



Foraging ecology of masked boobies (*Sula dactylatra*) in the world's largest "oceanic desert"

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Abstract

The South Pacific Gyre has the most hyper-oligotrophic waters in the world and is considered the largest "oceanic desert." Rapa Nui (Easter Island), located within the South Pacific Gyre, is a breeding ground for masked boobies (*Sula dactylatra*), which are seabirds with a foraging range that effectively confines them within the gyre. The foraging ecology of this species in the gyre was examined by attaching GPS and time-depth devices to chick-rearing adult birds (9 and 14 birds in 2016 and 2017, respectively) and by collecting regurgitates (18 and 15 samples in 2016 and 2017, respectively). In addition, the birds' foraging ecology between years was compared. Masked boobies traveled in various directions, dived at unspecific locations, and explored areas < 110 km from the colony. Local environmental conditions were not significantly different between years, and differences in foraging parameters (maximum foraging range, trip duration, and dive depth) were greater among individuals than between years. The foraging characteristics of masked boobies suggest that resources were ephemerally distributed around the colony, with similar abundances across years. Under these conditions, traveling to unspecific locations may increase the area covered and the probability of prey encounter. The spatial and temporal consistencies in environmental conditions explain the uniformity of foraging parameters between years. The ability of masked boobies to exploit ephemerally distributed resources in seascapes like Rapa Nui may help explain its pantropical distribution.

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Introduction

Optimal foraging theory suggests that predators make foraging decisions that optimize energy intake with minimal energy investment, thus maximizing energetic gain (Charnov 1976; Pyke et al. 1977; Louzao et al. 2014). In the tropical marine environment, prey can be concentrated in areas of enhanced primary productivity [high chlorophyll-*a* concentration (CHL) and lower sea-surface temperature (SST)] (Ballance et al. 2006), and seabirds may travel directly to these areas where prey encounters are likely to be higher (Weimerskirch 2007; Assali et al. 2017). However, the South Pacific Gyre may be an especially challenging region for seabirds. This region has the most hyper-oligotrophic superficial waters in the world (Claustre et al. 2008) and is considered to be the world's largest "oceanic desert" (Morel et al. 2010). The gyre covers an area of 37 million square kilometers (Longhurst et al. 1995; Reintjes et al. 2019), with Rapa Nui, also known as Easter Island, located at its center. While some seabird species breeding within the gyre, such as petrels, travel thousands of kilometers to forage at fronts with high productivity (Clay et al. 2017), other species with smaller

foraging ranges still manage to forage and breed successfully within the gyre (Jaramillo et al. 2008; Flores et al. 2014). Little is currently known about how seabirds adapt to survive in this tropical, low-productivity environment and how they modify their foraging strategies to fulfill their energetic requirements.

The masked booby (*Sula dactylatra*) preys mainly on flying fish and squid throughout its range but consumes other prey families according to localities (Nelson 1978; Priddel et al. 2005; Asseid et al. 2006; Weimerskirch et al. 2009; Young et al. 2010; Kappes et al. 2011). Masked boobies forage by plunge diving and have been reported at a maximum distance of 367 km from the colony (Asseid et al. 2006), meaning they are effectively confined within the gyre while breeding. Seabird species inhabiting low-productivity areas like Rapa Nui are expected to spend long periods searching for food because prey abundances are lower and more unpredictable than in productive areas (Ashmole 1971; Longhurst and Pauli 1987; Jaquemet et al. 2005). The waters around Rapa Nui have low variability in terms of CHL and SST at a mesoscale level (Testa 2014) and hence may not provide appropriate physical features for prey accumulation within the birds' foraging range. However, Rapa Nui forms the part of the Easter Seamount, comprising large seamounts that can reach > 3000 m above the surrounding seafloor (Rodrigo et al. 2014). Seamounts support a wide diversity of fish and other potential prey species and may thus act as a resource patch (Riotte-Lambert and Matthiopoulos 2019) providing enhanced foraging opportunities for marine top predators (Ballance et al. 1997; Pitcher et al. 2007; Clark et al. 2010). Seamounts can therefore be critical foraging areas for seabirds in the food-stressed environment of oligotrophic oceans (Pitcher et al. 2007).

Tropical regions typically experience variable environmental conditions (Hamer et al. 2002). During periods of lower productivity, which affect prey abundance, seabirds may forage further and for longer periods (Burger and Piatt 1990; Harding et al. 2007), use different areas to forage (Péron et al. 2012), or switch prey species and size (Burger and Piatt 1990; Croxall et al. 1999). However, conditions within the gyre are less well known than for other oceanographic regions (Mannocci et al. 2014; Clay et al. 2017; Reintjes et al. 2019), and the levels of variability of environmental conditions are poorly known (Testa 2014). It is possible that masked boobies may adjust their foraging movements and diet between years if considerable environmental variation occurs (Nelson 1978; Sommerfeld et al. 2015). However, adjustments in their foraging movements and diet can be costly, because spending more time foraging during poor years increases absence times from the nest, potentially leading to deferred reproduction, lower growth rates, and higher chick mortality (Quillfeldt and Masello 2013; Guillemette et al. 2018).

