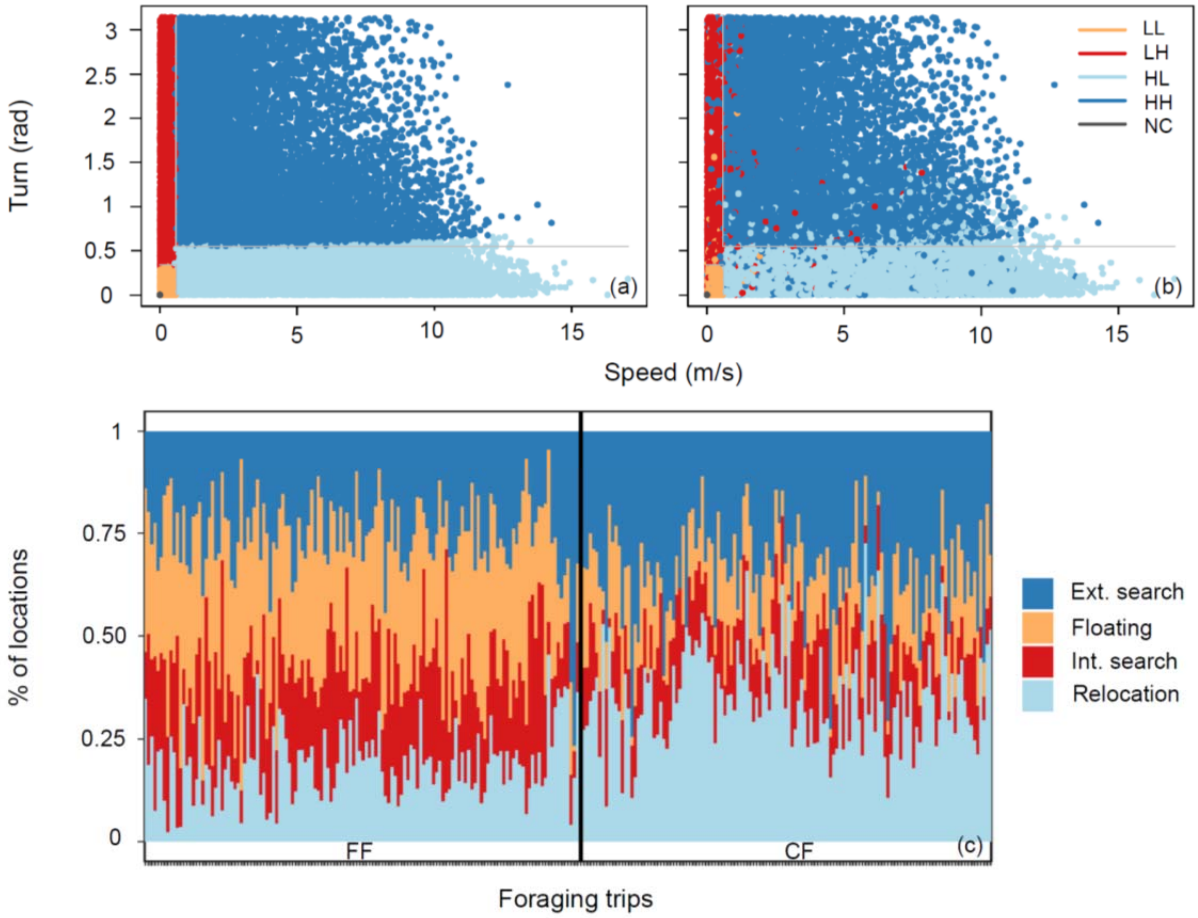


Figure 3. Sequences of coarse-scale (CF) and fine-scale (FF) foraging trips performed by individual shearwaters. Different lines show the sequence of consecutive foraging trips of each individual (Trip number). Individuals were grouped by sex (females: $N = 125$ trips and 23 individuals, males: $N = 140$ trips and 21 individuals). Red: CF trips, blue: FF trips.

