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INTRINSIC AND EXTRINSIC DRIVERS OF FORAGING MOVEMENTS IN COLONIAL BIRDS

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This thesis is dedicated to the memory of Franca and Marisa Chiarini, two special human beings that loved

all things feathery.

SUMMARY

INTRODUCTION

Foraging: a key for life history

Individuals from animal populations living in the wild face several challenges to maximize their fitness. Within this set of challenges, finding food plays a key role (Kramer 2001), not only assuring survival, but providing the necessary energy to accomplish vital life-history tasks, such as rear offspring, escape predators and migrate (Kramer 2001). The search for food can also favour social information exchange (Hasenjager et al. 2020), sometimes enhancing cooperation between individuals (Dumke et al. 2018), ultimately leading to drastic changes in species' ecology. For example, it has been suggested that shifting diet towards high-quality and difficult-to-acquire resources promoted a prolonged juvenile period, increased brain capacities and encouraged intergenerational information flows in human beings (Lancaster et al. 2000). Foraging behaviour may affect the life history of individuals and drive, in turn, demography of whole populations (Boggs 1992). Ultimately, the essence of life has been described as the ability to "capture energy from the environment and convert it into more organisms" (Ellison 2017, Alberts 2019). However, the search for such energy, which is acquired via food resources in heterotrophs, may be constrained by intrinsic and extrinsic factors. Indeed, to forage successfully, individuals should minimize energy expenditure and maximize energy intake (Stephens & Krebs 1986), and extrinsic and intrinsic elements act on this balance, finely modulating individuals' spatio-temporal foraging choices (Stephens & Krebs 1986).

Movement ecology is a relatively new and rapidly growing branch of ecology, aimed at understanding the "causes, mechanisms and spatiotemporal pattern of movement, and their role in various ecological and evolutionary processes" (Nathan et al. 2008, Avgar et al. 2013), and can be applied to foraging ecology, providing a valuable tool for investigating individual foraging movements in relation to their drivers. Long-ranging, large-bodied bird species, such as seabirds or raptors, have been widely used to investigate foraging movement patterns and their drivers. Their

large body enable the deployment of different type of biologgers (Phillips et al. 2003, Bodey et al. 2018), and since they operate in challenging and dynamic environments (e.g. the air, the sea), they may be particularly sensitive to the effect of different extrinsic and intrinsic agents on their foraging performances (Sergio 2003, Collet et al. 2020, Collins et al. 2020).

Intrinsic drivers: the individual's internal state

Intrinsic drivers are elements inextricably linked to individual's characteristics or qualities (individual's internal state), that often are a function of age or sex. For example, older animals are more experienced, resulting in greater foraging efficiency (Heise & Moore 2003) and foraging site fidelity, while immatures are more exploratory in their foraging modes (Votier et al. 2017). Indeed, during ontogeny, individuals transition from exploratory movements to an optimal movement strategy, a process mediated by memory and knowledge of foraging grounds (Votier et al. 2017). However, after an optimal age, senescence starts playing a role, and older individuals become less fit than younger ones, resulting in the adoption of different, less energetically demanding movement modes (Catry et al. 2011). Sex-based differences can affect shape, morphology, physiology or energetic requirements of individuals, resulting for example in different flight efficiency or aerial agility between individuals, that can alter foraging decisions (Temeles & Roberts 1993, González-Solís et al. 2000, Weimerskirch & Lys 2000, Raihani et al. 2006, Weimerskirch et al. 2006, Catry et al. 2016). Ultimately, sex dimorphism and related differences in size can result in persistent spatial and or temporal differences in foraging behaviour, leading to sex-specific foraging niches (González-Solís et al. 2000, Clark et al. 2021). This differentiation in foraging niches plays an important role in the ecology of populations, by reducing intra-specific competition and allowing e.g. partners to differ in time activity budgets or nutritional requirements related to their reproductive roles (Ruckstuhl & Neuhaus 2000, Clark et al. 2021). Moreover, social dominance, which often is the result of both sex and age, could drive individuals to adopt optimal foraging tactics, forcing subordinate individuals to adopt alternative or suboptimal foraging behaviours (Milligan et al. 2017). Finally, it has been shown

that animal personality can affect foraging decisions, with bold and shy individuals having different foraging site fidelity, propensity to explore the surrounding environment, responsiveness to environmental changes and foraging spatial intensity and scale (Van Overveld & Matthysen 2010, Patrick & Weimerskirch 2014, Villegas-Ríos et al. 2018, Harris et al. 2020).

Extrinsic drivers: the surrounding environment

Individuals, with their intrinsic characteristics, operate in a dynamic and complex environment, that collates both a biotic and an abiotic component. The abiotic component consists in a set of atmospherical or physical agents that can affect animal foraging decisions and movements in several ways. In birds, weather conditions and landscape features affect movements modes (Duerr et al. 2015, Scacco et al. 2019, Ventura et al. 2020), promoting the adoption of different foraging tactics (Hernández-Pliego et al. 2017, Clay et al. 2019). For example, seabirds modulate flight behaviour according to different wind conditions (Clay et al. 2020), and there is evidence that they use prior knowledge of the predictable regional windscape to optimize foraging trips on ocean wide scales (Ventura et al. 2020). Also, raptors have been shown to adjust their energetic expenditure to weather conditions, modulating the type of flight according to solar radiation and thermal updraft (Hernández-Pliego et al. 2017). The biotic component includes resources distribution and the presence of conspecifics/heterospecifics. Resources typically varies in time and space, and their distribution affect decisions on how, when and where to forage (Trevail et al. 2018). Particularly, resources predictability plays a key-role in shaping foraging decisions and foraging modes of animals. Environments where food resources are unpredictable or ephemeral, such as the marine one, promote social foraging, with individuals aggregating when searching for food (Egert-berg et al. 2018), exchanging information about resources (Overington et al. 2008), or following other species' movements to find foraging opportunities (Sakamoto et al. 2009). On the contrary, environments with predictable resources or with resources stable in space and time promote repetitive individual foraging behaviour and a more specialized diet (Overington et al. 2008, Egert-

berg et al. 2018). Similarly, heterogeneity of foraging areas modulates individual specialization. In homogeneous environments, individuals tend to behave similarly, likely to match the environment. In contrast, in heterogeneous environments, intraspecific competition and ecological opportunity facilitate divergent habitat specialisation among individuals (Trevail et al. 2021). Animals foraging decisions are also driven by the presence of other species. Landscape of fear (i.e. spatial variation in prey perception of predation risk), territoriality and competition or collaboration for resources may drive individuals to forage in specific areas or times, or to modulate their activity levels (Alatalo et al. 1987, van Overveld et al. 2018, Gaynor et al. 2019). Ultimately, other species may exert attraction and/or repulsion dynamics that deeply affect foraging behaviour (van Gils et al. 2015, Courbin et al. 2022).

Colonial life-style

Some animals exhibit a peculiar form of group living, known as coloniality, in which individuals breed close to each other in densely distributed territories that contain no resources other than nesting sites (Perrins & Birkhead 1983). Living in a colony is challenging, and present a trade-off between costs (e.g. competition for food, nest site and mates, increased risks of transmission of disease and parasites, cannibalism) and benefits (e.g. reduced predation risks and enhanced food finding) (Rolland et al. 1998). Colonial bird species offer a unique study system for investigating the effect of intrinsic and extrinsic drivers of foraging movements. They are central place foragers, meaning that they have to return to a central location (i.e. colony site) after each foraging bout (Orians & Pearson 1979). To maximize foraging efficiency, central place foragers should minimize transit time by selecting close foraging patches (Baird 1991, Elliott et al. 2009). Distant foraging patches will be used only if the net energy gain is higher than at closer patches (e.g. larger or more prey items) (Houston & McNamara 1985, Elliott et al. 2009). However, in colonies, the high density of individuals affects this balance, because of the strong competition when foraging on

shared grounds, often resulting in between and even within colony spatial segregation of foraging grounds (Cairns 1989, Grémillet et al. 2004, Wakefield et al. 2013, Conolly et al. 2018). Moreover, as the breeding season progresses, an area of depleted resources around the colony, the so called 'Ashmole's halo', expands as well (Ashmole 1963), further influencing foraging choices by increasing foraging ranges (Weber et al. 2021). Finally, since colonial bird species could be either terrestrial or marine, they also offer the unique opportunity to study how drivers of foraging decisions act in environments with different baseline ecological and physical rules.

Aim and outline of the thesis

Understanding what drives animals to forage in specific manners in time and space is a complex issue, further complicated by the interplay between intrinsic and extrinsic drivers. However, an in-depth knowledge of the relationship between foraging spatio-temporal choices, individual qualities and the external environment is a key point for predicting animal responses to future environmental changes. Anthropic pressures acting on the natural environment shape resources patchiness and distribution, or affect population composition in term of age and sex ratio (Veech & Crist 2007, Lambertucci et al. 2012), while the ongoing climate change affects physical components (e.g., temperature, rainfall, wind) (Scaife et al. 2012), all of which are expected to alter animals foraging decisions, with potential consequences for populations and communities. Predicting costs and potential shifts in foraging decisions is a key tool to implement effective mitigation or conservation strategies (Grémillet et al. 2006), but in order to make effective predictions, a baseline knowledge of the processes is mandatory. Aim of this thesis is to deepen the understanding of drivers of foraging spatio-temporal choices in some colonial bird species, covering different environments (i.e., terrestrial/marine, temperate/tropical). In the first chapters of the thesis, I focus on the interplay of different intrinsic and extrinsic drivers in different environments. Specifically, **Chapter I** focuses on the foraging tactics of a dimorphic seabird species. Individual tactic adoption was sex-specific and modulated by wind conditions. Indeed, different morphology of males and females results in

different energetic expenditure according to wind conditions, overall leading individuals to adopt the tactic more suitable energetically. Similarly, in **Chapter II,** I contributed to investigate foraging tactic adoption in a terrestrial colonial raptor. Here, tactic adoption was individual-specific but rather flexible, modulated by crosswind intensity and solar radiation, showing that individuals adopt different foraging tactics according to the contingent weather landscape. **Chapter III** focuses on the role of conspecific and heterospecific presence on foraging tactics, using an intriguing study system where two sympatric tropical seabird species (with contrasting population sizes) breed on neighbour islands. The two species, sharing the same trophic niche, adopted different foraging tactics. Likely, competition and different levels of sexual dimorphism and kleptoparassitistic pressure shaped species-specific foraging behaviour. In **Chapter IV,** I investigated the role of an overlooked but important weather component, rainfall intensity, on the foraging behaviour of a tropical seabird unable to waterproof its feathers. Individuals decreased time devoted to foraging and increased time spent perching with increasing rainfall, and flight mode was also affected, with individuals flying slower and at lower altitudes. In **Chapter V** I focused on how food resources can be found in the sea, a complex, dynamic and three-dimensional environment. Using a planktivorous seabird as a model species, I found that dynamic oceanographic features at different spatiotemporal scales, such as eddies, Lagrangian coherent structures and surface currents, interacting with predictable static features, can enhance foraging opportunities. Finally, in **Chapter VI,** I investigated the potential cost of associating to such dynamic structures, that aggregate both food (planktonic organisms) and environmental contaminants (floating microplastics). Indeed, almost half of the sampled individuals had ingested microplastics of different nature. Overall, this thesis provides a glance of how animals, operating with different constraints, manage to successfully forage, contributing to advance our knowledge on processes affecting foraging behaviour and decisions in the natural environment.

CHAPTER I: intrinsic and extrinsic drivers at sea

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

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A Scopoli's shearwater (*Calonectris diomedea*) colony in Spargiotto (La Maddalena Archipelago, IT) seen from above. Picture: A. Benvenuti.

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

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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) intraindividual 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 trips, from fine- to coarse-scale foraging (FF and CF, respectively). FF trips were characterized by lower flight activity, shorter travel distances and more intensive prey-searching behaviour compared to CF trips. Individuals did not consistently perform FF or CF trips. Males were more prone to perform FF trips than females, but both sexes shifted towards CF trips with increasing wind intensity, probably 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 in the niche overlap between the sexes. By adopting flexible, sex-specific foraging tactics, shearwaters probably optimize their energy expenditure during the energy-demanding chick-rearing stage. Our study outlines the importance of both intrinsic and extrinsic factors in shaping interindividual variability in foraging behaviour.

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Foraging behaviour is a key individual trait that is tightly linked to fitness and thus to population processes (Pyke, Pulliam, & Charnov, 1977; Stephens & Krebs, 1986; Weimerskirch, Louzao, de Grissac, & Delord, 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, resource abundance and distribution, predictability and luck can all affect foraging efficiency, making foraging behaviour an extremely plastic trait (Cook, Cherel, & Tremblay, 2006; Montevecchi, Benvenuti, Garthe, Davoren, & Fifield, 2009; Torres & Read, 2009; Weimerskirch, 2007; 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 (Austin et al., 2019; Heithaus & Dill, 2009; Boyd, Punt, Weimerskirch, & Bertrand, 2014), 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, Wiegand, Bartumeus, & Weimerskirch, 2014; Cecere et al., 2020).

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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 challenging, highly dynamic and three-dimensional environments, while rearing their altricial chicks (Weimerskirch, 2007). Moreover, these species commonly breed in large aggregations, resulting in strong intraspecific 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, Radersma, Cole, & Sheldon, 2017). Similarly, different nutritional and energetic requirements, individual specialization and personality can all affect the adoption of different foraging tactics (Patrick, Charmantier, & Weimerskirch, 2013; Louzao et al., 2014; Patrick & Weimerskirch, 2014; Alarcón, Morales, Donázar, & Sánchez, 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 prey, ultimately affecting foraging behaviour (Austin et al., 2019; Gonzalez-Solis et al., 2000; Lewis et al., 2005; Weimerskirch, Le Corre, Ropert-Coudert, Kato, & Marsac, 2006; Trefry & Diamond, 2017; Weimerskirch & Lys, 2000). 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 (Alarcón et al., 2017; Welcker, Steen, Harding, & Gabrielsen, 2009). Intrinsic traits can also vary with age, leading individuals of different age classes to adopt divergent foraging tactics (e.g. Skórka & Wójcik, 2008). In general, older animals are more experienced, resulting in greater foraging efficiency and foraging site fidelity (Woo, Elliott, Davidson, Gaston, & Davoren, 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, Granadeiro, Ramos, Phillips, & Oliveira, 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 seabirds' ability both to reach profitable foraging grounds and to locate and catch prey (Daunt, Afanasyev, Silk, & Wanless, 2006; Lewis, Phillips, Burthe, Wanless, & Daunt, 2015; Tarroux et al., 2016). The flying behaviour of dynamic soaring birds, in particular, is strongly affected by wind (Weimerskirch, Guionnet, Martin, Shaffer, & Costa, 2000; Richardson, Wakefield, & Phillips, 2018). For instance, Murphy's petrels, *Pterodroma ultima*, exploit favourable tail winds to perform long-distance foraging trips (Clay, Oppel, Lavers, Phillips, & Brooke, 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 differences in wing loading between males/females and juveniles/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. Ceia & Ramos, 2015; Patrick et al., 2014), the characterization of intrapopulation variation in foraging tactics and the analysis of their drivers are still poorly explored (Lewis et al., 2015).

We investigated whether foraging tactics differed consistently between 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 Mediterranean Sea. Like other procellariforms, the Scopoli's shearwater is a dynamic soaring bird, taking advantage of winds for travelling over long distances at reduced energetic costs (Paiva, Guilford et al., 2010). 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. Second, we investigated whether the adoption of a given foraging tactic affected spatiotemporal trip characteristics and the exploitation of different environments. Third, 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 both to be outcompeted by males due to their smaller size and to experience lower energy costs of flight. We also expected both sexes to perform foraging trips that involve reaching more distant areas under strong winds at departure, exploiting the energetic benefits of dynamic soaring.

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, Dell'Omo, Russo, Catoni, & Quillfeldt, 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, Rasband, & Eliceiri, 2012) and derived wing loading by dividing body mass by twice the wing area. Birds were sexed using individual or partner vocalizations (Cure, Aubin, & Mathevon, 2009). Three individuals could not be recaptured and their GPS loggers were not retrieved. Eight loggers did not contain any data due to

device failure or to the device being waterlogged. Overall, we obtained data from 44 of 55 individuals recruited for the study.

Following Lascelles et al. (2016), we identified a foraging trip 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 data set 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 26 June 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 chicks were probably 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, Palmer, Oltra, & Bartumeus, 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 (Bennison et al., 2018; Soldatini et al., 2019; de Grissac, Bartumeus, Cox, & Weimerskirch, 2017; Louzao et al., 2014; 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; 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 postprocessing 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'). Owing to some incorrect behavioural assignment from the 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 relabelled 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 relabelled them as 'floating'. These corrections led to relabelling of 1582 GPS locations (out of 48 208; 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 at night (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 1800 hours and within a 10 km buffer from the colony site. Night-time data were excluded because foraging is rare at night (Rubolini et al., 2015), when birds are either flying or floating on the sea surface. Hence, any behaviour performed at night 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 surroundings of the colony site before sunset, as they wait to enter their burrows with complete darkness (Brooke & Cox, 2004).

To identify 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 behaviours 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, Ghazzali, Boiteau, & Niknafs, 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 spatiotemporal 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, Catoni, Maggini, Imperio, & Gaibani, 2013; Cecere, Gaibani, & Imperio, 2014; Péron, Authier, & Grémillet, 2018), namely bathymetry, slope, chlorophyll *a* concentration, sea-surface temperature and mixed layer depth. We obtained bathymetry from the National Oceanic and Atmospheric Administration using R package 'Marmap' (Pante, Simon-Bouhet, & Irisson, 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 trip type on variation in spatiotemporal trip metrics and exploited environment was assessed by means of different linear mixed models, including bird identity as a random intercept effect to account for repeated trips performed by the same individual. Trip metrics and environmental variables were $\log_{10}$

transformed to improve normality of residuals. Mixed models were fitted using R package 'lme4' (Bates et al., 2015).

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 the colony at the time of departure. We accessed wind data through the Global Forecast System of the U.S.A.'s National Weather Service using the 'rWind' R package (Fernández-López & Schliep, 2018; Appendix Table A2). Trip departures were approximated to the nearest 3 h 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 R package 'RNCEP' (Kemp, Emiel van Loon, Shamoun-Baranes, & Bouten, 2012). For the first location of each trip outside a 10 km buffer from the colony, we calculated side wind (flow component perpendicular to the direction of movement) and tail wind (flow parallel along the direction of movement) intensity according to equations in Kemp et al. (2012). We used the absolute value of side wind and hereafter we refer to side wind and tail wind intensity as 'side wind' and 'tail wind', respectively. We modelled the probability of performing a given trip type by means of a binomial generalized linear mixed model (GLMM), with trip type as the binary dependent variable, bird identity as a random intercept effect, and sex, islet, wind intensity, tail wind and side wind as fixed effects. Wind intensity at the colony, tail wind and side wind were weakly correlated (wind intensity–tail wind: $r = 0.05$; wind intensity–side wind: $r = -0.02$; side wind–tail wind: $r = -0.37$) and could therefore be included simultaneously in the model. The initial model included all two-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}), using the observation level variance obtained via the delta method (Nakagawa, Johnson, & Schielzeth, 2017). Significance of R_{adj} was assessed by a likelihood ratio test (Zuur, Ieno, Walker, Saveliev, & Smith, 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, Video S1 in the Supplementary Material). Trips lasted on average 33 h (± 33 SD), spanning between 1 and 11 days. Overall, we obtained a mean of six foraging trips per individual (± 3 SD; range 1–10). Nine of 30 indexes suggested the presence of two clusters in the data set, 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) 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 versus FF: extensive search: 35.2 ± 12.4% versus 24.1 ± 8.0%; intensive search: 14.3 ± 7.0% versus 23.1 ± 11.1%; relocation: 34.8 ± 12.1% versus 18.6 ± 8.0%; floating: 15.5 ± 7.8% versus 34.1 ± 11.7%). These two trip types probably represented two main foraging tactics occurring
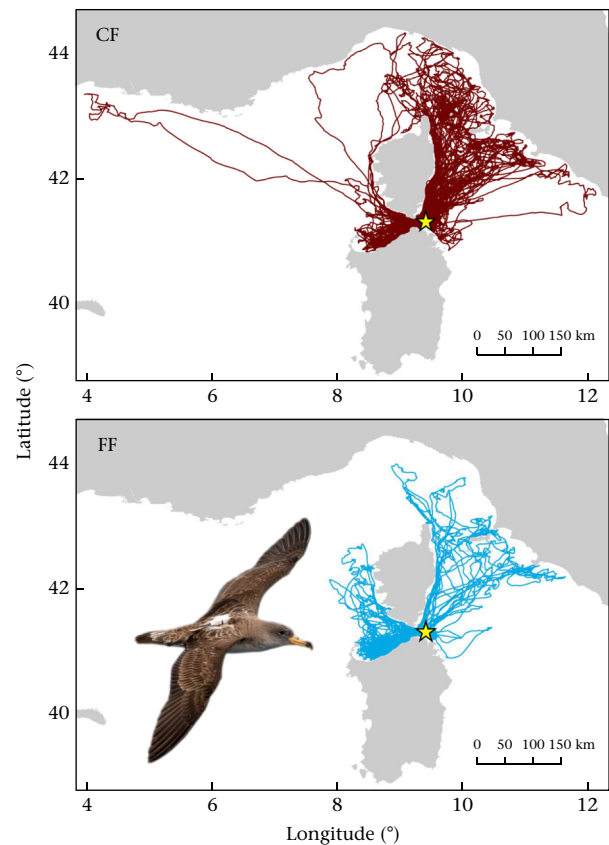

Figure 1. Maps of coarse-scale (CF) and fine-scale (FF) foraging trips. The sample size is 136 CF trips and 129 FF trips. The colony location is shown as a star. Credit for picture of GPS-tagged Scopoli's shearwater: M. Ugo.

in our study population. More details on the clustering procedure are shown in Appendix Fig. A3.

Supplementary data related to this article can be found at https://doi.org/10.1016/j.anbehav.2020.05.014.

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, deeper waters and steeper slopes compared to the other tactic (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 ($R_{adj} = 0$, $\chi^2_1 = 0$, $P = 1$), indicating a high behavioural plasticity. Sex, side wind and wind intensity at the 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 side wind at departure, 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 tail wind or islet effects were detected (Table 2).
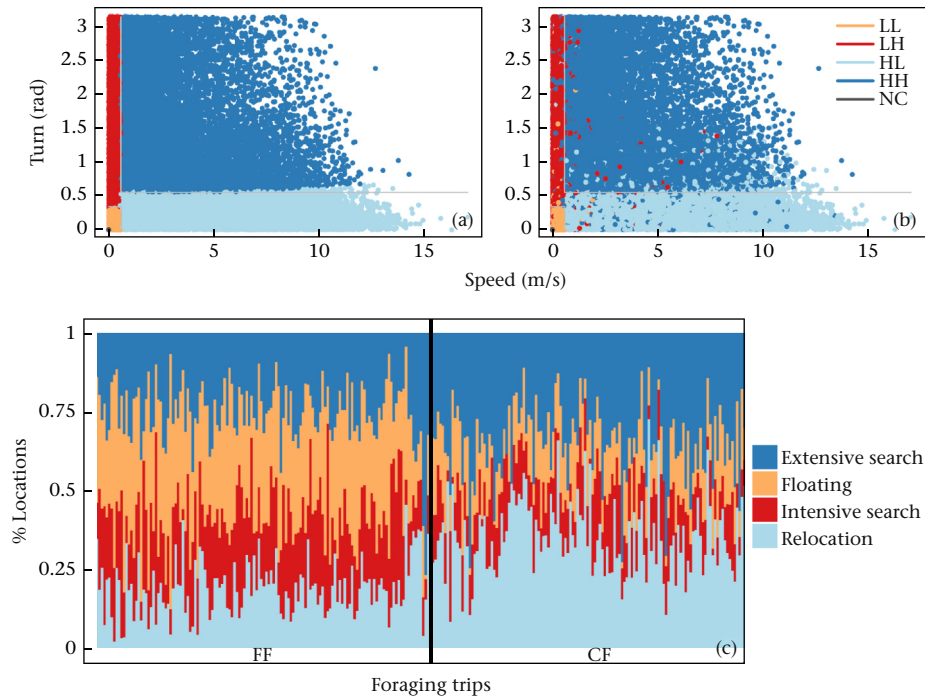
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Figure 2. Scatterplot of GPS locations in relation to turning angle and speed from EMbC algorithm, and percentage of estimated behaviours for each foraging trip. Behavioural modes (different colours) identified by the EMbC algorithm (a) before and (b) after the postsmoothing 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: unclassified data points, e.g. the last point of a trajectory. (c) 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).

DISCUSSION

We investigated intra- and interindividual variability in the foraging behaviour of a sexually size dimorphic seabird. Based on behavioural modes derived by movement data and subsequent clustering of behaviours at the trip level, we identified different types of foraging trip. These trip types, which we defined as coarse-scale (CF) and fine-scale (FF) foraging trips, probably 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 were characterized by high frequency of intensive search and floating on the sea surface. When performing CF trips, birds reached more distant foraging grounds and covered greater distances compared to FF trips. However, trip duration did not differ between trip types, indicating that birds performing foraging trips to more distant foraging grounds did not stay away from the nest for a longer time than those remaining around the colony (e.g. Appendix Fig. A1). Different trip types led individuals to explore areas with 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 behavioural gradient. Nevertheless, behavioural differences between trip types were substantial and resulted in huge differences in spatiotemporal trip metrics and exploited environments. We

Table 1
Effects of trip type (coarse-scale, CF, versus fine-scale, FF) on spatiotemporal trip metrics and environmental characteristics of exploited areas

Variables	CF trips ($N = 136$)	FF trips ($N = 129$)	χ^2	df	P	Marginal R^2	Conditional R^2
Spatiotemporal							
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
Chlorophyll a (mg/m^3)	0.045 ± 0.005	0.043 ± 0.003	9.13	1	0.002	0.04	0.12
Sea-surface temperature (°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 spatiotemporal 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 & Schielzeth, 2013). Values are mean ± SD.
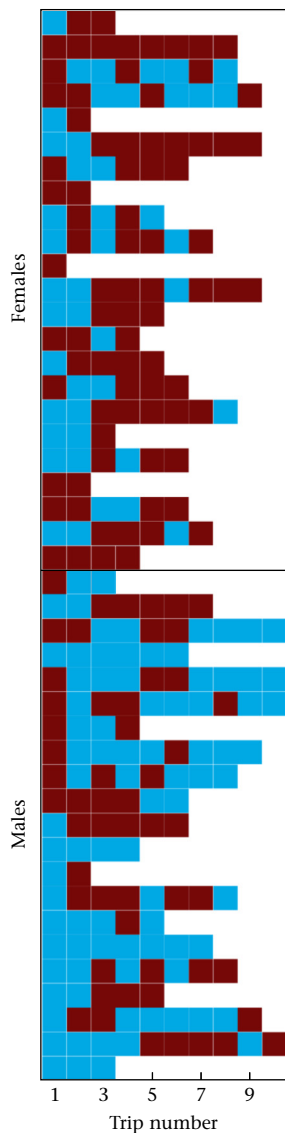
Figure 3. Sequences of coarse-scale (CF) and fine-scale (FF) foraging trips performed by individual shearwaters. Different lines show the sequence of consecutive foraging trips of each individual (trip number). Individuals were grouped by sex (females: $N = 125$ trips and 23 individuals; males: $N = 140$ trips and 21 individuals). Red: CF trips; blue: FF trips.

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	$\beta \pm SE$	χ^2	df	P	Effect size r
Sex	1.02 ± 0.27	14.75	1	< 0.001	0.24
Side wind	-0.34 ± 0.10	12.67	1	< 0.001	0.24
Tail wind	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 a 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 r obtained from the 'r2glmm' R package (Jaeger, Edwards, Das, & Sen, 2017).

thus believe that different trip types may represent different foraging tactics, and that they reflect a biologically meaningful distinction of foraging modes shared by individuals of our study population.

Overall, birds exploited areas with 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 the surface (Piatt et al., 2006). On the other hand, with FF trips birds on average frequented 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 (Cecere et al., 2014; Navarro & González-Solís, 2009), 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, Nunes, Silva, & Furness, 1998), the percentage of long trips (> 4 days) was very low in our data set (1.9%), with most birds performing short trips only. This may help explain the lack of differences in trip duration between CF and FF trips, even though, 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 procellariforms (Paiva, Pereira, Ceia, & Ramos, 2017; Weimerskirch & Lys, 2000) and can originate from the interplay between different energetic constraints linked to size and intersexual competition for resources (Pinet, Jaquemet, Phillips, & Le Corre, 2012). However, many previous studies on the foraging behaviour during breeding of *Calonectris* shearwaters failed to document sex differences (Navarro & González-Solís, 2009; Ramos, Granadeiro, Phillips, & Catry, 2009; Paiva, Geraldes et al., 2010; Paiva, Xavier et al., 2010; Cecere et al., 2013). This could be partly because sex differences in foraging behaviour may emerge only under specific environmental conditions (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 covaries positively with wing loading (Hertel & Ballance, 1999; Shaffer & Costa, 2001). This may explain why males mainly performed foraging trips characterized by less 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 resting and/or foraging by using the sit-and-wait prey-searching technique (Cianchetti-Benedetti et al., 2018; Pianka, 1966). 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 area selection during the incubation and chick-rearing stages, 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 the chick-rearing stage (Campioni et al., n. d.) may suggest that males and females target the same prey items, sharing
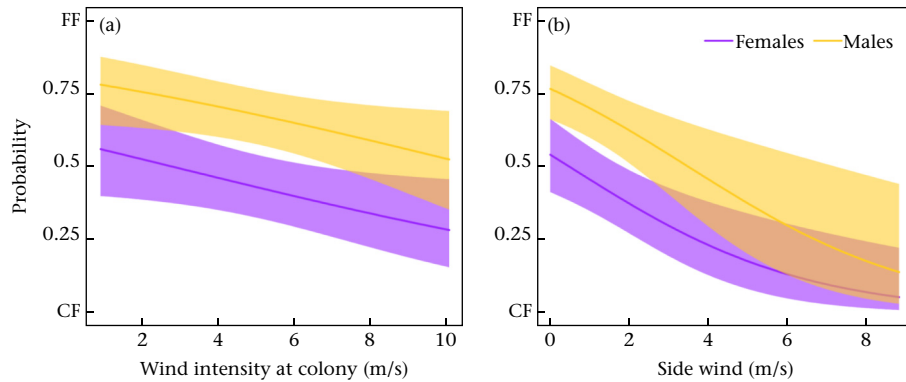
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Figure 4. Probability of performing fine-scale (FF) or coarse-scale (CF) foraging trips according to (a) wind intensity at the colony site or (b) a side wind at departure. Predicted probabilities (bold lines) and 95% confidence intervals (shaded areas) for each sex were derived from the fitted binomial GLMM model reported in Table 2.

the same trophic niche and implying that some 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 near the colony, where they might outcompete females.

On top of this sexual difference in foraging behaviour, the likelihood of performing CF trips increased in both sexes as wind intensity and side wind at trip departure increased. CF trips allowed birds to reach more distant foraging areas, probably exploiting the energetic advantages of dynamic soaring. Indeed, with a side wind, dynamic soaring birds may travel with small energetic costs using an S-shaped dynamic soaring manoeuvre (Weimerskirch et al., 2000; Wakefield, Phillips, & Matthiopoulos, 2009; Paiva, Guilford et al., 2010; Spivey, Stansfield, & Bishop, 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 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, Granadeiro, Padget, & Catry, 2020). Overall, our results suggest that Scopoli's shearwaters can flexibly adapt their foraging behaviour according to the winds, 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). Intersexual differences in foraging behaviour could be a way of expanding the ecological niche of breeding pairs and reducing intersexual 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).

Acknowledgments

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Appendix

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)	0.45 ± 0.03	0.52 ± 0.04	3.84	0.002

Mean ± SD values are reported. Sex differences were assessed by a Student t test. Wing loading was measured for a subsample of individuals only (six females, 11 males).

Table A2
Details of the environmental variables considered for this study

Variable	Unit	Spatial resolution	Temporal resolution	Data set details
Bathymetry	m	1 km	/	ETOPO1
Slope	°	1 km	/	ETOPO1
Chlorophyll *a*	mg/m³	4 km	1 day	MEDSEA_ANALYSIS_FORECAST_BIO_006_014
Sea-surface temperature	°C	4 km	1 day	MEDSEA_ANALYSIS_FORECAST_PHY_006_013
Mixed layer thickness	m	4 km	1 day	MEDSEA_ANALYSIS_FORECAST_PHY_006_013
Wind intensity (10 m)	m/s	50 km	3 h	NOAA/NCEP (GFS) Atmospheric Model collection
Wind direction (10 m)	°	50 km	3 h	NOAA/NCEP (GFS) Atmospheric Model collection

Data sets 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
Chlorophyll *a*	0.046 ± 0.016	0.13
Sea-surface temperature	26.17 ± 0.89	0.27
Mixed layer depth (m)	12.05 ± 0.80	0.11

Mean ± SD was calculated for each variable based on all GPS locations ($N = 49\ 790$) 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.
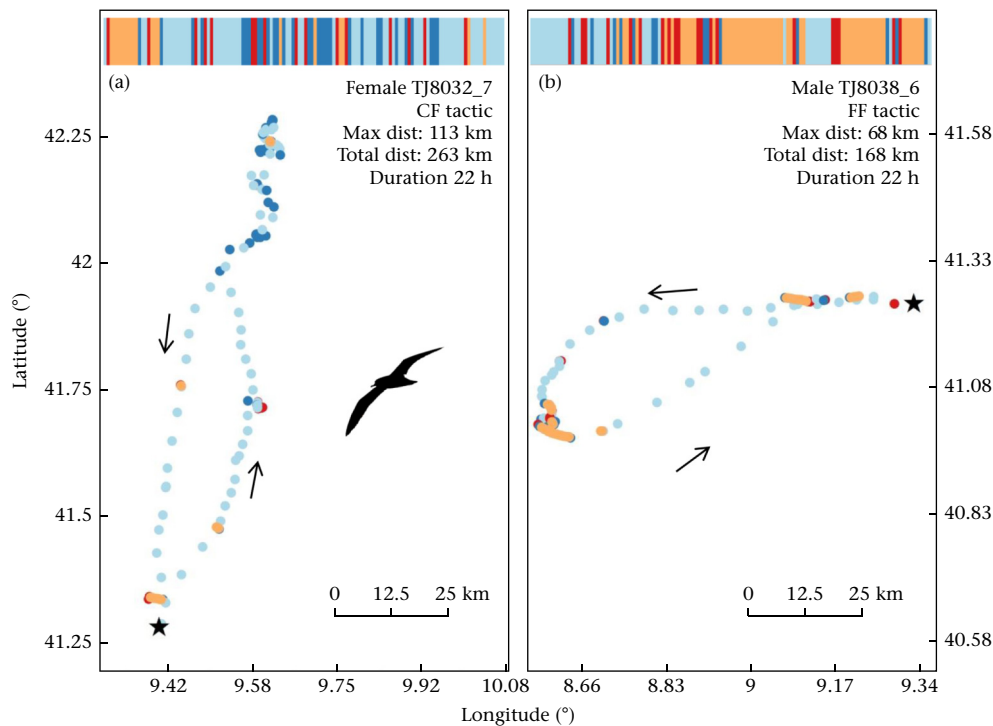
Figure A1. Representative examples of foraging trips with each GPS location coloured according to its assigned behaviour. Two foraging trips, identified as (a) coarse-scale (CF) and (b) fine-scale foraging (FF), performed by two individuals during the chick-rearing stage are shown. Colours represent 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.
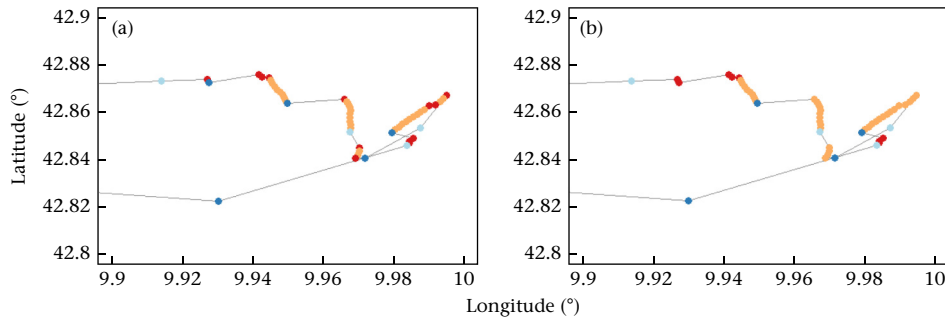
Figure A2. Representative examples of a segment of foraging trip (a) before and (b) after manual correction for behavioural state assignment. Behaviours are shown with different colours: floating (orange), intensive search (red), relocation (light blue) and extensive search (dark blue).
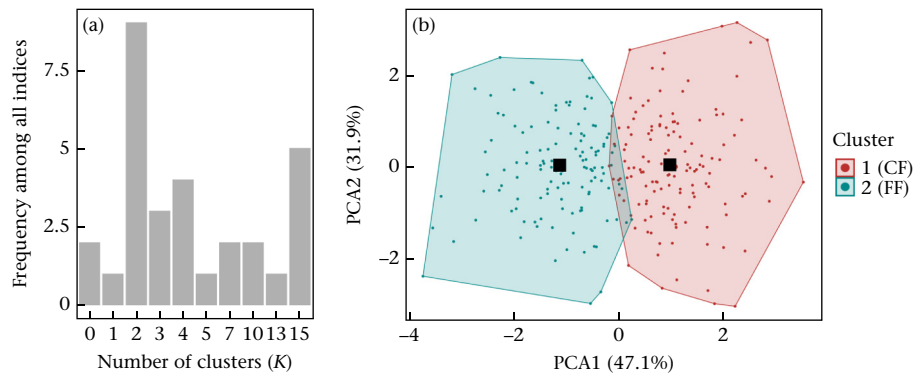

Figure A3. Choice of the optimal number of clusters and principal component plot of *K*-means clusters. (a) Graphical output of the NbClust procedure for estimating the optimal number of clusters (*K*), indicating $K = 2$ as the most frequent number of clusters proposed by the 30 indexes considered. (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 79% of the observed variance).
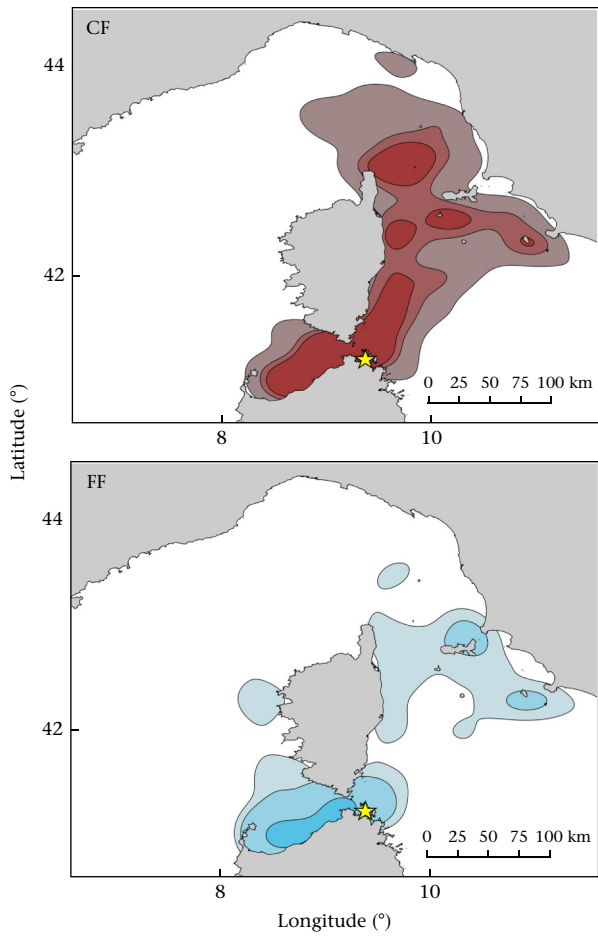
Figure A4. Kernel density estimate (KDE) of GPS locations from different trip types. Fixed KDEs (50, 70 and 90% contours) were calculated for coarse-scale (CF) and fine-scale (FF) foraging trips separately. The colony location is shown as a star. The covariance bandwidth matrix was obtained using the least-square cross-validation estimator with R package 'ks' (Duong, 2007). Projected coordinates were used to prevent spatial biases.

CHAPTER II: intrinsic and extrinsic drivers on land

Inter-individual differences in foraging tactics of a colonial raptor: consistency, weather effects, and fitness correlates

Movement Ecology 8(1): 1-14

Gravine, in the outskirt of Matera (IT), are one of the typical lesser kestrel (*Falco naumanni*) foraging grounds.

Movement Ecology

Inter-individual differences in foraging tactics of a colonial raptor: consistency, weather effects, and fitness correlates

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Abstract

Background: Consistent inter-individual differences in behavioural phenotypes may entail differences in energy efficiency and expenditure, with different fitness payoffs. In colonial-breeding species, inter-individual differences in foraging behaviour may evolve to reduce resource use overlap among conspecifics exploiting shared foraging areas. Furthermore, individual differences in foraging behaviour may covary with individual characteristics, such as sex or physiological conditions.

Methods: We investigated individual differences in foraging tactics of a colonial raptor, the lesser kestrel (*Falco naumanni*). We tracked foraging trips of breeding individuals using miniaturized biologgers. We classified behaviours from GPS data and identified tactics at the foraging trip level by cluster analysis. We then estimated energy expenditure associated to each tactic from tri-axial accelerometer data.

Results: We obtained 489 foraging trips by 36 individuals. Two clusters of trips were identified, one (SF) characterized by more static foraging behaviour and the other (DF) by more dynamic foraging behaviour, with a higher proportion of flying activity and a higher energy expenditure compared to SF. Lesser kestrels showed consistent inter-individual differences in foraging tactics across weather condition gradients, favouring DF trips as solar radiation and crosswind intensity increased. DF trips were more frequent during the nestling-rearing than during the egg incubation stage. Nestlings whose tracked parent was more prone to perform DF trips experienced higher daily mass increase, irrespective of nestling feeding rates.

Conclusions: Our study provided evidence that breeding lesser kestrels flexibly adopted different foraging tactics according to contingent weather landscapes, with birds showing consistent inter-individual differences in the tendency to adopt a given tactic. The positive correlation between the tendency to perform more energy-demanding DF trips and nestling growth suggests that individual differences in foraging behaviour may play a role in maintaining key life-history trade-offs between reproduction and self-maintenance.

Keywords: Dynamic foraging, Behavioural plasticity, Birds of prey, *Falco*, Foraging in flight, Foraging strategy, ODBA, Sit-and-wait

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Background

Inter-individual differences in behavioural phenotypes, that are consistent over time and across environmental contexts, have been frequently documented in animals [57]. Individuals can also consistently differ in how they modulate specific behaviours in accordance to spatial and temporal environmental gradients, the so-called contextual plasticity [64]. Ultimately, inter-individual differences in behavioural phenotypes and in contextual plasticity may be associated with fitness differences among individuals [63], with far-reaching ecological and evolutionary consequences [16]. For instance, individual differences in foraging behaviour may favour foraging specialization, resulting in a reduction of intraspecific competition by limiting resource use overlap [3, 8, 46].

In colonial species, where conspecifics gather in groups to reproduce close to each other and exploit shared foraging areas [11, 38], resource depletion around colony sites commonly occurs [4, 22]. Such depletion may favour the evolution and maintenance of individual foraging differences, which may be important in compensating the negative fitness effects of intraspecific competition. Indeed, individual differences in dietary preferences have been documented in several colonial vertebrates, including birds (e.g. [12]), pinnipeds (e.g. [14]) and terrestrial mammals (e.g. [15]). Individual foraging differences can also result in inter-individual differences in foraging tactics [5, 9, 17, 29], which we define as a distinguishable combination of behavioural patterns (i.e. multiple behaviours) shared by different individuals to search for food (similarly to [17, 39]). In northern gannets *Morus bassanus*, the analysis of both food boluses and blood isotopes, combined with the analysis of at-sea foraging behaviour, has uncovered individual differences in foraging tactics, with some birds exploiting consistently and more frequently than others fishing vessels discards [65]. In the same species, the analysis of foraging trips of birds breeding in two large colonies revealed consistent individual preferences in foraging areas during the nestling-rearing stage, but also large inter-individual differences in prey searching behaviour along environmental gradients [48]. Within-population differences in foraging behaviour can also be unrelated to individual preferences and rather arise from individual characteristics, such as sex [49], age [26], reproductive stage [25], personality [50] or physiological status differences [2].

The lesser kestrel *Falco naumanni* is a small (ca. 120 g) colonial diurnal raptor, which mostly breeds in holes and crevices of buildings in towns and cities, and forages in farmland areas surrounding breeding sites [11]. The species shows flexible foraging behaviour, whereby both flight and hunting mode vary in accordance to weather conditions: energy-saving soaring-gliding flight is more frequently adopted than energy-expensive flapping flight when solar radiation is high, and perch-hunting is more frequently used than flight-hunting when both wind speed and solar radiation are low [30]. However, it is as yet unknown whether individuals consistently differ in their foraging tactic across weather condition gradients, or whether individuals differ in their behavioural response to weather conditions.

In this study, we characterized the foraging tactics adopted by breeding lesser kestrels that were tracked by miniaturized biologgers (including both a GPS and a tri-axial accelerometer) across multiple foraging trips. We classified behaviours from movement data and identified tactics at the foraging trip level based on the combination of different behaviours occurring within each trip, while energy expenditure associated to each tactic was estimated by accelerometer data. According to previous knowledge about lesser kestrels foraging ecology [30], we expected birds to adopt two main foraging tactics: a more energy-demanding tactic whereby birds mainly search for prey while flying within a foraging trip (dynamic foraging, DF), and a less energy-demanding tactic, resulting from trips with prolonged perching while waiting for prey detection (static foraging, SF).

We then investigated 1) whether there were inter-individual differences in the tendency to adopt a given foraging tactic across weather condition gradients (solar radiation, rain, wind), expecting birds mainly to adopt the DF tactic whenever conditions are favourable for soaring-gliding, i.e. with high solar radiation [30] and wind assistance (tailwind or crosswind) at trip departure (e.g. [35]). Furthermore, we explored 2) whether the tendency to adopt a specific tactic was explained by individual characteristics, such as sex and breeding stage (incubation or nestling-rearing). Foraging behaviour of lesser kestrels can indeed vary markedly between males and females and between the incubation and nestling-rearing stages [31]. Finally, we investigated 3) the association between the tendency to perform a specific tactic and fitness-related traits. We expected the more energy-demanding DF tactic to be adopted preferentially by individuals in better body condition and to be associated with improved fitness, as estimated by higher breeding success and larger nestling body mass increase.

Methods

Target species, study area and general field methods

The lesser kestrel is a sexually dimorphic species, females being ca. 15% heavier than males [54]. Females lay up to 5 eggs that both parents incubate for ca. 30 days. After hatching, both parents feed the nestlings until fledging, which takes place at 35–40 days of age. The study was carried out in the city of Matera (southern Italy; 40°39′ N, 16°36′ E), hosting a colony of ca. 1000

breeding pairs [37]. We relied on nest-boxes placed on terraces of buildings in the old town, which were monitored 2–3 times per week to obtain detailed data about reproductive stage (laying date, incubation, hatching, nestling body mass at ca. 7 and ca. 14 days after hatching of the first egg) [53, 54]. Breeding individuals were captured by hand within nestboxes during the late incubation and early nestling-rearing stage. Upon capture, birds were individually marked, and body mass (using an electronic scale, accuracy 0.1 g) and keel length (using a dial calliper, accuracy 0.1 mm) were recorded.

GPS deployment and identification of foraging trips

We equipped 36 breeding lesser kestrels (13 females and 23 males) with Axy-Trek biologgers, including a GPS and a tri-axial accelerometer (TechnoSmArt Europe S.r.l., Rome, Italy), using a backpack Teflon harness. Devices (including the harness) weighed between 5.9 and 7.2 g, on average accounting for 4.5% of body mass (range: 3.8–5.5%) (hereafter, relative load of device). The accelerometer was set to record data at 25 Hz and the GPS to record one position per minute from 05:00 to 21:00 local time (i.e. ca. 20 min before sunrise and ca. 30 after sunset; devices were switched off during night-time to preserve battery power). Birds were tagged in the morning and devices were set to start the following day in order to collect data when the tagged birds were likely inured to the device. After 2–5 days, birds were recaptured and the device was removed. Movement data were collected during June 1–20 of the breeding seasons 2016, 2017 and 2018, when pairs were in the late incubation or early nestling-rearing stage. Only one member of each pair was tracked and none of the birds was tagged more than once.

Foraging trips were identified as those tracks starting and ending within a 50-m buffer around the nest or the roosting site, and heading to the rural surroundings, by means of ESRI ArcMap 10.2.1. Since the devices switched on at 05:00 local time, in some cases the first position of the first foraging trip of the day was already in the countryside surrounding the town; when the distance between such position and the nesting site was > 2 km, the foraging trip was discarded and not included in any analysis. We did not consider as foraging trips all those excursions which covered the urban area only, identified by means of the 2012 CORINE Land Cover (CLC) map (codes 111 and 112, respectively continuous and discontinuous urban habitat), because birds generally do not forage in the urban area (authors' pers. obs.). Each trip was classified as occurring during incubation if only eggs were present in the nest of the target individual on the date when the foraging trip was performed, or as occurring during the nestling-rearing stage if at least one nestling was present in the nest on the date when the trip was performed.

Identification and characterization of foraging tactics

To identify behaviours adopted by lesser kestrels during foraging trips, we applied the Expectation Minimization binary Clustering (EMbC) algorithm to GPS data by means of the R package "EMbC" [27]. The EMbC is a classification algorithm based on maximum likelihood which assigns a behavioural mode to each GPS position according to instantaneous velocity and turning angle between successive positions. The algorithm assigns positions to four behavioural modes (see Fig. S1): 1) low velocity and low turns, which we interpreted as 'perching' behaviour (see Fig. S2); low velocity and high turns, representing 'intensive search'; 3) high velocity and low turns, representing 'relocation'; 4) high velocity and high turns, representing 'extensive search' [27, 39]. As the EMbC algorithm disregards the temporal information, we accounted for the possible incorrect labelling of positions when a long-term predominant behavioural mode occurred by applying a post-processing smoothing using the *smth()* function (with default parameters) (see [27]; and Fig. S1).

To identify the foraging tactics, we applied a cluster analysis to the percentage of the four behaviours occurring in each trip [39]. Cluster analysis was performed with a K-means procedure by means of the R package "stats" [56]. The optimal number of clusters was assessed by means of the *NbClust* procedure from the R package "NbClust" [13], which computes 30 indexes for determining the optimal number of clusters, including the option of no clustering (one cluster only). It then suggests the best number of clusters based on the majority consensus rule. As the *NbClust* procedure identified two clusters as the best number, we applied the K-means algorithm with K = 2 over 10,000 iterations.

We then assessed whether the two identified trip clusters (trip types, hereafter) affected variation in spatio-temporal trip descriptors (trip duration, trip length, maximum distance from the nest site and tortuosity, i.e. ratio between total trip length and the maximum distance from the nest site [7];) by means of linear mixed models (LMMs), including individual identity as a random intercept effect to account for non-independence of trips performed by the same individual.

Based on tri-axis accelerometer data, we calculated the overall dynamic body acceleration (ODBA) for each foraging trip, smoothing total acceleration over 1 s [59, 68]. ODBA is considered a proxy of energy expenditure in birds [23, 68]. It positively correlates with O_2 consumption rates and CO_2 production in great cormorants (*Phalacrocorax carbo*) [68] and with heart rate in two vulture species (*Gyps fulvus* and *G. himalayensis*) [20].

We investigated whether energy expenditure was affected by trip type by means of a LMM including individual identity as a random intercept effect. Accelerometer data were available for 34 out of 36 tracked birds.

LMMs were fitted using the *lmer* function of the R package "lme4" [6]. Residuals did not significantly deviate from a normal distribution.

Environmental factors affecting foraging tactics

To investigate the effect of environmental conditions on the tendency to perform different trip types, we first associated to each trip the following variables: 1) solar radiation (W/m^2) at departure, which seems to be determinant for performing soaring-gliding flight [30]; 2) presence of rain during the trip (hereafter, 'presence of rain'; 0 = rain absent; 1 = rain present), which we hypothesized may negatively affect the likelihood of performing foraging in flight. Rain was not considered as a continuous variable since it occurred in 14% of foraging trips only, and considering it as continuous would have resulted in a very skewed variable with an excess of zeroes; 3) tail-wind (TWC) and 4) cross-wind components (CWC), both of which are known to affect movement activity in soaring-gliding raptors [35]. To control for potential differences in foraging behaviour between foraging habitats, we also computed 5) the percentage of positions in arable lands (the main habitat used for foraging, see below) for each trip (hereafter, 'time in arable lands'). Nestbox identity was not included in the models since all tagged birds belonged to different nests, with the exception of two nestboxes which were sampled twice in different years but they were occupied by different individuals.

Solar radiation and rain data were recorded at a weather station located at 8 km from the nest sites (Matera, Contrada Matinelle, 40°41′ N; 16°31′ E). Wind data (speed and direction) were recorded at a different weather station, located at 15 km from the nest sites (Grottole 40°37′ N; 16°26′ E). All weather data were recorded at hourly intervals, and were associated to the GPS position that was closest in time.

TWC and CWC were calculated for each trip based on the mean value of wind speed and direction (WS and WD respectively) at time of departure and at time of returning, and the direction of the trip (TD), as follows:

$$TWC = WS \times \cos(TD - WD)$$

$$CWC = | WS \times \sin(TD - WD) |$$

TD, which we assumed to reflect the direction of the goal area, was calculated as the angle between the N-S axis (directed northwards) and the position of the farthest point of the trip from the nesting site. Positive

TWC values imply that a bird flew globally with tail-wind on its way out of the colony towards the foraging grounds, whereas negative TWC values indicate the opposite (outgoing flights with headwinds). Large CWC values mean that a bird flew on average with high side-wind during the foraging trip.

To calculate the proportion of time spent in arable lands during each foraging trip, we assigned all GPS positions, excluding those identified as relocation by the EMbC, to the corresponding habitat type from CLC by means of ESRI ArcMap 10.2.1. We pooled together those CLC habitat types that were similar in habitat and structure, obtaining 6 habitat classes: artificial landscape (continuous and discontinuous urban fabric, infrastructures, industrial areas), arable lands, permanent crops (tree plantations, olive groves, vineyards), grasslands (pastures and natural grasslands), heterogeneous agricultural areas (annual crops associated with permanent crops, complex cultivation patterns, agro-forestry areas), and wooded areas (forests and bushes). Each trip was then characterized by the percentage of positions occurring in each habitat class (time spent in each habitat). While foraging, birds spent most of the time in arable lands (median 70.6%, 25th – 75th percentiles: 23.3 – 94.1%), and time in arable lands was negatively correlated with time in grasslands ($r = -0.69$, $n = 489$ trips), the second most frequently used habitat (median 0.0%, 25th – 75th percentiles: 0.0 – 25.0%).

The probability to perform a given trip type (0 = SF, 1 = DF) was modelled by means of binomial generalised linear mixed models (GLMMs), with solar radiation, TWC, CWC, and presence of rain as fixed predictors, controlling for time in arable lands, breeding stage, sex and sampling year. Individual identity was included as a random intercept effect to control for non-independence of prey searching behaviour performed by the same individuals. All predictors were standardized (mean = 0 and SD = 1). Because of size and morphological differences, sexes may differ in their behavioural response to environmental variables; we hence included in the initial model all two-way interactions between sex and each weather variable (solar radiation, TWC, CWC, and presence of rain). The final binomial GLMM was obtained after removing weak (95% CI of parameter estimates intersecting 0) interactions in a single step. GLMMs were not overdispersed (φ always < 1.05).

Individual differences in foraging tactics and their correlates

The random intercept effect of the final binomial GLMM describes the extent to which individuals preferentially perform different trip types (i.e. whether foraging tactics can be regarded as an individual-specific trait). Intra-individual consistency of the probability of

performing DF trips was estimated as the proportion of variance explained by the random intercept effect, accounting for variance explained by fixed effects (adjusted repeatability, R_{adj}). R_{adj} was computed using the observation-level variance obtained via the delta method [45] and significance was assessed by a likelihood ratio test [69].

To investigate individual differences in the behavioural response to environmental gradients (behavioural reaction norms), which represent the degree of contextual plasticity (see [18]), we ran four binomial GLMMs with trip type as the binary dependent variable and sex, breeding stage, sampling year and one weather variable (solar radiation, presence of rain, TWC, or CWC) at a time as predictors, while including an individual-level random slope effect for that weather variable. Random slope models were fitted by including in binomial GLMMs one weather variable at a time to avoid model overparametrization and lack of convergence [60]. Significance of the random slope effect was tested by a likelihood ratio test [69]. Models were not overdispersed (ϕ always < 1.05). All binomial GLMMs were fitted using the *glmer* function of the R package "lme4" [6].

The individual tendency to perform DF trips was expressed as the individual-level random intercept estimate (hereafter, individual intercept) from the final binomial GLMM, higher values implying a stronger tendency to perform DF trips. Individual intercepts were computed as the conditional modes of the random effect evaluated at the parameter estimates (a.k.a. Best Linear Unbiased Predictors in LMMs). Uncertainty of individual intercepts was estimated by a simulation approach ($n = 10,000$ simulations; see [36]), and expressed as the SD of the simulations, using the *REsim* function of the R package "merTools" [36].

We tested the associations between the individual tendency to perform DF trips by the tracked parent and several fitness proxies, namely body condition of the tracked individual, its breeding success, and the daily body mass increase (DBMI) of its nestlings during the early nestling-rearing stage. We also investigated the association of the tendency to adopt the DF tactic with feeding frequency (number of foraging trips/h during the tracking period) and with the relative load of device (mass of biologging device relative to body mass). The latter association was tested (separately for males and females) to assess the possible effects of device load on foraging behaviour. All these associations were tested by computing weighted correlation coefficients (r_w), where the weighting variable was the inverse of the SD of the individual tendency. Such weighting should at least partly account for uncertainty of conditional modes, as advocated by Houslay and Wilson [32]. Weighted correlation coefficients were computed using the *weightedCorr*

function of the R package "wCorr" [24]. Significance of r_w was tested by randomization, randomly shuffling variables 9999 times, and computing the probability of observing a more extreme value than the observed one [41].

To estimate body condition of tracked birds, we computed the scaled mass index (hereafter, SMI) (body mass scaled by a skeletal trait, in our case keel length [51]). SMI was calculated as in Podofillini et al. [54]. To remove heterogeneity in SMI related to sex (see [54]), we computed the residuals of a linear model of SMI with sex as a predictor (hereafter, residual SMI).

The breeding success of the tracked birds was estimated as the fate of the brood, which was either coded as failed (0 = no nestlings alive at 14 days) or successful (1 = at least one nestling alive at 14 days after hatching of the first egg).

Nestling DBMI was computed as the mean of the daily relative body mass increase among all nestlings of a brood k between ca. 7 (mean ± SD = 6.6 ± 1.8 days) and ca. 14 days (mean ± SD = 14.7 ± 1.7 days) from hatching, as follows:

$$\text{DBMI}_k = \frac{1}{m} \times \sum_{j=1}^{m} \frac{1}{i} \times \left[\frac{\text{BM}_{j,\text{day}(n+i)} - \text{BM}_{j,\text{day}(n)}}{\text{BM}_{j,\text{day}(n)}} \right]$$

where BM is body mass of nestling j, n is the day post-hatching at which the first record of BM was taken and i is the number of days elapsed between the first and second measure of BM of a nestling, m is the brood size at $\text{day}_{(n+i)}$ (range: 1–4). We assumed that nestling DBMI denoted the ability of parents to foster the growth of their offspring, and that large value of DBMI could be considered as a proxy for high parental investment and high nestling fitness. To remove heterogeneity among sampling years and different brood sizes on nestling DBMI, we computed the residuals from a linear model of nestling DBMI including year and brood size at day $n+i$ as predictors (hereafter, residual nestling DBMI). The correlation test was based on data from 22 parents whose eggs hatched and whose offspring were alive at 14 days from hatching of the first egg.

Feeding frequency was computed only for birds which were tracked during the nestling-rearing stage ($n = 14$). To remove heterogeneity among sampling years, sexes, and variation in brood size on feeding frequency (see [19, 31]), we computed residuals from a linear model of feeding frequency including year, sex, and brood size during the tracking days as predictors (hereafter, residual feeding frequency).

All analyses were ran on R ver 3.6.2 [56].

Cecere *et al. Movement Ecology*   (2020) 8:28

Page 6 of 13

Results

Identification and characterization of foraging tactics

We obtained 489 foraging trips from 36 breeding birds, the mean value being 14 trips (± 11 SD) per individual, ranging from a minimum of 1 to a maximum of 45 trips per individual (see also Table 1). The cluster analysis identified two clusters of trips, which we interpreted as two main foraging tactics (Fig. 1). The first cluster included trips characterized by high frequency of perching (mean ± SD proportion over all GPS positions of a trip: 0.53 ± 0.17), low frequency of intensive (0.15 ± 0.01) and extensive search (0.04 ± 0.05), and lower relocation positions (0.28 ± 0.12) compared to the other cluster. This cluster of trips was likely reflecting a relatively more SF tactic (Table 2). The second cluster was characterized by trips with a more dynamic and exploratory behaviour, with birds mostly searching for food while flying (perching: 0.07 ± 0.09; intensive search: 0.26 ± 0.16; extensive search: 0.07 ± 0.07; relocation: 0.60 ± 0.01), likely reflecting a relatively more DF tactic (Table 2). On average, SF trips lasted longer and were associated to lower values of ODBA compared to DF ones, whereas all other trip descriptors were not markedly different (Table 2). Figure 2 shows representative examples of DF and SF foraging trips performed by a single individual during both the incubation and the nestling rearing stages. Differences in the temporal sequence of behaviours clearly highlight that DF trips were characterized by more time actively spent searching for food, whereas SF trips showed prolonged perching periods (Fig. 2). There was no apparent spatial differentiation in exploited areas between SF and DF trips (Fig. 3).

Environmental factors affecting foraging tactics and individual differences in foraging behaviour
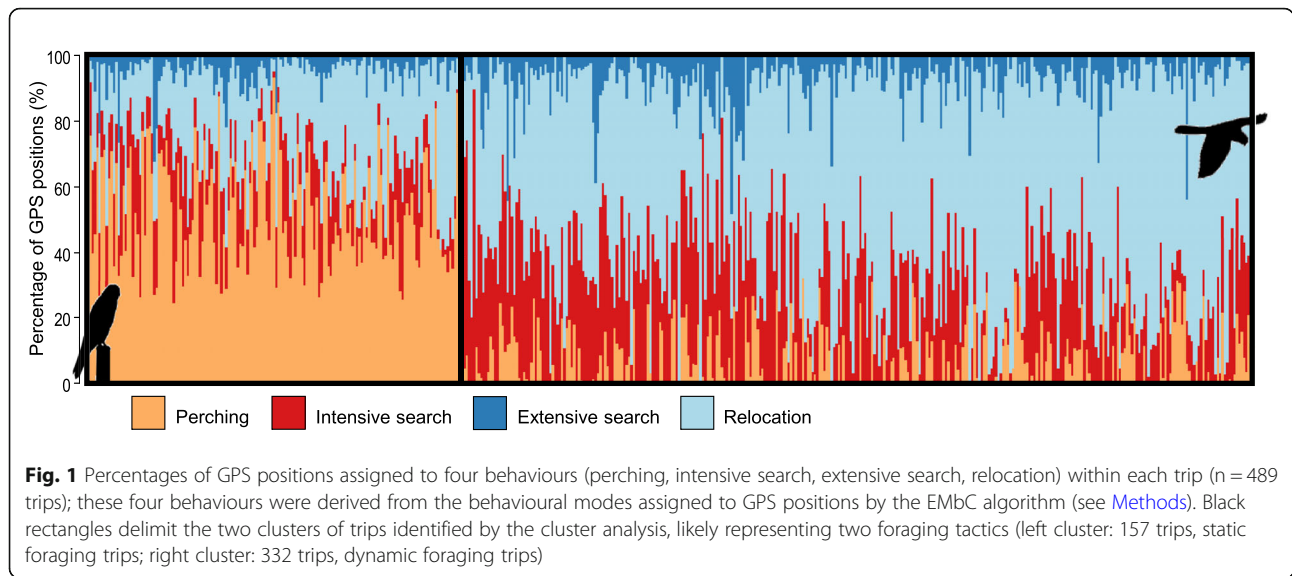
Tracked birds preferentially performed DF trips (65% of all trips; intercept-only binomial GLMM, estimate [95% CI] = 0.62 [0.18, 1.06], $Z = 2.76$, $P = 0.006$). The probability of performing DF trips varied among years and was moderately positively affected by solar radiation (effect size $r = 0.28$), with CWC and breeding stage having somewhat weaker effects ($r = 0.13$ and 0.20, respectively) (Table 3). With low CWC and solar radiation, birds mostly adopted SF, whereas the probability of adopting the DF tactic increased as CWC and solar radiation increased (Fig. 4). Birds were more likely to perform DF trips during the nestling-rearing compared to the incubation stage (Table 3). All other predictors had a negligible effect on the probability to perform DF trips (95% CI including 0, all $r < 0.06$). Males and females did not markedly differ in the probability to perform DF trips according to weather condition gradients (two-way interactions between sex and each weather variable, r always < 0.05, P always > 0.29).

The proportion of variance explained by individual identity was low ($R_{adj} = 0.13$, $\chi^2 = 15.17$, $df = 1$, $P < 0.001$), indicating that individuals mostly adopted a flexible foraging behaviour. However, variation among individuals in the tendency to perform DF trips was substantial, with values ranging between −1.15 and 1.65 (logit scale; Fig. S3). Individual differences in the behavioural response to weather conditions gradients were negligible in most cases (random slope effects, solar radiation: $\chi^2 = 0.09$, $df = 2$, $P = 0.96$; presence of rain: $\chi^2 = 2.02$, $df = 2$,

Table 1 Variation in spatio-temporal trip descriptors according to breeding stage (incubation and nestling-rearing) and sampling year (2016, 2017 and 2018)

	Trip duration (h)	Trip length (km)	Maximum distance (km)	Tortuosity
Incubation				
2016 ($n = 76$, 12)	2.40 ± 1.61 (0.21–9.76)	18.23 ± 9.78 (3.86–55.59)	5.26 ± 2.46 (0.90–17.62)	3.49 ± 0.94 (2.25–5.96)
2017 ($n = 91$, 11)	2.02 ± 1.54 (0.37–8.61)	22.93 ± 12.40 (2.79–74.79)	6.63 ± 2.51 (0.61–13.33)	3.44 ± 1.11 (2.20–8.69)
2018 ($n = 52$, 6)	1.72 ± 1.33 (0.29–7.55)	18.14 ± 8.15 (6.07–39.58)	6.09 ± 1.58 (1.69–8.82)	2.90 ± 0.72 (2.13–4.70)
Years pooled ($n = 219$, 29)	2.08 ± 1.54 (0.21–9.76)	20.16 ± 10.83 (2.79–74.79)	6.03 ± 2.37 (0.61–17.62)	3.33 ± 0.10 (2.13–8.69)
Nestling-rearing				
2016 ($n = 34$, 2)	1.37 ± 0.84 (0.20–3.21)	14.68 ± 8.18 (3.21–29.34)	4.75 ± 2.44 (1.43–8.18)	3.11 ± 0.68 (2.19–4.83)
2017 ($n = 78$, 6)	1.09 ± 0.61 (0.25–2.93)	16.87 ± 7.37 (5.77–39.84)	6.03 ± 2.20 (2.45–13.98)	2.78 ± 0.51 (2.12–4.14)
2018 ($n = 158$, 6)	0.89 ± 0.54 (0.13–4.06)	15.42 ± 6.07 (3.34–35.78)	6.15 ± 2.33 (1.49–9.72)	2.56 ± 0.60 (2.06–5.30)
Years pooled ($n = 270$, 14)	1.01 ± 0.62 (0.13–4.06)	15.75 ± 6.77 (3.21–39.84)	5.94 ± 2.35 (1.43–13.98)	2.69 ± 0.61 (2.06–5.30)

For each variable, the mean value ± SD (minimum and maximum value) are reported. Sample sizes of both foraging trips and tracked birds are reported in the first column (7 individuals have been tracked during both breeding stages)

Cecere *et al. Movement Ecology* (2020) 8:28

Page 7 of 13

Fig. 1 Percentages of GPS positions assigned to four behaviours (perching, intensive search, extensive search, relocation) within each trip (n = 489 trips); these four behaviours were derived from the behavioural modes assigned to GPS positions by the EMbC algorithm (see Methods). Black rectangles delimit the two clusters of trips identified by the cluster analysis, likely representing two foraging tactics (left cluster: 157 trips, static foraging trips; right cluster: 332 trips, dynamic foraging trips)

$P = 0.36$; TWC: $\chi^2 = 5.60$, $df = 2$, $P = 0.06$; CWC: $\chi^2 = 1.10$, $df = 2$, $P = 0.58$). Hence, individuals consistently differed in foraging tactic across solar radiation and CWC gradients (Fig. 4).

Correlates of individual variation in foraging tactics

The individual tendency to perform DF trips was very weakly correlated with residual SMI ($r_w = -0.03$, $n = 35$, $P_{rand} = 0.87$) and breeding success ($r_w = 0.15$, $n = 35$, $P_{rand} = 0.41$), but it was moderately positively correlated with the residual nestling DBMI ($r_w = 0.45$, $n = 22$, $P_{rand} = 0.038$) (Fig. 5). The body mass of nestlings increased on average by 11.4% (± 4.7 SD) between the two measurements, ranging between 4 and 29%. The latter correlation was not explained by a higher feeding frequency of birds performing more DF trips, as feeding frequency was weakly correlated with the tendency to perform DF trips ($r_w = 0.16$, $n = 14$, $P_{rand} = 0.58$) (Fig. 5).

Finally, the relative load of devices was very weakly associated with the individual tendency to perform DF trips in both sexes (males: $r_w = 0.08$, $n = 23$, $P_{rand} = 0.71$; females: $r_w = -0.07$, $n = 12$, $P_{rand} = 0.83$).
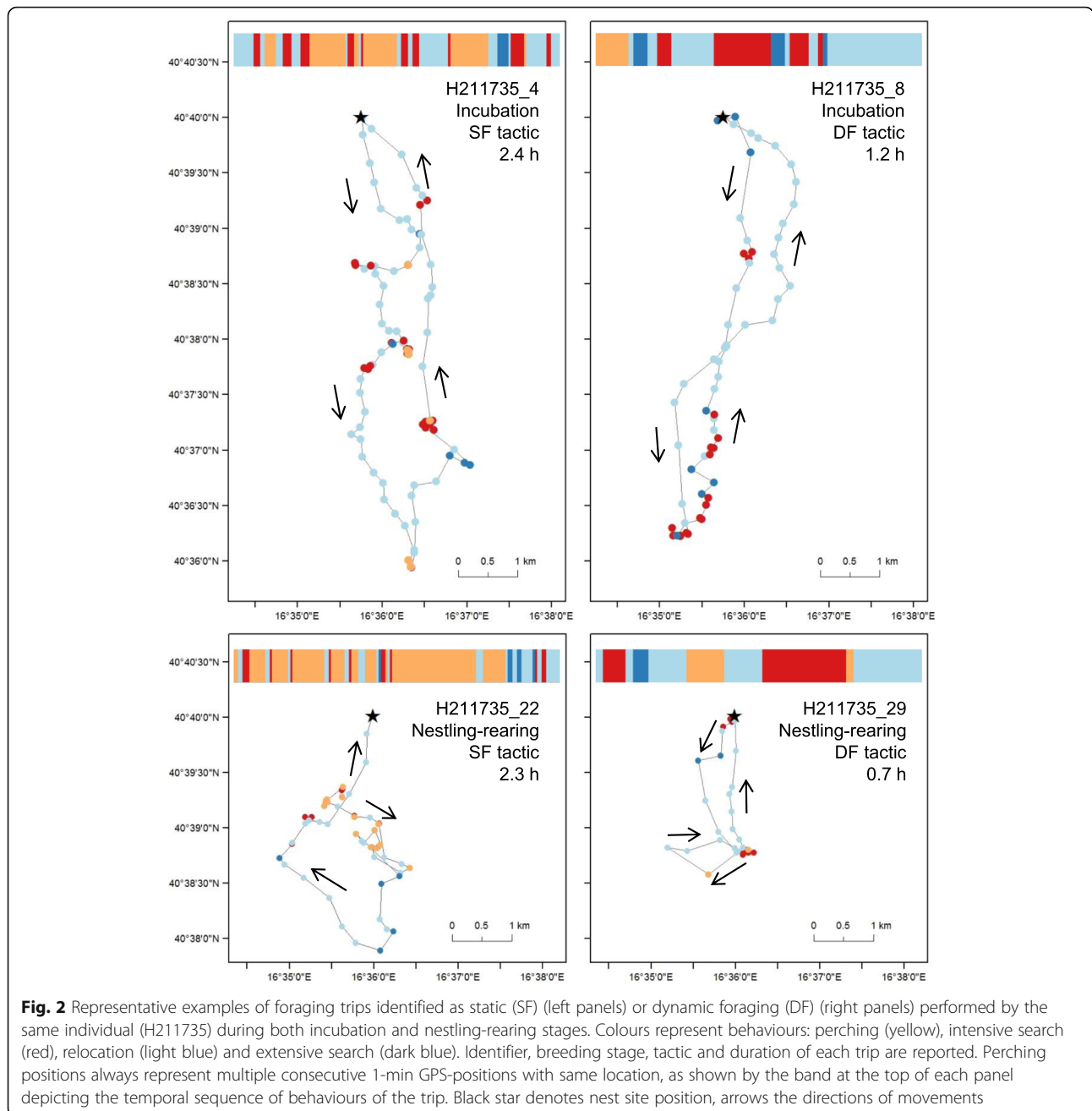
Discussion

By GPS-tracking individuals over multiple foraging trips, we investigated the degree of individual specialization in foraging tactics of breeding lesser kestrels. Foraging tactics adopted by birds during foraging trips varied between two extremes. On the one side, birds performed more static foraging (SF) trips, characterized by high frequency of perching and low proportion of searching behaviour, which were also long-lasting. On the other side, high frequency of both relocation and intensive search and low frequency of perching resulted in more dynamic foraging (DF) trips, that were short-lasting. Unsurprisingly, DF trips were associated with 1.7-fold higher ODBA compared to SF trips. Although birds performed more DF trips overall, the probability of performing DF trips increased with increasing solar radiation and cross-wind, and was higher during the nestling-rearing than

Table 2 Spatio-temporal descriptors and ODBA of static (SF) vs. dynamic foraging (DF) trips

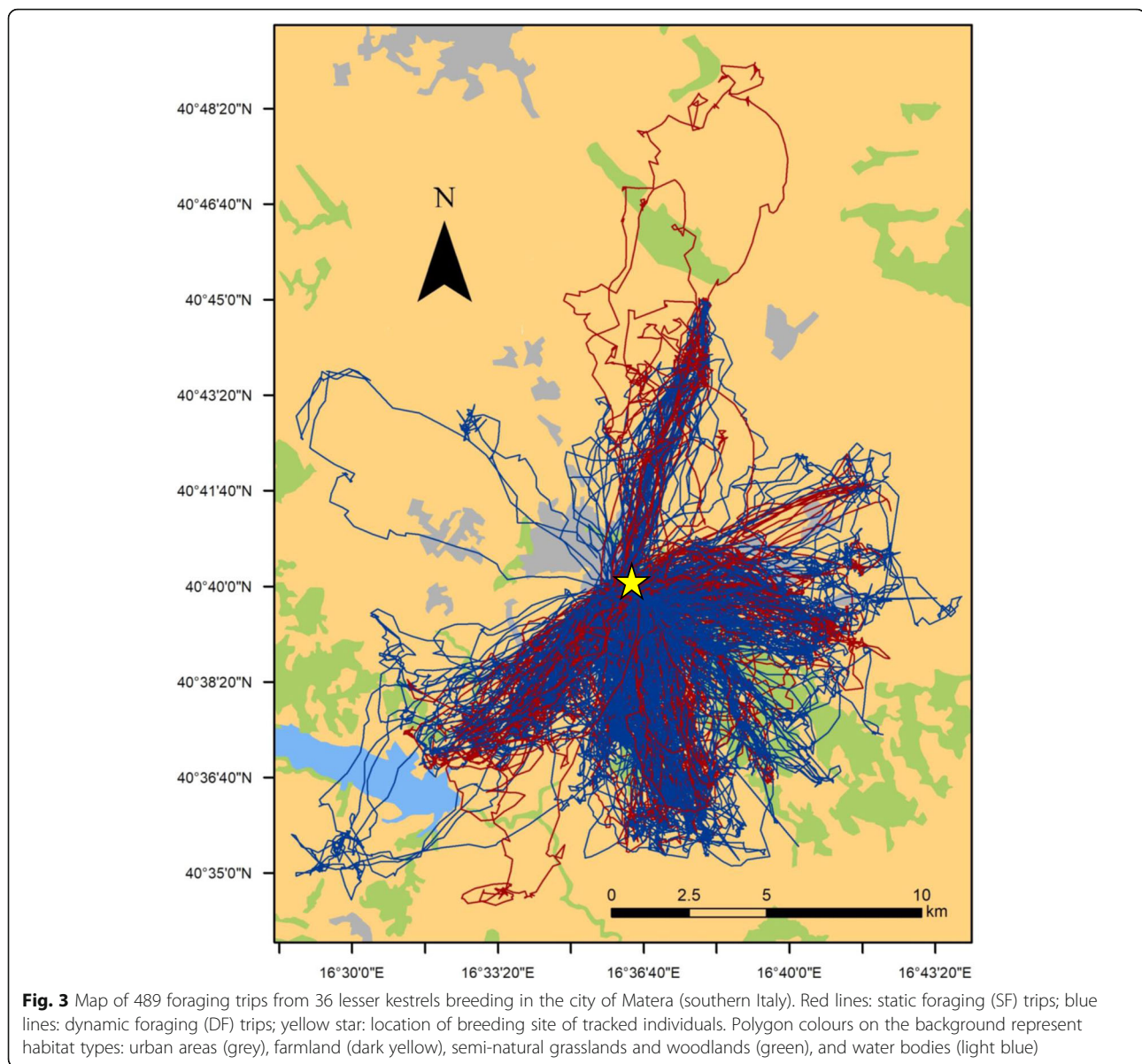| Variable	SF trips (n = 157)	DF trips (n = 332)	Estimate [95% CI]	F	df	P	Marginal R^2	Conditional R^2
Trip duration (h)	**2.44 ± 1.54**	**1.04 ± 0.74**	**−1.31 [−1.52, −1.11]**	**156.7**	**1, 485**	**< 0.001**	**0.24**	**0.37**
Trip length (km)	18.22 ± 9.83	17.49 ± 8.72	− 0.72 [−2.46, 1.02]	0.65	1, 486	0.42	0.01	0.18
Maximum distance (km)	5.73 ± 2.50	6.10 ± 2.28	−0.01 [−0.43, 0.42]	0.01	1, 486	0.99	0.01	0.26
Tortuosity	3.19 ± 0.90	2.88 ± 0.83	−0.10 [−0.25, 0.06]	1.55	1, 485	0.21	0.01	0.30
ODBA[a]	**0.21 ± 0.08**	**0.42 ± 0.09**	**0.14 [0.13, 0.16]**	**292.7**	**1, 426**	**< 0.001**	**0.38**	**0.56**

The effect of trip type (SF = 0, DF = 1) on trip descriptors and ODBA was assessed by linear mixed models including individual identity as a random intercept effect. 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" [44]. Mean values ± SD are reported. Degrees of freedom for the F-tests were estimated according to the Kenward-Roger approximation. Important effects (whose 95% CI do not include zero) are bolded

Fig. 2 Representative examples of foraging trips identified as static (SF) (left panels) or dynamic foraging (DF) (right panels) performed by the same individual (H211735) during both incubation and nestling-rearing stages. Colours represent behaviours: perching (yellow), intensive search (red), relocation (light blue) and extensive search (dark blue). Identifier, breeding stage, tactic and duration of each trip are reported. Perching positions always represent multiple consecutive 1-min GPS-positions with same location, as shown by the band at the top of each panel depicting the temporal sequence of behaviours of the trip. Black star denotes nest site position, arrows the directions of movements

during the egg incubation stage. On top of this, individuals significantly differed in their tendency to perform different trip types, with no evidence of contextual plasticity (i.e. all individuals modulated their foraging tactic in a similar way in relation to weather condition gradients). The tendency to perform energy-demanding DF trips by the attending tracked parent was associated with higher nestling body mass increase, but not with a higher nestling feeding frequency.

The occurrence of both wide-ranging and relatively more static foraging tactics has been documented in many predators, including reptiles (e.g. [52]), fish (e.g. [21]), birds (e.g. [42]) and mammals [67]. However, to our knowledge, the alternation of foraging tactics has seldom been analysed at the individual level. It is being increasingly appreciated that animal movement patterns and behaviour are shaped by the so-called 'energy landscape', i.e. the variation in the cost of transport across time and space, determined by the interaction between static landscape features and dynamic environmental conditions [1, 23, 61]. Lesser kestrels heavily rely on thermal soaring and gliding for foraging, especially when

Fig. 3 Map of 489 foraging trips from 36 lesser kestrels breeding in the city of Matera (southern Italy). Red lines: static foraging (SF) trips; blue lines: dynamic foraging (DF) trips; yellow star: location of breeding site of tracked individuals. Polygon colours on the background represent habitat types: urban areas (grey), farmland (dark yellow), semi-natural grasslands and woodlands (green), and water bodies (light blue)

solar radiation is high [30]. We showed that foraging lesser kestrels mainly performed SF trips when weather conditions were not ideal for soaring-gliding, i.e. with low solar radiation [30] and weak crosswinds, which are known to affect movement patterns in soaring raptors [35]. As expected according to previous studies [43, 66], performing SF trips was an energy-sparing tactic compared to performing DF trips. Birds may thus use DF or SF depending on the relative energy advantage, determined by the wind and solar radiation landscape surrounding the breeding colony. Birds were mostly adopting the more energy-demanding tactic (i.e. DF) only when the energy landscape surrounding breeding sites allowed it.

Inter-individual differences in foraging tactics of colonial vertebrates may originate from divergent selection

to mitigate intraspecific competition, by limiting resource use overlap among individuals sharing foraging areas (e.g., [3]). Under this scenario, we would not expect any significant fitness difference between individuals adopting preferentially one or the other foraging tactic. Although we did not measure other fitness components (i.e., parental survival), the higher body mass increase of nestlings whose parent was performing more DF trips might suggest that the tendency to adopt a given foraging tactic is related to individual characteristics, such as age/experience or physiological status [2, 26] rather than to the mitigation of intraspecific competition. Admittedly, the higher body mass increase of nestlings whose parent was preferentially performing DF trips should be viewed with caution because we could assess

Table 3 Final binomial generalized linear mixed model of the probability to perform dynamic foraging (DF) trips over static foraging (SF) trips

Predictors	Estimate [95% CI]	χ^2	df	P	Effect size *r*
Solar radiation	**0.70 [0.44, 0.97]**	**26.88**	**1**	**< 0.001**	**0.28**
Presence of rain	−0.12 [−0.35, 0.11]	1.09	1	0.30	0.06
TWC	−0.16 [−0.44, 0.12]	1.27	1	0.26	0.06
CWC	**0.32 [0.08, 0.56]**	**6.90**	**1**	**0.009**	**0.13**
Time in arable lands	0.13 [−0.13, 0.38]	0.97	1	0.32	0.06
Breeding stage	**0.53 [0.19, 0.86]**	**9.33**	**1**	**0.002**	**0.20**
Sex	0.04 [−0.36, 0.44]	0.03	1	0.86	0.01
Sampling year[a]	**–**	**8.84**	**2**	**0.012**	**–**
Intercept	−0.02 [−0.73, 0.69]				

[a]: estimated mean values (logit scale), LCL, UCL: 2016 = -0.179, -0906, 0.548; 2017 = 1.199, 0.377, 2.003; 2018 = 0.959, a 0.287, 1.631
Estimates refer to standardized variables. Breeding stage was coded as 0 = incubation or 1 = nestling-rearing, sex as 0 = males or 1 = females. Individual identity was included as a random intercept effect. The model was not overdispersed (ϕ = 1.0). Model R^2 was 0.24 (marginal) and 0.34 (conditional), while R_{adj} was 0.13 (all values estimated according to [45]). Effect size for covariates was calculated as the absolute value of Pearson's *r* obtained from semi-partial R^2 values from the "r2glmm" R package [34]. Important effects (i.e., with 95% CI of estimates not including zero) are shown in bold. One individual with a single foraging trip was excluded (*n* = 488 trips from 35 individuals)
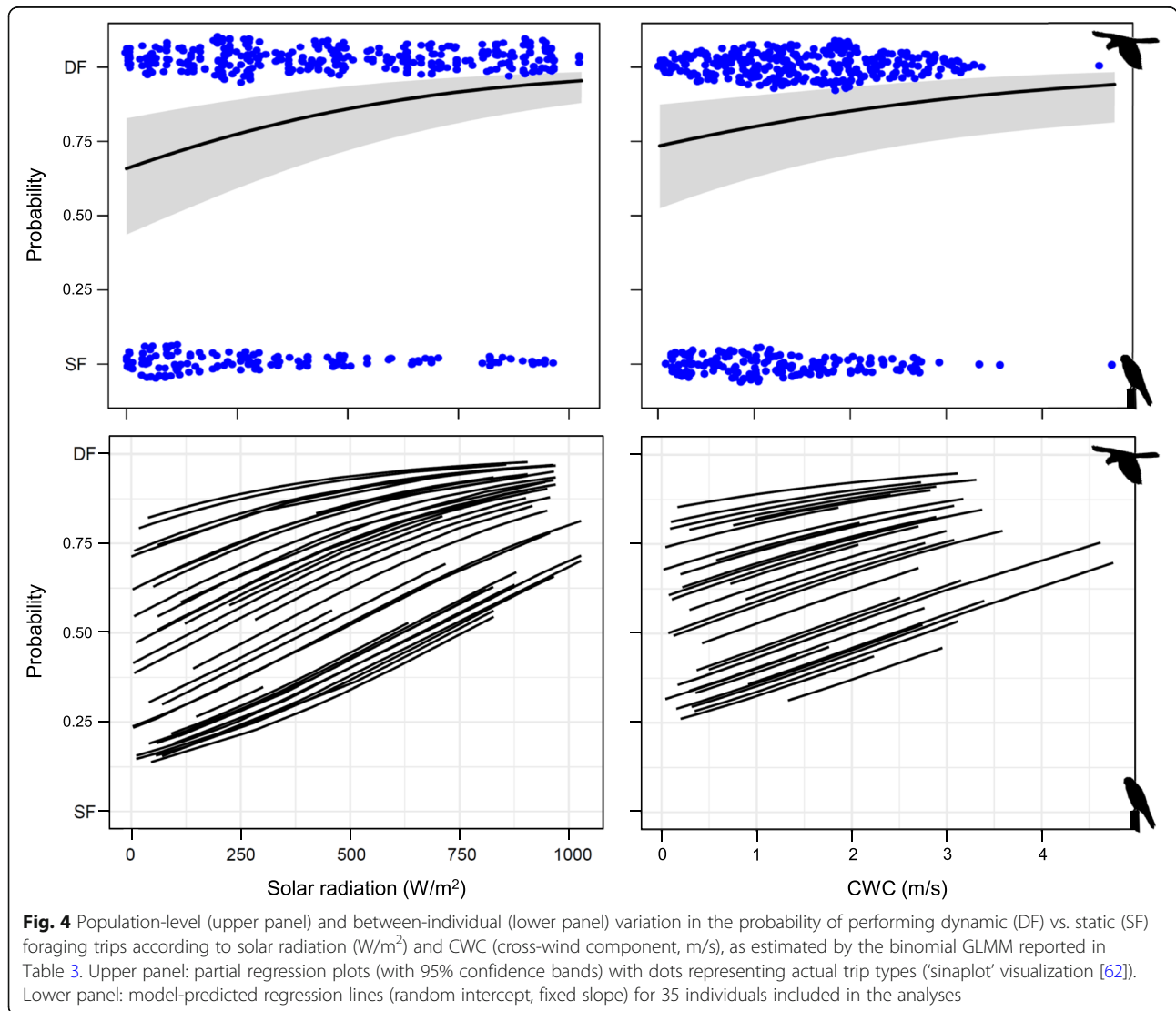
Fig. 4 Population-level (upper panel) and between-individual (lower panel) variation in the probability of performing dynamic (DF) vs. static (SF) foraging trips according to solar radiation (W/m²) and CWC (cross-wind component, m/s), as estimated by the binomial GLMM reported in Table 3. Upper panel: partial regression plots (with 95% confidence bands) with dots representing actual trip types ('sinaplot' visualization [62]). Lower panel: model-predicted regression lines (random intercept, fixed slope) for 35 individuals included in the analyses

Fig. 5 Association between the individual tendency to perform dynamic foraging (DF) trips and (left panel) residual nestling daily body mass increase (DBMI) or (right panel) residual feeding frequency (trips/hour). Sample size, weighted correlation coefficient r_w and P-value are reported within panels
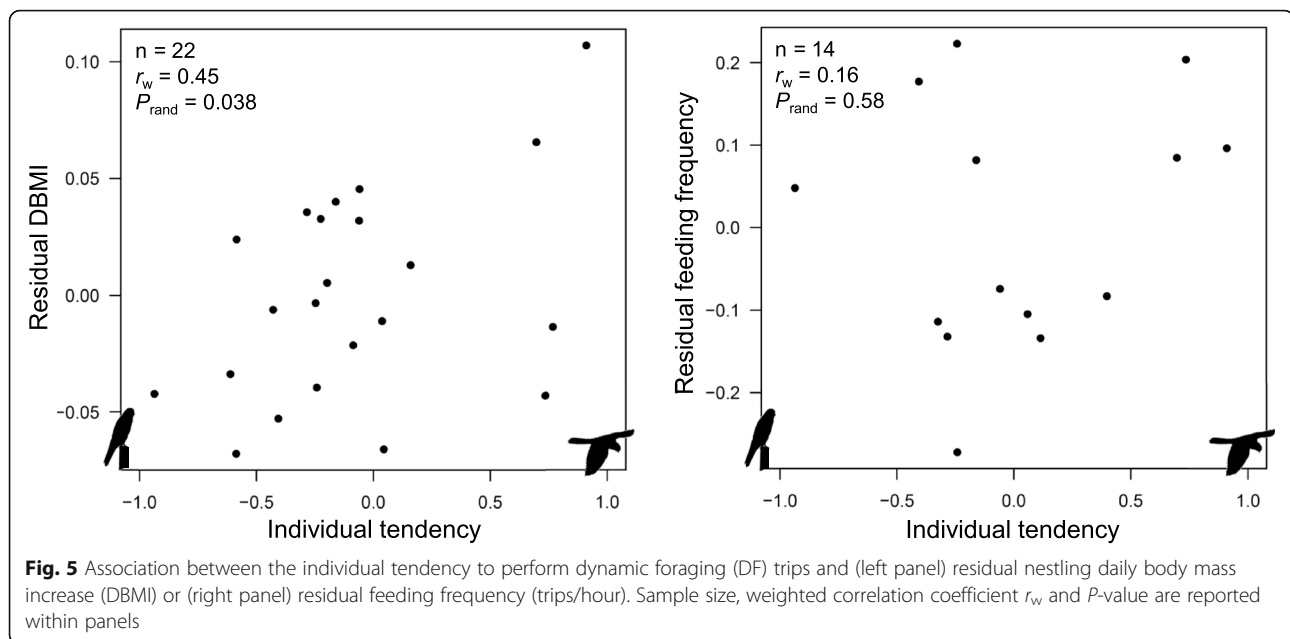
the behaviour of a single parent only. Notwithstanding, it suggests that, even when considering the uniparental contribution to nestling growth, an increased energy expenditure during foraging could result in faster nestling growth and thus better fitness prospects.

The higher body mass increase of nestlings of tracked parents was not a by-product of higher nestling feeding frequencies of birds preferentially performing DF trips. This raises the question of why nestlings reared by parents more prone to perform DF trips grew more. We may speculate that parents preferentially performing DF trips could have delivered more energy-rich prey to their nestlings than those performing more SF trips, resulting in faster mass growth. For instance, parents performing more DF trips may have been mostly targeting large crickets, that are the preferred lesser kestrel prey and have a higher fat content compared to e.g. vertebrate preys [58], whereas those performing more SF trips may have been targeting larger (but less energetic) prey items, such as lizards and mammals. Indeed, sit-and-wait predators generally catch larger prey compared to those taken by active predators [28].

The shorter duration of DF compared to SF trips could be related to the DF tactic being associated with group foraging by means of local enhancement processes for food finding [55]. Such processes imply that individuals searching for food are attracted by feeding aggregations of other individuals and do not need to spend time searching for productive food patches [33, 40]. Social foraging should increase individual foraging efficiency when exploiting ephemeral and unpredictable resources [47]. In the study area, we indeed regularly observed aggregations of foraging

lesser kestrels performing DF to catch large orthopterans flushed during harvesting operations (see also [10]), while birds perching on wires or poles were generally observed alone.

Conclusions

We provided evidence for both individual foraging specialization and high flexibility in foraging tactics, with individuals consistently modulating their foraging tactic according to the concomitant weather landscape. The two foraging tactics were not equivalent in term of energy expenditure and consequences for fitness. Parents preferentially performing DF trips may have exploited group foraging to target more profitable, energy-rich prey in a shorter amount of time, resulting in increased nestling growth, though at the cost of a higher energy expenditure for transport. We may speculate that parents mainly performing DF trips may favour offspring growth over self-maintenance, whereas those mainly performing SF trips may do the opposite. Our results therefore suggest that inter-individual differences in foraging tactics may play a role in maintaining variation within populations in key intergenerational life-history trade-offs, such as those between parental reproductive effort and offspring survival, or between offspring growth and parental self-maintenance.

Supplementary information

Supplementary information accompanies this paper at https://doi.org/10.1186/s40462-020-00206-w.

Additional file 1. Contains the scatterplot of GPS positions in relation to flight velocity and turning angle, highlighting the four behavioural

modes assigned by the EMbC algorithm (**Figure S1.**), the frequency histograms of ODBA values associated to GPS positions for each behavioural mode obtained by the EMbC algorithm, showing that behavioural modes largely differ in ODBA values (**Figure S2.**), and the 'caterpillar plot' illustrating the variation of the random effect estimates obtained by simulations from the final binomial GLMM (**Figure S3.**).

Authors' contributions
JGC conceived the study. JGC and DR wrote the paper with inputs from DM and SI; DM, SI, FDP, DR and JGC analysed the data; JGC, DM, CC, FDP, DR and MG carried out fieldwork. The author(s) read and approved the final manuscript.

Availability of data and materials
The datasets used and/or analyzed during the current study are available from the corresponding author on request.