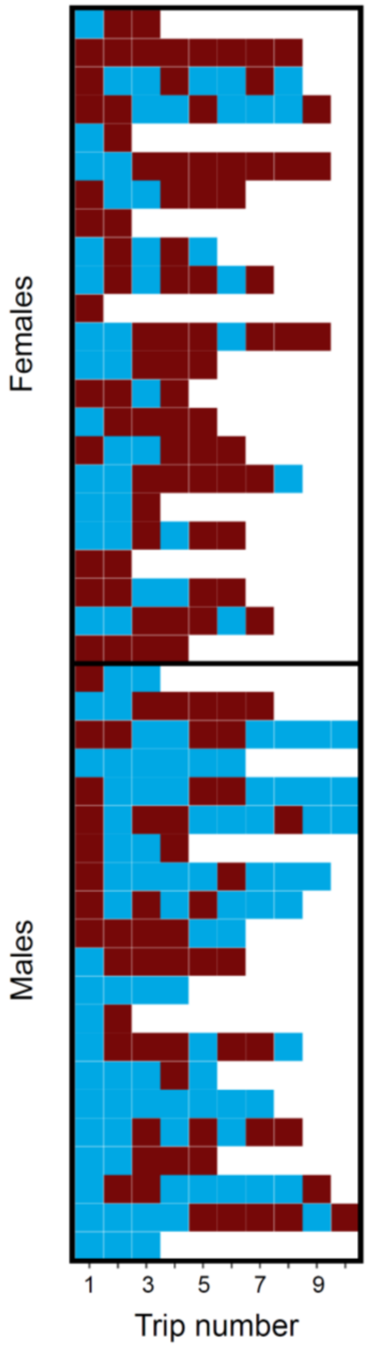


Figure 4. Probability of performing fine-scale (FF) or coarse-scale (CF) foraging trips according to wind conditions at trip departure. Variation in the probability of performing FF or CF trips in relation to wind intensity at the colony site (a) or sidewind at departure (b). Predicted probabilities (bold lines) and 95% confidence intervals (shaded areas) for each sex were derived from the fitted binomial GLMM model reported in Table 2.

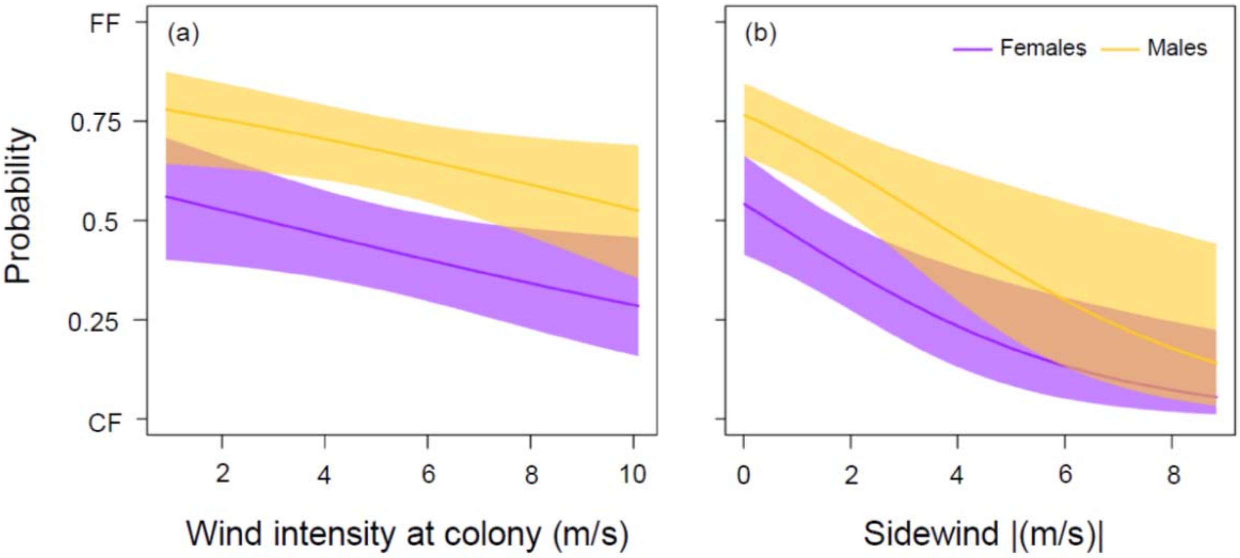


Figure A1. Representative example of foraging trips with each GPS location coloured according to its assigned behaviour. Two foraging trips, identified as coarse-scale (CF) (left panels) and fine scale foraging (FF) (right panels), performed by two individuals during chick-rearing stage are shown. Colours represent behaviours: floating (orange), intensive search (red), relocation (light blue) and extensive search (dark blue). The band on the top shows the behavioural sequence during the foraging trip. Sex, bird identity, tactic and metrics of each trip are reported. The black star shows the colony location and the arrows the direction of the trip.

Figure A2. Representative example of a segment of foraging trip before (a) and after (b) manual correction for behavioural state assignment. Behaviours are shown with different colours: floating (orange), intensive search (red), relocation (light blue), extensive search (dark blue).