Ethics approval and consent to participate
Capture, handling and tagging procedures were carried out 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. Birds were caught by hand at the nexboxes and released back into them within 15 min to minimize stress. They were handled by experienced staff only and no bird was injured by the capturing/handling procedure.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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Cecere *et al. Movement Ecology*   (2020) 8:28

Page 13 of 13

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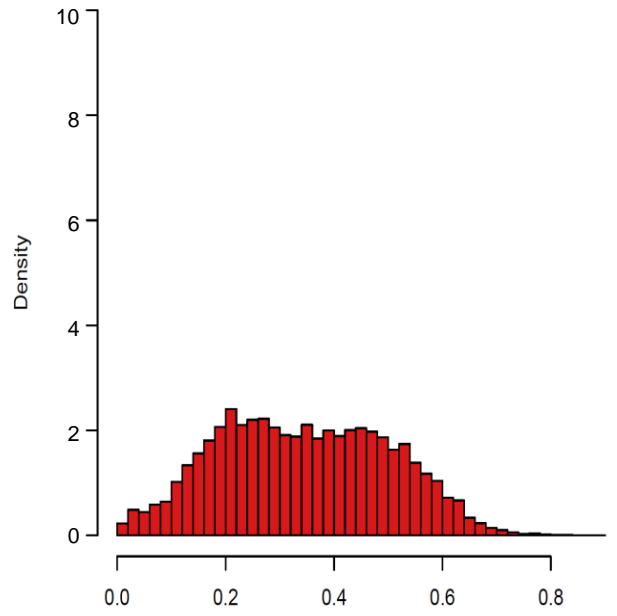# Supporting information accompanying Chapter II
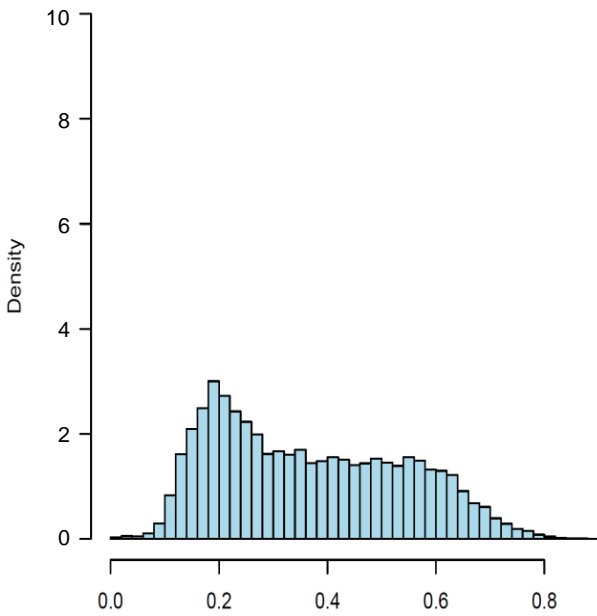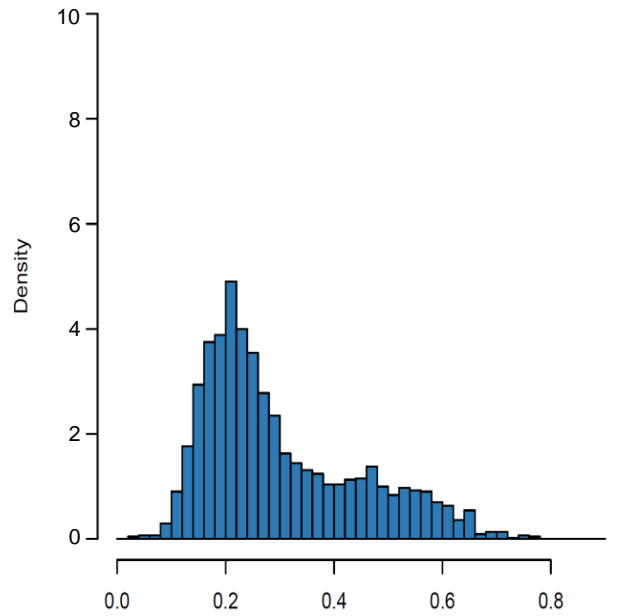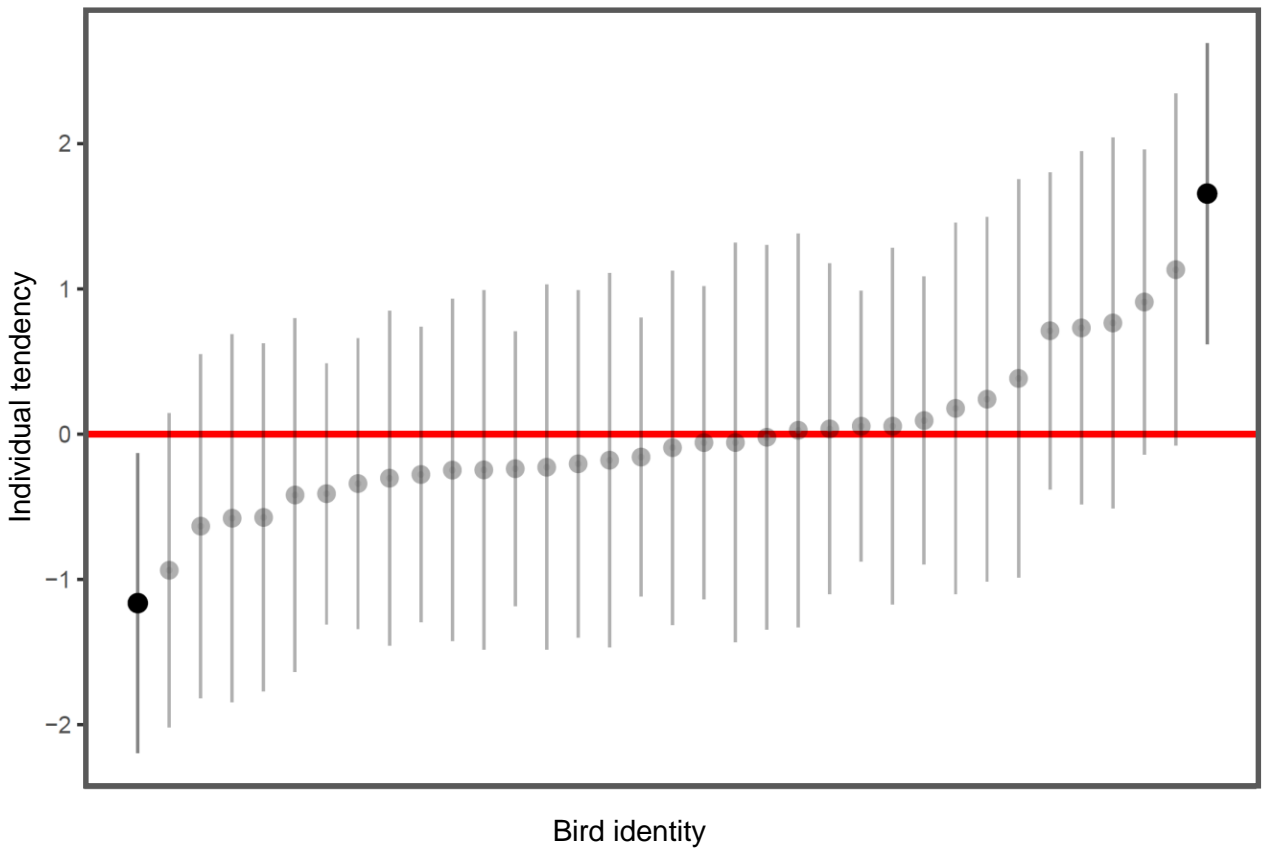
CHAPTER III: competition in neighbouring species

Interspecific and intraspecific foraging differentiation of neighbouring tropical seabirds

Movement Ecology 9(1): 1-16

Inter and intra specific interactions recorded from a bird-borne camera deployed on a brown booby (*Sula leucogaster*) on Cayman Islands. In the top left corner, another brown booby, a red footed booby (*Sula sula*) and a frigatebird (*Fregata magnificens*) are interacting during a feeding association. Picture: R. Austin & F. De Pascalis.

Interspecific and intraspecific foraging differentiation of neighbouring tropical seabirds

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Abstract

Background: Social interactions, reproductive demands and intrinsic constraints all influence foraging decisions in animals. Understanding the relative importance of these factors in shaping the way that coexisting species within communities use and partition resources is central to knowledge of ecological and evolutionary processes. However, in marine environments, our understanding of the mechanisms that lead to and allow coexistence is limited, particularly in the tropics.

Methods: Using simultaneous data from a suite of animal-borne data loggers (GPS, depth recorders, immersion and video), dietary samples and stable isotopes, we investigated interspecific and intraspecific differences in foraging of two closely-related seabird species (the red-footed booby and brown booby) from neighbouring colonies on the Cayman Islands in the Caribbean.

Results: The two species employed notably different foraging strategies, with marked spatial segregation, but limited evidence of interspecific dietary partitioning. The larger-bodied brown booby foraged within neritic waters, with the smaller-bodied red-footed booby travelling further offshore. Almost no sex differences were detected in foraging behaviour of red-footed boobies, while male and female brown boobies differed in their habitat use, foraging characteristics and dietary contributions. We suggest that these behavioural differences may relate to size dimorphism and competition: In the small brown booby population ($n < 200$ individuals), larger females showed a higher propensity to remain in coastal waters where they experienced kleptoparasitic attacks from magnificent frigatebirds, while smaller males that were never kleptoparasitised travelled further offshore, presumably into habitats with lower kleptoparasitic pressure. In weakly dimorphic red-footed boobies, these differences are less pronounced. Instead, density-dependent pressures on their large population ($n > 2000$ individuals) and avoidance of kleptoparasitism may be more prevalent in driving movements for both sexes.

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Conclusions: Our results reveal how, in an environment where opportunities for prey diversification are limited, neighbouring seabird species segregate at-sea, while exhibiting differing degrees of sexual differentiation. While the mechanisms underlying observed patterns remain unclear, our data are consistent with the idea that multiple factors involving both conspecifics and heterospecifics, as well as reproductive pressures, may combine to influence foraging differences in these neighbouring tropical species.

Keywords: Red-footed booby, Brown booby, Competition, Resource partitioning, Foraging ecology

Background

Understanding how coexisting species and individuals use and partition resources is central to knowledge of community structure in wild populations [1, 2], and a key component for identifying conservation priorities [3–5]. Consumers must adopt highly efficient strategies to acquire ample resources for survival and reproduction [6, 7]. Thus, it is often advantageous for animals to develop behaviours that minimise conflict with others [2]. For example, where multiple species with similar morphologies coexist, this can manifest as resource partitioning in space, time and/or diet, resulting in divergent ecological niches [1, 8–11].

Such pressures and outcomes also operate within species, and intraspecific segregation in resource use based on sex, life stage and even at the individual level is common within the animal kingdom [12–14]. Such resource partitioning has been widely associated with factors linked to body size differences [15, 16], and in communities with large populations may be driven by density dependence [17, 18]. While competitive pressures offer one potential explanation for interspecific and intraspecific differentiation in foraging, many other factors such as differing nutritional or physiological requirements [19], predation risk [4, 20], or sociality (e.g. avoidance of mating attempts: [21, 22]) have been proposed as causal factors, although a limited consensus exists between studies and systems.

For highly mobile marine vertebrates constrained to breed on land, such as seabirds, operating successfully within ocean systems is fraught with challenges. Access to suitable nesting habitat and widely-distributed prey can limit population processes [23–25], and these influences can become particularly pronounced during breeding periods when movements of central-place foragers are constrained in space and time [26]. Throughout the global oceans, these challenges result in the coexistence of multiple colonial seabird species within ecosystems, and thus in varied forms of ecological segregation [10, 11, 19]. Nevertheless, some communities in highly productive systems that offer abundant resources appear to lack niche divergence between their constituent species (i.e. [27, 28]).

In tropical and subtropical oceans, our understanding of factors that affect foraging differentiation and community structure lags behind that for many other regions [29, 30]. Yet these environments, characterised by low productivity and limited seasonal variability [31], support diverse communities of marine vertebrates including large populations of seabirds [32]. In comparison to the impressive dive depths common amongst temperate and polar seabirds, many tropical species feed at or near the ocean's surface, where social and commensal foraging in mixed aggregations is common [33–35]. This propensity for co-exploitation of resources contrasts with predictions of ecological niche divergence, and highlights a need for improved knowledge of multi-species interactions in these systems.

Two congeneric tropical seabirds, the red-footed booby (*Sula sula*, Linnaeus, 1766; hereafter referred to as the RFB) and brown booby (*S. leucogaster*, Boddaert, 1783; hereafter referred to as BB), commonly co-exist on islands throughout the tropics [36–38]. These species share similar morphological traits, the RFB being slightly smaller and more slender than the BB, yet exhibit striking differences in breeding behaviour [36, 37]: RFBs are arboreal nesters while BBs predominantly employ a ground-nesting strategy [37]. To be successful, these species must deal not only with constraints associated with securing suitable nest sites, but those imposed within the foraging environment in which they operate [39]. Thus, understanding the mechanisms by which these sulids coexist requires consideration of factors in both marine and terrestrial habitats. While RFBs and BBs have received considerable attention for tropical species, with some interspecific differences in foraging ecology reported [35, 40–44], the degree to which they coexploit and/or partition marine resources, both in terms of space use and diet, remains poorly understood [36, 45].

Here, we investigated whether coexisting populations of these two tropical species have evolved divergent foraging behaviour with high levels of segregation at sea, mirroring their separation in nesting habitat, or whether they overlap in their resource use. To answer this question, we studied interspecific and intraspecific differences in the spatial movements, dive behaviour, activity patterns, social interactions and diet of two neighbouring populations that breed contemporaneously in the Caribbean Sea. The Cayman Islands archipelago in the

Western Antilles has resident populations of both species that nest in close proximity on neighbouring islands, yet differ in their population sizes. The RFB booby population is over an order of magnitude larger than the BB population, and co-occurs at its nesting site with breeding magnificent frigatebirds, thus experiencing regular kleptoparasitic pressure from this predator. We hypothesise that the close proximity of the BB and RFB populations, and differences in both their densities and risk of kleptoparasitism, will introduce pressures that manifest through divergent foraging behaviours and/or dietary preferences within their environment.
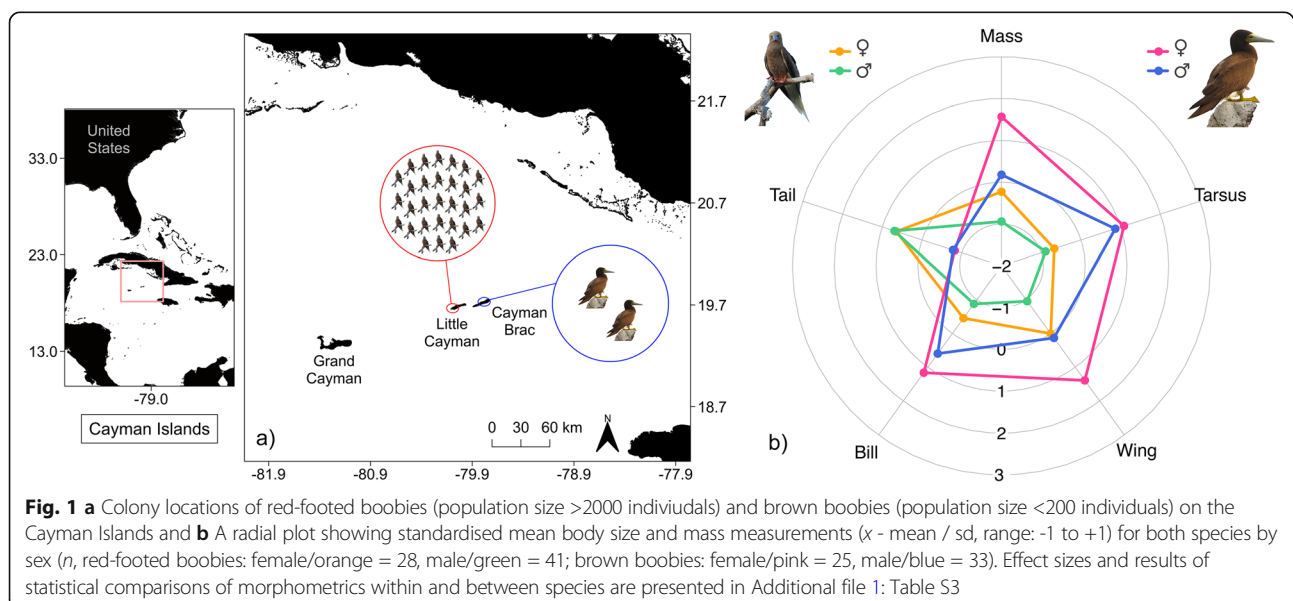
Methods

Study site and bio-logging

Data were collected from two closely-situated populations of boobies that breed at neighbouring sites (islands ~ 7 km apart, nests ~ 26–39 km apart) on the Cayman Islands in the Caribbean Sea: 1) the Booby Pond Nature Reserve on Little Cayman, a RAMSAR site that hosts an internationally important breeding population of RFBs (Fig. 1; Latitude: 19.663 °N, Longitude: 80.082 °W; estimated population size in 2017: 2094 breeding adults, [46]); and 2) beach and cliff locations on Cayman Brac that support a small scattered breeding population of BBs (Fig. 1; Latitude: 19.711 °N, Longitude: 79.801 °W; estimated population size in 2017: 146 breeding adults, [47]).

All fieldwork was performed under permissions of the Department of Environment, Cayman Islands Government and/or National Trust of the Cayman Islands, following established protocols to minimize disturbance. All handling procedures were undertaken following ethical guidelines of the Universities of Liverpool and Exeter. To assess the impact of device attachment on the reproductive performance

of tagged animals, the fledgling success (measured as the proportion of nests that hatched and fledged a chick) was recorded in experimental nests and unhandled closely matched control nests dispersed throughout the colonies. Fisher's exact tests were used to test for significant differences between groups.

During chick-rearing (Feb - April) between 2016 and 2019, RFBs ($n = 31$) and BBs ($n = 68$) were tracked with archival GPS loggers (Mobile Action iGotU GT-120 s; Mass = ~ 15 g; chick age range = 2 − 13 weeks, see Additional file 1, Appendix S1 for further details), set to record at intervals of either 30 s or 2 min. Incorporation of interpolated tracks originally recorded at ~ 2-min intervals had no notable effect on spatial analyses (Additional file 1, Appendix S2). Devices were attached to a small number of back contour feathers using waterproof tape, and were recovered after at least one foraging trip. A subset of boobies were simultaneously tracked in 2017, 2018 and 2019 with time-depth recorders to record dive activity (TDRs - Cefas Technology G5s; Mass = 2.5 g; Sampling interval = 1 Hz; n, RFBs = 20, BBs = 27), and immersion loggers to measure on-water activity (Migrate Technology C65s; Mass = 1 g; n, RFBs = 17, BBs = 15). Immersion loggers, set to record changes from wet to dry states every 6 s, were attached to a plastic ring on the tarsus, while TDRs were attached to the underside of the two central tail feathers using waterproof tape.

To assess the presence, rate and behavioural context of kleptoparasitic interactions with magnificent frigatebirds, 16 brown boobies (9 females, 7 males) were instrumented with a miniaturised video data logger in 2018 (Catnip Technologies, Hong Kong; Mass = 24.7 − 26.7 g). Twelve of these individuals (8 females, 4 males) were also tracked simultaneously with a GPS logger to obtain matching spatial locations (see above). Loggers were set to record

Fig. 1 a Colony locations of red-footed boobies (population size >2000 indiviudals) and brown boobies (population size <200 individuals) on the Cayman Islands and **b** A radial plot showing standardised mean body size and mass measurements (x - mean / sd, range: -1 to +1) for both species by sex (*n*, red-footed boobies: female/orange = 28, male/green = 41; brown boobies: female/pink = 25, male/blue = 33). Effect sizes and results of statistical comparisons of morphometrics within and between species are presented in Additional file 1: Table S3

for 30 min periods every 2 h during daylight (cumulative recording time of ~ 4 h). The total mass of combined loggers in the study did not exceed 3% body mass (Mean % body mass, BBs = 2.4 ± 0.8 g, RFBs = 2.3 ± 0.4 g), with the exception of 14 BBs that were fitted with either a video logger or accelerometer for a simultaneous study (in these cases device mass never exceeded 4.5% body mass). RFBs were not tracked with video loggers owing to size constraints.

Birds were weighed prior to device deployment, and a range of morphometric measurements, including flattened wing length, bill length, bill depth, bill width, tarsus length and tail length, were taken with dial calipers (± 0.01 mm) or a steel rule (± 0.1 mm) by the same researcher to determine body size. As the sex of RFBs cannot be reliably determined in the field, DNA sexing was undertaken on a subset of sampled birds ($n = 69$) using blood samples or three to four breast feathers collected during handling (Animal Genomics Laboratories, UK). The sex of birds that tissue was not extracted from ($n = 10$) was predicted based on results of a discriminant function analysis undertaken on morphometric data from birds of known sex (see Additional file 1, Appendix S3).

Dietary habits

To investigate trophic habits, carbon and nitrogen stable isotope values in blood samples of foraging birds were analysed (n, RFBs 2016 = 37, 2017 = 22; BBs 2016 = 11, 2017 =19). Blood was sampled from the tarsal vein of tracked individuals upon first capture, using a needle and syringe, and spun in a centrifuge for 15 min to extract red blood cells (RBCs) for analysis, before being frozen. RBCs were dried in an oven at low temperatures (35 – 40 °C) until reaching constant mass, ground into a powder and weighed into tin capsules in preparation for stable isotope analysis (0.5 – 0.8 mg).

A range of fish and squid prey species were sampled opportunistically from regurgitates of tracked birds (RFBs = 15, BBs = 30). To examine diet, samples were identified to the lowest taxonomic level possible, and subsequently analysed to determine stable isotope compositions. Small sections of dorsal white muscle tissue (~ 2 cm) were extracted, dried, ground and weighed into capsules following methods outlined above. To account for contributions from ^{13}C-depleted lipids in fish muscle samples, lipid extracted $\delta^{13}C$ values were predicted using lipid-normalisation equations from [48] (following methods in [49]).

Stable isotope analysis was performed at the Natural Environment Research Council Life Science Mass Spectrometry Facility, East Kilbride in 2016, and the University of Liverpool School of Environmental Sciences Isotope laboratory in 2017, using continuous-flow isotope mass spectrometry. Isotope ratios were expressed in δ notation in parts per thousand (‰) relative to V-

PDB ($\delta^{13}C$) or AIR ($\delta^{15}N$) scales. Multiple measurements of internal laboratory standards indicated that measurement error was ≤0.1 ‰ for both $\delta^{13}C$ and $\delta^{15}N$.

Data analysis

Less than 0.01% of GPS locations for BBs and 0.03% for RFBs were associated with ground speeds of > 95 km h^{-1} (consistent with existing reports of instantaneous flight speeds in these or similar species: [50–52]). Therefore, we filtered GPS locations for unrealistic speeds above this threshold. Prior to further processing, raw GPS data were also filtered to remove partial trips, colony-based movements (< 500 m from nest) and movements away from the colony < 30 min in duration.

To allow a direct comparison of foraging distributions between species, Hidden Markov Models (HMMs), based on step lengths and turn angles, were trained to estimate behavioural states in tracks using the 'momentuHMM' package in R [53]. Prior to fitting models, GPS locations were interpolated to 30 s intervals using cubic piecewise hermite polynomials (following [54]), and colony-based locations were removed. Step lengths were modelled using a gamma distribution, while turn angles were modelled with a von Mises distribution. HMMs were validated using dive and immersion data from birds tracked with simultaneously deployed TDRs and immersion loggers (see Additional file 1, Appendix S4 for details). Appropriate parameter priors for the final model were selected through a comparison of negative log-likelihood values of a number of candidate models run iteratively using a range of randomly selected mean and SD parameter values constrained within realistic limits ($n = 25$). Following the assignment of time points to behavioural states, all locations estimated to be associated with directed flight and rest were discarded, and bouts of movement associated with foraging were extracted to map density distributions.

Fixed Kernel Density Estimates (KDEs) were calculated on HMM-estimated foraging data. To prevent spatial biases, covariance bandwidth matrices were obtained using the least squares cross validation estimator ('ks' package in R, [55]) on projected coordinates. The overlap between kernel density estimates (50 and 90% KD contours representing the core and main foraging areas) of different sexes and species was calculated using Bhattacharyya's affinity [56]. Intra-annual comparisons of the core (50% KDE) and main (90% KDE) foraging areas for 2016 and 2017 (when both species were tracked) indicated that differences in space use between species were consistent across sample years (Fig. S3; Bhattacharyya's affinity, 2016: 50% = 0, 90% = < 0.1; 2017: 50% = 0, 90% = < 0.01). Thus, we pooled all data across years for comparison of species distributions. For each foraging track, total distance travelled, maximum distance from colony,

trip duration, mean distance from the nearest coastline, median underlying bathymetry (obtained via the marmap package in R: [57]) and time spent in different behavioural states (see below) were calculated. Mixed-effects models with a random individual intercept were run to compare trip characteristics between species and sexes.

To investigate the presence of different foraging tactics, we firstly used a PCA to extract appropriate variables for further behavioural clustering (see Additional file 1, Appendix S5). To identify clustering in the data, Gaussian Mixture Models were run on trips from both species using 'trip duration', 'distance to nearest coastline' and 'maximum distance' parameters. As BB trips clustered into two groups, we used Binomial GLMMs with a random intercept for individual on this species, to investigate differences in the probability of foraging coastally versus pelagically between the sexes.

Dives were classified using the 'diveMove' package in R [58]. Depth measurements were calibrated using a 'moving quantile' zero-offset correction method (following [59]) and a dive threshold of > 0.25 m. Dive and immersion data were matched to the nearest spatial location obtained from 30 s interpolated GPS data, and dive metrics were calculated within 30 s segments of track centred on each location for all subsequent spatial analyses. The mean dive rate (no. dives hr^{-1}) of each species was calculated and mapped within 5 km × 5 km grid cells.

Video footage was analysed frame-by-frame (~ 30 frames s^{-1}) using VirtualDub software (Avery Lee), and behaviour of the tagged bird was categorised for each second using a specifically designed ethogram. All data were analysed by a single observer and validated by an independent observer. For all kleptoparasitic interactions, we recorded time, duration, and the sex and age class of the attacking frigatebird. Interactions were considered discrete if there was a gap of 30 s. We also recorded the time of interactions with respect to the time when boobies were searching/foraging or engaging in prey capture. We compared differences in the proportion of male and female boobies targeted with a Fisher's exact test, and plotted the spatial distribution of kleptoparasitic interactions within 30 s curvilinear interpolated GPS data from tracked birds. Distance to nearest coastline, and the number of kleptoparasitic events within 5 km × 5 km grid cells over the foraging range of video-instrumented birds, were determined. Departure and arrival times to and from the colony (< 500 m from nest sites) were calculated from GPS data.

The isotope niche spaces occupied by sampled birds and their prey were estimated using standard ellipse areas (corrected for small sample sizes: SEAc) calculated in the SIAR package in R [60]. As isotopic discrimination factors between blood and prey muscle tissue have not been published for Sulids, the mean and standard deviations of discrimination factors for similar species in the literature (Additional file 1, Table S7) was applied to avian data to allow a comparison with reference prey data. Differences in bulk carbon and nitrogen isotope values between sexes, species and years were tested with generalised least squares models (weighted linear regression; GLS), with an added variance structure to allow for different variances per factor level. Repeated isotope values between years were sampled from only one BB, and only the first measure was used for this individual during modelling. Morphometric measurements of species and sexes were compared using either linear models or GLS models with variance structures for species or sex in cases of unequal variances between factor levels.

Results
Device effects
There was no significant difference between the fledgling success of experimental nests and control nests for the two study species, with the exception of RFBs in 2017 when control pairs had lower fledging success than experimental pairs (Additional file 1, Table S8). This suggests that handling and tagging disturbance had no notable detrimental effect on the ability of experimental birds to successfully raise a chick.

Body mass and size
Body mass and size differed significantly between species, and between sexes within species. BBs were heavier and larger than RFBs in all measures (Mass, Bill length, Tarsus length: GLS, $p < 0.001$; Wing length: LM, $p < 0.001$), except tail length which was longer in the latter species (GLS, $p < 0.001$, Fig. 1 & Table S3). Females of both sexes were also heavier and larger than males (GLS, $p < 0.001$), with the exception of tail length which did not differ with sex (GLS, $p = 0.681$, Fig. 1 & Table S3), and the degree of size dimorphism was greater in BBs than RFBs for most metrics (Cohen's d effect sizes all > 0.6, except for tail length comparisons where $d < 0$, and the BB tarsus length comparison where $d = 0.4$; see Table S3).

Interspecific and intraspecific partitioning of movement
Between 2016 and 2019, 217 full foraging trips from 58 BBs (13 partial) and 54 full trips from 24 RFBs (14 partial; Fig. S6) were recorded. For these GPS-tracked birds, 18 dive and 13 immersion traces were obtained for BBs, while eight dive and 10 immersion traces were obtained for RFBs (see Table S9 for a full summary of deployments and recoveries). On average, RFBs travelled significantly further from the nest,

foraged in deeper waters, had larger home ranges, and spent longer periods at sea than the more coastal short-ranging BBs (Fig. 2, Table 1). Both species exhibited shallow dive behaviour, with foraging occurring almost exclusively within the top 2 m of ocean (BBs = 98%, RFB = 99%; Table 1). BBs dived on average to greater depths than RFBs, however, differences in depth were small (< 30 cm on average), and no differences in dive rate or duration were detected (Table 1; Fig. S7). While RFBs often spent the entire day at sea (or multiple days, rafting at night; 60% trips > 8 h in duration), commonly departing and returning to the colony during crepuscular hours, BBs were exclusively diurnal foragers with more variable departure and return timings (Fig. S8). The two species showed high levels of spatial segregation with almost no overlap in both their core and main foraging areas (Overlap: 50% occupancy kernels = 0, 90% occupancy
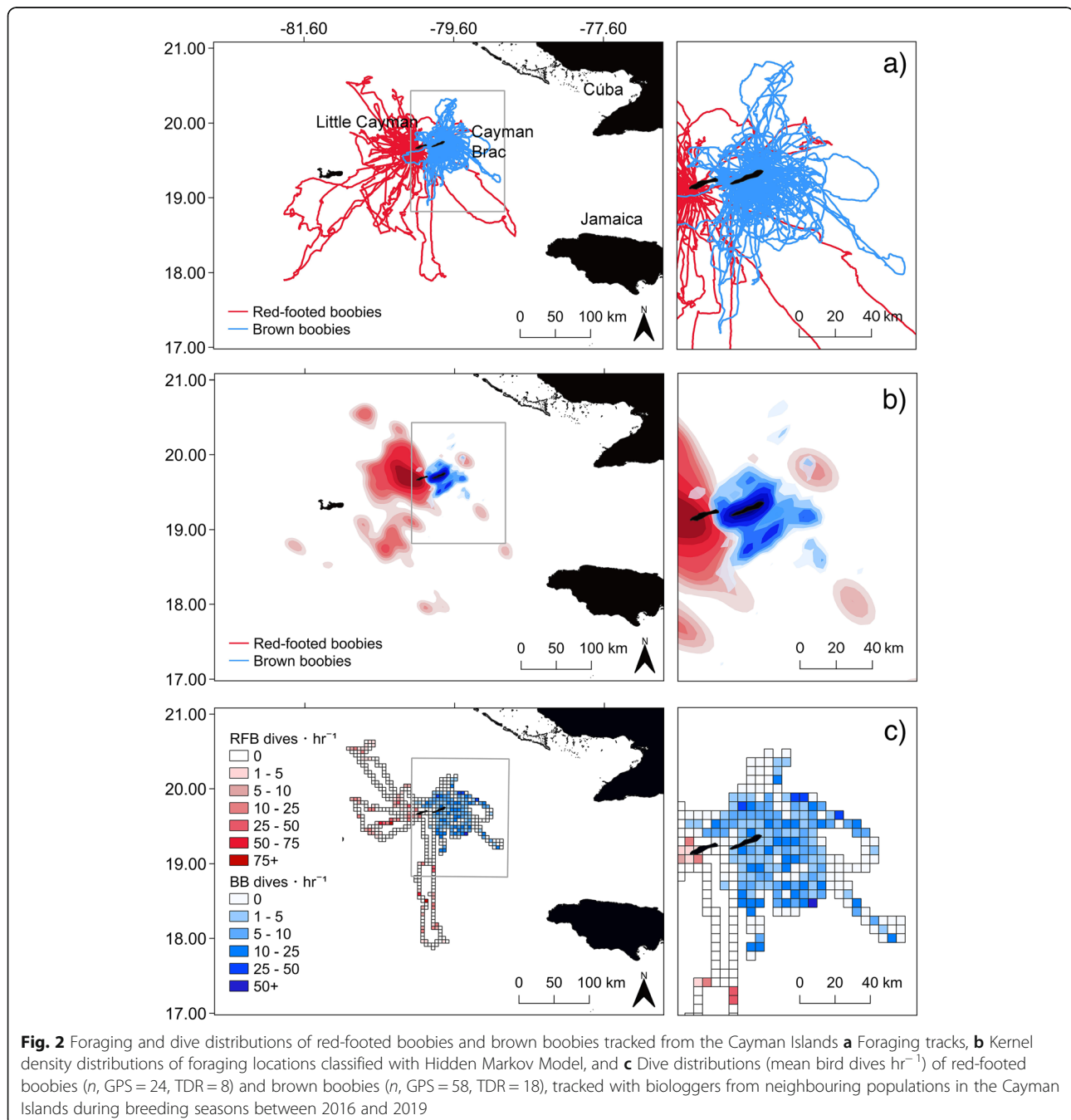

Fig. 2 Foraging and dive distributions of red-footed boobies and brown boobies tracked from the Cayman Islands **a** Foraging tracks, **b** Kernel density distributions of foraging locations classified with Hidden Markov Model, and **c** Dive distributions (mean bird dives hr^{-1}) of red-footed boobies (n, GPS = 24, TDR = 8) and brown boobies (n, GPS = 58, TDR = 18), tracked with biologgers from neighbouring populations in the Cayman Islands during breeding seasons between 2016 and 2019

Table 1 Foraging trip characteristics (mean ± SE) of red-footed and brown boobies by sex, and results of GLMMs

Parameter	Red-footed boobies			Brown boobies			χ^2_1 (p)		
	Female	Male	All	Female	Male	All	Sex RFB	Sex BB	Species
n (birds / trips)	5 / 8	19 / 46	24 / 54	27 / 124	31 / 93	58 / 217	–	–	–
Max dist. (km)	90.4 ± 34.0	57.4 ± 6.9	62.3 ± 7.7[b]	14.8 ± 1.4[a]	23.5 ± 1.7[a]	18.5 ± 1.1[b]	1.191 (0.275)[g]	**7.496 (0.006)**	**22.491 (<0.001)**
Dist. coast (km)	44.0 ± 17.0	31.8 ± 0.3	33.6 ± 3.8[b]	4.5 ± 0.9[a]	11.3 ± 0.1[a]	7.4 ± 0.7[b]	0.539 (0.463)	**6.298 (0.012)**	**28.91 (<0.001)**
Total dist. (km)	252.1 ± 83.4	194.5 ± 22.9	203.0 ± 22.8[b]	49.9 ± 3.9[a]	77.2 ± 5.5[a]	61.6 ± 3.4[b]	0.472 (0.492)	**5.729 (0.017)**	**26.33(< 0.001)**
Trip dur. (h)	14.6 ± 5.4	12.4 ± 1.8	12.7 ± 1.7[b]	3.0 ± 0.3[a]	4.4 ± 0.4[a]	3.6 ± 0.3[b]	0.041 (0.840)[g]	**4.311 (0.038)[g]**	**21.40 (<0.001)**
Prop. time forage*	0.41 ± 0.03	0.52 ± 0.02	0.50 ± 0.02	0.50 ± 0.02	0.50 ± 0.02	0.50 ± 0.01	3.807 (0.051)	0.141 (0.708)	0.230 (0.631)
Prop. time travel*	0.39 ± 0.03	0.29 ± 0.01	0.31 ± 0.01	0.32 ± 0.02	0.36 ± 0.02	0.34 ± 0.01	**4.813 (0.028)**	0.005 (0.945)	1.448 (0.229)
Prop. time rest*	0.23 ± 0.04	0.19 ± 0.02	0.20 ± 0.02	0.21 ± 0.02	0.17 ± 0.02	0.20 ± 0.01	0.885 (0.347)	1.653 (0.199)	0.964 (0.326)
Core HR (km²)	143.5 ± 66.3	61.2 ± 11.3	73.4 ± 14.0[b]	15.3 ± 3.4	30.4 ± 4.1	21.8 ± 2.7[b]	1.550 (0.213)	1.034 (0.309)	**9.197 (0.002)**
Main HR (km²)	827.3 ± 424.9	335.7 ± 71.9	408.5 ± 88.6[b]	58.2 ± 11.7	121.2 ± 14.4	85.2 ± 9.3[b]	1.366 (0.242)	1.853 (0.173)	**0.704 (0.001)**
Bathymetry (m)	2023 ± 476.0	2321 ± 209	2277 ± 190[b]	793 ± 98[a]	1634. ± 125[a]	1153 ± 82[b]	0.362 (0.548)	**12.342 (<0.001)**	**13.043 (<0.001)**
Dives hr.⁻¹	8.8 ± 2.8	6.7 ± 1.4	7.4 ± 1.3	7.2 ± 1.1	7.2 ± 0.9	7.2 ± 0.7	< 0.001 (0.993)	0.027 (0.868)	0.991 (0.970)
Max dive depth (m)	0.42 ± 0.03	0.50 ± 0.05	0.47 ± 0.03[b]	0.73 ± 0.05	0.73 ± 0.04	0.73 ± 0.03[b]	0.388 (0.534)	0.013 (0.909)	**16.219 (<0.001)**
Dive dur. (s)	5.8 ± 1.6	4.2 ± 1.7	4.8 ± 1.3	5.1 ± 2.2	2.1 ± 0.3	3.7 ± 1.2	0.591 (0.442)	1.702 (0.192)	1.171 (0.279)

Mean (±SE) foraging trip characteristics and parameters from generalised linear mixed-effects models (GLMMs), of chick-rearing red-footed boobies and brown boobies tracked from neighbouring populations in the Cayman Islands during breeding seasons between 2016 and 2019. Unless otherwise indicated, GLMMs were specified with a random 'individual' intercept and either a Gamma error distribution[g], or Gaussian distribution with a variance structure to allow the variance to vary by sex

Dist. Coast mean distance to nearest coastline, *Max dist.* maximum distance from nest, *Total dist.* total distance travelled, *Trip dur.* trip duration, *Prop. time forage/rest/travel* proportion of trip time spent in behaviour, *HR* home range, *Dive dur.* dive duration

*Beta-binomial GLMMs with a logit link. Shared superscript letters within each parameter indicate significant differences between [a]sexes and [b]species (p < 0.05)

kernels = 0.02). No differences were found in time spent engaging in different behaviours between species nor sexes, with the exception of higher travel time in female RFBs (Table 1).
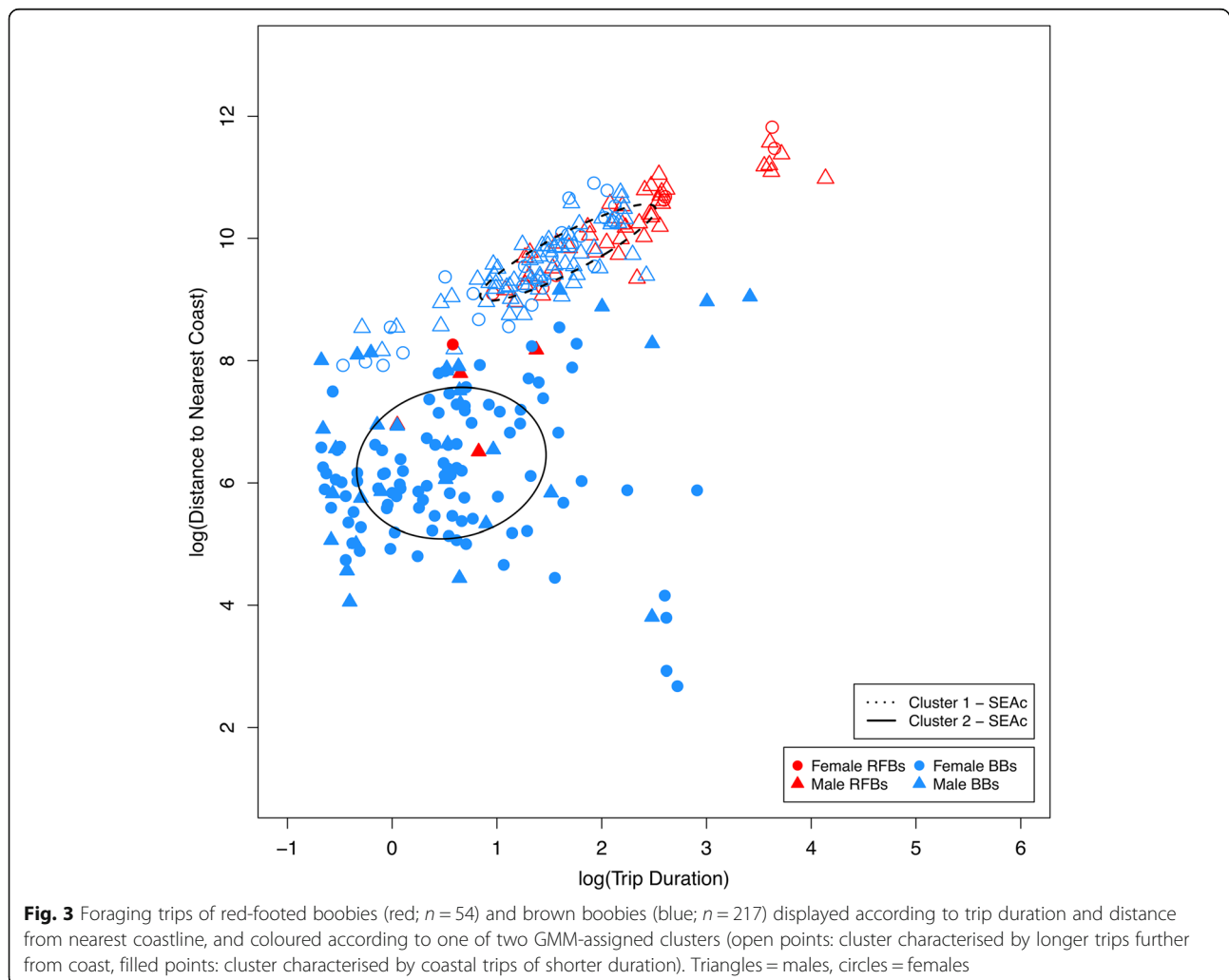
Foraging trips fell into two main clusters (C1 and C2) based on 'trip duration', 'distance to nearest coastline' and 'maximum distance' (see Additional file 1), illustrating divergence in foraging tactics. Almost all RFB trips clustered together (C1,: 91%) and were characterised by longer trip durations further from shore (also correlated with greater underlying water depths, larger home ranges, and greater distances travelled). In contrast, BB trips were variable in their characteristics, falling into the two clusters: neritic shorter trips (C2) and more extensive pelagic trips of longer duration similar to RFBs (C1; Fig. 3). For BBs, males and females undertook both types of foraging trips, although males had a significantly higher probability of engaging in the longer, more extensive trip
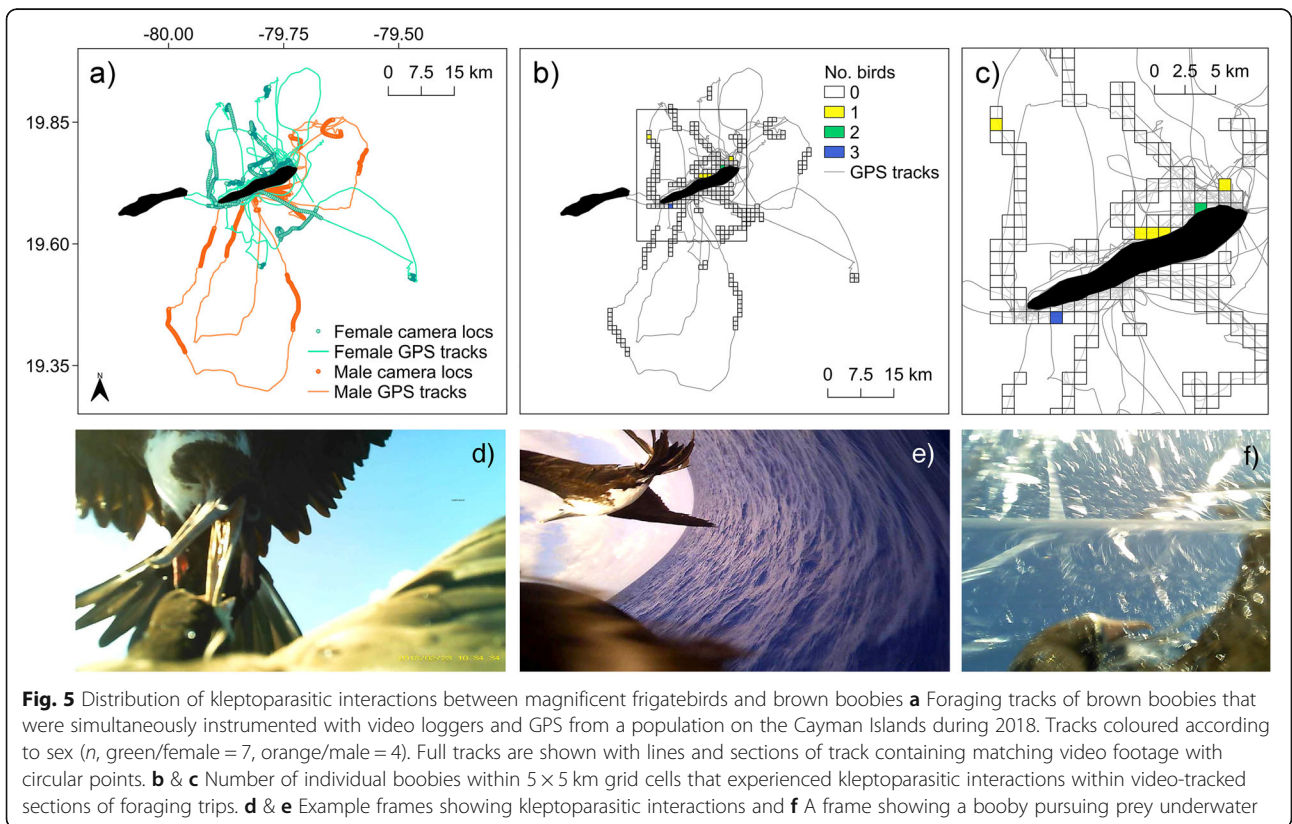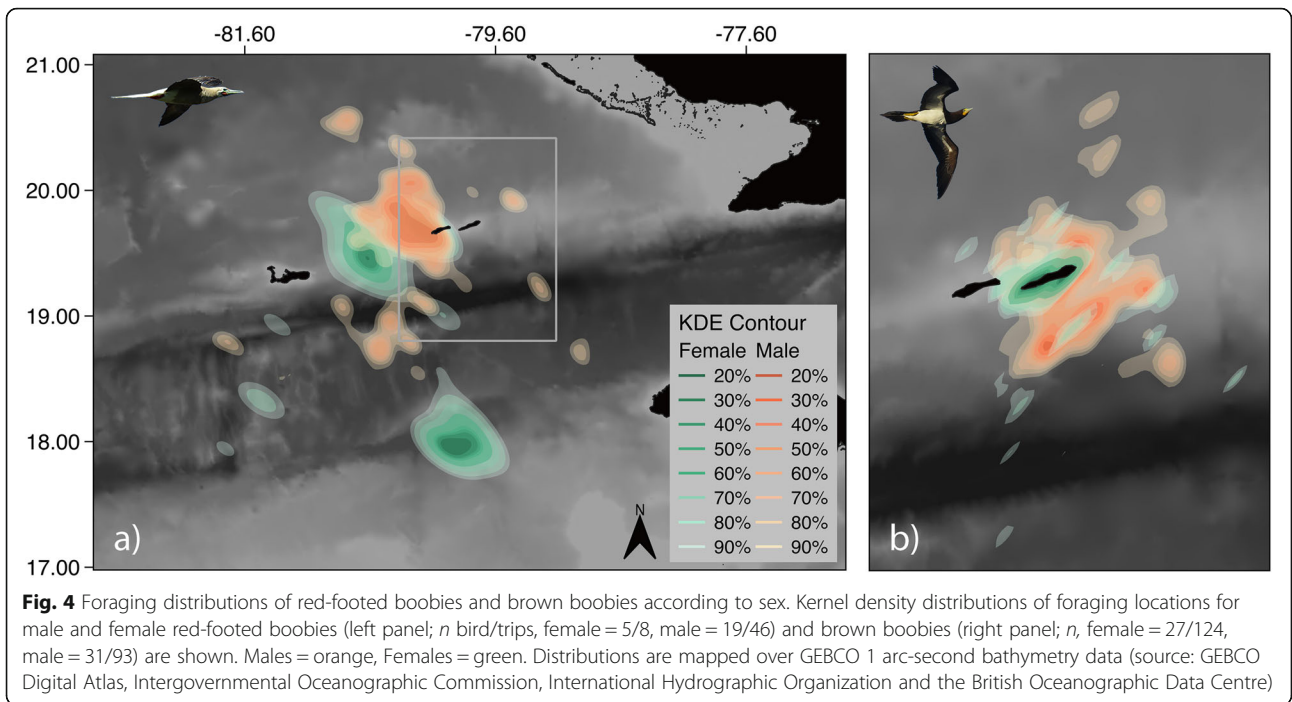
type than females (LRT, $\chi^2_1 = 21.299$, $p < 0.001$; C1, 67% of male trips, 22% of female trips).

Sex differences in spatial distributions and trip characteristics were marked in the highly size-dimorphic BB, the males of which undertook significantly longer trips than females, foraging further from the nest over deeper waters (Fig. 4 and Table 1). Intersexual differences in movements and trip characteristics were almost entirely absent in RFBs (Fig. 4 and Table 1).

Kleptoparasitic interactions
Twelve kleptoparasitic interactions between frigatebirds and brown boobies ($n = 5$ individuals) were detected in 19.5 h of video data, totalling 3.78 min (interaction duration range = 4 – 45 s; Additional file 1, Appendix S9). Frigatebirds only kleptoparasitised female boobies ($n = 5$ of 9 females vs 0 of 7 males; Fisher's exact test, $P = 0.034$), and all attacks were undertaken by adult female (n interactions = 10; Fig. 5) or juvenile frigatebirds

Fig. 3 Foraging trips of red-footed boobies (red; $n = 54$) and brown boobies (blue; $n = 217$) displayed according to trip duration and distance from nearest coastline, and coloured according to one of two GMM-assigned clusters (open points: cluster characterised by longer trips further from coast, filled points: cluster characterised by coastal trips of shorter duration). Triangles = males, circles = females

Fig. 4 Foraging distributions of red-footed boobies and brown boobies according to sex. Kernel density distributions of foraging locations for male and female red-footed boobies (left panel; *n* bird/trips, female = 5/8, male = 19/46) and brown boobies (right panel; *n,* female = 27/124, male = 31/93) are shown. Males = orange, Females = green. Distributions are mapped over GEBCO 1 arc-second bathymetry data (source: GEBCO Digital Atlas, Intergovernmental Oceanographic Commission, International Hydrographic Organization and the British Oceanographic Data Centre)

Fig. 5 Distribution of kleptoparasitic interactions between magnificent frigatebirds and brown boobies **a** Foraging tracks of brown boobies that were simultaneously instrumented with video loggers and GPS from a population on the Cayman Islands during 2018. Tracks coloured according to sex (*n*, green/female = 7, orange/male = 4). Full tracks are shown with lines and sections of track containing matching video footage with circular points. **b** & **c** Number of individual boobies within 5 × 5 km grid cells that experienced kleptoparasitic interactions within video-tracked sections of foraging trips. **d** & **e** Example frames showing kleptoparasitic interactions and **f** A frame showing a booby pursuing prey underwater

(*n* interactions = 2; Fig. 5). There were no differences in mass between parasitized and non-parasitized females (targeted = 1313 ± 117 g, not targeted: 1323 ± 120 g; Wilcoxon rank-sum test, $W = 8$, $p = 1$).

All kleptoparasitic interactions observed on birds with matching spatial data (*n* interactions = 10; *n* birds = 11) occurred when the tracked booby was in coastal waters, with only one interaction occurring > 1.5 km from shore (Fig. 5). All kleptoparasitic interactions took place during booby searching and foraging activity, or soon before/after these behaviours (< 2.4 min; see Additional file 1, Fig. S9), although the success of the frigatebird was unclear. In two cases, the targeted booby was observed catching prey < 30 s from the start of the interaction (Fig. 5). See Additional file 2, Video S1 for example footage of a kleptoparasitic interaction.

Dietary partitioning

The 45 regurgitates collected (*n* birds, BBs = 30, RFBs = 15) contained 196 individual prey samples identifiable to at least the family level. Ballyhoo (family: Hemiramphidae) and flying fish (family: Exocoetidae) were most abundant overall. RFBs ate more flying fish, while BBs ate more ballyhoo, additionally consuming a small number of inshore and reef-associating species including triggerfish (family: Balistidae) and needlefish (family: Belonidae) (Chi-squared test, $\chi^2 = 21.363$, $df = 2$, $p < 0.001$; Fig. 6 & Table S11). For RFBs, 27% regurgitates contained ≥2 prey types, while for BBs 46% regurgitates contained ≥2 prey types. Male and female RFBs showed no significant difference in the numerical abundance of flying fish, ballyhoo and other prey types in their regurgitates (Chi-squared test, $\chi^2 = 0.462$, $df = 2$, $p = 0.794$; Fig. 6 &

Fig. 6 The numerical abundance of different prey types in regurgitate samples (expressed as the proportion of each prey type out of total prey sampled) of tracked red-footed boobies (RFB *n* = 15) and brown boobies (BB *n* = 30) from colonies on the Cayman Islands, during chick-rearing periods between 2016 and 2018. For each species, data are shown for all individuals combined (left sub-figure), and according to sex (right sub-figures; RFB *n*, female = 6, male = 6; BB *n*, female = 18, male = 9). Values on bars show the frequency of occurrence (percentage of birds with a prey type present in their regurgitate) of flying fish and ballyhoo

Table S11). However, male BBs consumed comparatively fewer flying fish and ballyhoo, and a higher proportion of other prey, than females (Chi-squared test, χ^2 = 17.896, df = 2, p < 0.001; Fig. 6 & Table S11).

RFBs were significantly more enriched in ^{15}N than BBs in both sample years (GLS, χ^2_4 = 26.347, p < 0.001; Fig. 7a and Table 2). RFBs were also more depleted in ^{13}C than BBs in 2017 (GLS, χ^2_1 = 46.047, p < 0.001), although no significant differences were found in ^{13}C in 2016 (GLS, χ^2_1 = 0.833, p = 0.361; Fig. 7a & Table 2). In both species, females had higher $\delta^{15}N$ (GLS, χ^2_4 = 32.647, p < 0.001) and $\delta^{13}C$ values (GLS, χ^2_1 = 10.909, p < 0.001) than males (Fig. 7a), with no significant interactions between sex and year nor species detected. Despite this, a comparison of avian isotope values in both species with those of their prey showed that fractionation-corrected blood values (and their incorporated uncertainties) overlapped with the largely identical isotopic niche spaces occupied by their two main prey types (flying fish and ballyhoo; Fig. 7b).

Discussion

This study shows that BBs and RFBs engage in different foraging behaviours - the small population of sexually-dimorphic BBs have sex-specific foraging areas close to the coast, while the larger population of weakly dimorphic RFBs travel further offshore and show almost no sex differences in foraging behaviour. These patterns can be explained by differences in dimorphism, reproductive roles, kleptoparasitism and interspecific and intraspecific competition. We discuss these potential drivers below.

Competition and size dimorphism

Unlike some tropical seabird populations that breed throughout the year or sub-annually [61, 62], BBs and RFBs show some breeding seasonality [37, 61], resulting in potential for competition in areas of coexistence. In the Cayman Islands, the RFB population size is an order of magnitude greater than the BB population. This could lead to local prey depletion requiring RFBs to travel further from the colony, particularly during chick rearing [17, 63, 64]. This form of indirect 'exploitative competition' [63] may also partly explain why BBs seldom venture into coastal waters to the west of their island used by RFBs. Nevertheless, exploitative competition does not fully explain observed patterns, and segregation could arise because of species-specific differences in foraging habitat that emerge due to historical competition.

Like many tropical seabirds, BBs and RFBs both exhibit reverse sexual size-dimorphism, the former species being notably larger (this study, [37, 65]). Direct competition, whereby individuals are inhibited from access to prey by others (termed 'interference competition' [8]) is often attributed to body size differences [66, 67], and thought to be the main competitive force in tropical
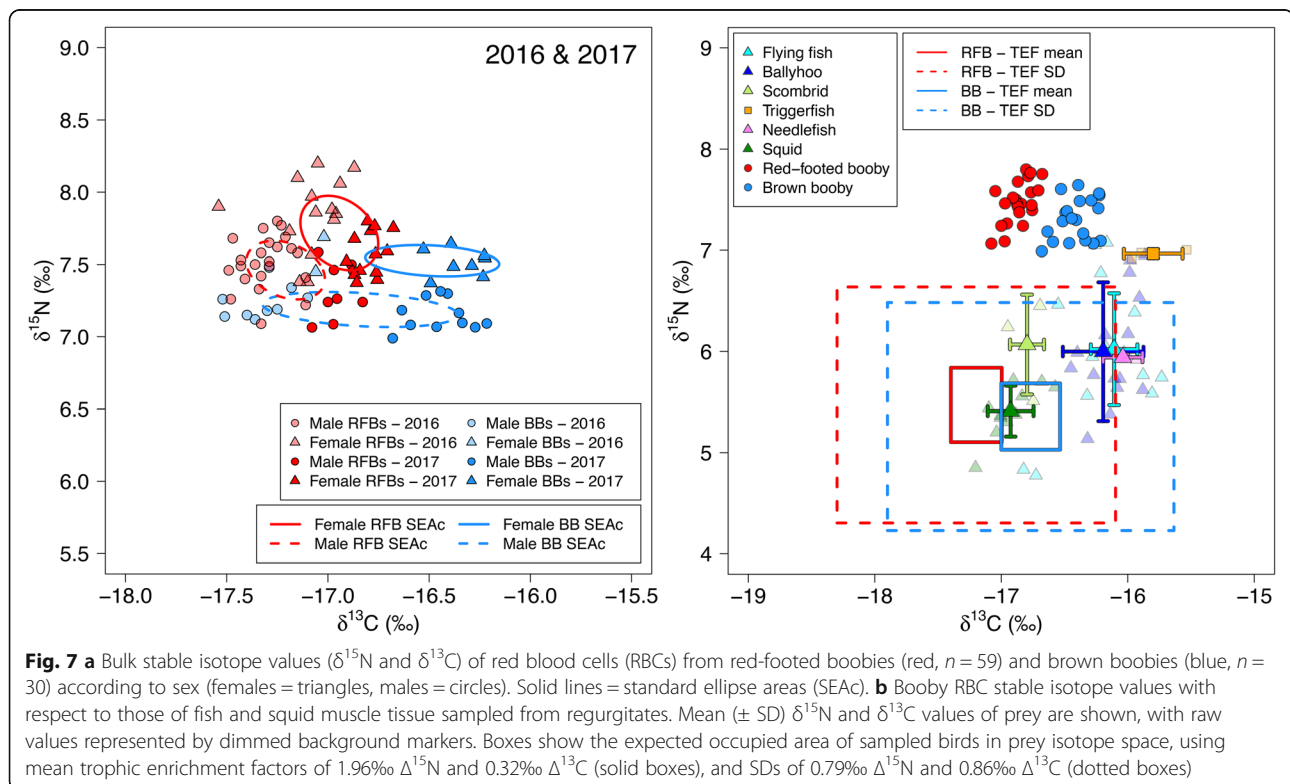

Fig. 7 a Bulk stable isotope values ($\delta^{15}N$ and $\delta^{13}C$) of red blood cells (RBCs) from red-footed boobies (red, n = 59) and brown boobies (blue, n = 30) according to sex (females = triangles, males = circles). Solid lines = standard ellipse areas (SEAc). **b** Booby RBC stable isotope values with respect to those of fish and squid muscle tissue sampled from regurgitates. Mean (± SD) $\delta^{15}N$ and $\delta^{13}C$ values of prey are shown, with raw values represented by dimmed background markers. Boxes show the expected occupied area of sampled birds in prey isotope space, using mean trophic enrichment factors of 1.96‰ $\Delta^{15}N$ and 0.32‰ $\Delta^{13}C$ (solid boxes), and SDs of 0.79‰ $\Delta^{15}N$ and 0.86‰ $\Delta^{13}C$ (dotted boxes)

Table 2 Stable isotope compositions of blood from red-footed boobies and brown boobies from the Cayman Islands

Isotope ratio	Year	Red-footed boobies			Brown boobies		
		Female	Male	All	Female	Male	All
$\delta^{15}N$ (‰)	2016	7.8 ± 0.3 (14)	7.5 ± 0.2 (23)	7.6 ± 0.3 (37)	7.6 ± 0.2 (2)	7.2 ± 0.1 (9)	7.3 ± 0.2 (11)
	2017	7.6 ± 0.2 (13)	7.3 ± 0.2 (9)	7.5 ± 0.2 (22)	7.5 ± 0.1 (8)	7.1 ± 0.1 (11)	7.3 ± 0.2 (19)
	All	7.7 ± 0.3 (27)	7.5 ± 0.2 (32)	7.6 ± 0.3 (59)	7.5 ± 0.1 (10)	7.2 ± 0.1 (20)	7.3 ± 0.2 (30)
$\delta^{13}C$ (‰)	2016	−17.1 ± 0.2	− 17.3 ± 0.1	− 17.2 ± 0.2	−17.0 ± 0.1	− 17.3 ± 0.1	−17.3 ± 0.2
	2017	−16.8 ± 0.1	− 17.0 ± 0.1	− 16.9 ± 0.1	−16.3 ± 0.1	− 16.4 ± 0.1	−16.4 ± 0.1
	All	−16.9 ± 0.2	−17.2 ± 0.2	− 17.1 ± 0.2	− 16.5 ± 0.3	− 16.9 ± 0.5	−16.7 ± 0.5

Mean (± SD) carbon and nitrogen stable isotope values for red blood cells sampled from chick-rearing red-footed boobies and brown boobies in 2016 and 2017 from populations on the Cayman Islands. Sample sizes are given in parentheses

environments [68, 69]. Size differences may confer competitive advantages to BBs allowing interference with foraging opportunities for RFBs [70]. However, present day population sizes of the two species on the Cayman Islands (the BB population being small and in decline owing to anthropogenic impacts: [47, 71]) suggest that direct competition alone is unlikely to explain observed foraging differences. Furthermore, there is little evidence for intersexual competition as a driver for niche partitioning in tropical sulids [44, 72]. Rather than being driven by present day competition, the respective pelagic and coastal strategies of RFBs and BBs may instead be a ghost of competition past, or other processes that caused them to diverge.

Body size differences are also regularly suggested as an explanation for intraspecific differences in foraging behaviour [73, 74]. The relative degree of sex differences in foraging of RFBs and BBs accords with their differing degrees of dimorphism [75], as well as earlier comparisons of basic trip metrics [36, 45]. In theory, high levels of size dimorphism in BBs (23–38%, this study, [36, 76]) could allow larger females to outcompete males in colony-adjacent habitat (e.g. [73]). In comparison, the more weakly dimorphic RFBs (~ 14%, this study, [40]) exhibited almost no sex differences in foraging behaviour, which would accord with lower intraspecific competition. However, how such interference competition may operate remains unclear, although vocalisations could play a role in conveying information about size, status or sex [77, 78]. Alternatively, RFBs may have reduced scope for behavioural variation, since foraging at greater distances might cause them to experience physiological constraints on flight time, limiting scope for spatial segregation (see [79]).

Division of labour and physiological constraints

Differing levels of sex differentiation in foraging may also relate to division of parental care [44, 80]. In both species, the larger females play greater roles in chick provision [41, 81, 82], although this division of labour is more marked in highly dimorphic BBs [41, 82]. Higher provisioning requirements may cause female BBs to remain closer to the nest, a response likely not required in RFBs that vary only slightly in their parental participation [41]. Some BB populations show an opposite pattern of foraging differentiation to those found here, with males remaining closer to shore than females [83, 84], or spending more time at the nest [35]. These cases have been attributed to selection on males to defend nest sites, and females to undertake greater roles in chick provisioning (i.e. through increased food payload capacity or more extensive travel [85, 86]). However, we propose that in the Cayman Islands ecosystem where kleptoparasitism from heterospecifics occurs (see discussion below), the need for risk aversion that likely differs with body size and sex may override relationships between payload and travel distance. Here, smaller males may undertake more distant foraging trips to minimise risks of kleptoparasitism that larger females are better able to cope with [35]. Furthermore, the longer foraging trips of males seen here, in addition to indications that male BBs have lower or similar aggressive tendencies than those of females [37, 87], suggests that territory defence may not be as biased towards males as suggested amongst sulids [35, 80, 83].

Physiological differences associated with body size and wing morphology are believed to drive resource partitioning in some seabirds (i.e. [19]). In the strongly dimorphic BBs, the smaller body size of males may confer greater aerial agility to this sex for exploiting offshore environments, where associations with conspecifics and heterospecifics likely differ from those inshore [40, 70, 88]. In comparison, in weakly dimorphic RFBs, physiological differences with sex may be less prominent. Physiological drivers could also explain interspecific differences in foraging, with smaller, more agile RFBs exploiting pelagic waters where lower wing loadings allow greater manoeuvrability during prey pursuit, which may be less important in highly coastal environments [89].

52

Kleptoparasitism

Sex-based differences in kleptoparasitism may also influence observed intraspecific differences in foraging, based on the observation in 16 video-instrumented birds that all kleptoparasitic attempts were on female BBs in coastal waters. Under theories of risk aversion, the sex most vulnerable to predation pressure is predicted to minimise risk by selecting resources within safer environments [90–92]. Thus, the tendency of male brown boobies to forage further from the coast may represent risk-aversion, seeing that female frigatebirds, the only sex that we observed kleptoparasitising boobies (and a bias seen in other populations [93–95]), show a higher propensity for coastal foraging [96]. This is consistent with evidence that frigatebird density becomes more diffuse with distance from coasts [97]. Smaller, less aggressive male boobies [37, 87] may be less capable of successfully defending themselves against a challenger than females. Similarly, female frigatebirds (also the larger sex) may be more successful in, and capable of balancing the costs of, kleptoparasitism than smaller males.

Male brown boobies must still travel through coastal waters in which kleptoparasites predominantly operate to reach foraging sites, suggesting that they do encounter frigatebirds. However, all kleptoparasitic interactions occurred during or closely timed with booby foraging activity (Fig. S9). This foraging-related context of piracy may allow transiting males to avoid regular kleptoparasitism, while short-ranging foraging females experience higher exposure. Frigatebirds are known to wait aloft near colonies to attack boobies as they return from foraging trips ladened with food [94, 98]. However, in our study system, brown booby nests are scattered along large stretches of coast, with no defined travel corridor or focal point to target. Therefore, use of a 'waiting tactic' is unlikely to yield higher benefits for kleptoparasites over one where frigatebirds target foraging individuals or feeding aggregations.

This mechanism could also help to explain the observed interspecific differences in behaviour. While we could not equip RFBs with video loggers, casual observations at or near nesting sites suggest that rates of kleptoparasitism in coastal waters near colonies may be higher on smaller-bodied RFBs than larger BBs (Austin et al. unpublished observation), the former of which nest side-by-side with magnificent frigatebirds on Little Cayman [99]. Frigatebirds congregate in large groups near the RFB colony and regularly partake in kleptoparasitic attempts on RFBs as they return from foraging trips, as seen in other co-existing populations [93, 100, 101]. This stressor is likely to influence foraging behaviour (see also [98]), and may drive a pelagic avoidance tactic in both sexes of RFBs. Kleptoparasitism might also explain differences in diel activity patterns of the two species: RFBs predominantly leave and return to the colony in crepuscular hours or under cover of darkness (Additional file 1 and see [98]), while BBs show more variability in departure and return times, which largely occur during daylight (Additional file 1). Nevertheless, the role of kleptoparasitism in shaping behaviour of the two species warrants further investigation.

Dietary partitioning

Partitioning in diet can alleviate competitive pressures in communities [10, 102], but we found weak evidence for this in our dietary data with both species targeting similar prey (see also [30, 72, 103, 104]). In accordance with their neritic distribution, there was a higher diversity of prey in regurgitates of coastal BBs, including reef-associating species, and a higher incidence of squid in pelagic RFBs (consistent with [105, 106]). While no sex differences were found in the diet of RFBs, there were differences in the relative contribution of different prey in female and male BBs, likely relating to sex differences in habitat use. Nevertheless, both species predominantly targeted flying fish and ballyhoo that occupy similar ecological niches [107].

Stable isotope values of both species fell within similar isotope prey space seen in our reference data, further indicating that the two populations do not substantially differ in their dietary resources. This broad similarity in diet likely reflects the flexible and opportunistic foraging strategies required in oligotrophic tropical environments where prey are widely distributed [24, 103]. Thus, it is unlikely that differences in habitat use are driven by exploitation of differing target prey. Differences between isotopic values of RFBs and BBs are consistent with commonly observed inshore-offshore gradients in food web isotopes [108, 109], with pelagic RFBs being more enriched in ^{15}N than coastal feeding BBs across sampling years, and more depleted in ^{13}C in 2017. Overarching between-year differences in both species most likely reflect variability in oceanographic conditions and associated biogeochemical processes. In both species, females had higher $\delta^{15}N$ and $\delta^{13}C$ values than males. While this pattern may be explained in BBs by the tendency of females to stay closer to the coast, RFBs did not show significant differences in space use with sex. Nevertheless, the larger size of females may allow exploitation of larger prey, which could be reflected in nitrogen isotope values. Small sample sizes prevented a comparison of prey size between sexes, but evidence in tropical seabirds of a strong correlation between body mass and prey length [30] supports this suggestion. Alternatively, overriding sex differences may be associated with reproductive processes such as egg synthesis, should fluctuations in isotopic routing and fractionation span multiple months for RBCs [110]. While there was little evidence for a role of diet in driving foraging differences in the two focal

Austin *et al. Movement Ecology*   (2021) 9:27

Page 14 of 16

sulids, differing nutritional requirements could still influence use of habitats and foraging strategies, as is now being discussed and tested in seabirds [111, 112].

The fact that little inter- and intraspecific segregation in dive behaviour was found, with the exception of slightly greater dive depths in BBs (which can be explained by body mass differences or consumption of reef-associating prey), further supports the conclusion that these two seabirds have not evolved vastly different dietary niches, and are likely constrained in the diversity of prey that they can access within tropical surface waters [30].

Conclusions

An improved understanding of foraging diversification between coexisting species in tropical environments may help to predict how future change in marine environments may impact species distributions and the functioning of communities, and thus their vulnerability to environmental perturbation. For example, should coastal habitats in the study system offer more predictable resources than those offshore, BBs and RFBs may show differing levels of specialism and differing adaptive capacities to prey field lability (e.g. [113]). Devising explicit tests of the mechanisms underlying foraging segregation in natural systems remains challenging, but our data suggest that a combination of factors linked to population size and body size may contribute, including division of labour, exploitative competition and kleptoparasitism. This is supported by evidence of local adaptation in both species indicated through a range of intraspecific behavioural patterns reported amongst populations [35, 36, 42, 43, 83, 84, 114]. This highlights the need for further comparative studies within and across a range of marine environments, including within the tropics, to improve knowledge of processes acting on seabird community structure and the vulnerability of constituent species to environmental change.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40462-021-00251-z.

Additional file 1. Supporting materials. Supporting materials in the form of figures, tables and text compiled in a single document.

Additional file 2: Video S1. Description of data: example video sequence showing kleptoparasitic interaction between a magnificent frigatebird and brown booby.

Availability of data and materials
The datasets supporting the conclusions of this article are available upon request from the corresponding author.

Declarations

Ethics approval and consent to participate
All procedures performed in this study were in accordance with the ethical standards of the institutions and/or applicable national guidelines for the care and use of wild animals. Fieldwork was performed under permissions of the Cayman Islands Government's Department of Environment following established protocols. All handling procedures were undertaken according to ethical guidelines of the Universities of Liverpool and Exeter.

Consent for publication
Not applicable.

Competing interests
Authors declare that there are no competing financial or non-financial interests in relation to the work described.

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Publisher's Note

Supporting information accompanying Chapter III

Interspecific and intraspecific foraging differentiation of neighbouring tropical seabirds

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Appendix S1 – Chick age range

Table S1. Number of tracked breeding red-footed boobies and brown boobies with respect to chick age.

Species	Small chicks (1-3 wks)	Medium chicks (4-8 wks)	Large chicks (9-13 wks)
Red-footed booby	2 (0.08)	21 (0.88)	1 (0.04)
Brown booby*	15 (0.26)	33 (0.57)	10 (0.17)

*No evidence to suggest that chick age influenced trip duration significantly within the range of ages sampled in the study (GLMM with a random individual intercept, LRT, $\chi^2_2 = 1.099$, $p = 0.147$). Formal statistical testing not possible with red-footed boobies owing to small sample sizes in small and large chick categories.

Appendix S2 – Comparison of interpolated 'original' and 'down-sampled' GPS tracks
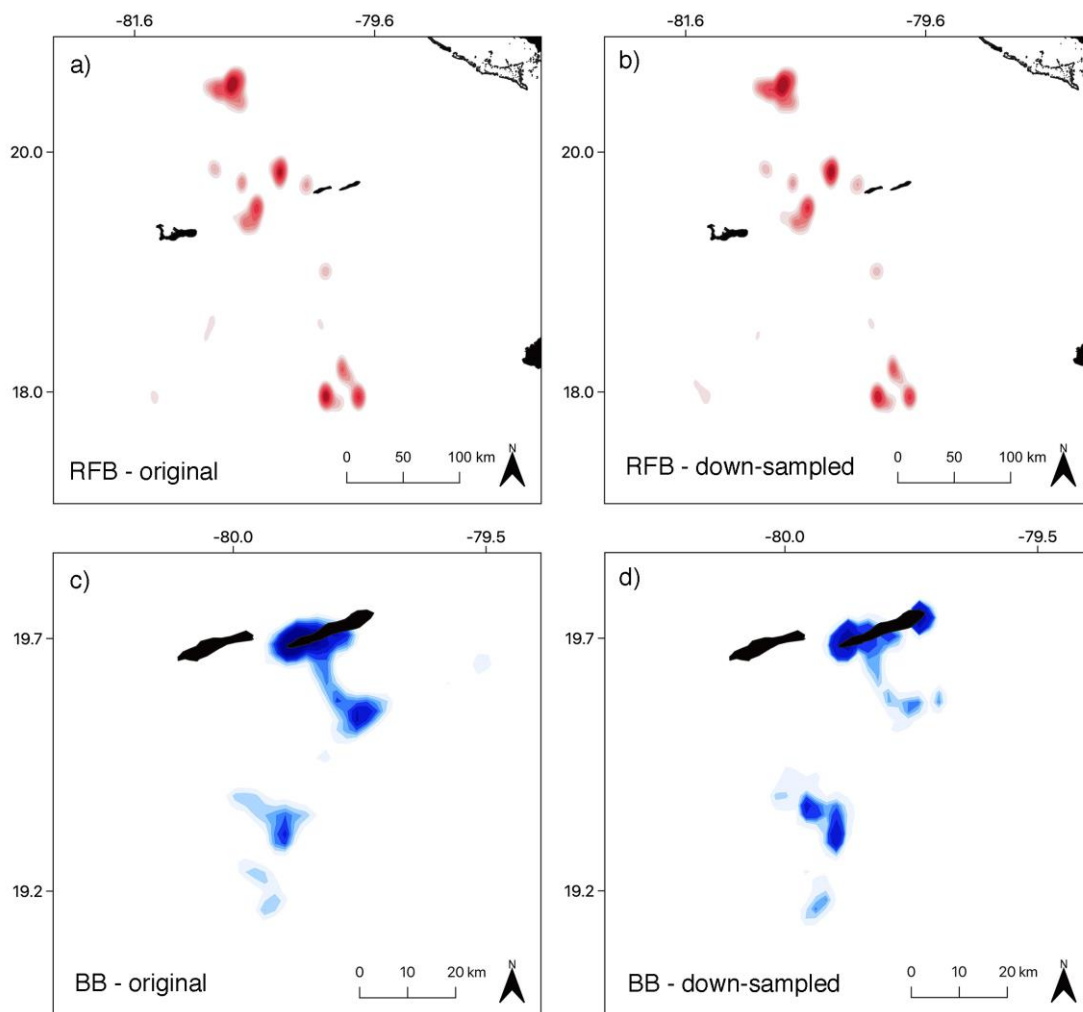
Fig S1. Comparison of Kernel Density Estimates of foraging locations from a-b) red-footed boobies ($n = 3$) and c-d) brown boobies ($n = 3$) for the same foraging trips processed at different sampling rates prior to curvilinear interpolation. Original = 30 s interpolated GPS locations recorded at ~30-40 s intervals prior to interpolation. Down-sampled = 30 s interpolated GPS locations down-sampled to ~2 min intervals from 'original' data prior to interpolation.

For both species, the majority of foraging tracks were recorded at ~30-40 s resolution (RFBs = 92% of birds, BB = 60% of birds). However, to investigate whether inclusion of 2 min tracks influenced the resulting Kernel Density Estimates (KDE) of foraging trips, we undertook the following analysis: Three tracks for each species recorded at ~30-40 s resolution were randomly selected. We then compiled two sets of data for each individual prior to interpolating the data to the same time intervals: 1) 'original' data recorded at ~30-40 s intervals and 2) 'down-sampled' versions of 'original' data that had been sub-sampled to ~2 minute intervals. Both sets of data were then interpolated to 30 s intervals, and behavioural states were estimated for locations using 3-state Hidden Markov Models following the method described for the full GPS dataset in the main text. For each species, locations estimated to be associated with foraging were then used to create KDEs for the two datasets. Bhattacharyya's affinity was calculated as a measure of overlap between 50% and 90% kernel contours, and for both species there was little difference in the resulting KDEs (BA overlap: RFBs, 50% KDE contour = 99%, 90% contour = 99%; BBs, 50% contour = 67%, 90% contour = 85%). Thus, we concluded that inclusion of the different sampling rates did not result in misleading interpretations about levels of segregation and space use between our two study species (Fig S1).

Appendix S3 - Discriminant Function Analysis

We trained a Discriminant Function Analysis (DFA) on morphometric measurements from RFB individuals of known sex (classified using DNA sexing; n = 69), in order to predict the sex of RFBs that blood or feather tissue were not collected from. The morphometric measurements used in the DFA were chosen from a pool of candidates (mass, wing length, bill length, bill depth, bill width, tail length, tarsus length) using a Wilks Lambda stepwise forward variable selection method. The variables that contributed significantly to separating the two sexes were body mass, wing length and bill length. The DFA on training data (containing birds of known sex) correctly assigned 94% of individuals to their true sex (Wilks' Lambda = 0.357, F = 39.07, P < 0.001; Table S2). Similarly, a leave-one-out cross validation on the data had 93% accuracy. The discriminant function obtained from this analysis was then used to predict the sex of 10 unsampled birds (3 of which had matching spatial data), and the assignments were used in subsequent analyses. Fisher's classification coefficients for the two sexes are given in equations 1 and 2.

Table S2. Outputs of a Discriminant Function Analysis on training data using morphometric measurements (wing length, bill length and body mass) of red-footed boobies of known sex. Proportions of males and females that were accurately assigned to their true sex are shown. Numbers in brackets show frequencies.

		Predicted	
		Female	Male
Actual	Female	0.96 (27)	0.04 (1)
	Male	0.07 (3)	0.93 (38)

Fisher's classification coefficients:

Equation S1.
$$D_{Female} = 0.043 * Mass + 4.502 * WingLength + 0.124 * BillLength - 1455.604$$

Equation S2.
$$D_{Male} = 0.008 * Mass + 4.379 * WingLength + 12.046 * BillLength - 1345.112$$

Table S3. Summary of the morphometric characteristics (mean ± SD) of adult red-footed boobies (n, F = 28, M = 41) and brown boobies (n, F = 25, M = 33) from breeding populations on the Cayman Islands. The mean percent difference between metrics for females and males, and effect sizes (Cohen's d) for species (d_{spp}) and sex (d_{sex}) comparisons are shown. All measurements except body mass are given in mm. Parameters from generalised least squares (GLS) models and linear models to compare between species and sex are shown.

Species	Sex	Mass (g)**	Tarsus length*	Wing length*	Bill length*	Tail length
Red-footed booby	Female	914 ±49	36.3 ±2.4	395 ±10	87.9 ±2.8	231 ±18
	Male	795 ±55	35.0 ±1.9	380 ±9	84.6 ±2.4	232 ±15
	All	**843 ±78.5**	**35.5 ±2.2**	**386 ±12**	**85.9 ±3.0**	**231 ±16**
	% size diff.	15.0	3.7	4.0	3.9	0.4
	d_{sex}	2.3 (1.6 – 2.9)	0.7 (0.2 – 1.2)	1.6 (1.1 – 2.2)	2.4 (2.0 – 2.9)	-0.1 (-0.5 – 0.4)
Brown booby	Female	1213 ±96	47.6 ±4.4	417 ±7	100.7 ±8.1	200 ±11
	Male	982 ±98	46.1 ±3.3	397 ±10	96.2 ±4.7	201 ±10
	All	**1081 ±151**	**46.8 ±3.8**	**406 ±13**	**98.2 ±6.7**	**201 ±10**
	% size diff.	23.5	3.3	5.0	4.7	0.5
	d_{sex}	2.4 (1.7 – 3.1)	0.4 (-0.2 – 0.9)	2.3 (1.6 – 3.0)	0.7 (0.2 – 1.2)	-0.1 (-0.6 – 0.4)
	d_{spp}	2.0 (1.6 – 2.5)	3.7 (3.1 – 4.3)	1.6 (1.2 – 2.0)	1.3 (0.8 – 1.8)	-2.2 (-2.6 - -1.7)
LRT (p)	Species	93.75 (<0.001)	131.30 (<0.001)	96.76 (<0.001)	152.32 (<0.001)	96.73 (<0.001)
	Sex	99.78 (<0.001)	9.53 (0.002)	82.49 (<0.001)	12.57 (0.002)	0.169 (0.681)
	Sex:Species	224.95 (<0.001)	---	---	---	---

***Models with terms for Species, Sex, **Model with terms for Species, Sex and Species:Sex. A correlation structure to allow unequal variances for species was used for tarsus, mass and tail length models, and correlation structures for both species and sex were used for bill length (GLS models). No correlation structure was needed for wing length (linear model).

Appendix S4 - Behavioural classification in booby foraging trips

Hidden Markov Models, based on correlated step lengths and turning angles, were fit to estimate behaviour in foraging tracks of RFBs and BBs and identify foraging bouts for use in further analyses (R package 'momentuHMM'). Model-estimated states were validated using dive and immersion data from a subset of individuals simultaneously tracked with TDR (dive activity) and GLS (immersion patters) loggers. Following a comparison of the negative log-likelihood values of candidate models with between 2 and 5 states (see model selection methods outlined in Dean et al 2013), HMMs with 3 hidden states were used to estimate behaviour.

Table S4. Mean ($\pm$ SD) step lengths, and concentrations of turn angles, for the three states classified by HMMs for GPS-tracked red-footed boobies and brown boobies.

	Red-footed booby		Brown booby	
HMM state	Step length (km)	TA Conc.	Step length (km)	TA Conc.
Travel - 1	0.30 ± 0.06	38.03	0.30 ± 0.09	38.16
Forage - 2	0.08 ± 0.09	1.19	0.11 ± 0.08	1.68
Rest - 3	$0.01 \pm {<}0.01$	14.06	0.01 ± 0.01	0.72

RFB	1	2	3
1	0.963	0.037	<0.001
2	0.024	0.931	0.045
3	<0.001	0.057	0.944

BB	1	2	3
1	0.937	0.063	<0.001
2	0.050	0.912	0.038
3	<0.001	0.044	0.955

State at t (row labels, both matrices)

Table S5. State transition matrix from the three-state Hidden Markov Model, showing the probability of changing from state at time t to state at time t +1. State, 1 = travel, 2 = forage, 3 = rest. Proportion of locations assigned to states: RFB, 1 = 0.27, 2 = 0.41, 3 = 0.32; BB, 1 = 0.31, 2 = 0.38, 3 = 0.32.
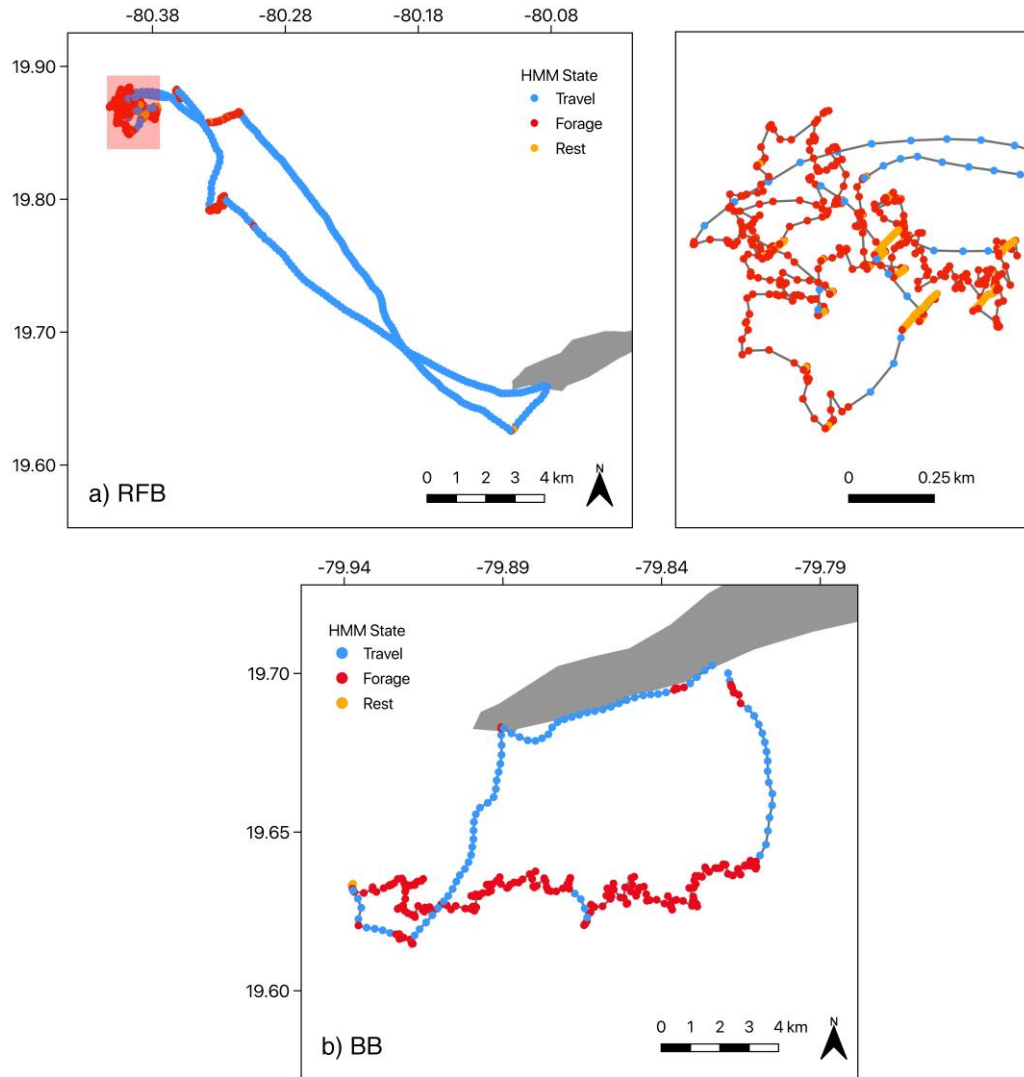
Fig. S2 Example tracks from a a) red-footed booby (RFB) and b) brown booby (BB), coloured according to behavioural states estimated from 3-state HMMs. The pink box in the left RFB figure highlights the position of the zoomed in figure on the right.

Table S6. The proportion of GPS locations associated with dive activity (Dives$_p$; n birds, RFBs = 8, BBs = 18), and the mean (± SD) proportion of time spent on-water in 30 s sections of GPS tracks (OW$_t$; n birds, RFBs = 10, BBs = 13), for the three behavioural states estimated by Hidden Markov Models (HMM).

State	RFB		BB	
	Dives$_p$	OW$_t$	Dives$_p$	OW$_t$
Travel	0.13	0.01±0.02	0.15	0.02±0.02
Forage	0.77	0.39±0.14	0.80	0.17±0.11
Rest	0.10	0.98±0.03	0.05	0.44±0.44
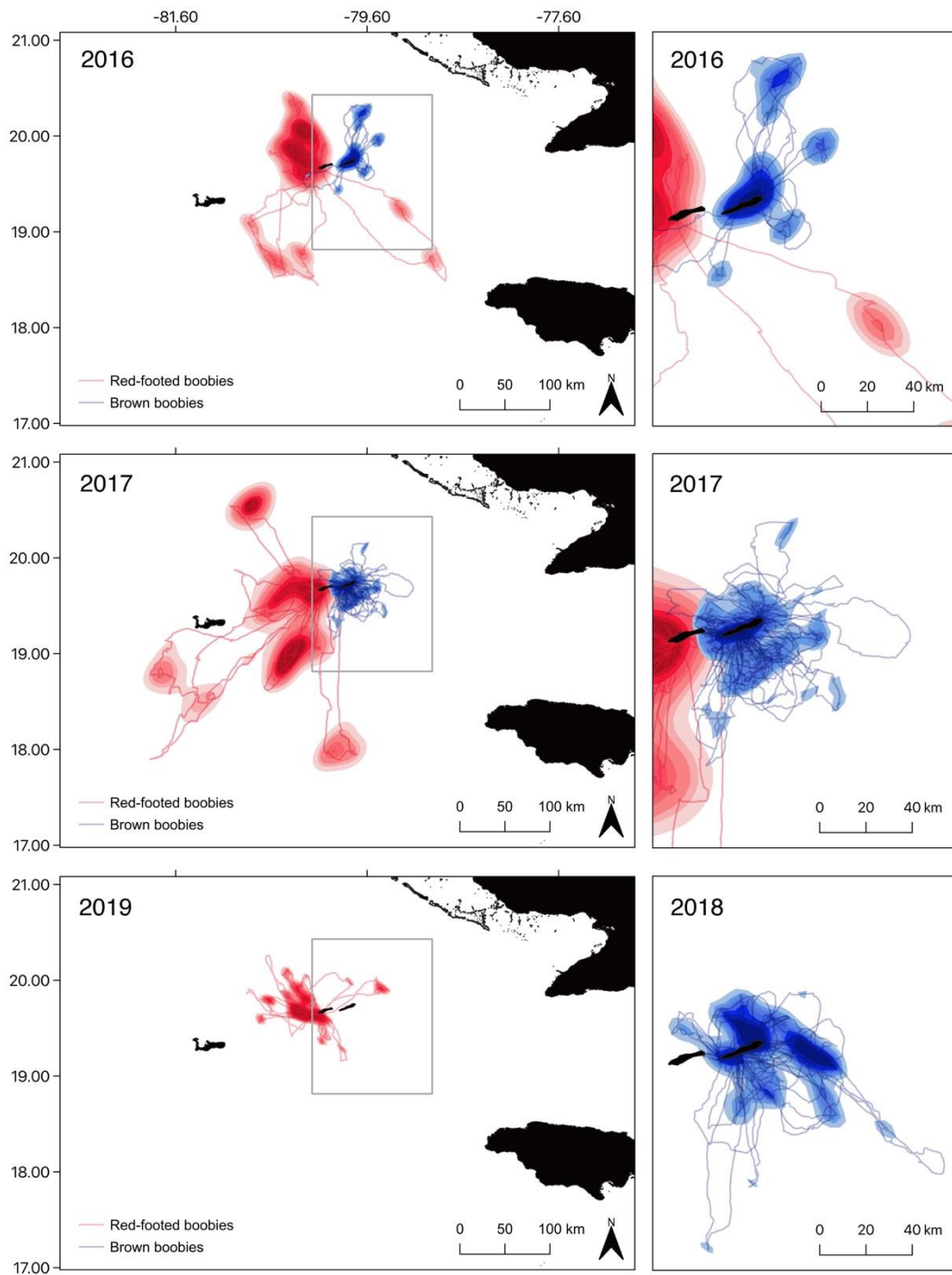
Fig. S3 Foraging tracks and Kernel Density Estimates of red-footed boobies and brown boobies, tracked with GPS from neighbouring populations in the Cayman Islands during breeding seasons between 2016 and 2019. Data are presented separately for each tracking year. Only BBs were tracked in 2018 and only RFBs in 2019 (bottom row).