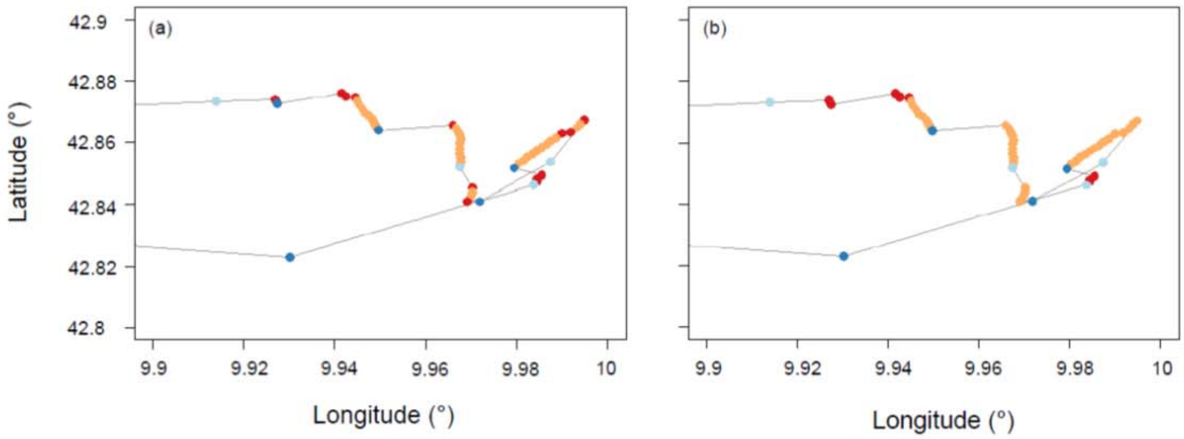


Figure A3. Choice of the optimal number of clusters and Principal Component plot of K-means clusters. Panel (a): Graphical output of the NbClust procedure for estimating the optimal number of clusters (K), indicating K = 2 as the most frequent number of clusters proposed by the 30 indexes considered. Panel (b): K-means clusters of foraging trips based on the percentages of four behaviours per trip (dots, $N = 265$). Convex hulls, grouping foraging trips, were coloured according to the assigned cluster. Cluster centroids are represented as black squares. For visualization purposes, the multivariate data are plotted on the two main axes of a Principal Component Analysis, performed on the percentages of four behaviours per trip (overall explaining the 79% of the observed variance).