Appendix S5 - Trip clustering

A PCA was run on rescaled trip characteristics to identify collinearity and redundancy, and extract appropriate variables for further clustering of foraging trips. All variables contributed relatively equal contributions to the first principle component (PC1), with the exception of 'mean underlying bathymetry', which also contributed little to the second principle component (PC2). Trip duration contributed >42% to PC2 (Fig S4). Trip duration (TripDuration_hr), mean distance to nearest coastline (meanNDist) and maximum distance (Maxdist) were chosen for use in subsequent analysis. While trip duration and maximum distance were correlated, incorporation of both variables improved the clustering and allowed us to mitigate potential errors introduced by averaging 'distance to nearest coastline' within tracks.
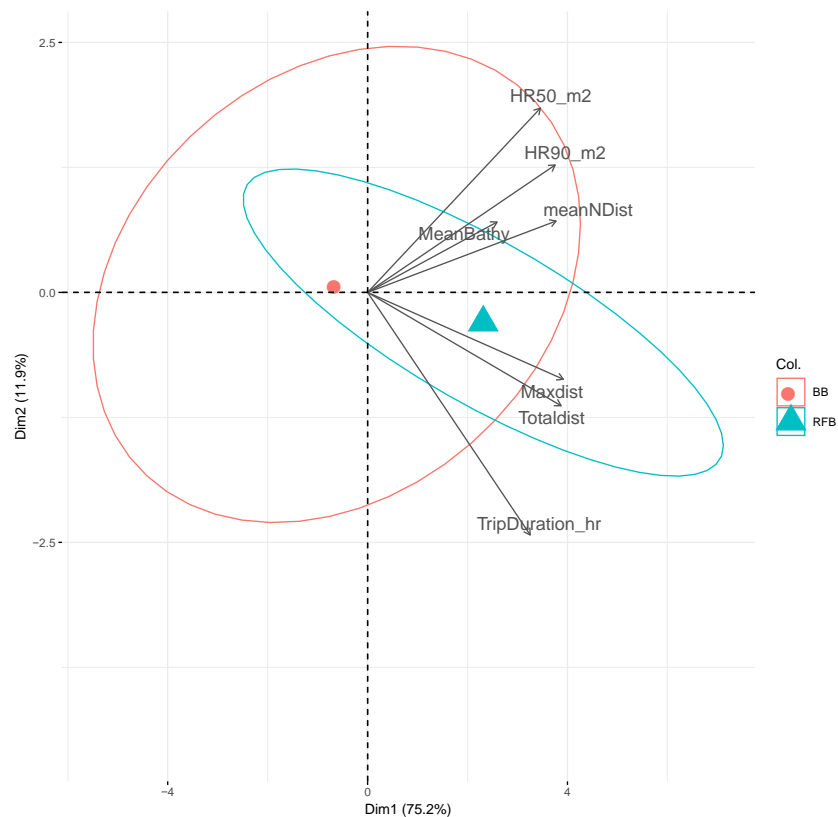
Fig S4. PCA biplot showing the variables used in the analysis (indicated with arrows and labels) and position of individual data points coloured according to species (BB = red, RFB = blue). 95% ellipses are given for the two species. Arrow lengths from the origin indicate the quality of each variable on the map and representation on the principle components.
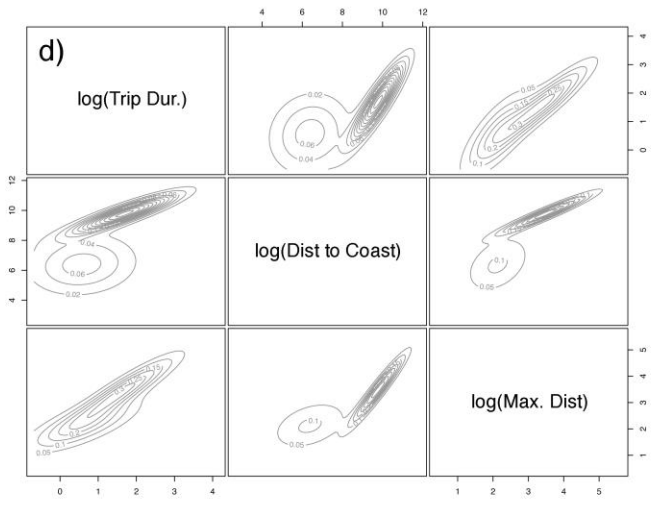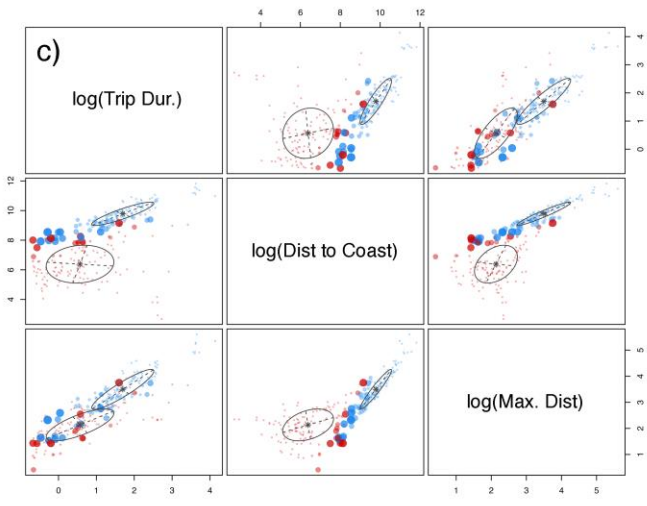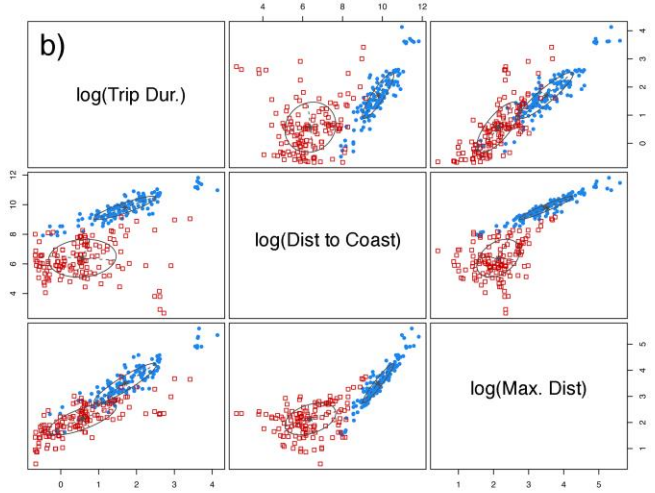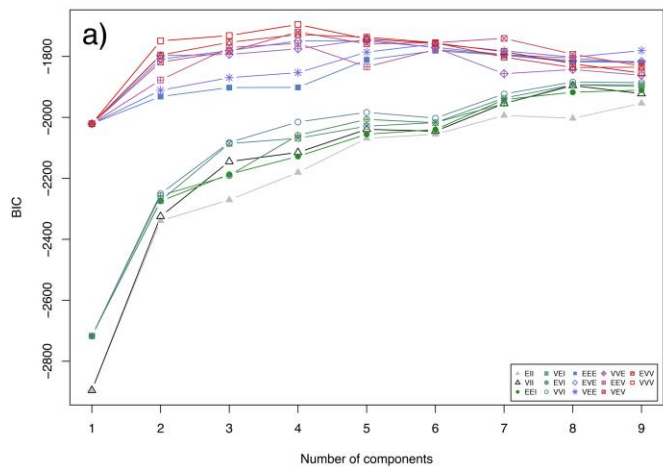
Fig. S5 Results from Gaussian Mixture Model (GMM) selection procedures, and outputs of the final two-state model. a) Bayesian Information Criteria (BIC) for candidate GMMs with 1 to 9 components, b) GMM-assigned clusters based on 'trip duration', 'mean distance to nearest coastline' and 'maximum distance', c) uncertainty of belonging to one of the two GMM-assigned clusters and d) estimated density based on 'trip duration', 'mean distance to nearest coastline' and 'maximum distance'. State: blue = 1, red = 2.

Appendix S6 – Isotopic discrimination

Table S7 Published carbon and nitrogen stable isotope discrimination factors between seabird blood to prey muscle tissue.

Seabirds	Diet	Diet tissue	Avian tissue	Condition	*n*	Δ15N	Δ13C	Source
Ring-billed gull (Larus delawarensis)	Perch†	Whole*	Whole blood	Captive	14	3.1±0.2	0.3±0.8	Hobson & Clark, 1992
Greak skua (*Catharacta skua*)	**Sprat**	**Whole***	**Whole blood**	**Captive**	**9**	**2.8**	**1.1**	**Bearhop et al., 2002**
	Beef	NA	Whole blood	Captive	9	4.2	2.3	Bearhop et al., 2002
King penguin (*Aptenodytes patagonicus*)	**Herring**	**Muscle***	**Whole blood**	**Captive**	**10**	**1.23**	**-0.61**	**Cherel et al., 2005**
		Whole*	Whole blood	Captive	10	2.07	-0.81	Cherel et al., 2005
Rockhopper penguin (*Eudyptes chrysocome*)	**Capelin**	**Muscle***	**Whole blood**	**Captive**	**9**	**1.86**	**0.46**	**Cherel et al., 2005**
		Whole*	Whole blood	Captive	9	2.72	0.02	Cherel et al., 2005
Rhinoceros auklet (*Cerorhinca monocerata*) ††	Silverside	Whole	Red blood cells	Captive	18	2.84-3.49		Sears et al., 2009
Mean ± SD (lipid extracted, marine diet, adults)^						**1.96 (±0.79)**	**0.32 (±0.86)**	

*Lipid extracted tissue; †also fed vitamin supplements; ††blood sampled from chicks & juveniles.

^Mean ± SD calculated from studies with lipid-corrected carbon isotope values from adults fed on a marine diet

Table S8 Fledgling success (number of eggs that hatched and fledged / total number of eggs laid) of experimental and control nests for red-footed boobies and brown boobies from colonies on the Cayman Islands. Sample sizes are given in brackets. Bold treatments in each column are those used for statistical comparisons.

Treatment	Brown boobies			Red-footed boobies		
	2016	2017[†]	2018[†]	2016	2017	2019
Control	**0.93 (43/46)**	**1.00 (13/13)**	**0.79 (15/21)**	**0.78 (32/41)**	**0.32 (52/163)**	**---**
Experimental	---	**0.96 (27/28)**	**---**	---	**0.71 (24/34)**	**1.00 (24/24)**
GPS	**1.00 (11/11)**	1.00 (11/11)	---	**0.82 (23/28)**	0.82 (9/11)	1.00 (14/14)
Combined	---	0.94 (16/17)	**0.95 (19/20)^**	---	0.65 (15/23)	1.00 (10/10
P	1.000	1.000	0.093	0.767	<0.001	---
Power	0.06	0.07	0.07	0.89	0.99	---

[†]Control group consisted of birds monitored over the same time period as tracked nests; ^Fledging data not collected for one study nest in 2018.

Appendix S8 – Tracking

Table S9 Summary of tracked red-footed boobies and brown boobies during the study. The number of working loggers recovered is given in brackets.

	Brown boobies			Red-footed boobies		
Tags	2016	2017	2018	2016	2017	2019
GPS	13 (8)	36 (32)	36 (28)	20 (11)	36 (13)	24 (7)
TDR	---	18 (15)	12 (12)	---	27 (18)	10 (2)
GLS	---	18 (15)	---	---	24 (17)	---
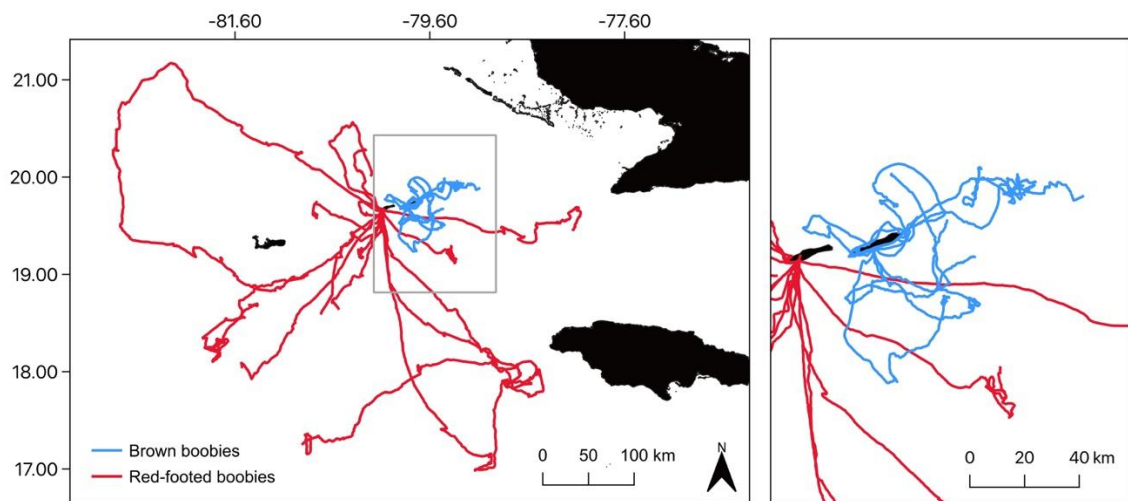
Fig. S6 Partial foraging trips for red-footed boobies (red; $n = 14$) and brown boobies (blue; $n = 13$) tracked with GPS loggers between 2016 and 2019.
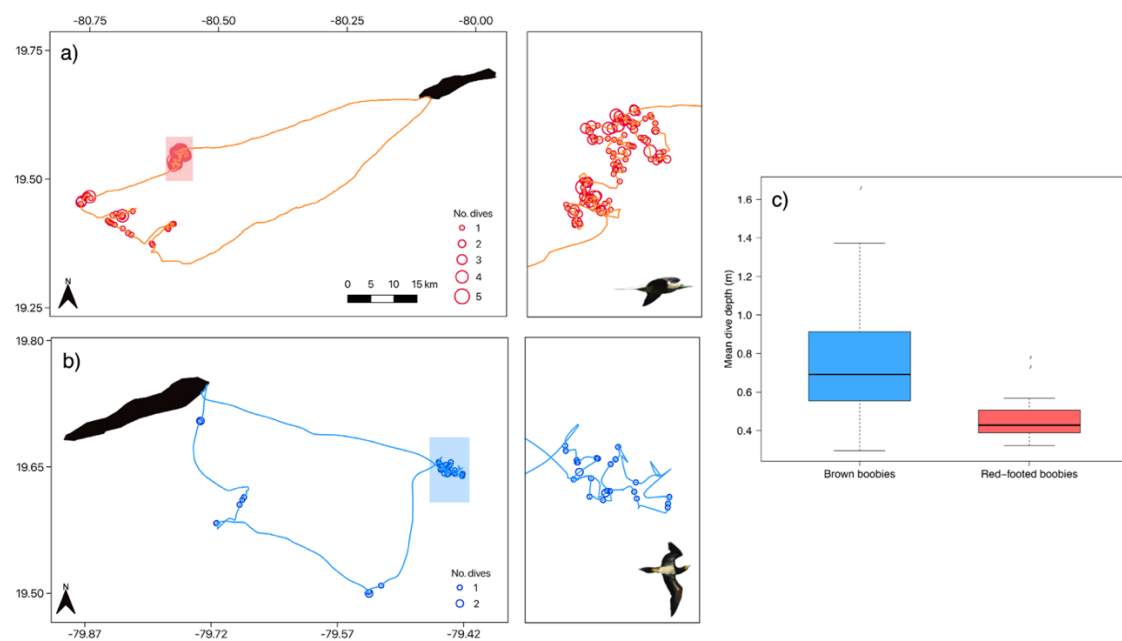
Fig. S7 Example tracks of a) red-footed boobies and b) brown boobies, showing the spatial distribution and number of dives (circles), and c) the distribution of maximum dive depths for the two species (red = red-footed boobies, $n = 8$; blue = brown boobies, $n = 18$).
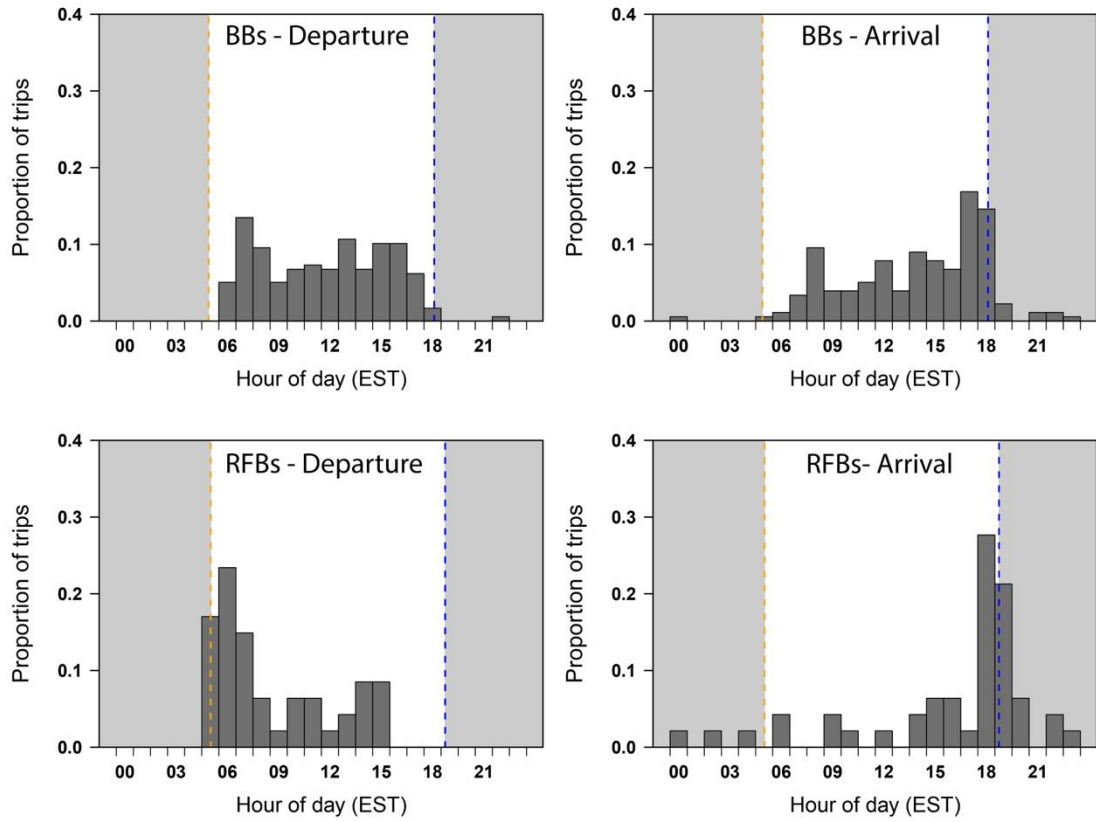
Fig. S8 Departure and arrival times of foraging trips from breeding red-footed boobies and brown boobies, tracked with GPS loggers from populations on the Cayman Islands between 2016 and 2019. Dotted lines show average dawn (orange) and dusk (blue) times over tracking periods.

Appendix S9 – Kleptoparasitism

Table S10. Summary of kleptoparasitic interactions between magnificent frigatebirds (FB) and video-instrumented brown boobies from the Cayman Islands.

Attempt	Date	Bird ID	Start time	Dur (s)	FB Life Stage	No. FBs	Evasive Landing	Victim	Body Contact	Coast dist. (km)
1	19/02/2018	1	10:34:00	31	I	1	Y	F	N	NA
2	19/02/2018	1	13:20:36	7	A	2	Y	F	N	NA
3	20/02/2018	2	09:33:26	14	A	1	N	C/F	Y - wing	1.5
4	17/02/2018	3	11:36:35	8	I	1-2	Y	F	Unknown	12.9
5	23/02/2018	4	12:00:43	32	A	1	Y	F	N	0.4
6	23/02/2018	4	12:08:20	30	A	3	Y	F	Unknown	0.5
7	23/02/2018	4	12:10:39	6	A	1	Y	F	Unknown	0.5
8	23/02/2018	4	12:12:28	45	A	1	Y	F	Y - bill/wing	0.5
9	23/02/2018	4	12:14:28	6	A	1	Y	F	N	0.5
10	23/02/2018	4	14:11:26	4	A	1	Y	F	N	0.5
11	22/02/2018	5	17:51:14	36	A	1	Y	F	Unknown	0.8
12	22/02/2018	5	17:52:43	4	A	1	Y	F	N	0.9

A = adult, I = immature; C = conspecific, F = focal booby, Dur = duration, Coast dist . = distance to nearest coastline.
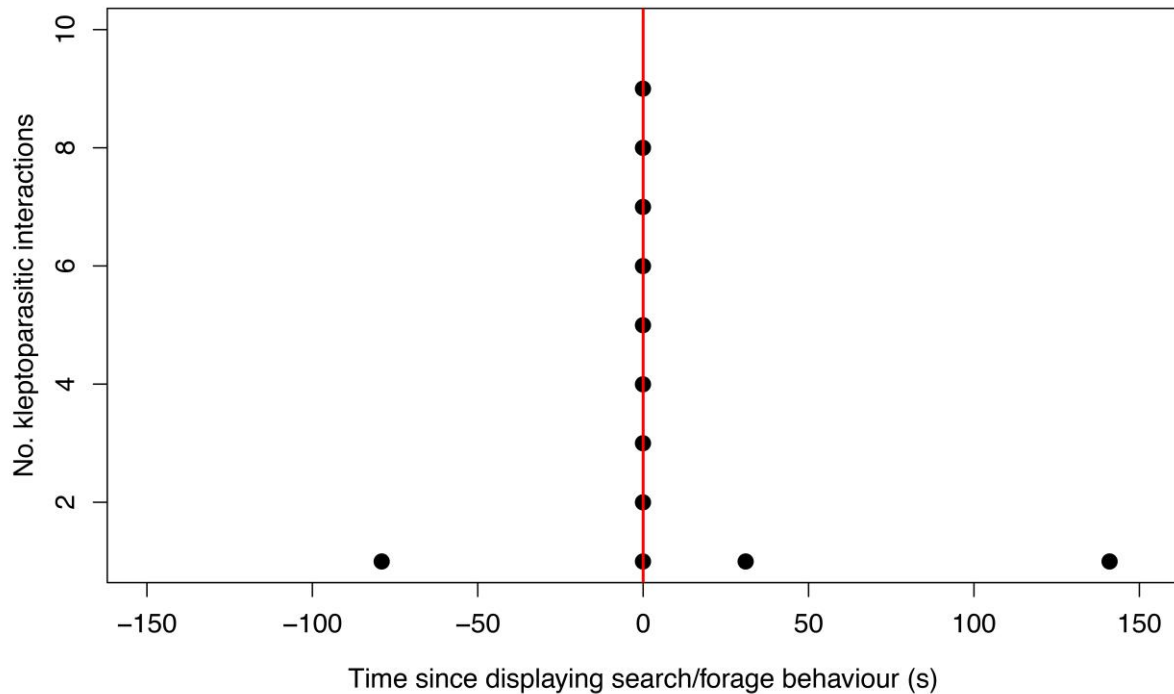
Fig. S9 Time that video-instrumented brown boobies were assessed as engaging in search or foraging behaviour relative to the start of kleptoparasitic interactions with magnificent frigatebirds (red line; $n = 12$).

Appendix S10 - Summary of diet

Table S11 Contribution of different prey types to the diet of red-footed boobies ($n = 15$) and brown boobies ($n = 30$) as found in regurgitate samples collected between 2016 and 2018. The numerical abundance (N%; the percentage of a prey type out of all prey sampled) and frequency of occurrence (O%; the percentage of birds with a prey type present in their regurgitate) of each prey type is given.

Prey type*	Red-footed boobies						Brown boobies					
	♀ ($n = 6$)		♂ ($n = 6$)		All ($n = 15$)		♀ ($n = 18$)		♂ ($n = 9$)		All ($n = 30$)	
	N%	O%	N%	O%	N%	O%	N%	O%	N%	O%	N%	O%
BH	13	17	12	17	11	13	43	72	14	44	33	63
FF	54	67	65	83	60	73	24	56	12	56	20	53
DF	0	0	0	0	0	0	0	0	2	11	1	3
TU	13	33	0	0	9	20	1	6	14	44	6	20
MS	0	0	0	0	0	0	17	6	0	0	10	3
SQ	20	17	6	17	11	13	0	0	5	11	2	3
NF	0	0	0	0	0	0	7	17	10	33	7	20
TF	0	0	0	0	0	0	0	0	2	11	1	3
UN	0	0	17	33	9	13	8	6	41	33	20	17

*BH = ballyhoo, FF = flying fish, DF = dolphinfish, TU = Tuna, MS = mackerel scad, SQ = squid, NF = needlefish, TF = Triggerfish, UN = unidentified. Birds of unknown sex = 3x red-footed booby, 3x brown booby.

CHAPTER IV: the role of weather

Influence of rainfall on foraging behavior of a tropical seabird

Behavioral Ecology, in press.

A cloud front arrives over a brackish mangrove pond on Little Cayman (Cayman Islands), a habitat typically exploited by frigatebirds (*Fregata magnificens*). Picture: F. De Pascalis.

Original Article

Influence of rainfall on foraging behavior of a tropical seabird

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Acquiring resources for self-maintenance and reproduction is a key challenge for wild animals, and the methods that individuals employ are, in part, shaped by environmental conditions that vary in time and space. For birds, rainfall may affect behavior, impairing senses and increasing energetic costs, but its consequences on movement patterns are poorly explored. We investigated the influence of rainfall on the foraging behavior of the magnificent frigatebird, *Fregata magnificens*. This peculiar tropical seabird lacks feather waterproofing and is known to track environmental conditions while searching for food. Thus, its foraging behavior should be highly sensitive to the effects of rainfall. By GPS-tracking chick-rearing adults, we showed that frigatebirds did not avoid areas with rainfall during foraging trips, nor did rainfall influence trip characteristics. However, rainfall decreased time devoted to foraging and increased time spent perching. Moreover, it affected flight mode, inducing birds to fly slower and at lower altitudes. Wind speed, which was not correlated with rainfall, only affected behavior during night-time, with strong winds decreasing time spent perching. Our results indicate that rainfall does not affect the spatial distribution of foraging frigatebirds but does alter fine-scale foraging behavior by reducing flight activity. We suggest that the ongoing environmental change in this region, including an increase in rainfall events, has the potential to impair foraging and negatively affect fitness.

Key words: environmental drivers, Hidden Markov Models, magnificent frigatebird, precipitation, Resource Selection Function, spatial behavior, wind speed.

INTRODUCTION

Wild animals must overcome a range of challenges to maximize their fitness. Locating ample food is one such challenge, essential not only for survival but also for successfully rearing offspring, evading predators, and migrating (Kramer 2001). The search for food can favor cooperation between individuals (Dumke et al. 2018), such as social information exchange (Hasenjager et al. 2020), potentially leading to drastic changes in species' ecology (Lancaster et al. 2000). Acquiring ample resources is however hindered by several factors, including inter- and intra-specific interactions (e.g.,

competition and predation: Ashmole 1963; Krebs 1980), physiological constraints, prior experience (Smith and Metcalfe 1994; Aubret et al. 2015), luck (Wilson et al. 2018) and environmental conditions. The latter include climatic and atmospheric components, which can act indirectly on foraging by affecting trophic interactions, influencing food webs, and potentially driving long-term change in communities (Zhang et al. 2007; Bogdziewicz et al. 2020). Moreover, environmental conditions can alter foraging behavior more directly, promoting or disrupting foraging activities at fine spatial and temporal scales, by affecting the timing of feeding (e.g., ground air temperature: Kasper et al. 2008) or selection of foraging areas (Sunde et al. 2014; Udyawer et al. 2015). In birds, weather conditions and landscape features are well-known drivers of foraging behavior (Duerr et al. 2015; Scacco et al. 2019; Ventura

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et al. 2020), with a growing number of studies demonstrating flexibility in the behavioral responses to a varying external environment (Clay et al. 2019; Cecere et al. 2020; De Pascalis et al. 2020).

Rainfall is a key weather component, known to affect avian activity and movement patterns (Elkins 2010). Wet plumage can result in severe heat loss (Stalmaster and Gessaman 1984; Wilson et al. 2004), impair locomotor performance and flight capabilities, and increase body mass and consequently wing loading (Mahoney 1984; Ortega-Jiménez et al. 2010; Ortega-Jimenez and Dudley 2012a), all conditions that are expected to increase energy expenditure (Hertel and Ballance 1999). In addition to direct effects on energy expenditure, rainfall has the potential to impair vision and hearing, reducing the perceptive accuracy of the surrounding environment (Yorzinski 2020). Overall, rain can reduce foraging efficiency in several ways, for example by impairing the localization of prey, inhibiting detection of predators and thus increasing the need for vigilance, or inducing shifts in preferred foraging areas (Hilton et al. 1999; Sergio 2003; Whittingham et al. 2004; Fernández-Juricic 2012).

Despite its potential to disrupt foraging and alter time-activity budgets, the behavioral strategies that birds have evolved to cope with rainfall are poorly investigated. Avoidance of rain by sheltering has been documented (e.g., Cauchard and Borderie 2016; Wilkinson, et al. 2019), especially in the tropics where intense but transient downpours can take place (Elkins 2010). If sheltering is not possible due to habitat and/or body size (e.g., large raptors), individuals can remain perched to minimize exposure to rain (Elkins 2010). Relocating to more distant areas, to avoid strong rain and wind, has been observed in some species prior to the arrival of perturbation fronts, as birds are believed to be capable of sensing—to some extent—the arrival of storms (Blomqvist and Peterz 1984; Streby et al. 2015; Weimerskirch and Prudor 2019). Finally, some species have evolved morphological or behavioral adaptations to cope with rainfall. For example, birds with high feeding rates such as hummingbirds can actively fly and forage in the rain, using both aerial and perched shaking techniques to expel water from their plumage (Ortega-Jimenez and Dudley 2012b). While most of the existing studies provide anecdotal evidence for behavioral responses to rainfall, or performed investigations at the foraging trip level (Pistorius et al. 2015; Lane et al. 2019), a fine-scale understanding of the influence of rain on foraging behavior, particularly during energy-demanding periods of the life cycle such as chick-rearing, is currently lacking.

Frigatebirds are intriguing candidate species to investigate the effect of rainfall on foraging, given their ecology and life-history traits. They are large-bodied marine predators (1–1.9 kg; Diamond and Schreiber 2002) widely distributed across the tropics, an area that experiences fluctuating and sometimes heavy rates of rainfall (Mandeep et al. 2011). Owing to their unusual morphological characteristics (limited feather waterproofing and partially webbed feet), frigatebirds are obligate opportunistic surface feeders that rely heavily on visual cues to detect prey (Diamond and Schreiber 2002). They are highly efficient flyers due to their low wing loading (Weimerskirch et al. 2004) and are thus capable of ranging over large distances to search for food (Weimerskirch et al. 2016; Austin et al. 2019). Furthermore, they are known to track environmental components such as frontal regions and transport fronts to increase foraging opportunities (Tew-Kai et al. 2009; De Monte et al. 2012) and may be one of the few bird species able to ride out a storm (Cramp and Simmons 1977). While provisioning offspring, frigatebirds behave as central-place foragers, implying that they have spatial and temporal constraints on their movements (Orians and Pearson 1979). To meet the high energetic demands associated with this phase of

the life cycle, frigatebirds are expected to adjust foraging behavior to maximize efficiency in the spatiotemporally variable environments that they exploit (Weimerskirch et al. 2003a; De Monte et al. 2012). However, their functional traits may render them particularly susceptible to foraging disruption caused by rainfall.

In this study, we investigated whether rainfall alters the foraging behavior of chick-rearing magnificent frigatebirds (*Fregata magnificens*, hereafter referred to as "frigatebirds"). Assuming that searching for food under rainy conditions results in increased energy expenditure, and given that frigatebirds show some capability to anticipate the arrival of perturbation fronts (Weimerskirch and Prudor 2019), we hypothesize that chick-rearing frigatebirds should: 1) avoid foraging in areas subjected to heavy rainfall; and 2) modify their at-sea behavior when encountering rain. The latter could be achieved by a) increasing flight height above the rainy cloud front and avoiding rainfall (frigatebirds are capable of flying at very high altitudes; Weimerskirch et al. 2003b) or b) reducing activity until the unfavorable conditions are over. Rainfall events can be associated with light-to-strong changes in wind intensity, since clouds form in frontal depression systems where air masses move (Ahrens 2011). Thus, to account for confounding effects of wind speed on fine-scale behavioral responses to rain, we included wind speed in our analysis.

MATERIALS AND METHODS
Animal capture, handling, and data preparation

During the main chick-rearing periods (February to May) in 2017 and 2019, 44 (2017: $n = 22$; 2019: $n = 22$) breeding adults were equipped with solar-powered GPS-GSM biologgers (Movetech Telemetry) at a colony on Little Cayman, Cayman Islands, in the Central Caribbean (19° 39.8'N, 80° 4.9'W). Individuals were caught on the nest with a noose-pole, and devices were attached to a small number of contour feathers on the back using waterproof tape (mean ± SD handling duration: 15 ± 3 min). In all cases, birds were observed returning to attend the chick shortly after release. Owing to difficulties in recapturing birds after first capture, loggers were not retrieved and were assumed to have been shed when transmissions ceased. Devices were set to record positions on three dimensions (latitude, longitude, and altitude) every 15 min. Device mass ranged between 23.2 and 25.8 g, and relative device load (including attachment) was 2.9 ± 0.4 % (mean ± SD) of body mass. To assess the potential impact of handling and device attachment, we recorded breeding success (proportion of nests that fledged a chick) of all experimental nests and a group of unhandled control nests. No significant difference in fledging success of experimental and control nests was observed (2017: Austin et al. 2019; 2019: control, $n = 99$, fledging success = 0.63; experimental, $n = 22$, fledging success = 0.45, Fisher's exact test, $P = 0.16$, odds ratio = 0.50, power = 0.27). Fieldwork was performed under permissions of the Department of Environment, Cayman Islands Government and National Trust of the Cayman Islands.

Foraging trips were identified as movements ≥1 km from the colony, lasting ≥ 30 min (Austin et al. 2019). Incomplete trips and very short trips (≤2–3 locations; $n = 33$), likely to represent colony-based movements inside the reef, were also removed from further analyses. Only foraging trips undertaken when the tracked bird was actively rearing a chick were retained. For birds that lost their chick during the tracking period, we only included trips performed before the last date the chick was recorded alive. Duplicate and unrealistic locations based on derived ground speed were identified and

removed using the "SDLfilter" R package (Shimada 2019). Overall, we obtained information on 517 complete foraging trips from 33 birds (15 males and 18 females; mean ± SD; trip duration: 30 ± 43 hours; foraging trips per individual: 16 ± 35; Figure 1). The tracking period spanned March to late May in 2017 (*n* = 14 individuals) and March to late October in 2019 (*n* = 19 individuals). GPS locations were matched to gridded environmental data (cell size: 0.25° × 0.25°; ~27 km × 27 km, temporal resolution: 1 h). Precipitation data (mm/h, a measure of rainfall), and both U and V wind component data, from the ERA5 dataset (Hersbach et al. 2020) were downloaded from the Copernicus Climate Change Service (https://cds.climate.copernicus.eu/cdsapp#!/home). Wind speed (m/s) was then derived from U and V wind components using the "rWind" R package (Fernández-López and Schliep 2019).

Statistical analyses

Effect of rainfall on spatial distribution

A Resource Selection Function (RSF) approach was used to investigate whether frigatebirds avoided areas with high rainfall during foraging trips. Environmental features at locations visited by the animal (i.e., "used locations") were compared to the features at a set of random locations drawn from an area assumed to be available to the animal (i.e., "available locations") (Muff et al. 2020). Defining

an availability domain for frigatebirds is challenging, since they are long-distance foragers that exploit a wide range of environments, including pelagic waters, coasts, islands, and inland areas (see Austin et al. 2019). Therefore, to achieve the highest possible ecological realism, we generated two sets of random locations by rotating each foraging trip (anchored at its initial location, i.e., the colony site) by a randomly selected angle (Freeman et al. 2010; Cecere et al. 2018). For each real trip, we calculated the proportion of locations falling on land, and then constrained each rotated trip to have a similar number of locations on land (± 10%). If the original trip had less than 10% of locations on land, we allowed the rotated trip to fall entirely over sea. If the above conditions were not met after 1000 iterations of random rotations, the trip was discarded (*n* = 46). This approach allowed us to work on raw presence data, and prevented biases being introduced by any unrealistic overlap with—or absence of—land. We generated two rotated trips for each real trip, confirming that these were different from each other by visual inspection. For both the real and simulated trips, the time of each location was rounded to the nearest hour, and the most central location in each hourly time bin was retained with all others discarded. This method was followed to avoid excessive temporal autocorrelation between subsequent consecutive locations and to ensure that the temporal resolution of rainfall data matched that of the GPS data.
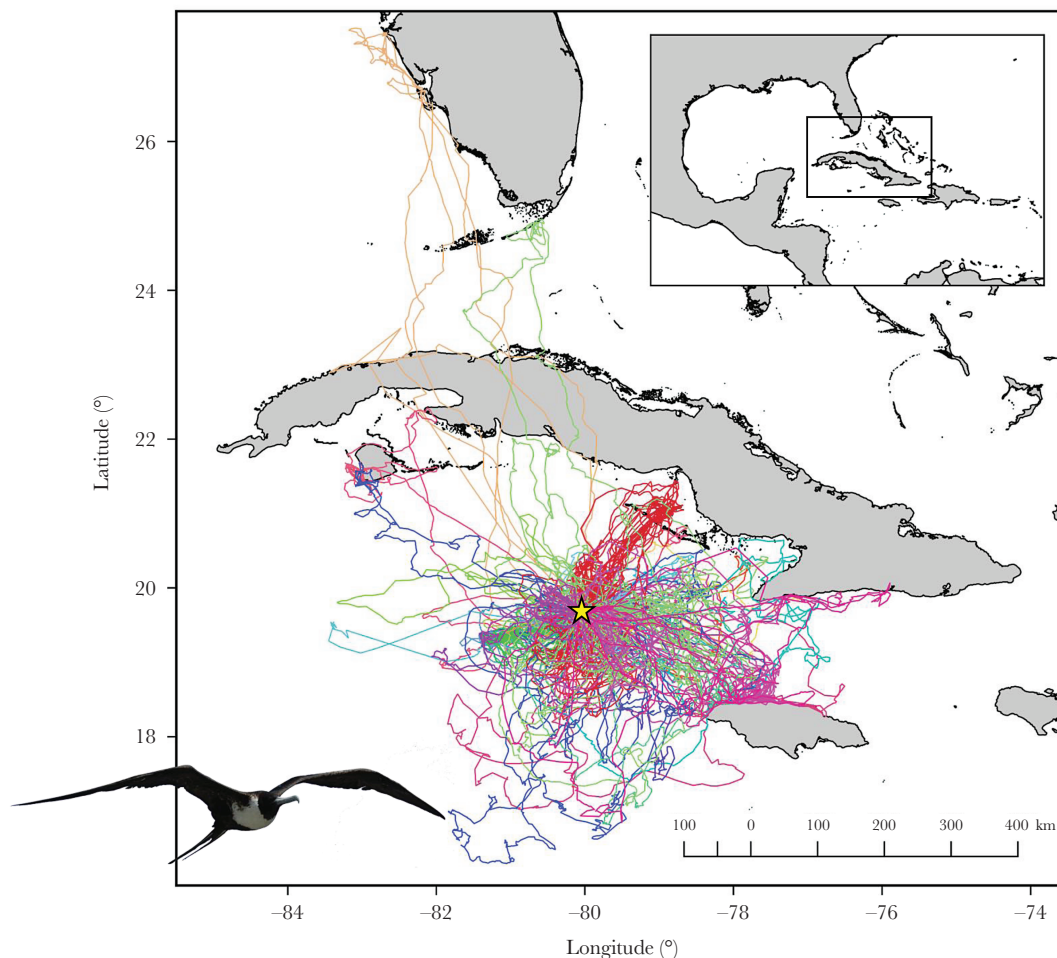
Figure 1
Foraging trips of chick-rearing magnificent frigatebirds. Foraging trips (*n* = 517) of chick-rearing magnificent frigatebirds (*n* = 33) tracked with GPS-GSM loggers during 2017 and 2019 from a colony on Little Cayman, Cayman Islands (colony location indicated with a star). Trips from different individuals are displayed with different colors.

Overall, the dataset used for the RSF analysis contained 13 330 used (471 trips from 33 individuals) and 26 660 available (942 trips from 33 individuals) locations (see Supporting information). To investigate the effect of rainfall on the spatial distribution of frigatebirds, we fitted a weighted logistic regression model to the data, modeling the probability of having a used vs. available location in relation to rainfall, and including a by-individual random intercept and slope. The model was fitted with the *glmmTMB* function in the "glmmTMB" R package (Magnusson et al. 2020), using the parametrization recommended by Muff et al. (2020) for RSFs.

Effect of rainfall on foraging trip characteristics

To assess the broad-scale effect of rainfall on foraging behavior, we calculated the following characteristics for each foraging trip: trip duration (h), mean distance from colony (km), maximum distance from colony (km), and total distance travelled (km). We then fitted GLMMs using the "lme4" R package (Bates et al. 2018), with each trip characteristic as the response variable, and mean rainfall experienced during each foraging trip as an explanatory variable. Bird identity was included as a random intercept, and significance was assessed using likelihood ratio tests. After visual inspection of frequency distributions, we fitted a Gamma error distribution with a log-link function. Model assumptions were checked using the "performance" R package (Lüdecke et al. 2020).

Effect of rainfall and other environmental variables on behaviors

Generalized Hidden Markov Models (HMMs) were used to test the effect of two environmental variables associated with perturbation fronts and potentially affecting foraging behavior of frigatebirds (i.e., rainfall and wind speed) using the "momentuHMM" R package (McClintock and Michelot 2018). As HMMs require regular time steps, we linearly interpolated and re-sampled the dataset at 15-min intervals, using the "adehabitatLT" R package (Calenge 2006). To each interpolated location, we then assigned the closest matching real-time altitude, rainfall, and wind speed values. Since frigatebirds are highly visual predators, and considering that they can spend a prolonged time aloft (up to 2.1 months, Weimerskirch et al. 2016), it is likely that circadian rhythms and ambient light could influence their behavioral responses to weather variability. Therefore, we determined if each location occurred during daytime (coded 1) or night-time (coded 0), using the *crepuscule* function (astronomical twilight) from the R package "maptools" (Bivand and Lewin-Koh 2018). A three-state multivariate HMM was run using the Viterbi algorithm to estimate the most likely behavioral state sequence (Zucchini et al. 2017). The number of states was chosen based on *a priori* knowledge of frigatebird behavior (Austin et al. 2019). Initial parameter priors used in the model were chosen after comparing negative log-likelihood values of several candidate models ($n = 20$), run iteratively using a range of randomly selected reasonable prior values.

Data streams used in the model were step length (i.e., distance travelled), turning angle (i.e., change of movement direction), and altitude (i.e., meters above sea level). Despite GPS-derived altitude being less accurate when compared to latitude and longitude, it can be reliably used in HMMs (Clark et al. 2019). A Gamma distribution was used to model step length and altitude, while a Von Mises distribution was used to model turning angle, and a zero-mass parameter was applied to step length to account for zero inflation. We modeled the transition probabilities as a function of daytime/night-time, rainfall, and wind speed. The two latter variables were

very weakly correlated ($r = 0.03$), hence our results were unaffected by collinearity. To test the relative influence of environmental variables (as well as their combined effect) on model performance, a set of ecologically meaningful candidate models were compared. Starting from a null model, we sequentially added each covariate, as well as their two-way interaction, and used AIC to select the most parsimonious model. To assess how environmental covariates affected the proportion of time spent in each behavior, we calculated and plotted the stationary-state probabilities (representing the equilibrium of the process) for each covariate. When plotting rainfall, wind speed was kept at its mean value (5.11 m/s). When plotting wind speed, rainfall was kept at its mean value (0.09 mm/h). When plotting daytime/night-time, both rainfall and wind speed were kept at their mean values. Finally, for each covariate we extracted the predicted stationary probability (with 95% CI) for the minimum and maximum actual values recorded (rainfall: 0 and 6 mm/h; wind speed: 0 and 13 m/s) during both daytime and night-time. To assess the effect of covariates on state transition probabilities, we plotted transition probabilities as a function of each covariate (keeping the other at its mean value) during both daytime and night-time, and extracted the transition probability (with 95% CI) on the real (i.e., natural) scale for the maximum and minimum values recorded. All analyses were performed using R software version 3.5.1 (R Core Team 2018).

RESULTS

Effect of rainfall on spatial distribution and trip characteristics

Frigatebirds encountered rainfall events (>0.005 mm/h) during the majority of foraging trips (94 %, Figure 2). The mean number of hourly intervals with rain per trip was 17 ± 23 SD (56.6 % of the mean trip duration). Overall, used locations were similarly rainy (0.085 mm/h ± 0.002 SE) as available ones (0.084 mm/h ± 0.002 SE). At the population level, frigatebirds were not significantly more likely to occur in less rainy locations (weighted logistic regression analysis; = –0.026 ± –0.06 SE, $P = 0.68$). At the individual level, frigatebirds were rather homogeneous in their lack of a spatial response to rainfall (random slope effect: $\sigma^2 = 0.08 \pm 0.29$ SD). The spatial distribution of foraging frigatebirds was thus largely independent of rainfall.

There was no significant effect of rainfall on foraging trip characteristics (trip duration: estimate = 0.60 ± 0.03 SE, $\chi^2 = 3.5$, df = 1, $P = 0.06$; mean distance from colony: estimate= -0.10 ± 0.20 SE, $\chi^2 = 0.1$, df = 1, $P = 0.70$; total distance travelled: estimate = 0.10 ± 0.30 SE, $\chi^2 = 0.1$, df = 1, $P = 0.80$; maximum distance from colony: estimate = –0.10 ± 0.20 SE, $\chi^2 = 0.2$, df = 1, $P = 0.70$).

Characterization of behaviors

The fitted HMM assigned each location to one of three states, which were considered to represent the following behaviors: searching/foraging (moderate step length and altitude, and high turning angle); traveling (large step length, high altitude and low turning angle); perching (very low step length and altitude, and high turning angles) (Table 1, see also Supplementary Material). Locations assigned to each behavior were visually inspected. The vast majority of locations classified as perching (95.7%) were tightly clustered on land, while only 4.3% were interspersed within other behavioral states at sea, reflecting either infrequent inaccuracies in
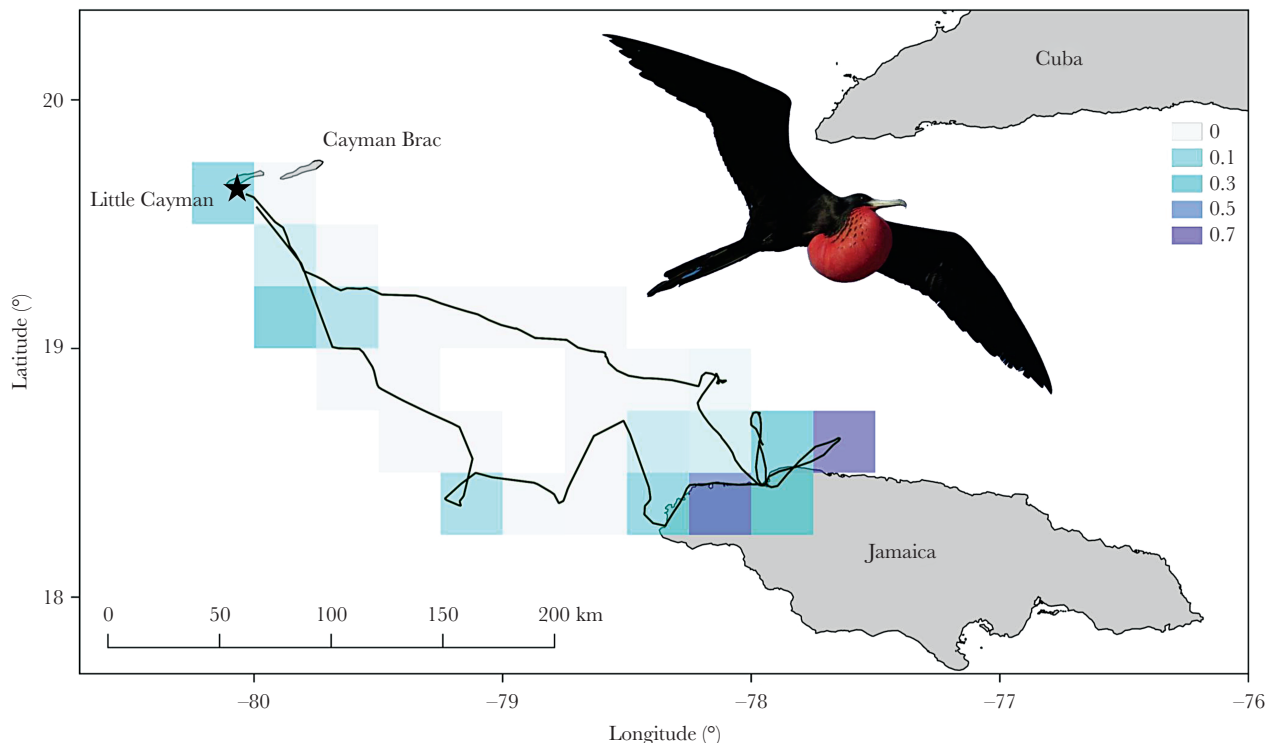
Figure 2

Rainfall experienced during a foraging trip of a chick-rearing magnificent frigatebird. Mean rainfall experienced per cell (0.25° × 0.25°) while the bird was present is reported in mm/h. Colony location is represented with a star.

Table 1

Estimated parameters from the fitted three-state Hidden Markov Model. Parameter estimates (means) of step length (kilometers), turning angle (radians) and altitude (meters above sea level) from the fitted three-state HMM, with standard deviation (concentration for turning angle) in parenthesis.

Variable	Searching/foraging	Traveling	Perching
Step length (km)	1.56 (1.30)	4.60 (2.16)	0.01 (0.01)
Turning angle (rad)	−0.02 (1.42)	−0.01 (12.83)	0.03 (0.57)
Altitude (m a.s.l.)	125.63 (112.90)	255.66 (244.88)	23.61 (24.98)

behavioral assignment and/or perching on boats or other floating objects (e.g., channel markers, buoys). We are therefore confident that most perching events were correctly identified by the model.

Effect of rainfall and other environmental variables on behaviors

Including environmental covariates strongly improved model fit (ΔAIC = 1042.5 compared to the null model). The best fitting model included all candidate environmental covariates, as well as a two-way interaction between wind speed and daytime/night-time (Table 2). Overall, time spent in each behavior changed according to daytime/night-time, with higher probability of perching during night-time than during the day (Supplementary Material). Changing levels of rainfall (range 0.0–6.9 mm/h) affected the time spent in each behavior in a similar fashion during both day and night (Figure 3a,b): with increasing rainfall, perching probability increased almost to 1 while traveling and foraging/searching probability decreased to near zero. During daytime, the probability of being in a given behavioral state remained relatively constant as wind speed increased (Figure 3c). However, during

Table 2

AIC comparison of a set of candidate three-state Hidden Markov Models. List of 8 ecologically meaningful candidate models with their AIC and respective difference in AIC (ΔAIC) from the best-fitting model (highlighted in bold).

Model	AIC	ΔAIC
Null model	837378.9	1042.5
Rainfall	837358.7	1022.3
Rainfall + wind speed	837171.1	834.7
Rainfall + wind speed + daytime/night-time	836357.1	20.7
Rainfall + wind speed + daytime/night-time + (rainfall × wind speed)	836367.1	30.7
Rainfall + wind speed + daytime/night-time + (rainfall × daytime/night-time)	836353.2	16.8
Rainfall + wind sspeed + daytime/night-time + (wind speed × daytime/night-time)	836336.4	0

night-time (Figure 3d), the probability of perching decreased from 0.78 (95% CI 0.71–0.84) when there was no wind (0 m/s) to 0.07 (95% CI 0.04–0.12) at high wind speeds (13 m/s). In contrast,

78
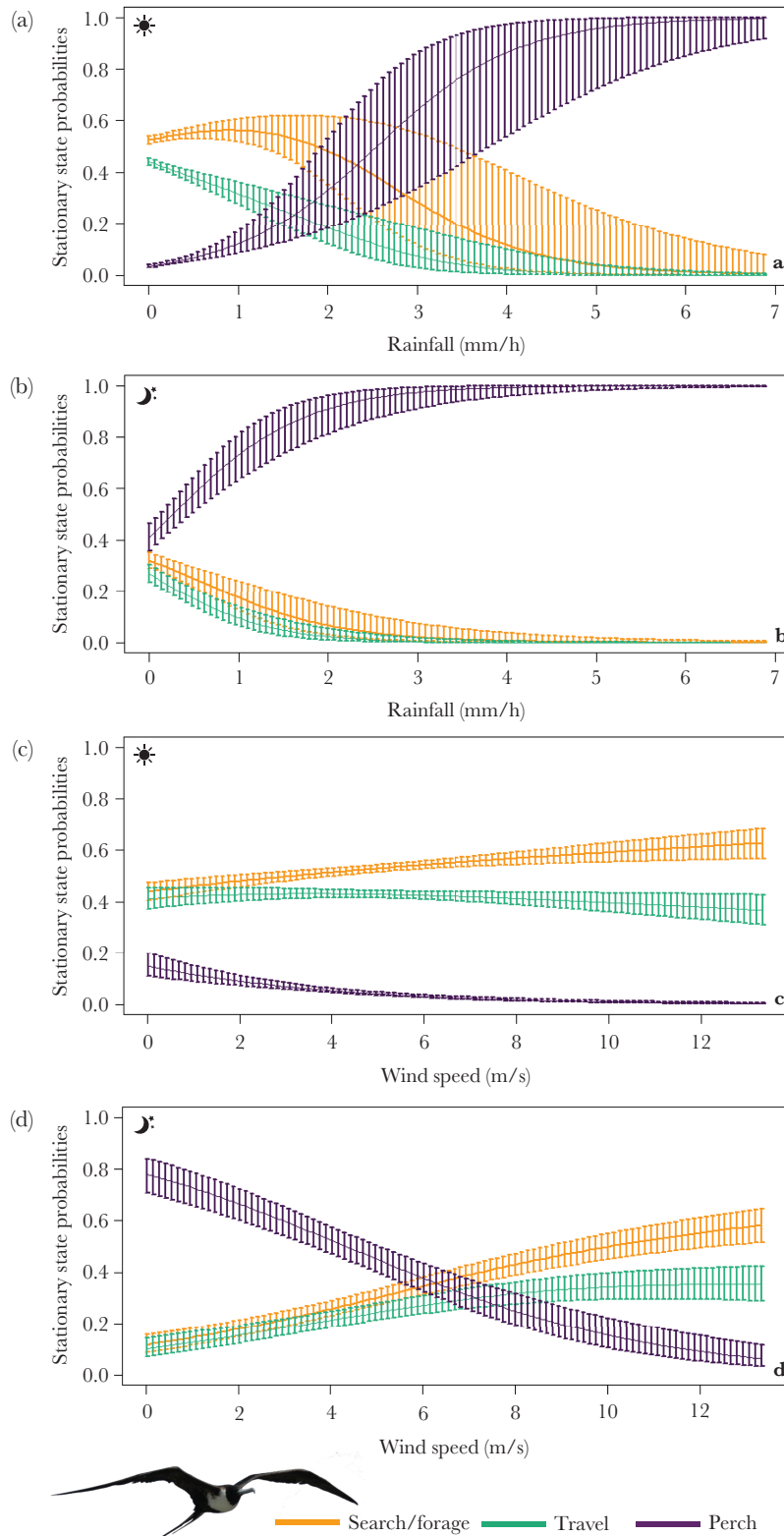
Figure 3

Stationary state probabilities for three HMM-estimated behaviors of magnificent frigatebirds (orange: search/forage, green: travel, purple: perch) with respect to differing rates of rainfall and wind speed (a: daytime rainfall rate, b: night-time rainfall rate, c: daytime wind speed, d: night-time wind speed). Solid lines show means and error bars show 95% confidence intervals. For rainfall plots (panels a & b), wind speed was kept at its mean value (5.11 m/s), and for wind speed plots (panels c–d) rainfall was kept at its mean value (0.09 mm/h).

the probabilities of traveling and search/foraging increased with increasing wind speed: traveling increased from 0.10 (95% CI 0.07–0.15, 0 m/s) to 0.35 (95% CI 0.29–0.42, 13 m/s), while search/foraging increased from 0.12 (95% CI 0.09–0.16, 0 m/s) to 0.58 (95% CI 0.51–0.64, 123 m/s).

Transition state probabilities were only weakly influenced by wind speed (see Supplementary Material) and ambient light conditions (see Supplementary Material), while a small effect was found for rainfall (see Supplementary Material): the probability of remaining in a traveling state decreased with increasing rainfall, from 0.86 (95% CI 0.85–0.86, 0 mm/h) to 0.51 (95% CI 0.27–0.75, 6 mm/h) during daytime, and from 0.92 (95% CI 0.91–0.93, 0 mm/h) to 0.61 (95% CI 0.30–0.85, 6 mm/h) during night-time. In contrast, the probability of transitioning from traveling to search/foraging slightly increased with increasing rainfall, from 0.14 (95% CI 0.14–0.15, 0 mm/h) to 0.40 (95% CI 0.17–0.68, 6 mm/h) during daytime, and from 0.07 (95% CI 0.07–0.08, 0 mm/h) to 0.23 (95% CI 0.08–0.50, 6 mm/h) during night-time. The probability of transitioning from traveling to perching slightly increased with increasing rainfall, but the confidence interval around mean values was large (see Supplementary Material).

DISCUSSION

We provide novel evidence for the influence of rainfall on the fine-scale foraging behavior of a seabird which we expected to be especially sensitive to rainfall. Foraging frigatebirds did not avoid areas with rain, nor was there an effect of rainfall on foraging trip characteristics. However, when encountering rainfall, individuals modified their activity patterns, increasing time spent perching and decreasing time devoted to foraging. In addition, with increasing rain intensity, birds were more likely to switch from traveling to either perching or foraging/searching. The responses of birds to rainfall were similar during both daytime and night-time. In contrast, wind speed did not affect behaviors during daytime. However, during night-time birds engaged more frequently in traveling and foraging/searching, and spent less time perching with strong winds.

The observed fine-scale response to rainfall suggests that foraging frigatebirds do not avoid rain by riding storms and flying high above perturbation fronts. In contrast, birds searched for a perching site above a certain rainfall threshold (~2 mm/h), presumably to wait until the rain event was over, adopting a strategy that minimizes energy expenditure and rain exposure. This suggests that the time-activity budget of frigatebirds during foraging trips is flexible, possibly allowing individuals to buffer the costs of short-term adverse environmental conditions. This is further supported by the lack of an overall effect of rainfall on trip characteristics. However, it remains to be elucidated to what extent such rainfall-mediated reduction of foraging activity affected chick provisioning rates, and hence chick growth and survival.

Individuals that encountered heavy rainfall while traveling were more likely to switch not only to perching but also to foraging/searching (despite large CI). This could be explained by the direct effect of rain on flight mode rather than an actual switch to foraging: with rainfall, rain drops may force downward momentum of the body, increasing the power required to stay airborne (Ortega-Jimenez and Dudley 2012a). In addition to reduced visibility, this downward force may cause individuals to fly slower at lower altitudes with higher turning angles, which may appear similar to searching and foraging behavior. Alternatively, rainfall may cause birds to circle more, as they exploit maritime cumulous clouds that

are associated with thermals and often form in rain (Rauber et al. 2007). The effect of rainfall on marine fish is still poorly known, but it has been shown that rainfall events can alter diel rhythm and vertical movements of fish, resulting in a rain-mediated increased catchability of some species (Payne et al. 2013; Payne et al. 2015). Therefore, we cannot rule out the possibility that the increased surface-availability of some prey species with rain, coupled with reduced in-air visibility and increased water turbidity (Corbari et al. 2016), may inhibit the ability of frigatebirds to spot prey aggregations from high altitudes, causing them to switch to a lower altitude search mode and increase foraging effort (Ortega et al. 2020). The same mechanisms appeared to operate during both daytime and night-time. This is consistent with evidence for night-time foraging in frigatebirds, which are known to scavenge on fishery discards and target vertically migrating species with the aid of moonlight (Gilmour et al. 2012) or bioluminescence, and are often on the wing during darkness (Weimerskirch et al. 2004).

The spatial distribution of foraging frigatebirds was unaffected by rainfall, implying that birds did not actively avoid perturbation fronts. In an oligotrophic environment with scattered resources, such as the Caribbean Sea (Longhurst and Pauly 1987; Bertrand et al. 2002), the ability to cover large areas in search of food likely overrides the need to regularly adapt movements in response to a highly dynamic (and frequently occurring) environmental component (i.e., rain). Furthermore, the high probability of perching in heavy rainfall predicted by our model (daytime: 0.98, 95% CI 0.85–1.00; night-time: 1.00, 95% CI 0.99–1.00) may suggest that, when there is a strong perturbation front, frigatebirds are mostly close to areas where they can rapidly perch. Therefore, despite not avoiding rainfall, their ability to track environmental conditions (Tew-Kai et al. 2009; De Monte et al. 2012; Weimerskirch et al. 2016) could help them sense the arrival of strong perturbation fronts, and pre-emptively position themselves closer to land. Frigatebird associations with mesoscale transport fronts and cumulous clouds (Tew-Kai et al. 2009; De Monte et al. 2012; Weimerskirch et al. 2016) makes them particularly likely to encounter rainfall. Warm ocean eddies can provide heat (and therefore energy) to storms, intensifying them (Wu et al. 2007), and shallow maritime cumulous clouds often form rain (Rauber et al. 2007). Therefore, a mechanism of sensing potentially dangerous perturbation fronts and then moving close to land seems plausible in these species. However, we did not detect an effect of rainfall on distance to the coast at the trip scale (Supplementary Material). Therefore, if such a mechanism is present, it is likely to operate at a very fine spatial scale that is difficult to detect with our tracking data.

The behavioral responses to rainfall were not explained by an increase in wind speed, often linked to barometric depressions that favour rainfall. Rather, wind speed, which was not associated with rainfall in the present dataset, had a distinct effect on behavior during night-time, when individuals were more likely to spend time searching/foraging with increasing wind speed. Since wind facilitates take-off capabilities in seabirds, reducing energy expenditure (Diamond and Schreiber 2002, Shaffer 2011, Clay et al. 2020), frigatebirds could take advantage of it during night-time to become airborne, starting their foraging trips in darkness and commuting to areas where they then forage under stronger light conditions.

Fully understanding how animals react to environmental conditions, such as rainfall, is important for assessing their resilience to climate change, and it is currently considered a research priority in behavioral studies (Buchholz et al. 2019). Severe increases in the rate and extent of rainfall, as well as changes in rainfall seasonality

(Feng et al. 2013), are expected to occur in the near future within tropical regions (Collins et al. 2013; Fischer and Knutti 2016). Under this scenario, increasing rainfall rates may disrupt foraging and negatively affect chick survival and fitness. These potential negative effects of rainfall, coupled with predicted increases in extreme climatic events such as hurricanes (Stocker et al. 2015), increasing rates of chick mortality following storms (Schreiber and Burger 2001) and a wide range of other human-induced pressures, may contribute to threaten frigatebird populations, some of which are already experiencing declines (Birdlife International 2018).

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Supporting information accompanying Chapter IV

SUPPORTING INFORMATION

Figure S1. Real and simulated foraging trips of chick-rearing magnificent frigatebirds. a) Real foraging trips (a, *n* = 471), and b & c) simulated foraging trips (*n* = 471) from adult magnificent frigatebirds (*n* = 33) tracked with GPS-GSM biologgers from a colony on Little Cayman, Cayman Islands in 2017 and 2019. Colony location (i.e. rotation centre) is indicated with a star.
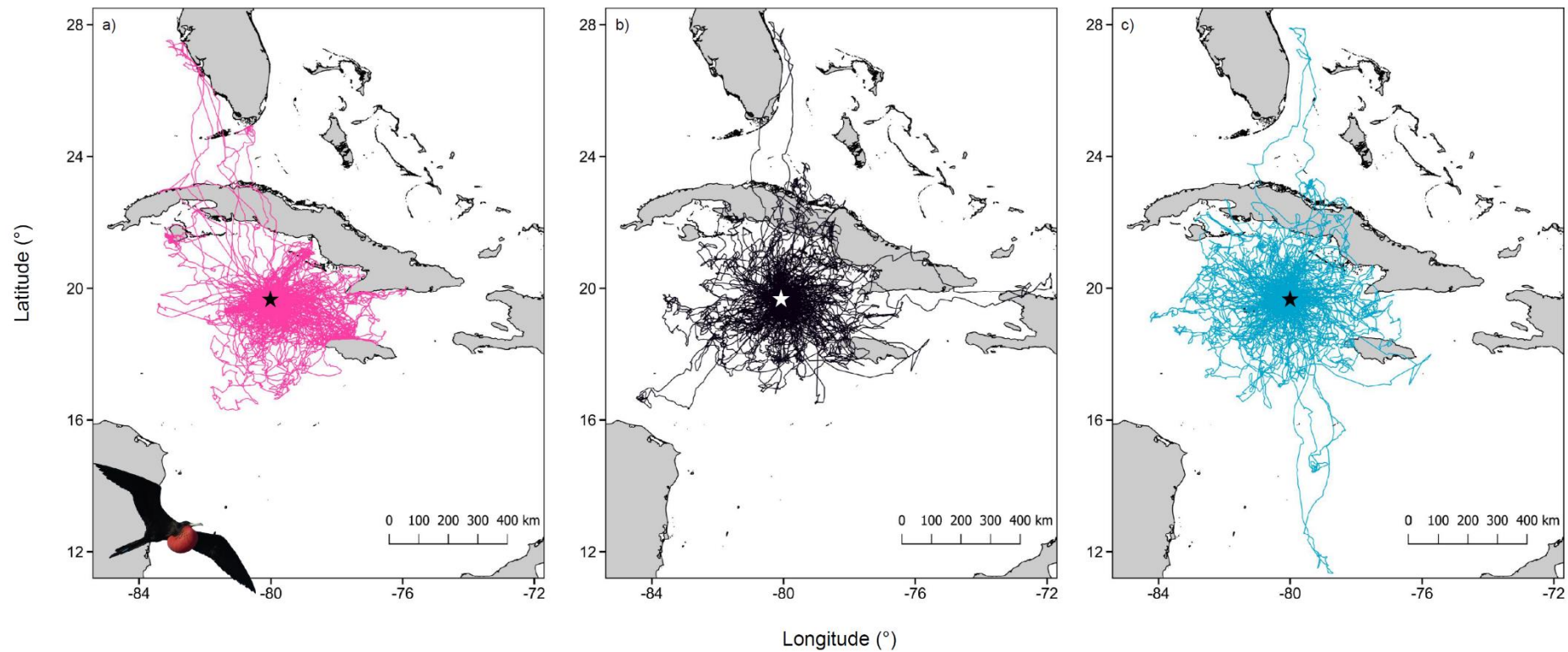
Figure S2. Probability distributions of three behaviors estimated with a Hidden Markov Model using step length, turning angle and altitude. Density distributions of a) step length, b) turning angle and c) altitude in magnificent frigatebird GPS data. Solid lines show the estimated state-dependent probability distributions of three identified behaviors from a Hidden Markov Model. State 1 (orange) = search/forage, state 2 (green) = travel, state 3 (purple) = perch.
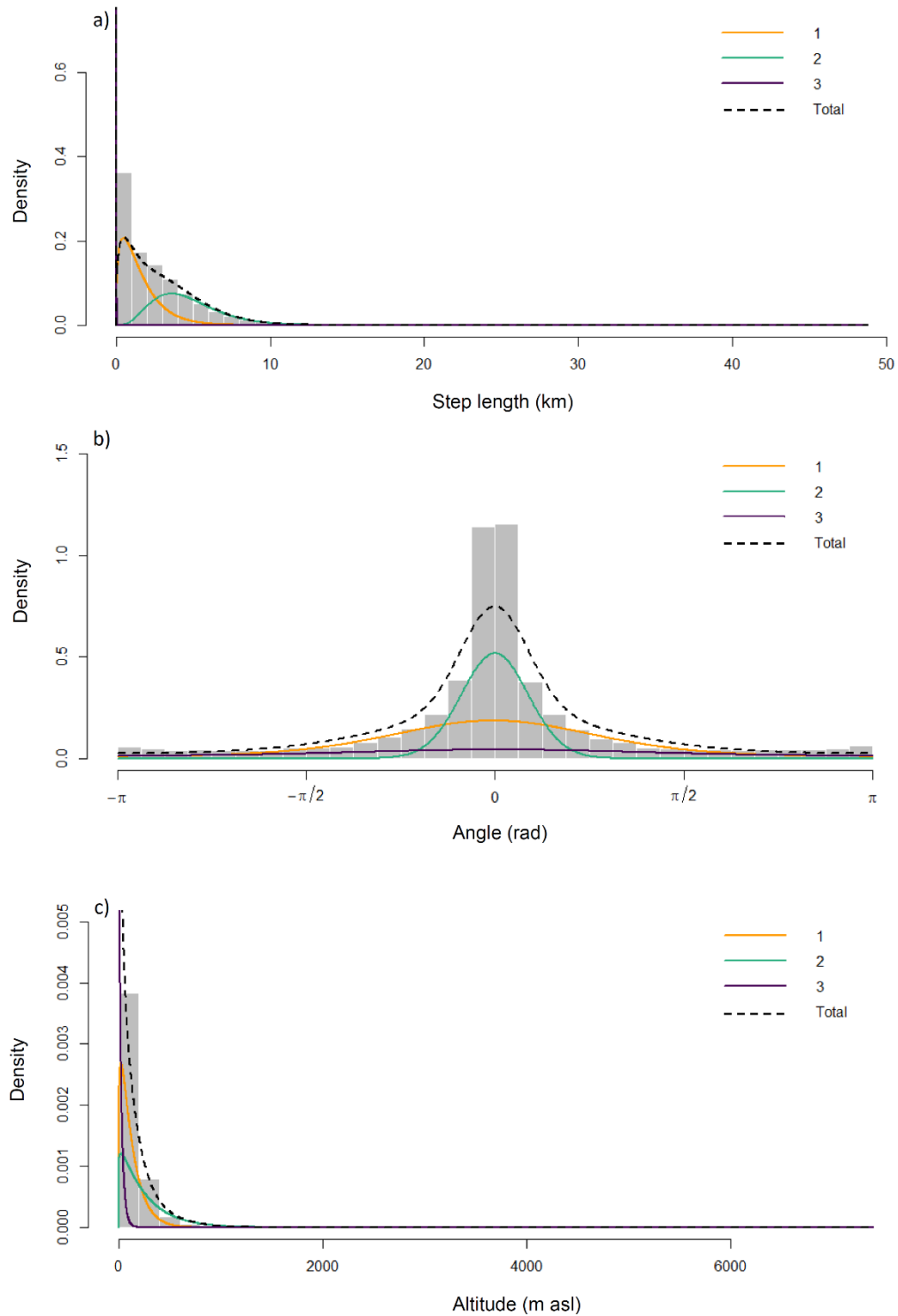
Figure S3. Example foraging trip of a magnificent frigatebird breeding on Little Cayman (Cayman Islands). Example foraging trip (12 days, clockwise movement) of a chick-rearing GPS-tracked male magnificent frigatebird**,** coloured according to estimated underlying behavioral states from the fitted three-state HMM. The higher-resolution subplot shows a section of track where the individual is perched on land. The colony location is indicated with a star.
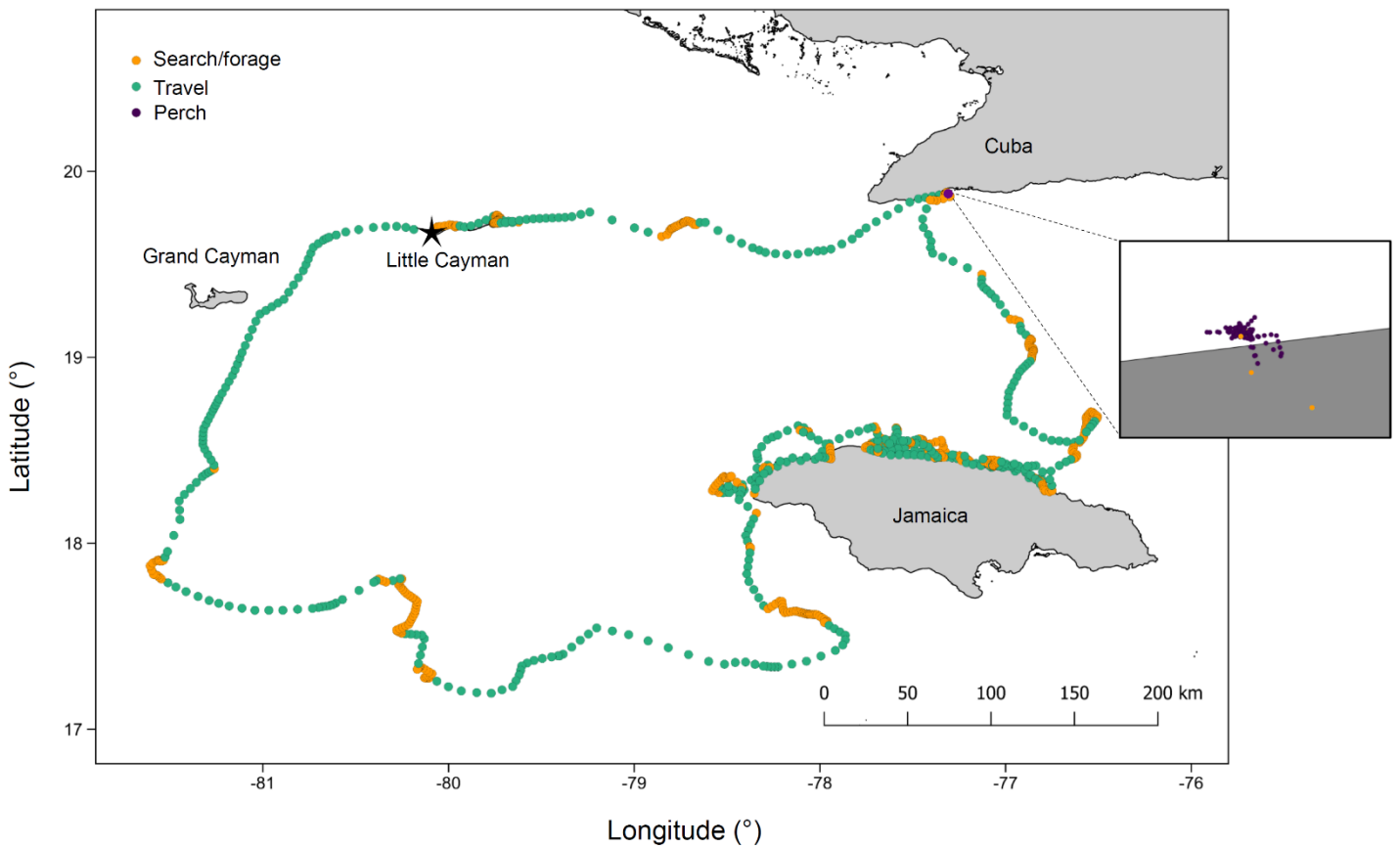
Figure S4. Effect of wind speed on state-transition probabilities from a three-state HMM during daytime. The estimated effects of wind speed (m/s) on the state-transition probabilities during daytime from the three-state HMM. Solid lines represent probability estimates and error bars indicate 95% confidence intervals. Rainfall was kept at its mean value (0.09 mm/h). State 1 = search/forage, state 2 = travel, state 3 = perch.
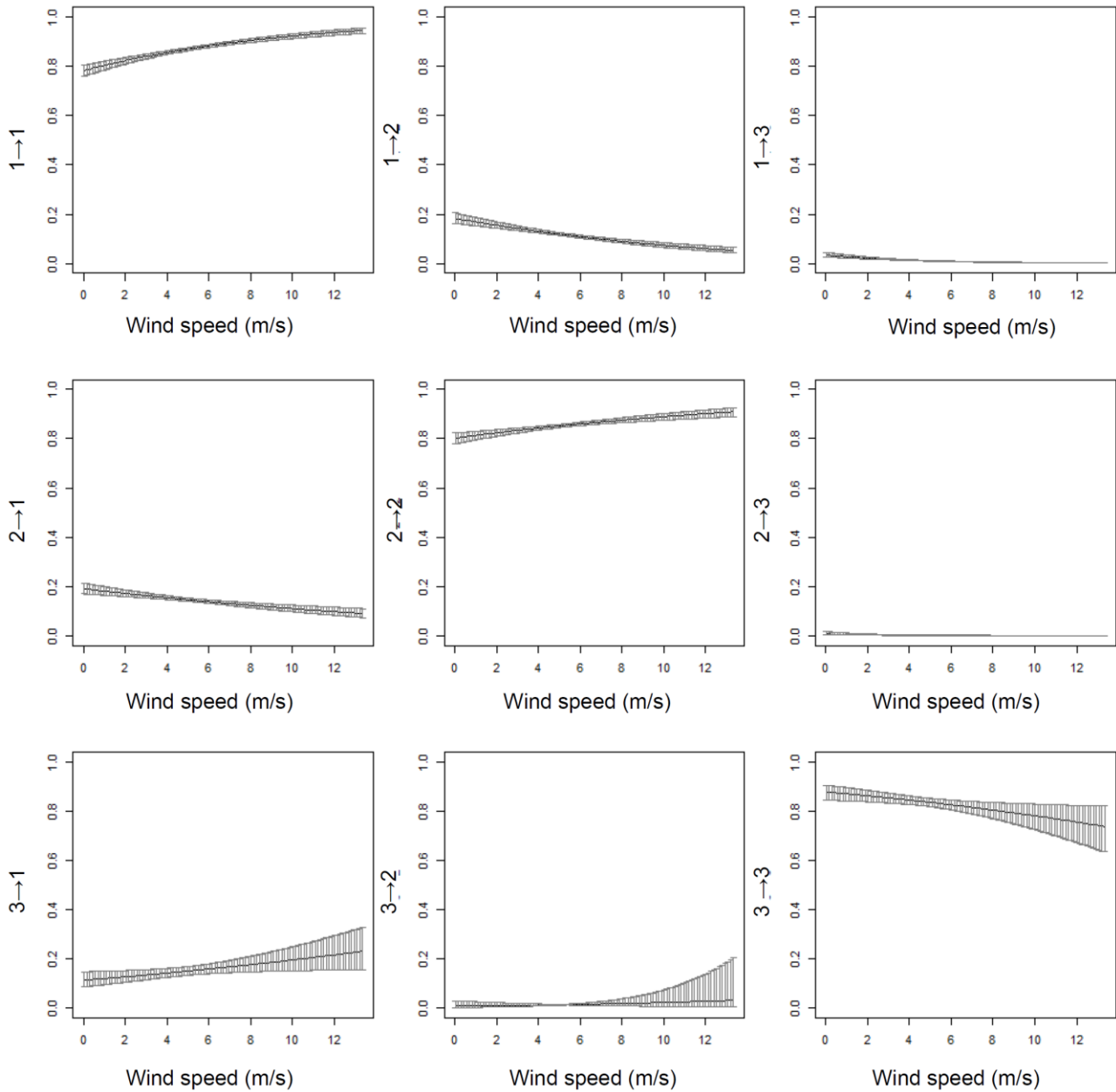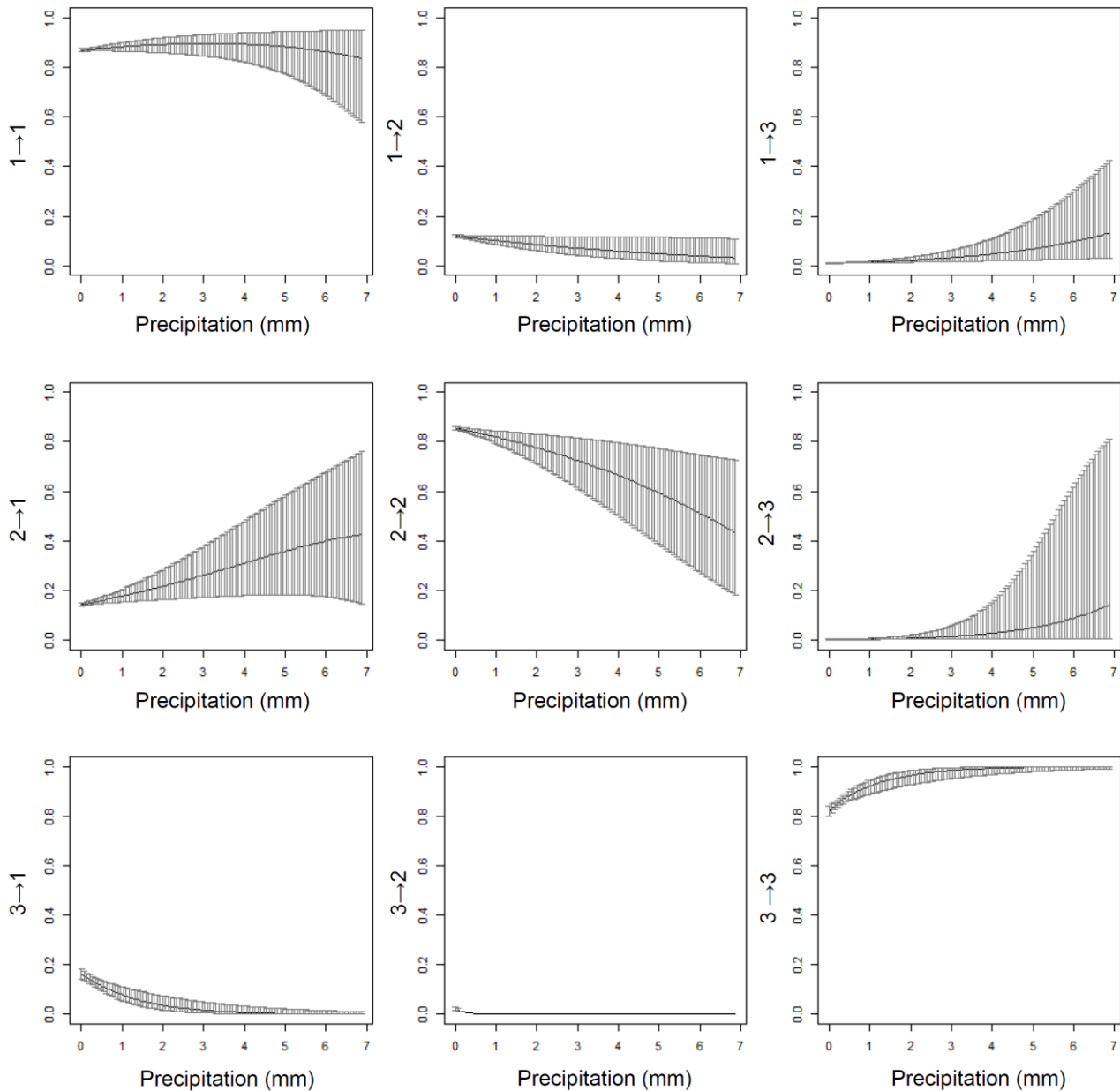
Figure S5. Effect of wind speed on state-transition probabilities from a three-state HMM during night-time conditions. The estimated effects wind speed (m/s) on the state-transition probabilities during night-time from the three-state HMM. Solid lines represent probability estimates and error bars indicate 95% confidence intervals. Rainfall was kept at its mean value (0.09 mm/h). State 1 = search/forage, state 2 = travel, state 3 = perch.
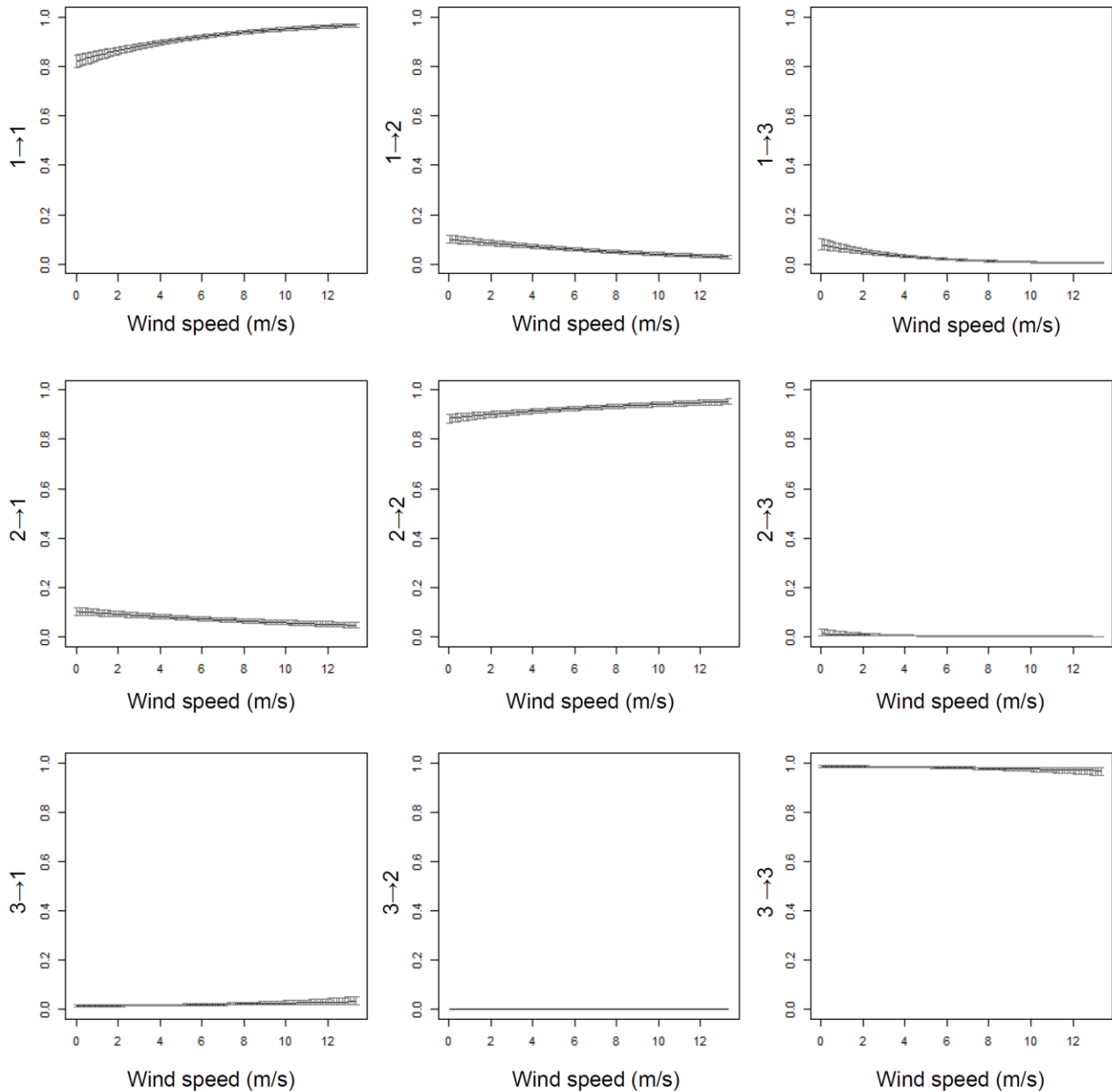
Figure S6. Effect of ambient light conditions on state-transition probabilities from a three-state HMM. The estimated effects of ambient light conditions (daytime/night-time) on the state-transition probabilities from the three-state HMM. Solid lines represent probability estimates and error bars indicate 95% confidence intervals. Environmental covariates were kept at their mean values (rainfall = 0.09 mm/h, wind speed = 5.11 m/s). State 1 = search/forage, state 2 = travel, state 3 = perch.
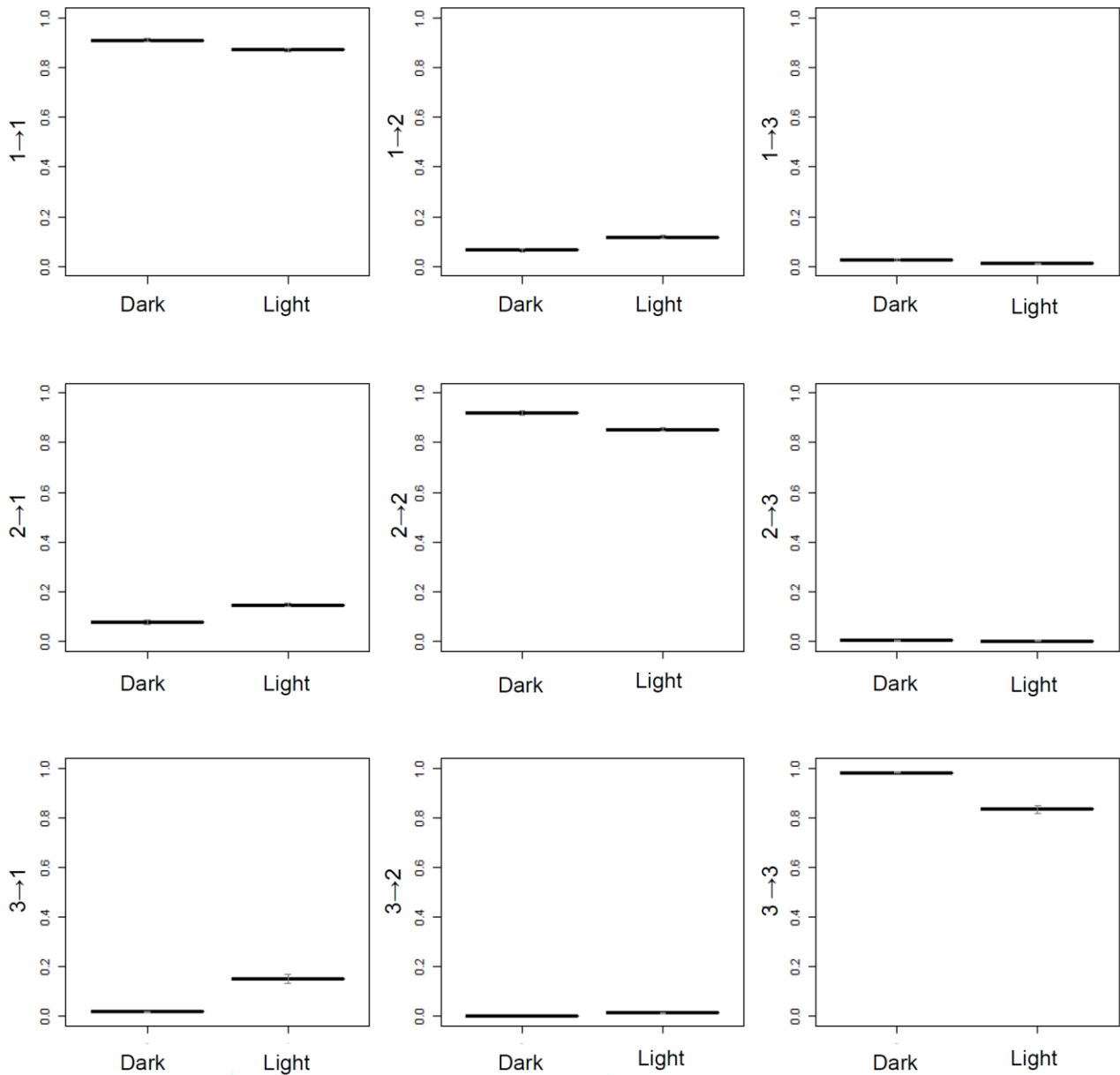
Figure S7. Effect of rainfall on state-transition probabilities from a three-state HMM during daytime. The estimated effects of rainfall (mm/h) on the state-transition probabilities from a three-state HMM during daytime are shown. Solid lines represent probability estimates and error bars indicate 95% confidence intervals. Wind speed was kept at its mean value (5.11 m/s). State 1 = search/forage, state 2 = travel, state 3 = perch.

Figure S8. Effect of rainfall on state-transition probabilities from a three-state HMM during night-time. The estimated effects of rainfall (mm/h) on the state-transition probabilities from a three-state HMM during night-time. Solid lines represent probability estimates and error bars indicate 95% confidence intervals. Wind speed was kept at its mean value (5.11 m/s). State 1 = search/forage, state 2 = travel, state 3 = perch.
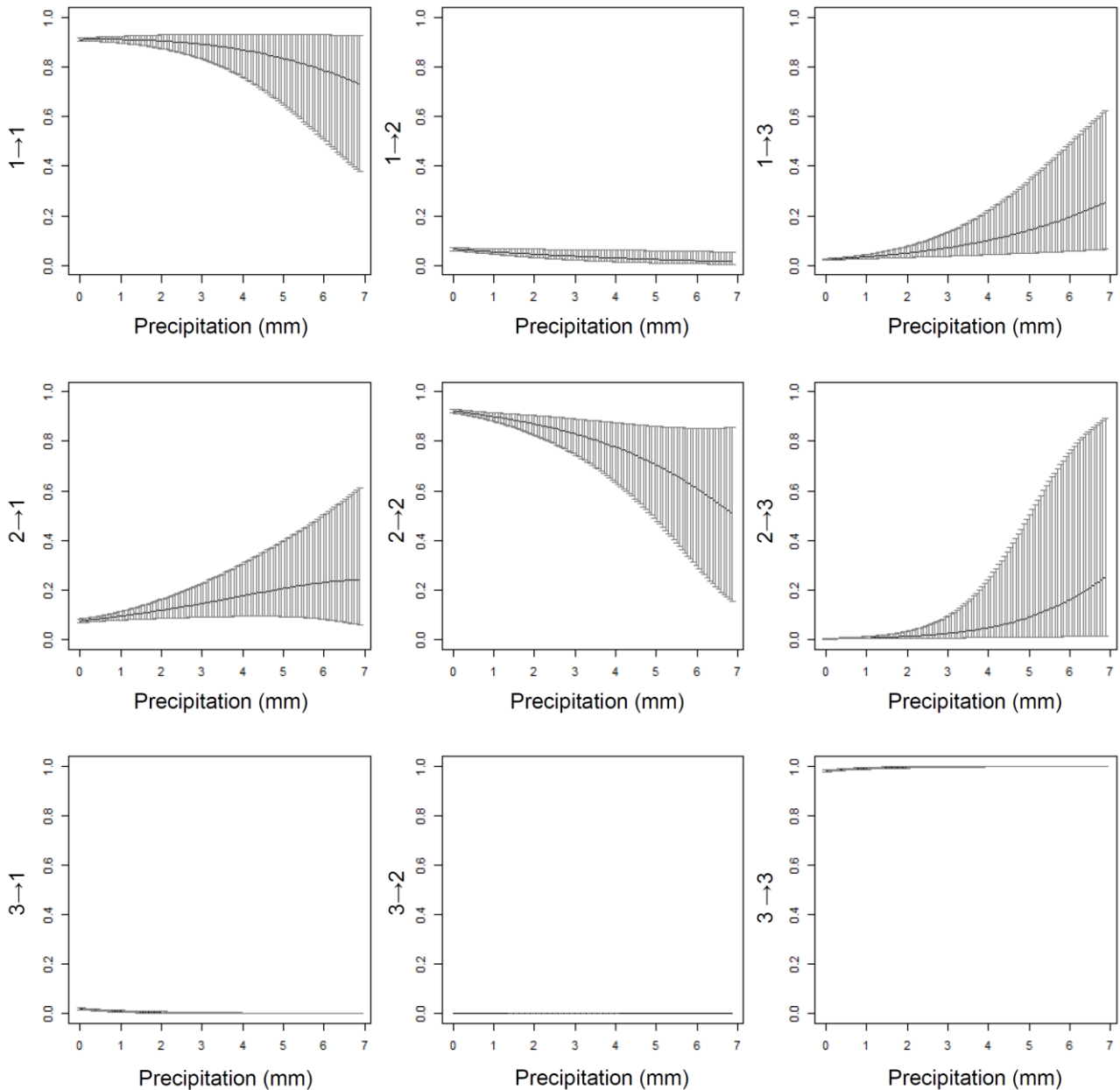
Appendix S10. Testing the effect of rainfall on distance from the coast during foraging trips

To test the effect of rainfall on the distance from the coast, the mean distance from coast (km) was calculated for each foraging trip, and a GLM with a gamma error distribution and log-link function was fitted ("lme4" R package; Bates et al., 2015), with distance from the coast as the response variable, mean rainfall during trip as an explanatory variable, and bird identity as a random intercept. Model assumptions were checked using the "performance" R package (Lüdecke, Makowski, & Waggoner, 2020). There was no significant effect of rainfall on distance from the coast at the trip scale (estimate = 0.23 ± 0.30 SE, χ^2 = 0.62, df = 1, P = 0.43).

CHAPTER V: finding food in a dynamic environment

Searching on the edge: dynamic oceanographic features increase foraging opportunities in a small pelagic seabird

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Wave breaking on a cliff during a powerful mistral swell in Sardinia. Picture: A. Benvenuti.

Searching on the edge: dynamic oceanographic features increase foraging opportunities in a small pelagic seabird

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ABSTRACT: Ocean mesoscale and submesoscale features, such as eddies and filaments, play a key role in the foraging ecology of marine predators, by concentrating nutrients and acting as aggregative structures for pelagic organisms. Highly pelagic seabirds may exploit these features to find profitable food patches in a dynamic and complex 3-dimensional spatial environment. Using miniaturized GPS loggers, we investigated whether foraging habitat selection of the Mediterranean storm petrel *Hydrobates pelagicus melitensis*, one of the smallest (ca. 28 g) seabirds worldwide, was affected by different static and dynamic oceanographic features during the breeding period. Individuals performed long foraging trips (up to 1113 km) in a relatively short time (1 to 2 d), covering large home ranges (up to 34 370 km²), particularly during incubation. Different oceanographic features affected the at-sea distribution of storm petrels at different spatio-temporal scales. During incubation, individuals selected areas characterized by shallow waters and strong currents, conditions that may enhance vertical water mixing and increase food availability. During chick-rearing, they foraged closer to the colony, selecting shallow and productive areas, where increasing Lagrangian coherent structures and eddy kinetic energy enhanced foraging probability. These features could play an important role in storm petrels' foraging habitat selection, especially during chick-rearing, given their need to find predictable food patches in a short timespan. Overall, our results suggest that marine circulation processes are key drivers of the at-sea distribution of this small pelagic surface predator.