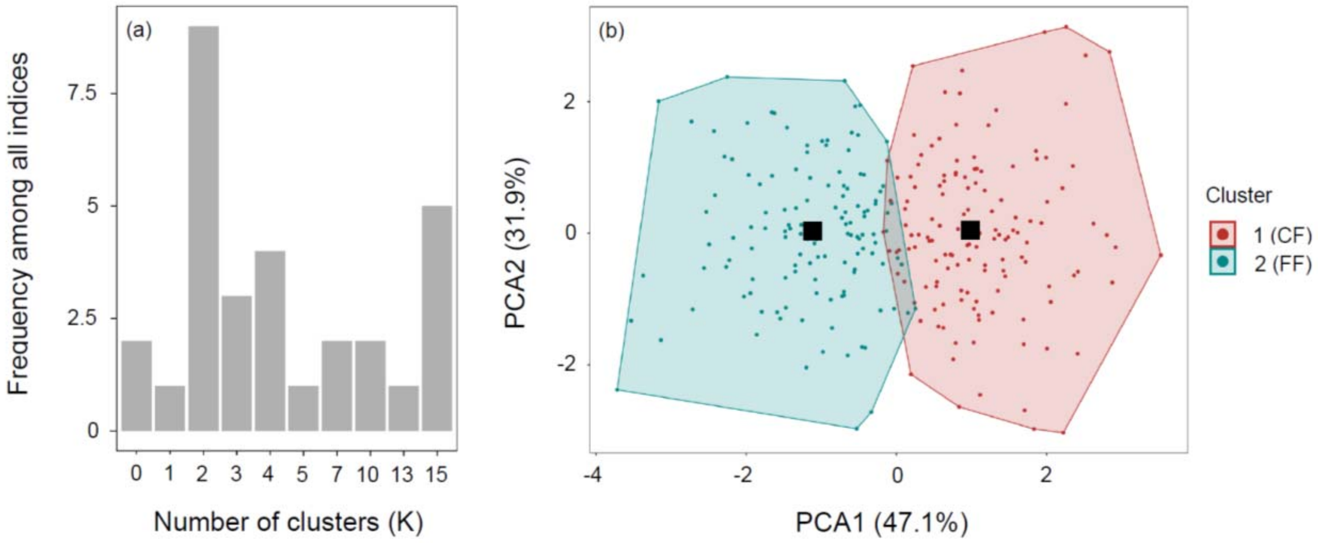
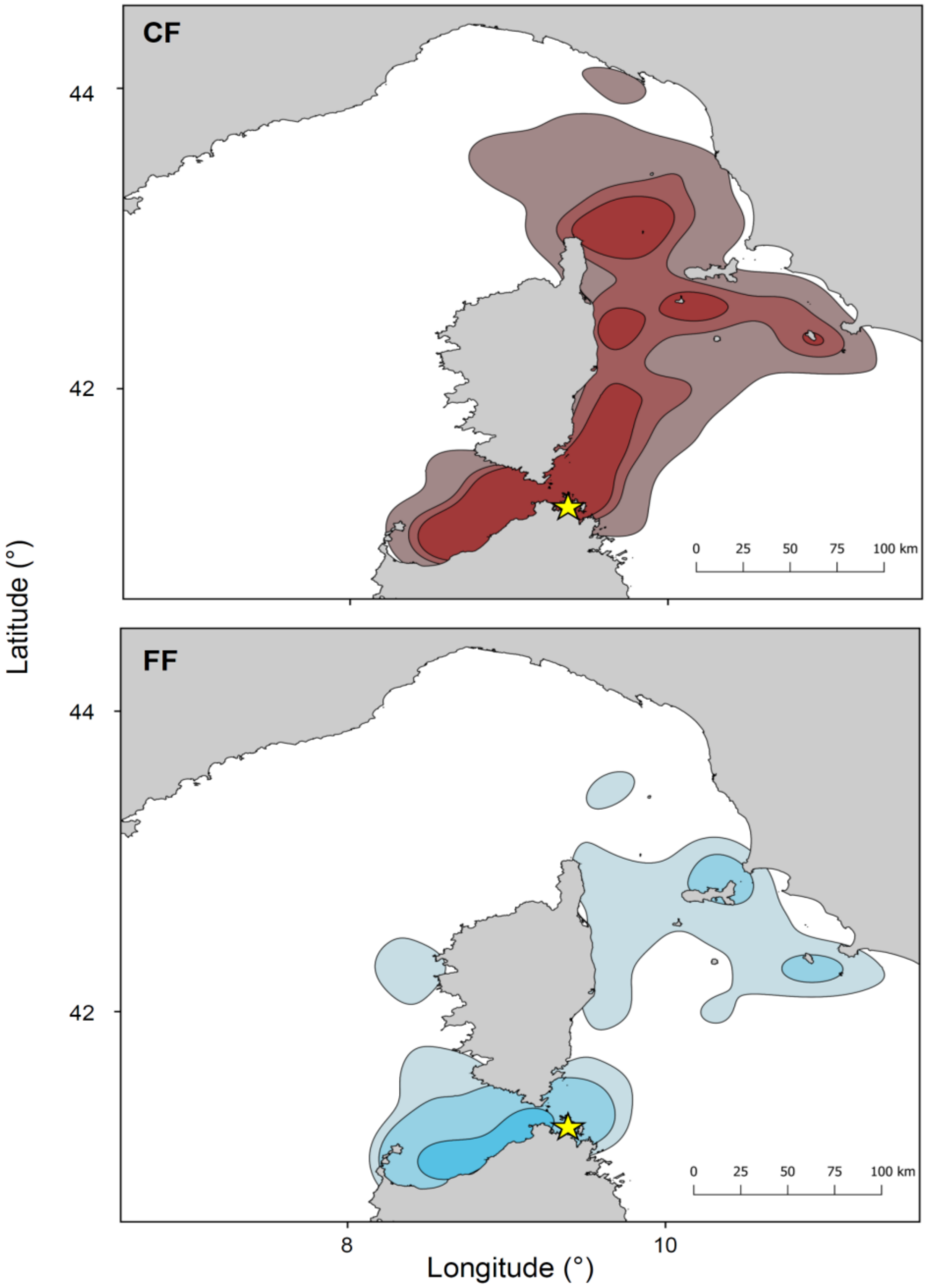


Figure A4. Kernel density estimate (KDE) of GPS locations from different trip types. Fixed KDEs (50, 70 and 90% contours) were calculated for CF and FF trips separately. The colony location is shown as a star. Covariance bandwidth matrix were obtained using the least square cross validation estimator with R package “ks” (Duong, 2007). Projected coordinates were used to prevent spatial biases.



Supplementary materials

S1 Video. Animation showing foraging trips of chick-rearing Scopoli's shearwater. Each dot represents an individual bird performing foraging trips (*N* = 264) during the chick-rearing stage in July/August 2018 from the colony in La Maddalena archipelago, Italy. One long foraging trip, where the individual reached the Gulf of Lion, was removed to aid visualization of smaller-scale movements. This animation was realised using R package "moveVis" (Schwalb-Willmann, 2018).

References

Schwalb-Willmann, J. moveVis: Movement Data Visualization. (2018). Available from: https://cran.r-project.org/package=moveVis