KEY WORDS: Ocean dynamics · Mesoscale features · Submesoscale features · Behaviour · Habitat selection · Storm petrel · Hidden Markov Model · *Hydrobates pelagicus melitensis*

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1. INTRODUCTION

In seas and oceans, apex predators search for patchy and ephemeral food resources over large areas (Block et al. 2011). The marine realm is funda-mentally a turbulent system (Stewart 2008) where complex ocean dynamics move water masses (and therefore nutrients) in 3 dimensions, shaping the distribution of marine organisms (Haury et al. 1978, McManus & Woodson 2012, Bertrand et al. 2014).

Pelagic marine predators like seabirds can take advantage of such dynamicity, exploiting cues of the presence of food at different spatio-temporal scales (Fritz et al. 2003, Tew Kai & Marsac 2010, Scott et al. 2013). At the mesoscale extent (~100 km, weeks to months) for example, seabirds can predict the presence of productive areas (Weimerskirch 2007), likely exploiting features such as frontal regions and eddies (Schneider 1990, Cotté et al. 2007, Tew Kai & Marsac 2010, Scales et al. 2014). Eddies are turbulent spinning circulations, found almost everywhere in the ocean (Stewart 2008). They can enhance vertical fluxes of nutrients, increasing and modulating phytoplankton aggregations and structuring mesopelagic communities (Falkowski et al. 1991, Della Penna & Gaube 2020). Moreover, interactions between eddies generate, at their edges, strong dynamic interfaces that form submesoscale (<10 km, 1 to 10 d) structures of high biological activity (Lima et al. 2002) that seabirds may be able to track using visual/olfactory cues or atmospheric changes (Tew Kai et al. 2009). These structures, known as Lagrangian coherent structures (e.g. filaments, vortex boundaries, transport barriers), are of great ecological importance, not only because they are nutrient-enriched, but also because they aggregate plankton and marine propagules (Harrison et al. 2013) and have therefore strong bottom-up aggregative effects on higher trophic levels (Scales et al. 2018).

Procellariforms are seabirds with a highly pelagic lifestyle (Warham 1990) that rely on the ocean–atmosphere interface to find food resources, efficiently exploiting winds to fly with minimal metabolic costs across large distances through the so called 'dynamic soaring' flight (Richardson 2011, Richardson et al. 2018). Most procellariforms are surface feeders that exploit only the upper layer of the water column and have an extremely developed sense of smell, which is used to track different concentrations of dimethyl sulphide (an odorous compound released into the air by phytoplankton, especially when grazed by zooplankton), thereby finding profitable food patches over the ocean surface (Nevitt & Bonadonna 2005). Therefore, planktonic aggregative features such as eddies and Lagrangian coherent structures can be particularly important for procellariforms, which are likely to make use of a combination of olfactory and oceanographic cues at the (sub)mesoscale to locate areas where prey aggregate (Bastos et al. 2020)

We focused on one of the world's smallest (ca. 28 g; Cramp & Simmons 1977) procellariforms, the Mediterranean storm petrel *Hydrobates pelagicus meli-*

tensis (hereafter storm petrel). The planktivorous food habits and the olfactory ability of storm petrels (D'Elbée & Hémery 1998, Bonadonna & Sanz-Aguilar 2012, Bolton 2021) make them suitable candidates to investigate whether they exploit dynamic mesoscale and submesoscale features to locate profitable food patches. Using miniaturized GPS dataloggers, we tracked foraging trips of incubating (2020) and chick-rearing (2019) individuals from a colony in the Mediterranean Sea, a semi-enclosed basin characterized by an oligotrophic water regime with localized upwelling areas (Antoine et al. 1995, Casella et al. 2011). First, we described the movement patterns of breeding storm petrels. Second, we assessed the foraging habitat selection considering a range of oceanographic features at the meso- and submesoscale, accounting for the different effect of breeding stage/year. Different breeding stages are characterized by different spatio-temporal and energetic constraints (Shaffer et al. 2003). Typically, constraints are more relaxed during incubation than during chick-rearing, potentially leading birds to forage over broader areas. Indeed, incubating seabirds perform long-lasting foraging trips (up to 3 times longer than birds rearing chicks), travelling larger distances at greater range from the colony (Guilford et al. 2008, Ito et al. 2010, Sommerfeld & Hennicke 2010, Pinet et al. 2012), likely resulting in different features being exploited to locate food. Moreover, stage-specific nutritional requirements may lead individuals to exploit different food resources (Navarro et al. 2009), potentially resulting in stage-specific foraging habitat selection patterns. We expect meso- and submesoscale features to be key determinants of foraging behaviour, particularly during the more energy-demanding and time-constrained chick-rearing stage, when individuals have to minimize time at sea while maximizing foraging efficiency to regularly provide food to offspring, besides finding enough food for self-provisioning.

2. MATERIALS AND METHODS

2.1. General methods and GPS deployment

We GPS-tracked storm petrels breeding at the colony of Capo Caccia (Sardinia, Italy; 40° 35′ 18″ N, 8° 10′ 24″ E), hosting approximately 400 pairs (F. De Pascalis et al. unpubl. data) which nest both in rock crevices and on the ground of a marine cave. Birds were captured by hand while incubating their eggs or attending chicks and ringed with a unique metal

ring. We tagged 13 chick-rearing birds in July to August 2019 and 16 incubating birds in July to August 2020 (different individuals from those tracked in 2019). We deployed PathTrack (Otley) nanoFIX® GEO-MINI GPS loggers (ca. 0.9 g) set to record 1 fix every hour during incubation and 1 fix every 20 min during chick-rearing (accounting for the expected differences in trip duration during different breeding stages). Devices were attached to the basal section of 4 central tail feathers (being careful not to cover the uropygial gland papilla) using 2 to 3 thin (ca. 2 to 3 mm) strips of Tesa® tape (Tesa). Device relative weight (including attachments) was around 4% of bird body mass (incubation: 3.4%; chick-rearing: 4.4%). During incubation, we tagged only birds with eggs where the embryo was clearly visible but not fully grown (assessed by egg candling) to avoid tracking individuals that had just laid the egg or had clutches that were too close to hatching. During handling, the egg was covered with a wool layer to avoid heat dispersion. After handling, individuals were carefully placed back on their nests and covered for approximately 5 min to make them settle back. Chick-rearing birds were tagged only if the chick body mass was over 10 g (mean ± SD: 16.3 ± 6.2 g chick body mass from tracked birds) to avoid subjecting chicks to thermal stress when left alone by the captured parent. To minimize tracking duration, device retrieval started the second day following deployment during incubation and the first night during chick-rearing, aiming at obtaining a single foraging trip per individual. To minimize colony disturbance, we visited the colony for only 7 non-consecutive days (or nights during chick-rearing) after deployment. Individual body mass was recorded to the nearest 0.1 g before and after GPS deployment using an electronic scale, while standard morphometric measurements (including head–bill length [HBL], to the nearest 0.1 mm) were taken only at GPS retrieval. We recovered 12 (out of 16) devices during incubation and 11 (out of 13) during chick-rearing. During incubation, the 4 missing devices were from birds that abandoned their nest soon after capture and were not seen again. The 2 missing devices during chick-rearing were from birds that had likely returned only for a short period of time to feed the chick (that was seen alive) and were therefore missed. We decided not to attempt further device recovery to minimize disturbance to the colony. All the retrieved devices contained data obtained during incubation while only 7 contained data obtained during chick-rearing. We recorded 13 foraging trips during incubation and 9 during chick-

rearing, from a total of 19 individuals (see Fig. 1). Capture, handling and tagging procedures were carried out under the supervision of 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, and with permission of Parco Naturale Regionale di Porto Conte. Given the small size of storm petrels and their sensitivity to disturbance, possible detrimental effects of GPS-deployment on 3 parameters (body mass, foraging trip duration, hatching success) were investigated (see Appendix for details). We found no direct evidence of a negative effect of device on these traits. The tracking dataset is available upon request on the BirdLife Seabird Tracking Database (www.seabird-tracking.org).

2.2. Foraging trip characterization and variation according to breeding stage

Foraging trips were visually identified using QGIS v2.18 (QGIS Development Team 2009). Spatial and temporal duplicates, as well as unrealistic fixes according to derived ground speed, were identified and removed from the dataset using the 'SDLfilter' R package (Shimada 2019). To homogenize sampling interval and to account for irregular sampling rate (particularly severe during 2019, when gaps were frequent; mean ± SD sampling rate, 2019: 36 ± 128 min, 2020: 67 ± 60 min), we linearly interpolated and re-sampled the dataset at 1 h intervals (both for incubation and chick-rearing) using the 'adehabitat-LT' R package (Calenge 2006). We then calculated, for each complete foraging trip (i.e. starting and ending at the colony, n = 20), the following spatio-temporal trip metrics: trip duration (h), total trip length (km), mean and maximum linear distance from the colony (km), mean and maximum linear distance from the nearest coast (km), and mean and maximum speed between subsequent steps (m s^{-1}).

The effect of breeding stage on variation in spatio-temporal trip metrics was assessed by means of different linear mixed models (LMMs) using the 'lme4' R package (Bates et al. 2015), including individual identity as a random intercept effect. Significance was tested by likelihood ratio tests. Mean and maximum distance from the coast were log$_{10}$-transformed to ensure normality of residuals. For each bird, we calculated individual home ranges (km^2) using kernel density estimation (KDE, 90% contours) from the 'KernSmooth' R package (Wand

2015). Optimized covariance bandwidth matrices were obtained using the least squares cross validator estimator from the 'ks' R package (Duong 2007) on projected coordinates, to prevent spatial biases. The effect of breeding stage on individual home range was tested using a linear model, after $\log_{10}$-transforming home range areas to improve normality of residuals. Cumulative (all individuals pooled together) 25, 50, 70 and 90% KDEs for the 2 breeding stages were computed to illustrate differences in spatial behaviour between incubation and chick-rearing. All model assumptions were inspected for each fitted model using the 'performance' R package (Lüdecke et al. 2020).

To assess if body condition affected foraging behaviour, we computed the scaled mass index (SMI) (Peig & Green 2009) for each individual. We calculated the SMI by scaling body mass at device deployment with HBL (distance between the back of the skull and the tip of the bill). HBL was positively correlated with body mass (r = 0.64, n = 17), resulting in the SMI for individual i being computed as: $SMI_i =$ body mass$_i \times (HBL_0/HBL_i)^{2.14}$, where $HBL_0 = 325.59$ mm (mean HBL of the sample population). We then calculated the Spearman's rank correlation coefficient between each trip metric and the SMI. In the case of multiple trips per individual, only the first trip was considered.

2.3. Identification of at-sea behaviours

We identified at-sea behaviours from tracking data by means of Hidden Markov Models (HMMs) using the 'momentuHMM' R package (McClintock & Michelot 2018). Before running models, trips that prior to interpolation had temporal gaps exceeding 3 h were identified and split into separate bursts (before and after the gap) to avoid affecting behavioural estimation. We ran a 2-state HMM using the Viterbi algorithm to estimate the most probable behavioural state sequence (Zucchini et al. 2017). The number of states was based on *a priori* knowledge of procellariform at-sea behaviour (Pohle et al. 2017) and took into account the coarse temporal resolution of data. Optimal prior selection was checked after comparing negative log-likelihood values of a set of candidate models (n = 50), run iteratively using a range of randomly selected priors with reasonable values. Data streams used in the model were step length (i.e. distance travelled, modelled with a Gamma distribution) and turning angle (i.e. change of direction, modelled with a Von Mises distribution).

2.4. Foraging habitat selection

To assess the foraging habitat selection of storm petrels, we compared environmental features associated with searching/foraging (use) to those associated with travelling (non-use) locations, which were identified with the HMMs (see Section 3.2). We then associated each location with the corresponding value of the following features that were likely to affect storm petrel foraging behaviour. (1) Chlorophyll *a* concentration (mg m^{-3}; temporal resolution: daily; spatial resolution: 0.04°) and (2) sea surface temperature (°C, hourly, 0.04°) were both accessed through the EU Copernicus Marine Service Information (www.copernicus.eu). (3) Sea depth (m, 0.01°) was obtained from a NOAA dataset using the 'marmap' R package (Pante et al. 2018) and (4) slope (°, 0.01°) was calculated using the 'raster' R package (Hijmans 2018). (5) Eddy kinetic energy (EKE; m^2 s^{-2}, daily, 0.125°) was derived from the sea surface height anomaly field based on the geostrophic relationship and commonly used, despite some limitations, as a direct measure of number and intensity of mesoscale eddies (Qiu & Chen 2010, Tew Kai & Marsac 2010, Ding et al. 2020). EKE was computed as

$$\frac{1}{2}\left(U_a^2 + V_a^2\right) \tag{1}$$

where U_a and V_a are the zonal and meridional horizontal velocity (altimetry derived) components of the geostrophic current (obtained from SSALTO/Duacs products available from the Copernicus repository; m s^{-1}, daily, 0.125°). We also considered (6) the absolute value of backward finite-size Lyapunov exponents (FSLE; d^{-1}, 0.04°) as a proxy of submesoscale Lagrangian coherent structures (Boffetta et al. 2001, d'Ovidio et al. 2004), available from CLS/CNES Aviso (www.aviso.altimetry.fr). FSLE is a Lagrangian diagnostic technique that measures dynamic structures, and ridges of FSLE identify Lagrangian coherent structures (Tew Kai et al. 2009). Finally, we considered (7) current speed (m s^{-1}, daily, 0.04°), calculated as:

$$\sqrt{U_b{}^2 + V_b{}^2} \tag{2}$$

where U_b and V_b are the zonal and meridional horizontal velocity components (derived from the physical component of the Mediterranean Forecasting System available from the Copernicus repository).

Binomial Generalized Additive Mixed Models (GAMMs) were then used to assess if the selected environmental variables predicted the probability of use vs. non-use. We used GAMMs to account for potential non-linear relations between probability of use and

environmental variables. Environmental variables were not collinear (variance inflation factors [VIFs] ≤1.5; Hair et al. 2010). Separate models were fitted for incubation and chick-rearing stages using the 'mgcv' R package (Wood 2019). The response variable was coded as 1 if the HMM-identified behaviour was 'searching/foraging' (use), and as 0 if it was 'travelling' (non-use). Cubic regression splines with shrinkage were used in the models to avoid over-fitting. Two full models were fitted, and only the response curves of variables strongly (p ≤ 0.05) influencing foraging behaviour were plotted. To account for temporal auto-correlation, an inherent characteristic of tracking data, the model incorporated an auto-regressive AR1 correlation structure applied to each individual foraging trip (random effect) at regularly spaced time steps. All analyses were carried out using R 3.5.1 (R Core Team 2018).

nearest coastline), directed towards the Liguro-Provençal Basin and the Balearic Islands (NW, W). In 2020, incubating storm petrels engaged in long-lasting foraging trips (50.8 ± 11.1 h; mean ± SD), travelling large distances (737.0 ± 217.3 km) at high speed (4.0 ± 0.9 m s^{-1}). Conversely, in 2019, chick-rearing individuals engaged in much shorter foraging trips (24.4 ± 12.3 h), travelling less (255.2 ± 155.4 km) at lower speed (2.63 ± 0.9 m s^{-1}) and remained closer to the colony compared to incubating birds (Table 1, Fig. 1). These differences resulted in individual home ranges being 3 times larger during incubation (2020) compared to chick-rearing (2019) (Table 1, Fig. 1). Inter-individual differences in body condition did not significantly covary with trip metrics ($|r_S|$ always ≤ 0.42, p ≥ 0.18; see Table S1 in the Supplement at www.int-res.com/articles/suppl/m668 p121_supp.pdf).

3. RESULTS

3.1. Foraging trip characteristics and variation according to breeding stage

Breeding storm petrels performed highly pelagic foraging trips (approximately 60 km away from the

3.2. Identification of at-sea behaviours

We interpreted the 2 states estimated by the HMM as proxies of the following behaviours: State 1, characterized by small step length and high angle concentration, identified locations likely associated with food searching and/or foraging; State 2, character-

Table 1. Differences in spatio-temporal trip metrics between 2 breeding stages of storm petrels. Differences were assessed by means of linear mixed effects models, with individual identity as a random intercept effect. Significance was tested by likelihood ratio tests. The effect of breeding stage (incubation, chick-rearing) on home range size (from the 90% kernel density estimation [KDE]) was assessed by means of a linear model. Values are mean ± SD and range (minimum−maximum values observed). Only complete trips were considered in these analyses (n = 20)

Trip metric	Incubation (n = 12 trips)	Chick-rearing (n = 8 trips)	χ^2	df	p
Trip duration (h)	50.8 ± 11.1 (40.0−70.0)	24.4 ± 12.3 (12.0−44.0)	9.4	1	0.002
Total trip length (km)	737.0 ± 217.3 (299.1−1112.9)	255.2 ± 155.4 (48.5−480.3)	14.9	1	<0.001
Maximum distance from colony (km)	297.6 ± 82.3 (166.7−406.2)	123.4 ± 69.4 (29.0−215.5)	13	1	<0.001
Mean distance from colony (km)	177.1 ± 58.7 (74.2−271.6)	85.4 ± 51.8 (24.8−271.6)	9.4	1	0.002
Maximum distance from coast (km)	129.0 ± 60.8 (38.7−211.2)	102.9 ±55.3 (21.8−166.6)	1	1	0.3
Mean distance from coast (km)	58.0 ± 36.1 (15.9−124.4)	64.9 ± 35.2 (11.3−104.0)	0.1	1	0.78
Maximum speed (m s^{-1})	9.8 ± 2.0 (6.7−12.5)	7.38 ±1.7 (4.5−9.8)	7.7	1	0.006
Mean speed (m s^{-1})	4.0 ± 0.9 (2.1−5.2)	2.63 ± 0.9 (1.1−4.1)	8.5	1	0.003
Home range size (km^2)[a]	16458 ± 10650 (3460−34370)	4835 ± 3535 (933−9320)	3.3[b]	1	0.002

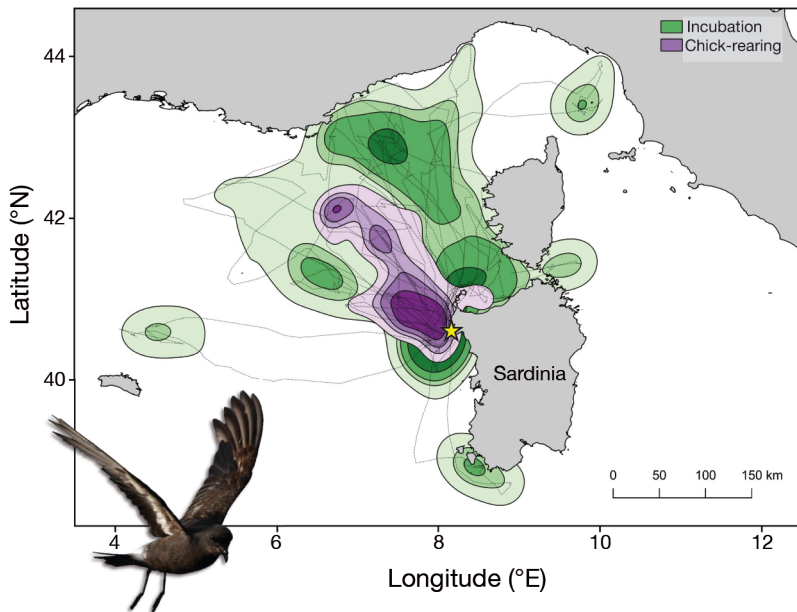[a]Incubation: n = 12; chick-rearing: n = 7 individuals; [b]*t*-value

Fig. 1. GPS tracks and cumulative kernel density estimates from breeding storm petrels. Kernel density estimates (25, 50, 70, 90% contours, from darker to lighter shades of colour) of incubating (2020, n = 12 individuals) and chick-rearing (2019, n = 7 individuals) storm petrels. (Dashed grey lines) GPS tracks; (★) colony location. Photo courtesy of Andrzej Tajchert

ized by high step length and low angle concentration, likely corresponded to sustained travelling/relocation (Table 2, Fig. 2). For incubating birds in 2020, the proportion of searching/foraging locations per foraging trip was 0.60 ± 0.14 (mean ± SD) (n = 658), while it was 0.76 ± 0.15 for chick-rearing ones in 2019 (n = 183) (Mann-Whitney U-test; W = 50490, p < 0.001).

3.3. Foraging habitat selection

Different meso- and submesoscale features affected foraging habitat selection during the breeding period (see Figs. S1, S2 & S3 in the Supplement for the spatial distribution of the retained variables over different years and Table S2 for the output of full

Table 2. Parameters from the fitted 2-state Hidden Markov Model (HMM). Parameter estimates of step length and turning angle from the 2-state HMM with SD (concentration for turning angle) in parenthesis

Parameter estimate	State 1 (searching/ foraging)	State 2 (travelling)
Step mean (km)	8.82 (8.06)	24.01 (6.69)
Turning angle mean (rad)	0.09 (0.81)	−0.03 (12.55)

models). During incubation, foraging probability increased with decreasing sea depth (i.e. shallower waters) and current speed, and decreased with increasing temperature and FSLE (Fig. 3, model r^2 = 0.17). However, the association between foraging probability and FSLE was highly non-linear with large standard errors (Fig. 3c), implying a relatively weak pattern. During chick-rearing, a mixture of meso- and submesoscale dynamic oceanographic features, as well as biotic and static features, affected foraging behaviour of storm petrels (Fig. 4, model r^2 = 0.16). In particular, foraging probability increased with increasing EKE, FSLE (despite large standard errors for high FSLE values) and chlorophyll a concentration, and decreased with increasing sea depth.

4. DISCUSSION

Mediterranean storm petrels from our study population showed a highly pelagic lifestyle, as observed in previous studies (Bolton 2021, Rotger et al. 2020). They engaged in foraging trips of short duration (~1 or 2 d depending on the breeding stage) and travelled long distances (up to 1113 km), suggesting that the species has an extremely efficient flight performance as well as a high foraging efficiency. As commonly observed in procellariiforms (e.g. Guilford et al. 2008, Cecere et al. 2013), breeding storm petrels travelled 3 times more and engaged in 2 times longer foraging trips during incubation compared to chick-rearing, when parents are more constrained to the nest by the need for frequent chick provisioning. Previous studies on the movement patterns of the species during breeding were conducted in the western Mediterranean waters (Rotger et al. 2020) and in the Atlantic Ocean (Bolton 2021). Differences in distance travelled and trip duration between populations during incubation were observed (Rotger et al. 2020: 73 h and 992 km; this study: 51 h and 737 km; Bolton 2021: 49 h and 562 km). Such differences could result from annual and individual variation, or reflect different energetic costs associated with different environments. Indeed, biotic (e.g. prey distribution) and abiotic (e.g. wind fields) factors can shape foraging costs for seabirds, affecting individual decision making (Afán et al. 2021).
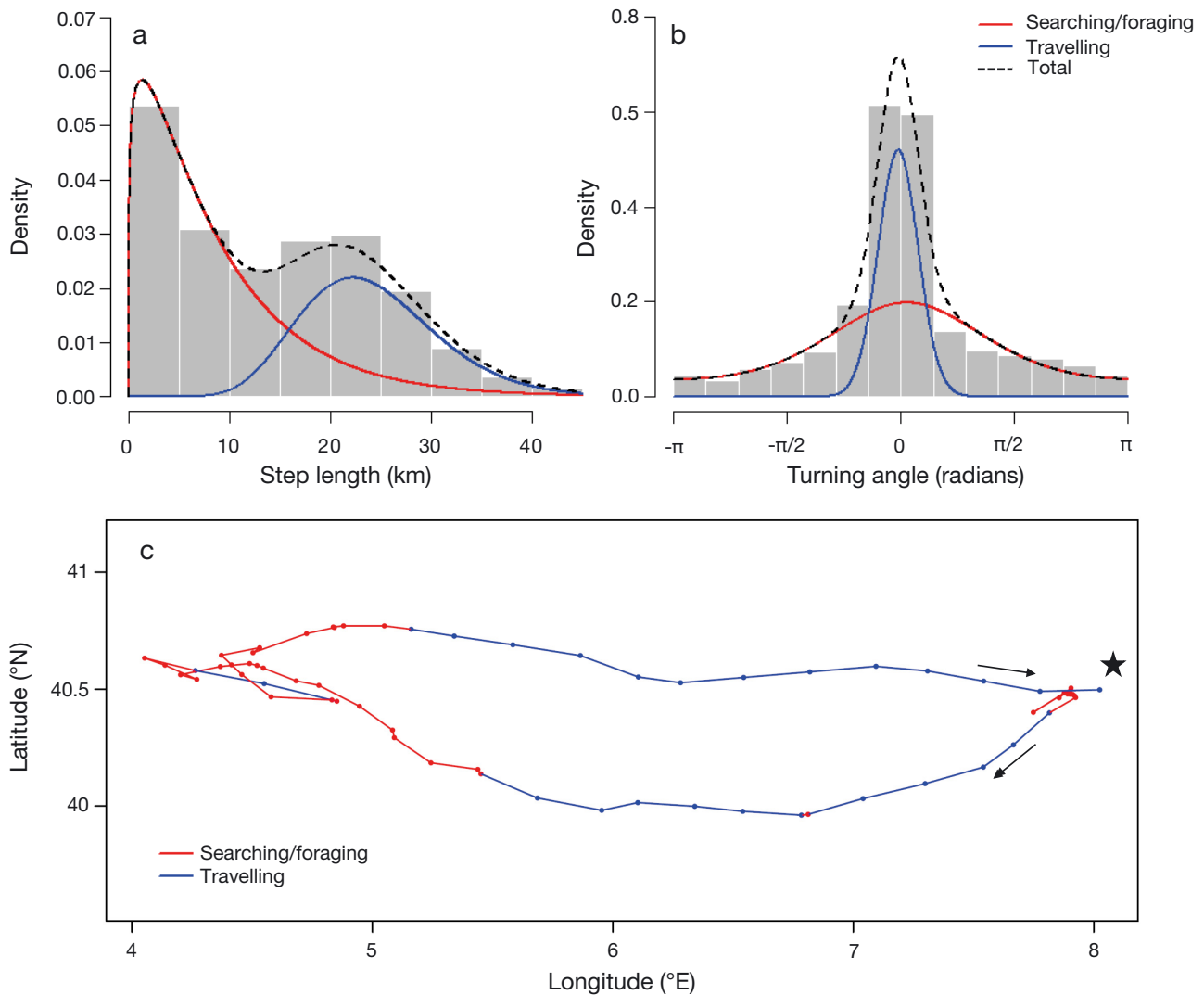
Fig. 2. Probability distributions of behaviours estimated with a Hidden Markov Model (HMM) and example track. Density distributions of (a) step length and (b) turning angle in GPS data from 22 foraging trips of 19 storm petrels. Solid lines correspond to the estimated state-dependent probability distributions of the 2 identified behavioural states from the HMM. State 1: searching/foraging; State 2: travelling. (c) Example of a foraging trip coloured according to estimated underlying behaviours from the fitted HMM. (arrows) Trip direction; (★) colony location

Storm petrels foraged in areas characterized by water mixing and stirring, and their at-sea distribution was influenced by different oceanographic features. In 2020 (during incubation), foraging individuals selected areas characterized by cool and shallow waters and strong currents. The combined effect of strong currents and low sea depth (continental shelf or seamounts, for example) may increase vertical water mixing, generating upwelling and creating areas of elevated sub-surface primary production (Scott et al. 2010, Waggitt et al. 2018) or directly bringing zooplankton close to the sea surface. Similar dynamics have been observed for other plankti-

vorous and/or surface-feeding seabirds in the ocean, where tidal currents interact with banks or shallow waters, increasing prey availability in the upper water layer (Hunt et al. 1998, Embling et al. 2012, Scott et al. 2013) (see Fig. S4 in the Supplement for further evidence supporting this combined effect). In 2019 (during chick-rearing), individuals concentrated on shallow and relatively more productive areas, with increasing EKE and FSLE values that are known to be associated with increased primary production and prey aggregation. Indeed, interactions between eddies and filamentation processes at eddy edges create packets of high biological activity, with
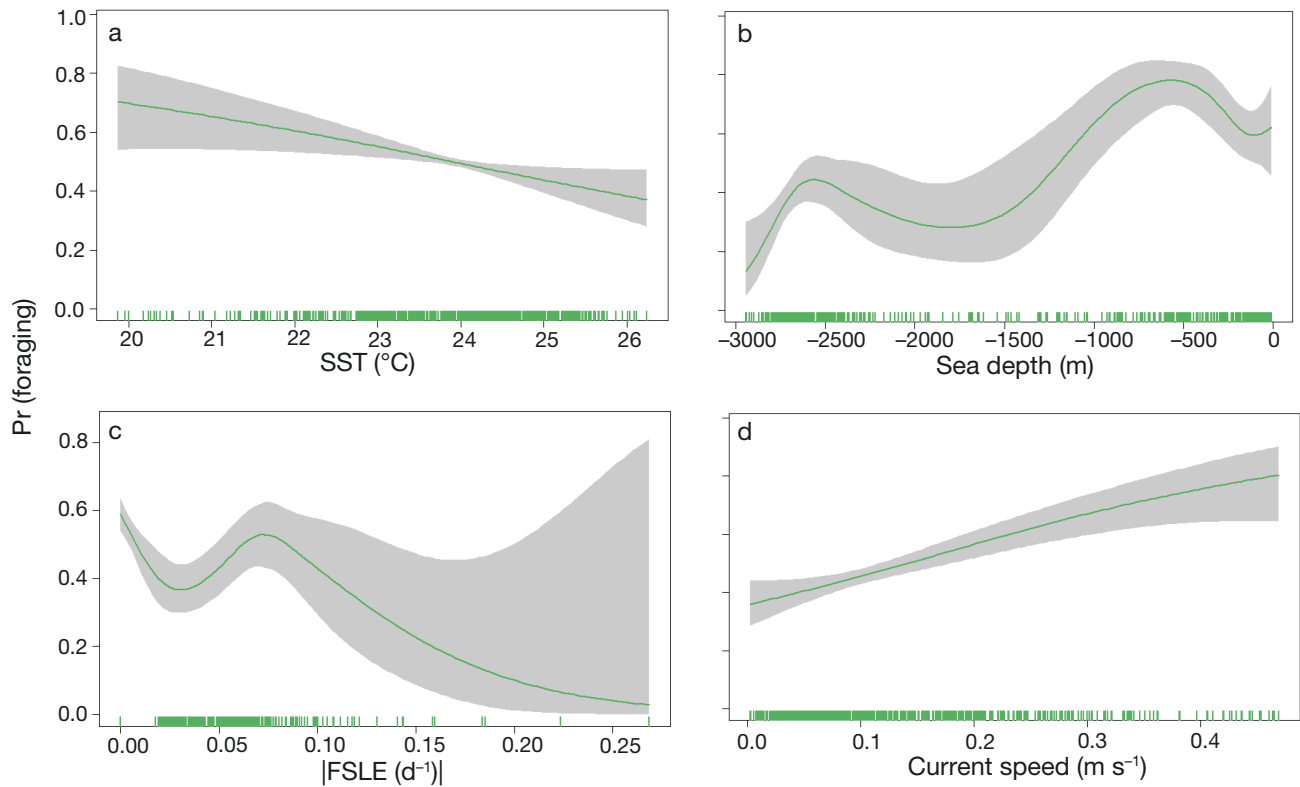
Fig. 3. GAMM response curves for key environmental predictors (p < 0.05) affecting foraging habitat selection of incubating storm petrels in 2020. Response curves (n = 12 trips) of the probability of foraging (0: non-use i.e. travelling, 268 fixes; 1: use i.e. searching/foraging, 390 fixes) according to (a) sea surface temperature (SST), (b) sea depth, (c) finite-size Lyapunov exponents (FSLE) and (d) current speed. Shaded areas correspond to the standard error of the estimate (green line), while ticks on the *x*-axis show the overall distribution of the data

marine larvae of different ages and origin clustered together in a small portion of the sea (Harrison et al. 2013). The observed differences between the 2 breeding stages may have multiple origins. Inter-annual differences in oceanographic features could influence the observed differences in habitat selection patterns (see Figs. S1–S3). In addition, the time constraints during chick-rearing likely promote the search for efficient proxies of prey availability, such as eddies and filaments, enabling individuals to quickly detect food resources close to the colony and be back at the nest, maintaining a positive energy balance. During incubation, individuals need to provision only for themselves, and they can roam over large areas opportunistically, looking for ephemeral but potentially highly rewarding prey aggregations, or even looking for other food sources that may not be available close to the colony (e.g. fishery discards, scavenging). Moreover, the different nutritional requirements of the 2 stages (chicks need highly energetic and lipid-rich food items; Wanless et al. 2005) could also promote the consumption of different prey

types occurring in different seascapes. Therefore, it is likely that a combination of different factors (i.e. year, breeding stage, foraging requirements) lead to the observed differences in foraging habitat selection between birds tracked in different breeding stages, and it is not possible to fully disentangle them. Regardless of these differences, we found that a set of static and dynamic oceanographic features at different spatio-temporal scales affected the at-sea distribution of foraging storm petrels. Such features increase the surface availability of prey, enabling this small predator to successfully forage even during periods of elevated energy demand. However, care must be taken in the interpretation of these results, given the small sample size and coarse GPS sampling rate. Finally, we point out that some other factors could affect storm petrel foraging decisions. Fishing vessels and fish farms could attract birds at sea, providing an alternative food source. Moreover, it is likely that wind speed and direction play a key role in foraging decision, restricting the search for food of this small-bodied species to specific locations and
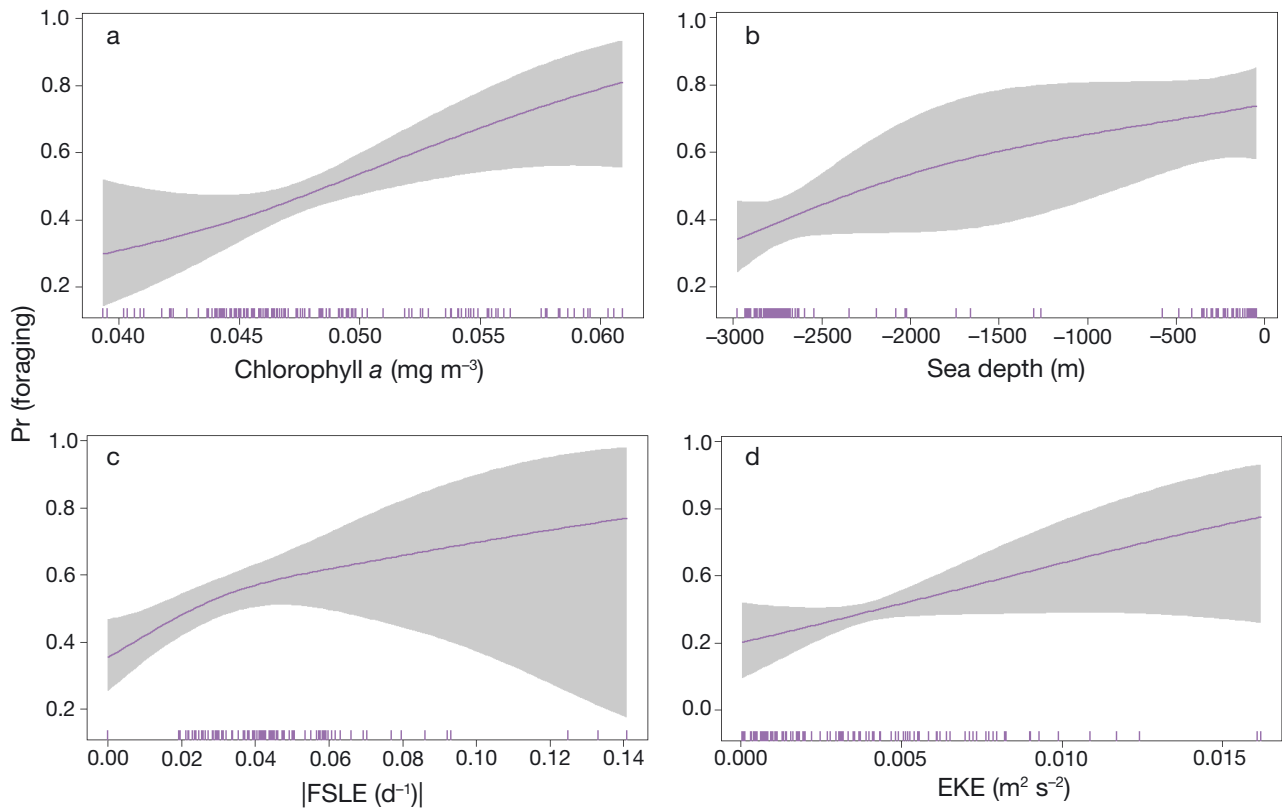
Fig. 4. GAMM response curves for key environmental predictors (p < 0.05) affecting foraging habitat selection of chick-rearing storm petrels in 2019. Response curves (n = 9 trips) of the probability of storm petrel foraging (0: non-use i.e. travelling, 45 fixes; 1: use i.e. searching/foraging, 138 fixes) according to (a) chlorophyll *a* concentration, (b) sea depth, (c) finite-size Lyapunov exponents (FSLE) and (d) eddy kinetic energy (EKE). Shaded areas correspond to the standard error of the estimate (purple line), while ticks on the *x*-axis show the overall distribution of the data

affecting the olfactory landscape and sea current formation (Nevitt 2008, Stewart 2008, De Pascalis et al. 2020). Therefore, an in-depth study investigating the energetic consequences of different wind conditions for the species is recommended.

Our results raise some pressing conservation concerns. The highly pelagic nature of this species during the breeding season (more than any other procellariform species breeding in the Mediterranean Sea; Louzao et al. 2006, Péron et al. 2013, 2018, Cecere et al. 2014), and the broad home ranges result in a wide range of threats encountered at sea. Such threats cannot be mitigated with area-based management, and require large-scale approaches (Oppel et al. 2018). Moreover, their tight foraging association with marine circulation processes (currents and eddies), coupled with surface-feeding constraints and a planktivorous diet, foster the risk of microplastic ingestion and bioaccumulation (Miller et al. 2020). Indeed, the central Mediterranean is highly contaminated by plastic debris, and microplastic movements and accumulation hotspots heavily depend on circu-

lation patterns (Guerrini et al. 2019, Caldwell et al. 2020). Broad-scale studies are needed to gain a better understanding of the species′ at-sea ecology, in order to develop effective conservation plans at the entire Mediterranean scale. Given the importance of storm petrel foraging grounds for marine predators of different taxa (e.g. large pelagic fish and cetaceans; Notarbartolo di Sciara et al. 2003, Royer et al. 2004, Cotté et al. 2011), such conservation efforts will likely have top-down effects on whole trophic webs, enhancing across-taxa conservation in one of the most degraded marine ecosystems worldwide (Claudet & Fraschetti 2010).

della Tutela del Territorio e del Mare (PNM n. 28399 del 10/10/2019 - Gestione dei Siti di Interesse Comunitario/Zone Speciali di Conservazione che ricadono all'interno delle Aree Marine Protette).

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Appendix. Evaluating GPS device effect on storm petrels

We assessed the effects of GPS devices on breeding storm petrels checking for differences in (1) body mass, (2) foraging trip duration and (3) hatching success between tagged and control birds.

For a subset of birds (n = 13), for which the device was removed immediately after the foraging trip, we compared body mass change (g) between GPS deployment and retrieval using a paired t-test. However, we did not measure body mass from a group of control birds to reduce any additional disturbance, since storm petrels are very sensitive to disturbance and handling (Blackmer et al. 2004).

We compared foraging trip durations of tagged and control birds during incubation. One of the main detrimental effects of device loading observed on seabirds is an increase in the energetic costs associated with foraging trips, resulting in longer foraging trip duration (Barron et al. 2010, Heggøy et al. 2015). During incubation, we deployed 2 camera traps in front of 3 active nests (with eggs), set to take time-lapse pictures every 20 min. We carefully marked 1 individual for each nest with a small white dot on the back of the head (without removing the animal from the nest) and we calculated foraging trip duration of 6 individuals, following De Pascalis et al. (2018). Foraging trip durations of tracked and control birds were then compared using an LMM with bird identity included as a random intercept effect. Significance was tested by the likelihood ratio test.

During incubation, we visited the colony in late August (22) to check the hatching success of tracked (n = 16) and control (n = 40) nests, and we used Fisher's exact tests to check for differences between the 2 groups. Control nests were located in an undisturbed nesting chamber that was accessed only twice, to count nests and to check hatching success.

Individuals did not decrease body mass after returning from a foraging trip (mean ± SD; deployment: 28.9 ± 2.8 g; retrieval: 29 ± 2 g; paired-samples t-test, t_{12} = −0.08, p = 0.93). With time-lapse cameras, we recorded 9 foraging trips from 9 incubating birds. Durations did not differ between control and experimental foraging trips (mean ± SD; control: 44.3 ± 19.4 h, n = 9; experimental: 51.4 ± 11.3 h, n = 12; df = 1; χ^2 = 0.78; p = 0.38). We found no difference in hatching success between tracked (25%, n = 16) and control (28%, n = 40) nests (Fisher's exact test, p = 1, odds ratio = 0.89).

Overall, we did not find any direct evidence of a detrimental GPS effect on storm petrels, a reassuring result that should nonetheless be taken with care, due to the small sample sizes considered. Tagged birds did not show a decrease in body mass, nor show longer trip durations, and had a similar hatching success to the control group. However, GPS-tagging individuals in natural nesting sites is difficult and challenging. Birds nest in high numbers on the ground of small caves (up to 100 nests in a single chamber), and natural egg loss due to movement of other birds (eggs are moved and then lost in crevices) is relatively common (F. De Pascalis et al. unpubl. data). Indeed, the eggs of the 4 birds that abandoned their nest after GPS-tagging had disappeared, and handling could lead to a momentary nest abandonment shortly afterwards that results in the egg being moved by other birds. Therefore, extreme care must be taken when tracking storm petrels in natural breeding sites such as caves. Researchers should preferentially target experienced individuals not at an early stage of incubation and breeding in shielded corners of the colony, preferably far from other clusters of nests.

Supporting information accompanying Chapter V

Fig. S1. Mean environmental variables in the central Mediterranean sea during storm petrel tracking periods. Mean chlorophyll-a concentration (mg m^{-3}) for 2019 (22/07/2019-11/08/2019) and 2020 (11/07/2020-23/07/2020) are shown in panels a) and b) respectively. Mean surface temperature (°C) for 2019 (23/07/2019-11/08/2019) and 2020 (11/07/2020-22/07/2020) are shown in panels c) and d) respectively. Mean environmental variables were calculated using 'Raster' R package (Hijmans 2018). Colony location is indicated with a star and black lines show foraging trips. To aid visualization, chlorophyll-a concentration was plotted using 1-99% values via the QGIS "*cumulative count cut*" function, in order to remove outliers.

1
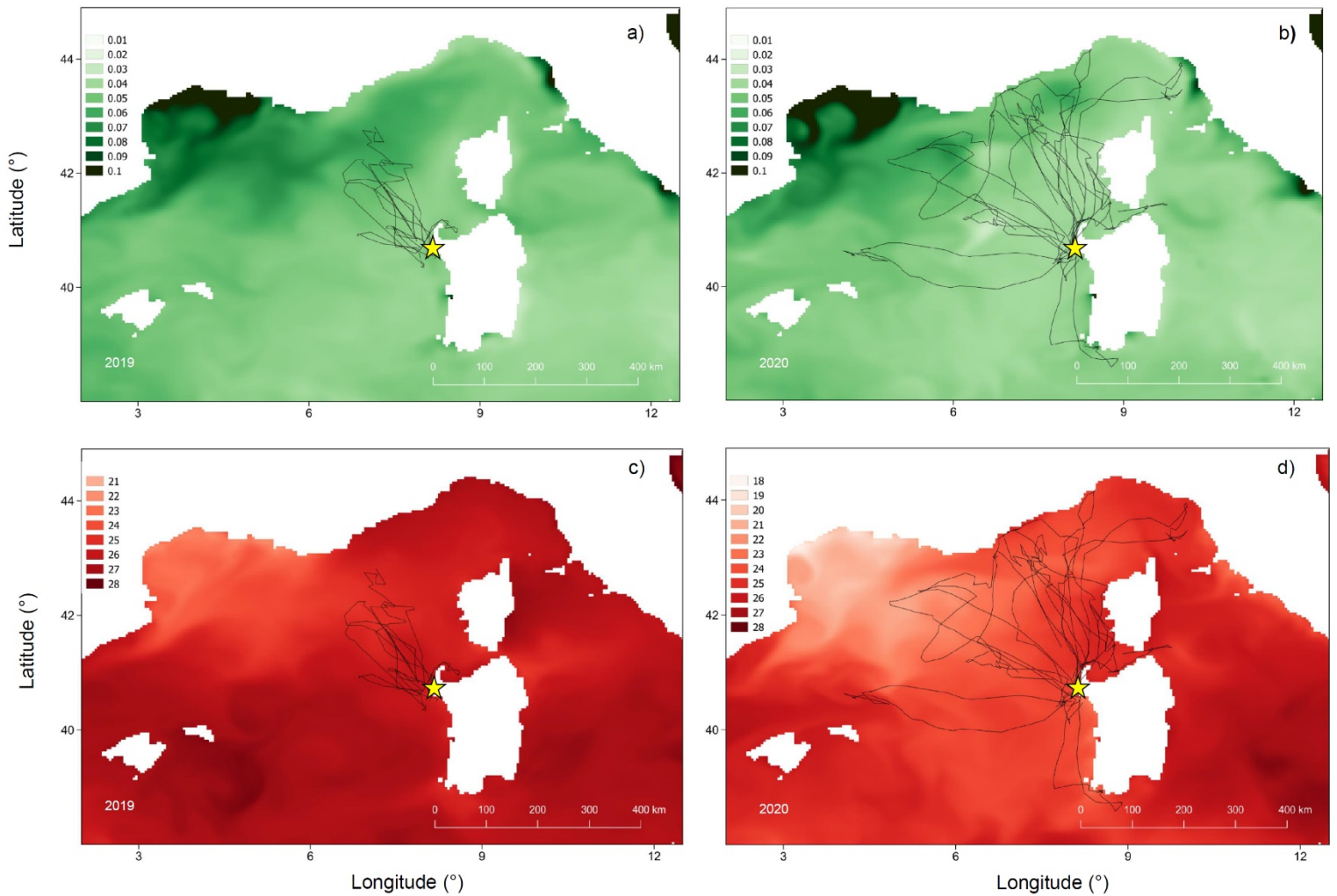
Fig. S2. Mean dynamic meso- and submesoscale oceanographic features in the central Mediterranean sea during storm petrel tracking periods. Mean current speed (m s^{-1}) for 2019 (23/07/2019-10/08/2019) and 2020 (11/07/2020-22/07/2020) are shown in panels a) and b) respectively. Mean eddy kinetic energy (EKE, m^2 s^{-2}) for 2019 (23/07/2019-10/08/2019) and 2020 (11/07/2020-22/07/2020) are shown in panels c) and d) respectively. Mean finite-size Lyapunov exponents (FSLE, day^{-1}) for 2019 (23/07/2019-10/08/2019) and 2020 (11/07/2020-23/07/2020) are shown in panels e) and f) respectively. Mean environmental variables were calculated using 'Raster' R package (Hijmans 2018). Colony location is indicated with a star and black lines show foraging trips. To aid visualization, EKE and FSLE were plotted using 1-99% values via the QGIS "*cumulative count cut*" function, in order to remove outliers.

2
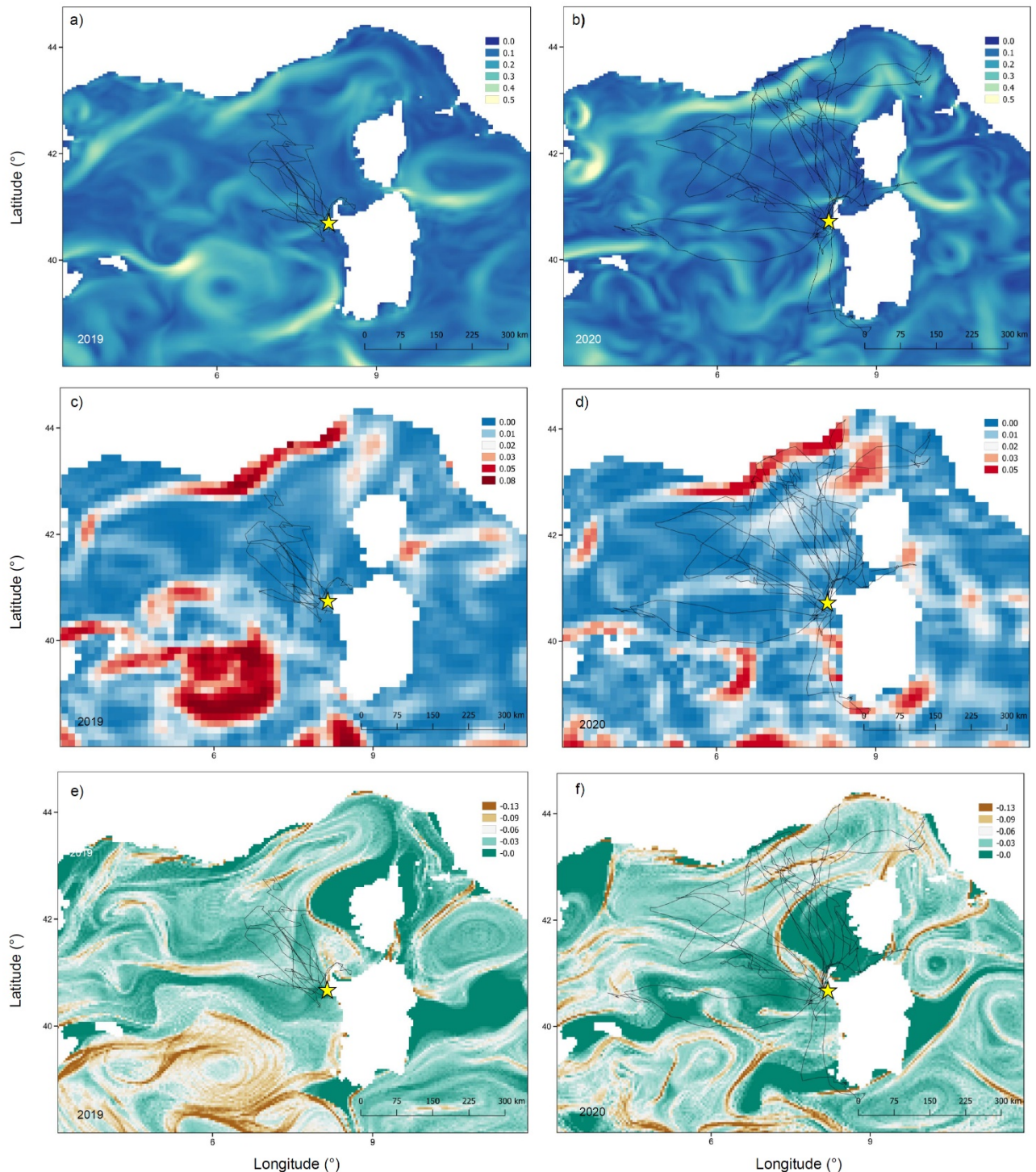
Fig. S3. Depth of the central Mediterranean sea (m). The colony location is indicated with a star and grey lines show foraging trips.
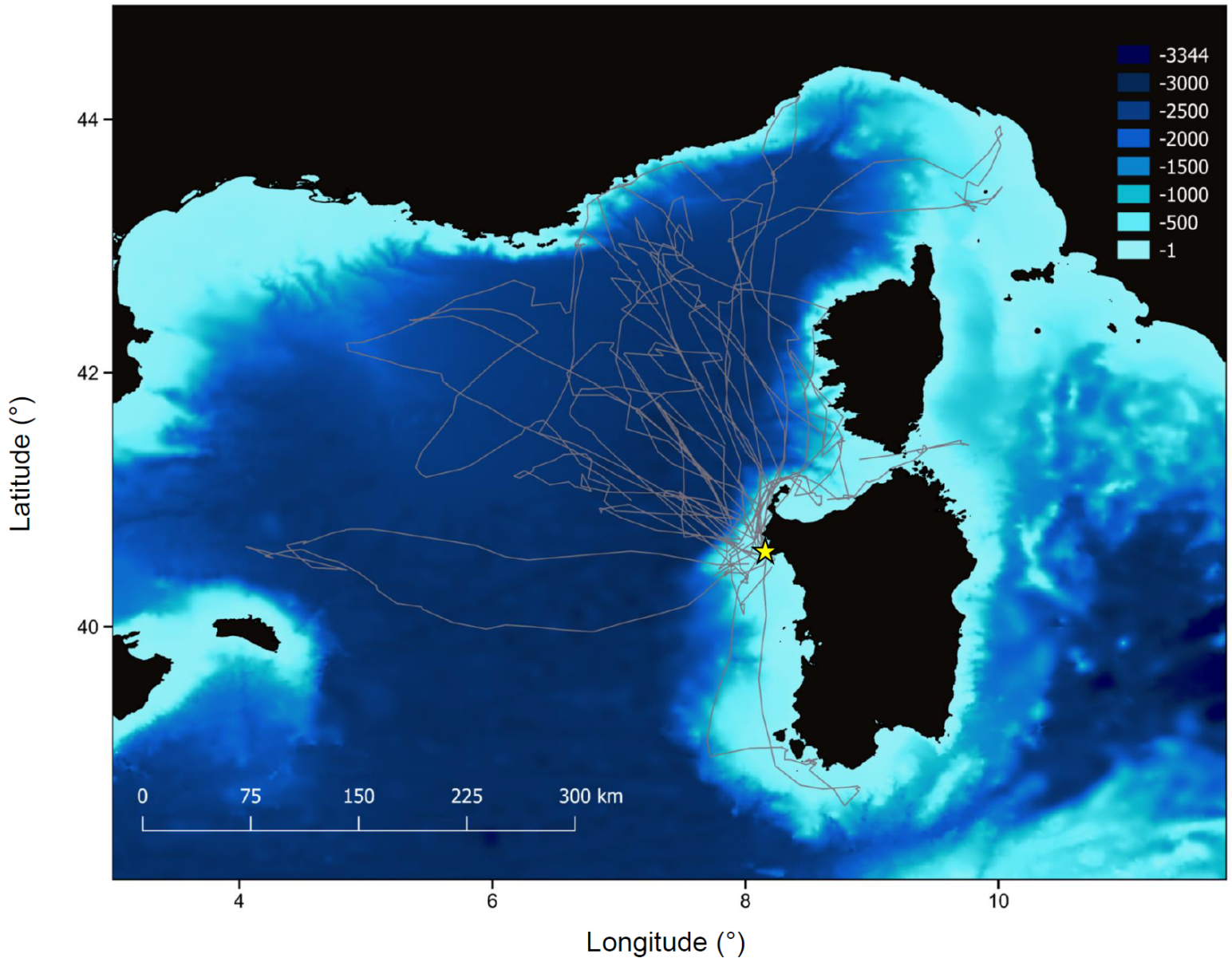
Fig. S4. Contour plot of the combined effect of sea depth (m) and current speed (m s^{-1}) on foraging behaviour of incubating storm petrel from a fitted GAMM. A binary GAMM was fitted (0: non- use i.e. travelling, 268 GPS fixes; 1: use i.e. searching/foraging, 390 GPS fixes) with sea depth and current speed fitted as a bivariate tensor (with cubic regression splines with shrinkage, and an auto-regressive AR1 correlation structure applied on each individual foraging trip at regularly spaced time-steps) to data collected during incubation (model r^2 = 0.10; p < 0.001, edf = 8.28; n = 12 trips). This graph provides some evidence that the combined effect of shallow waters and high current speed could increase foraging probability in incubating storm petrels.

te(sea depth, current speed, 8.28)
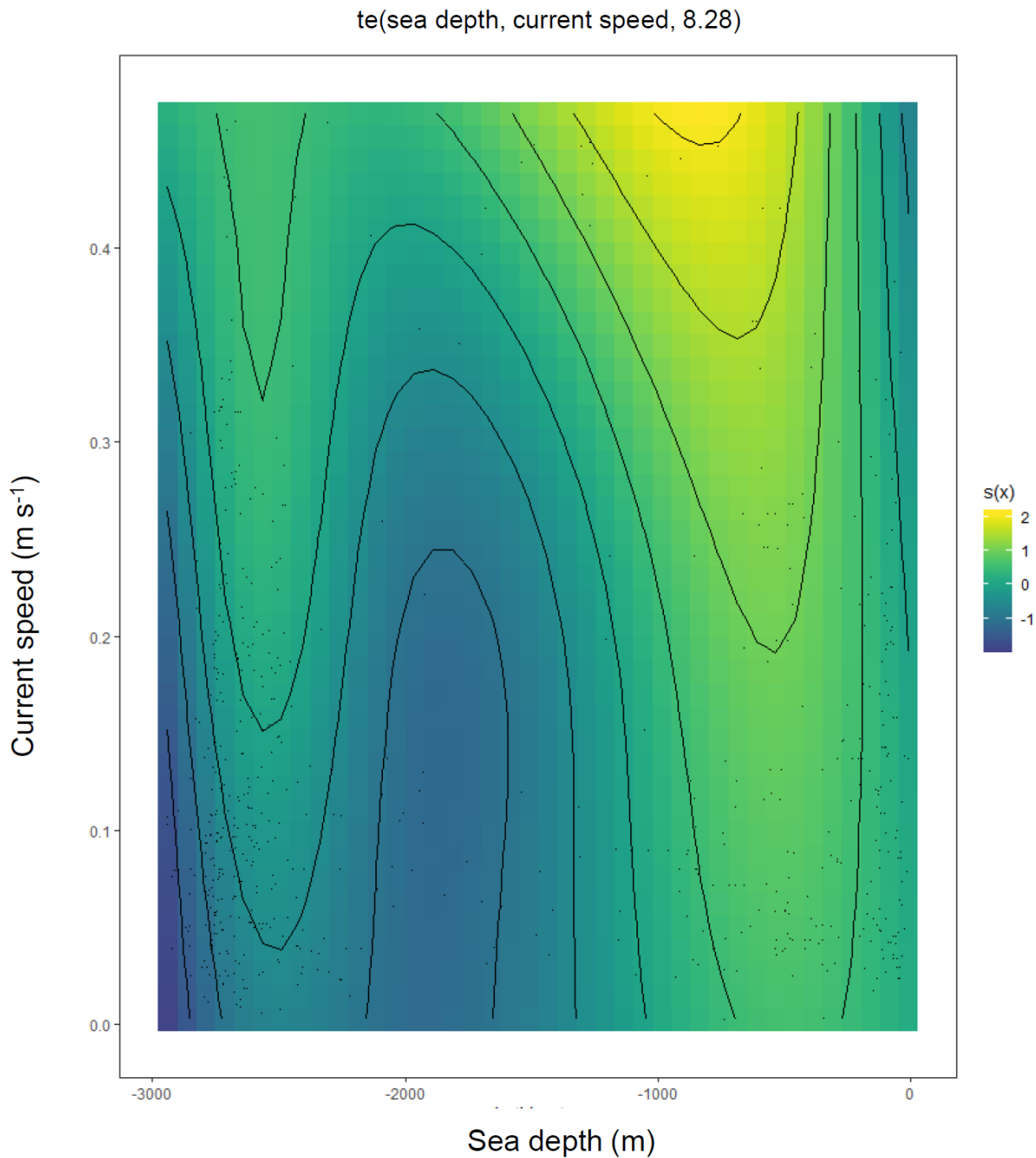
Table S1. Effect of body condition on foraging trip metrics. Spearman rank correlation coefficients between each trip metric and the scaled mass index (SMI) are shown. We considered only data from 2020 (n = 12) since in 2019 the sample of individuals with available SMI was too small (n = 5).

Trip metrics	r_s	p
Trip duration (h)	-0.01	0.96
Total trip length (km)	0.17	0.60
Maximum distance from colony (km)	0.19	0.54
Mean distance from colony (km)	0.42	0.18
Maximum distance from coast (km)	-0.31	0.32
Mean distance from coast (km)	0.05	0.87
Maximum speed (m s^{-1})	0.35	0.27
Mean speed (m s^{-1})	0.19	0.54
Home range size (km^2)[a]	0.25	0.43

Table S2. Full fitted binomial GAMMs. Models predicting the probability of use (1) vs. non-use (0) according to seven static/dynamic environmental variables during incubation (use: 390, non-use: 268 fixes) and chick-rearing (use: 138, non-use: 45 fixes). Cubic regression splines with shrinkage were used, and an auto-regressive AR1 correlation structure was applied on each individual foraging trip. Model r^2; incubation: $r^2 = 0.17$; chick-rearing: $r^2 = 0.16$.

Environmental variable	Incubation		Chick-rearing	
	edf	p	edf	p
Chlorophyll-a	1.75	0.25	1.04	0.01
Sea surface temperature	0.91	0.02	0.01	0.55
Sea depth	6.63	< 0.001	1.39	< 0.001
Slope	1.75	0.25	0.79	0.08
Eddy kinetic energy	1.00	0.91	1.00	0.02
Finite-size Lyapunov exponents	3.83	< 0.001	1.17	0.01
Current speed	1.35	< 0.001	0.46	0.18

CHAPTER VI: foraging in the Anthropocene

The hidden cost of following currents: microplastic ingestion in a planktivorous seabird

In review (2nd revision): Marine Pollution Bulletin

A Mediterranean storm petrel (*Hydrobates pelagicus melitensis*) forages close to drifting human artifacts. Picture: A. Benvenuti.

The hidden cost of following currents: microplastic ingestion in a planktivorous seabird

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Abstract

Plastic is an increasing and pervasive pollutant with detrimental effects on marine organisms. We assess dietary microplastic ingestion in the Mediterranean storm petrel (*Hydrobates pelagicus melitensis*), a small pelagic seabird from the Mediterranean sea, one of the most polluted seas worldwide. We collected spontaneous regurgitates from 30 chick-rearing individuals and used GPS tracking data from 7 additional individuals to locate foraging areas. Birds foraged in pelagic areas characterized by water stirring and mixing, and regurgitates from 14 individuals (i.e. 45%) contained microplastics, mostly blue and transparent items. Fibers were the dominant shape (56%) with polyester, polyethylene and nylon being the most frequent polymers. Our findings highlight the potential sensitivity of this species of conservation interest to plastic pollution and suggest that storm petrel regurgitates can be a valuable matrix to investigate microplastic ingestion in planktonic foragers, providing a characterization of spatio-temporal patterns of microplastic exposure in pelagic environments.

Introduction

Plastics polymers are among the most ubiquitous and pervasive pollutants occurring in seas and oceans (Rios et al. 2010, Eriksen et al. 2014). In 2019, global plastic production reached 368 million tonnes (Plastic Europe, 2020), and its manufacture, use and presence in the marine environment are increasing (Moore 2008, Patrício Silva et al. 2021). Plastic litter poses a transboundary and diffuse threat to marine species (Laist, 1987; Hermabessiere et al., 2017) and the detrimental effects of macro (> 25 mm) and mesoplastic (5-25 mm) ingestion on marine animals have been observed and studied since the 1970s (Kenyon & Kridler 1969). However, in the past two decades, awareness has risen on the presence of small and less obvious particles of plastics, known as microplastics (< 5 mm), that have now been reported in almost every basin worldwide (Ryan, 2015; Provencher et al. 2018). These small plastic fragments can enter the ocean directly, released from outlet water of Waste Water Treatment Plants (WWTPs) as they are structural components of cosmetics and cleaning products (Fendall & Sewell 2009) and commonly released from clothes after domestic and industrial washing (De Falco et al. 2018, Zambrano et al. 2019). They could also derive from the degradation of larger plastic items that experience chemical, physical and biological wearing (Ryan 2015).

Microplastics are abundant in the neuston (Ryan et al. 2009), where they can behave similarly to planktonic organisms, passively drifting on the sea surface and being carried by currents, waves and transport fronts (Iwasaki et al. 2017). Indeed, they are ingested indirectly by large planktonic foragers of different taxa (Fossi et al. 2014, Amelinau et al. 2016), but they could also enter the trophic web bottom-up (Nelms et al. 2018), as zooplankton is highly susceptible to their ingestion (Botterell et al. 2019). While the potential negative effects of microplastics on organisms is subtle, and still largely unclear for large vertebrates, taxa-specific negative effects on foraging, growth, reproduction and survival has been reported in fish and invertebrates (Foley et al. 2018). These negative effects could result directly from the leaching of toxic plastic additives

73 and/or to the fact that microplastic can enhance the transport and bioavailability of toxic

74 compounds, such as persistent organic pollutants (POPs) and trace elements (Ivar Do Sul & Costa

75 2014, Neumann et al. 2021).

76   Mediterranean storm petrels (*Hydrobates pelagicus melitensis,* hereafter "storm petrels") are

77 small planktonic procellariform seabirds inhabiting almost year-round the Mediterranean basin

78 (Lago et al. 2019, Martínez et al. 2019), one of the most polluted marine areas worldwide, with high

79 plastic contamination (Claudet & Fraschetti 2010, Lebreton et al. 2012). Their long life-span can

80 chronically expose them to the ingestion of microplastics, similarly to other long-lived marine

81 species (Fossi et al. 2012). Moreover, they forage in the neuston and they associate with pelagic

82 marine meso- and submesoscale features, such as eddies, surface currents and Lagrangian coherent

83 structures (D'Elbée & Hémery, 1998; Albores-Barajas et al., 2011, De Pascalis et al., 2021), where

84 both zooplankton and drifting microplastics can be found in high concentration (Collignon et al.

85 2012, Suara et al. 2020). Previous studies suggested that procellariforms in general, and storm

86 petrels in particular, are very sensitive to macro- and mesoplastic ingestion (Kühn et al. 2015), but

87 there is no information on microplastic ingestion. Furthermore, information about plastic ingestion

88 by seabirds in the Mediterranean basin is scanty (but see Codina-García et al. 2013). The storm

89 petrel is considered as a threatened species in Europe (Annex I of the Birds Directive

90 2009/147/EC), and the conservation status of genetically and phenotypically distinct Mediterranean

91 populations is poorly known (Cagnon et al. 2004). In this study, we aimed to assess the sensitivity

92 of storm petrels from the Mediterranean Sea to microplastic pollution. We collected spontaneous

93 regurgitates of chick-rearing storm petrels to 1) assess microplastic occurrence in diet and 2)

94 provide a qualitative and quantitative assessment of ingested microplastics (if any). Given the

95 ecology and life history traits of the Mediterranean storm petrel, we expected a relatively high

96 incidence of microplastics in regurgitates.

97

Materials and methods

Regurgitates collection

In July-August 2019, during the chick-rearing stage, we collected regurgitates from 30 breeding birds (one per individual). Birds were caught by hand at night in a colony in Sardinia, Italy (40°35'18"N; 8°10'24"E). Storm petrels provision their chicks with a diet-derived, lipid-rich fluid, that is stored in the proventriculus and then regurgitated in the chick mouth (Aguado-Giménez et al. 2016). Regurgitates were collected in single glass vials (25 ml, one per vial), previously washed with acetone to remove any plastic contamination. Regurgitates can be easily and non-invasively collected, as they are spontaneously expelled during handling (each handled bird spontaneously regurgitated). Sampled individuals were induced to regurgitate directly into the glass vials or sometimes in a metal spoon previously washed in acetone (i.e., we did not collect regurgitates from the cave floor or from clothes). Vials were filled with 90% EtOH (10 ml, previously stored in glass) upon regurgitate collection and stored at -20 °C until further analysis.

Microplastic identification and characterization

All the glassware, stainless forceps and pins used during the analytical procedure were washed with acetone, rinsed with ultrapure water previously filtered on cellulose filters (StonyLab, pore size 1 µm; Ø = 47 mm) and wrapped in tinfoil until analyses to avoid laboratory contamination. Each regurgitate (ca. 5 - 15 ml) was transferred to a 150 ml beaker, then 75 ml of pre-filtered (cellulose filters, StonyLab, pore size 1 µm; Ø = 47 mm) saturated sodium chloride solution (density =1.2 g/cm^3; 365 g/l) were added. Each beaker was stirred for 30 min using a glass-covered magnetic stirring rod, and the solution was left settling overnight. The supernatant was then transferred to a clean beaker, and 2 ml of Fenton's reagent and 2 ml of 30% hydrogen peroxide solution pre-filtered on cellulose filters (StonyLab, pore size 1 µm; Ø = 47 mm) were added, according to Prata et al. (2019). After 5 min, additional 2 ml of hydrogen peroxide were added, and the solution was heated

at 50 °C for 1 h. The obtained solution was left settling overnight at room temperature, and then filtered on cellulose filters (StonyLab, pore size 1 µm; Ø = 47 mm) through a water-jet pump. The beaker was washed three times with pre-filtered ultrapure water (10 ml each) and the washing aliquots were filtered on the same filter used for the sample. The filter was placed in a glass petri dish (Ø = 50 mm) and dried into a desiccator for 48 h.

Regurgitate samples were processed in four batches of (6-10 samples per batch). A procedural blank was run with each batch of regurgitates processing the same volume of saturated sodium chloride solution. Preliminary visual inspection (according to shape and colour of items) of the filters was performed under a Leica EZ4 W stereomicroscope to check for the presence of putative microplastics. The detection and isolation limit of putative microplastics through the preliminary visual inspection of filters was 20 µm in size. Items identified as putative microplastics during the preliminary visual inspection were transferred individually to Anodisc membrane filters (Whatman®; Ø = 13 mm, pore size = 0.2 µm) with stainless pins. A picture of each single item transferred to the filter was captured to allow the measurement of size (expressed as the maximum length of the item) with the image processing package Fiji freeware software (Schindelin et al. 2012).

To support inter-comparability of studies (Provencher et al., 2017), items isolated form regurgitates were grouped according to their shape in two main categories, i.e. fragments and fibers. No pellets and films were found in regurgitates. Items were also categorized according to their colour. A Munsell chart was used to specifically assign a colour to each item, which felt into one of the eight broad colour designations (i.e., white-transparent, grey-silver, black, blue-purple, green, orange-brown, red-pink, and yellow), and gradients were used to determine a light or dark tone classification (Verlis et al. 2013).

As an additional quality control, to check for potential aerial contamination from the laboratory environment, a cellulose filter was placed on a tinfoil next to the equipment used during

the whole duration of the analytical procedure (Winkler et al. 2020). Such filter was inspected as described above to check for the presence of external contamination, and none was found. During the regurgitate analysis, some blue fibers were found in the procedural blanks, but none was isolated from the filters used to check for aerial contamination of the laboratory. As µ-FTIR analyses (see below) showed that these fibers were made by cellulose, they were excluded from the regurgitate samples analysis.

The polymeric structure of the isolated items was obtained with a Fourier Transformed Infrared microscopy (µ-FTIR) analysis, using a Nicolet iN10 Infrared Imaging Microscope (Thermo Scientific). The analyses were performed in reflection mode in a wavenumber range of $4,000 - 675$ cm^{-1}. The instrument was controlled by OMNIC Picta software. A total of 256 scans were acquired for each single spectrum, with a spectral resolution of 4 cm^{-1}. The dimensional limit of the items for a correct identification was 20 µm. Polymer identification was performed by comparing the obtained spectrum with those of libraries with a matching > 70%. The following libraries were used to identify the polymeric composition of each microplastic item: HR Aldrich Polymers, HR Coatings Technology, HR Hummel Polymer and Additives, HR Industrial Coatings, HR Polymer Additives and Plasticizers, HR Rubber Compounding Materials, HR Spectra Polymers and Plasticizers, Hummel Polymer sample Library and Polymer Laminate Films.

Identification of foraging areas

To identify the foraging areas exploited by individuals from the study population, we equipped 13 chick-rearing adults with PathTrack nanoFIX® GEO-MINI GPS loggers (ca. 0.9 g, accounting for ca. 4% of storm petrel body mass), set to record 1 location every 20 min. To avoid excessive disturbance and manipulation on this sensitive species during the critical breeding period , we tracked different individuals from the one used to collect regurgitates (see De Pascalis et al., 2021 for further information on GPS tracking). We obtained GPS tracks of 9 foraging trips from 7 individuals. Foraging trips were visually identified, and locations were inspected and spatio-

172 temporal duplicates removed using 'SDLfilter' R package (Shimada 2019). Foraging/searching

173 behaviour was identified from the 1-h interpolated GPS tracks using Hidden Markov Models,

174 (HMMs) following De Pascalis et al. (2021). To identify foraging areas, all the locations identified

175 by the fitted HMM as "foraging/searching" where pooled together and the ones identified as

176 "travelling" where removed, since they do not identify areas where the animals feed/search for

177 food. Kernel Density Estimates (KDEs, 95% contours) were then calculated using 'KernSmooth' R

178 package (Wand 2015). The least squares cross validator estimator from 'ks' R package (Duong

179 2007) was used to obtain optimised covariance bandwidth matrices, and projected coordinates were

180 used to avoid spatial biases.

Results

Microplastic identification and characterization

183 Overall, microplastics were found in regurgitates from 14 individuals out of the 30 sampled (45%).

184 Regurgitates with microplastics contained on average 1.86 ($\pm$ 1.03 SD) microplastic items per

185 sample (range: 1-4 items), for a total of 25 microplastic items isolated and characterized (details in

186 Table 1). Fragments represented 44% of the microplastic items, while the remaining were fibers.

187 The size of microplastics (maximum length of items, independently of shape) ranged between 39

188 and 3582 µm (mean $\pm$ SD: 583 $\pm$ 947 µm, N = 25 items). Fiber length ranged between 73 and 3582

189 µm (mean $\pm$ SD: 956 $\pm$ 1144 µm, N = 14), while fragment size ranged between 39 and 220 µm

190 (mean $\pm$ SD: 107 $\pm$ 63 µm, N = 11). Most of the microplastics were blue and transparent (24%

191 each), followed by pink (16%) and purple (12%). White, green, grey and red microplastics were

192 less represented in regurgitates (i.e., only one item per each colour). Polyester (20%) was the most

193 abundant polymer, followed by polyethylene (16%), nylon (12%), polyethylene terephthalate (8%)

194 and polyurethane (8%), while a lower contribution was given by ethylene-propylene diene

195 monomer (EPDM), polyacrylate, polyvinyl acetate, polyvinylidene fluoride and polystyrene (only

one item per each polymer) (Fig. 1). It was impossible to unequivocally identify the polymeric

composition of four items (16%) because of a too low matching with the spectra in the libraries.

Likely, they were items made by composite materials or multilayers, particularly difficult to analyse

given the superimposition of several spectra, and therefore their origin (i.e., industrial, consumer,

etc) is impossible to guess. In addition to microplastics, 23% of regurgitates contained microfibers

of natural origin (i.e., cellulose-based microfibers).

Figure 1. Percentages of each polymer type identified in Mediterranean storm petrel regurgitates

with microplastics (N = 14 regurgitate samples, same colours represent the same percentage).

Polymer types were identified through Fourier Transformed Infrared (FTIR) microscopy.
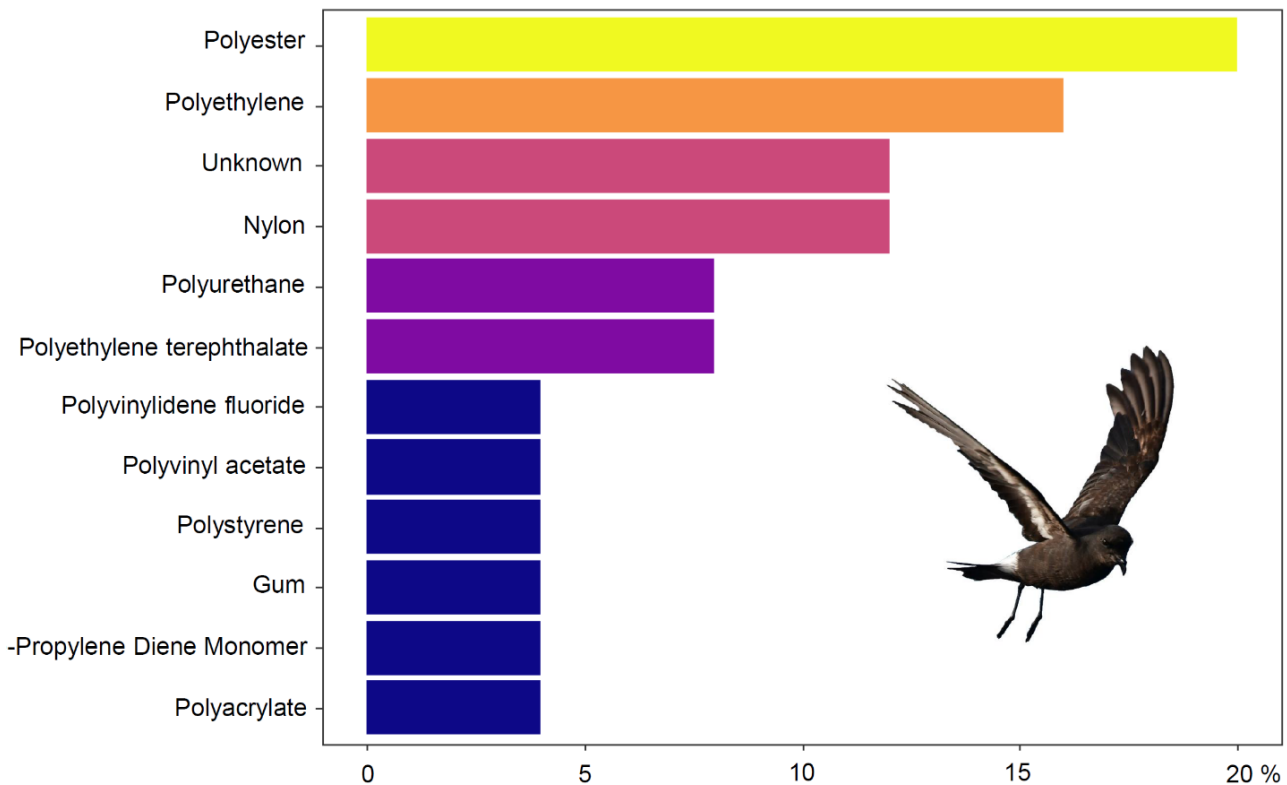
207 **Table 1**. Characteristics of each identified microplastic item (N = 25 items) in storm petrel

208 regurgitates (N = 14 regurgitates samples).

Sample	Shape	Colour	Length (µm)	Polymer
1	Fiber	Blue	73	Polyester
2	Fragment	Pink	220	Unknown
3	Fragment	Purple	65	Polyurethane
4	Fragment	White	99	Unknown
4	Fragment	Blue	104	Polyethylene
4	Fiber	Transparent	272	Polyester
4	Fiber	Blue	687	Ethylene-Propylene Diene Monomer
5	Fragment	Blue	39	Polyethylene
5	Fiber	Purple	216	Polyethylene terephthalate
6	Fiber	Transparent	1430	Polyethylene
7	Fragment	Blue	59	Acrylate
7	Fragment	Grey	86	Polyethylene
8	Fragment	Green	46	Unknown
8	Fiber	Pink	411	Nylon
9	Fragment	Purple	175	Polyethylene terephthalate
9	Fiber	Pink	228	Polyester
10	Fragment	Blue	80	Polyurethane
11	Fiber	Transparent	3582	Polystyrene
11	Fiber	Transparent	2194	Nylon
12	Fiber	Transparent	2972	Nylon
12	Fiber	Red	374	Polyester
13	Fiber	Pink	414	Polyester
14	Fragment	Transparent	202	Gum
14	Fiber	White	376	Polyvinyl acetate
14	Fiber	Black	160	Polyvinylidene fluoride

209

Identification of foraging areas

We identified two main putative foraging areas. One is a pelagic area located almost in the middle of the Liguro-Provençal basin, while the other extends from the Sardinian coast towards West (Fig. 2). This region is characterized by a strong mesoscale and submesoscale activity, with eddies generating strong vertical velocities that can induce water exchanges between the deeper layer and the surface (eddy pumping mechanism) (Falkowski et al. 1991; Casella et al. 2014).

Figure 2. Foraging areas of Mediterranean storm petrels (95% KDEs contours) from GPS-tracked individuals (2019, N = 7 individuals) are shown in orange. In the background, mean current speed for the tracking period is plotted (lighter shades of colour indicates stronger currents). The star indicates the colony location and foraging locations of individuals are shown (each colour represents a different individual).
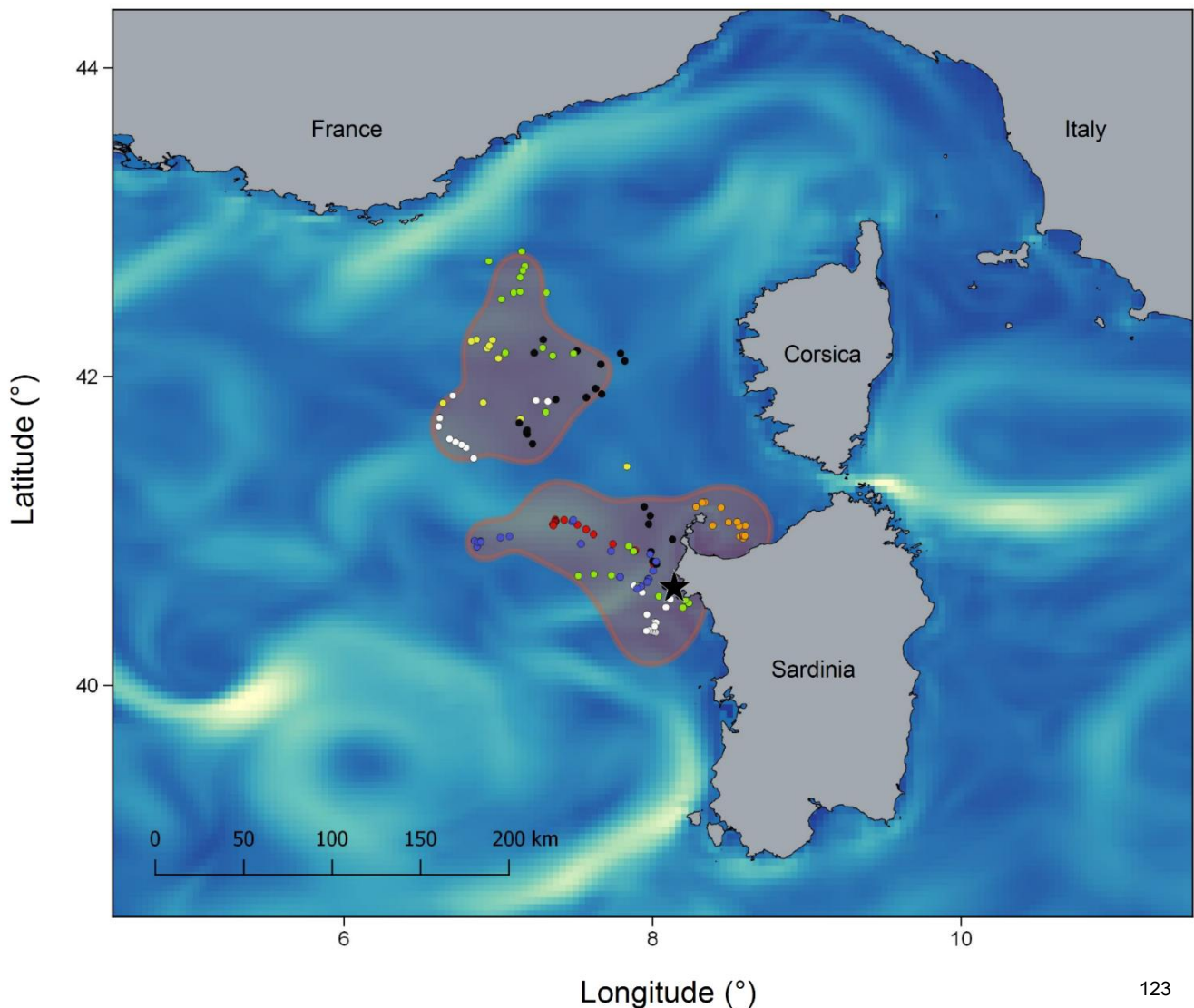
Discussion

We found that 45% of the sampled storm petrels ingested microplastic items of different nature during the chick-rearing stage. Our results highlight that breeding storm petrels from the Mediterranean Sea are exposed to microplastics via dietary ingestion. As storm petrels are planktonic and opportunistic feeders (D'Elbée & Hémery, 1998; Carreiro et al., 2020), both direct and indirect microplastic ingestion may occur.

Fibers were the most frequently ingested microplastic shape, similarly to other seabird species (albeit using different sampling matrixes; Codina-García et al., 2013; Amélineau et al., 2016), while the most ingested plastic polymers were polyester, polyethylene and nylon. Polyester is one of the most common man-made plastic fibers, widely used in the textile industry (Dalla Fontana et al. 2020) and particularly abundant in the marine environment (Dalla Fontana et al. 2020, Ross et al. 2021). Polyethylene is the most abundant plastic type present in the marine environment (Erni-Cassola et al. 2019), mainly used in disposable food packaging industry and widespread in Mediterranean waters (Suaria et al. 2016). Worryingly, polyethylene microplastic have a high affinity for hydrophobic compounds and its absorption ability of polycyclic aromatic hydrocarbons (PAHs), polychlorinated biphenyl (PCBs), naphthalene and perfluorooctylsulfonamide (FOSA) is higher than that of other plastic compounds (Wang et al. 2020). Finally, nylon fibers in the marine environment mostly originate from the fishing industry, where this polymer is widely used due to its strength and low degradation potential when exposed to saltwater (Kor et al. 2020).

The enclosed nature, the high coastal anthropization and the intense shipping and fishing activity in the Mediterranean favour the accumulation of plastic litter, with potential negative consequences for marine organisms (Ramirez-Llodra et al. 2013, Roman et al. 2021). The main foraging grounds exploited by storm petrels from the studied population were located in a deep and

highly dynamic marine region, where two surface circulation structures (Gulf of Lyon gyre and the
Liguro-Provençal-Catalan current) and one intermediate depth circulation structure (Western
Corsica Current) move water masses (Pinardi et al. 2015). The area is characterized by strong water
mixing and stirring, with localized upwelling areas and strong frontal activity (Casella et al., 2014;
Casella, Molcard, & Provenzale, 2011). Such features aggregate planktonic organisms, and attract a
series of planktonic foragers of different taxa (Falkowski et al. 1991, Della Penna & Gaube 2020).
Interestingly, simulations used to map microplastic presence in the area using Lagrangian particle
tracking suggest that the species' foraging grounds were located in an area with relatively low
microplastic density and contaminant concentration than the surrounding marine regions (Guerrini
et al. 2021). Considering that 45% of the sampled individuals ingested microplastics, this raises
concerns on ingestion levels in storm petrels foraging in more polluted areas, such as the Western
Mediterranean (Guerrini et al. 2021). While the fitness effects of microplastic ingestion in seabirds
are yet unclear, it has been shown that a set of hazardous additives can leach from ingested
microplastic to stomach oil (Kühn et al. 2020). Once in the stomach, such substances could be
assimilated and may accumulate in tissues (Tanaka et al. 2015), ultimately with the potential to act
as endocrine disruptors and negatively affect fitness.

In conclusion, our findings suggest that storm petrel regurgitates could be used as an
efficient and reliable indicator of microplastic exposure in pelagic seabirds, highlighting the
potential sensitivity of this species of conservation interest to plastic pollution. However, since there
is a lack comparative studies testing the effectiveness of different matrixes to capture the ingestion
of microplastics in storm petrels (and thus their reliability), some caution in the interpretation of the
results must be taken. Nevertheless, standardized sampling of regurgitates from different storm
petrel colonies across the broad distribution range of this species could provide the opportunity to
study microplastic ingestion at broader scales and to highlight spatial and temporal trend of
microplastic ingestions.

Author contribution

Conceptualization: DR, MP, JGC, FDP. Investigation: FDP, BDF, MP, JGC, DPI, DPA, LI, GM, LS. Formal analysis: FDP, BDF, MP, DA, EP, VG. Writing - original draft: FDP. Writing - review & editing: all coauthors.

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CONCLUSION AND FINAL REMARKS

Overall, my thesis highlights that the fundamental process of making optimal spatio-temporal foraging decisions (i.e., to decide where, when and how to forage to obtain the maximum energetic gain), is complex and finely modulated by several factors. This process is particularly intricate in colonial bird species, where high densities of hetero- and conspecifics generate pressures of different nature, that are often density dependent and that deeply affect foraging choices. We showed that red-footed boobies from a large population (2094 breeding pairs) segregated from, and foraged further from the colony, than brown boobies from a small neighbouring population (146 breeding pairs, ca. 4 km distance), despite sharing the same trophic resources. This suggests that inter-specific competition could drive foraging segregation between populations, whereas intra-specific competition in large colonies drive individuals to travel larger distances from the colony to find food, in accordance with Ashmole's hypothesis (Ashmole 1963). Additionally, sexual dimorphism likely resulted in sex-specific foraging areas in brown boobies, a process not observed in the monomorphic red-footed boobies. Sex-based differences in foraging behaviour are often observed in seabird species. These differences could help in the reduction of intra-specific competition between sexes, being at the same time a convenient way of expanding the ecological niche of breeding pairs, allowing a steady chick provisioning under fluctuating environmental conditions, buffering the risk of offspring starvation. Some of the intrinsic elements that create these sex-based differences in foraging behaviour (i.e. morphology, structure, size, physiology or parental roles; González-Solís et al. 2000, Lewis et al. 2005, Austin et al. 2019) can interact with external conditions (extrinsic elements), for example shaping asymmetric energetic costs based on individual characteristics. We observed that males Scopoli's shearwater tend to use a foraging tactic that likely meets their energetic optima (lower flight activity and more floating on the sea surface), probably because males experience higher flight cost, given their higher wing loading. However, when wind conditions are strong enough, they switch to a tactic that involves more flight activity and longer

distance travelled (usually adopted by females), exploiting the advantages of dynamic soaring. In lesser kestrels, a combination of high solar radiation and strong crosswind promoted a dynamic foraging mode. Such foraging tactic entails a higher energetic expenditure, but ultimately leads to a larger increase in body mass of nestlings. These findings suggest that individuals adopted the more suitable foraging tactic according to the weather landscape in their foraging grounds, and the strong inter-individual variability in tactic adoption was likely related to age, experience or physiological status, again highlighting the fine interplay between intrinsic and extrinsic elements, that is often difficult to disentangle.

Birds move in an extremely dynamic medium (i.e. the air) and different atmospheric components that vary in strength and directionality across different time-scales (Clay et al. 2020) have a huge impact on their locomotion. The work contained in this thesis suggests that atmospheric agents, such as wind and rainfall, can alter foraging movements and decisions and that birds cope with such agents in different ways. For example, individuals can take advantage of a sudden favourable condition, such as an increase in wind speed, to perform costly activities, like taking off from perches or reaching favourable foraging grounds earlier, as we observed in frigatebirds. Moreover, they can exploit favourable wind conditions (speed and/or direction) to adopt a specific foraging tactic. Alternatively, when unfavourable conditions happen, birds can adopt a "waiting strategy", waiting for the unfavourable condition to finish. For example, our findings on frigatebirds suggest that in the presence of heavy rainfall they stop their foraging activities and perch, avoiding the additional energetic loss created by such adverse condition and minimizing rain exposure. Atmospheric challenges are important for bird species, that must cope with them regularly and frequently. However, in the wild, the ultimate challenge is locating food, particularly in environments where resources are scattered and/or ephemeral, such as in seas and oceans. These habitats have also the further complexity of being 3-dimensional and extremely dynamic. Our findings on storm petrels suggest that individuals can take advantage of such dynamicity, exploiting both dynamic and static features (as well as their interactions) to forage, enhancing food finding

opportunities. Indeed, fronts, filaments, currents and eddies, thanks to their dynamicity, aggregate planktonic organisms and their predators, increasing foraging opportunities for different taxa. However, in a world becoming more and more dominated by human presence, such dynamic structures host not only foraging benefits, but hidden risks too. Unfortunately, eddies and filaments aggregate plankton, marine propagules (Harrison et al. 2013) and micro and macro plastics as well (Collignon et al. 2012, Suara et al. 2020). Microplastics are an emerging diffuse threat for marine organisms, and seabirds can ingest large quantity of this pollutants, whose effect on organisms, albeit still unclear, can be detrimental (Ryan 2015; Provencher et al. 2018). Indeed, 45% of the sampled storm petrels ingested microplastics of different nature, suggesting that planktonic surface foragers could be particularly exposed to this emerging threat.

Ultimately, in this thesis, I investigated variation in foraging behaviour of different species operating in contrasting habitats. Observed differences are mainly due to dissimilar functional traits and to their interaction with the ecological mechanisms at play within the environments they live in. Nesting behaviour, body size, sexual dimorphism, wing morphology, utilization of visual, olfactory or auditory cues to forage, and the consequent development of specific sensory traits, all affect the way in which external factors alter foraging behaviour. For example, dynamic soaring species with a developed sense of smell, could be more affected by wind conditions than tropical species relying on thermal updrafts or flapping flight to search for visual cues of prey presence. However, despite the specie-specific differences, individuals tend to flexibly adjust their foraging behaviour to maximize their energetic gain, modulating their movements according to the interplay of internal and external factors.

In conclusion, understanding the connection between individual qualities, foraging movements and external agents is particularly important given the predicted global changes for future years. Ultimately, behavioural flexibility in foraging could be an important trait to successfully cope with such changes and could contribute to increase the resilience of populations over time. It is important to keep investigating drivers of foraging decisions, with a particular focus

on their interplay and combined effect, to shed light on the processes at play and obtain key baseline information for effective mitigation and conservations strategies.

APPENDIX

Complete chronological list of publications in ISI-ranked journals published during the PhD period (October 2018-December 2021). The asterisk indicates manuscripts included as chapters in this thesis.

1. Assandri, G., Cecere, J. G., Sarà, M., Catoni, C., **De Pascalis, F**., Morinay, J., Berlusconi, A., Cioccarelli, S., Mercogliano, A., Pazhera, A., Terras, A., Imperio, S., Morganti, M., Rubolini, D. (2022). Context-dependent multi-scale of habitat selection in a farmland raptor along an agricultural intensification gradient. **Agriculture, Ecosystems and Environment**, *326, 107782.*

2. **De Pascalis, F**., Austin, R., Green, J. A., Arnould, J. P. Y., Imperio, S., Maugeri, M., Haakonsson, J., Cecere, J. G., Rubolini, D. (2021)*****. Influences of rainfall on foraging behaviour of a tropical seabird. **Behavioral Ecology.** *In press.*

3. Ilahiane, L., **De Pascalis, F**., Pisu, D., Pala, D., Ferrario, F., Cucco, M., Rubolini, D., Cecere, J. G., Pellegrino, I. (2021). No evidence of avian malaria occurence in two Mediterranean endemic seabirds. **Marine Ornithology,** *50, 13-17.*

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