With around 70 breeding pairs, the masked booby is the most numerous of the few native species on Rapa Nui (Jaramillo et al. 2008). It has a predictable presence on the island and is large enough to carry tracking devices that can be used to research their foraging strategies. These characteristics make the masked booby an ideal species for determining (1) if foraging incidents occur in relation to static marine features like seamounts in Rapa Nui and (2) if the birds' foraging ecology remains consistent between years based on environmental characteristics. It was expected that (1) masked boobies would travel directly to seamounts, reducing foraging times, with lower variability in foraging behavior than if prey patches were unknown (Sommerfeld et al. 2013; Patrick et al. 2014; Oppel et al. 2015), and (2) that their foraging parameters would adapt to inter-annual environmental conditions.

Materials and methods

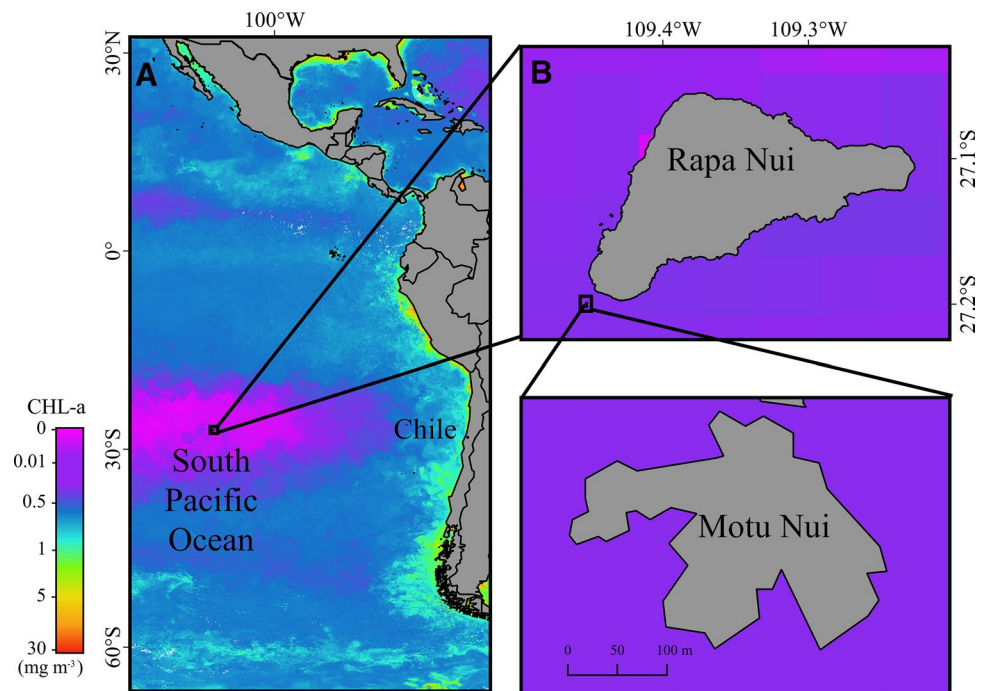
Data collection

Rapa Nui is the highest point of the Easter Seamount chain, reaching > 400 m above sea level (Rodrigo et al. 2014). Moai and the Pukao are the closest seamounts to Rapa Nui, reaching > 2000 m above the sea floor, with summits at 261 and 623 m depths, respectively (Rodrigo et al. 2014). Seamounts produce local turbulence and recirculation patterns that promote the entry of nutrients at relatively shallow depths, thus enhancing the primary productivity at Rapa Nui (Testa 2014). The seamounts at Rapa Nui are considered important marine conservation spots due to their diversity of fish (Friedlander et al. 2013) and are used sporadically by local fishermen (Mecho et al. 2019).

Data were collected at Motu Nui (109.4° W, 27.2° S, Fig. 1), a 3.9 ha islet covered with grass and surrounded by sea cliffs, located southwest of Rapa Nui. On Motu Nui, masked boobies nest in areas free from grass on the top of the islet and on the cliffs. Similar to Rapa Nui, Motu Nui has introduced species, including the Argentine ant (*Linepithema humile*) and the Chimango caracara (*Phalacrocorax chimango*), which can be potential predators of seabird chicks and eggs (Luna et al. 2018). There were 56 breeding pairs of masked boobies in 2016 and 77 breeding pairs in 2017.

The foraging movements of masked boobies were studied by attaching GPS CatLog-S devices sealed in a heat-shrink epoxy casing (3.7×2.2×0.8 cm, Catnip Technologies, Hong Kong) to nine chick-rearing birds (3 females and 6 males) in October and November of 2016 and to 14 chick-rearing birds (8 females and 6 males) in November of 2017. Chicks from tagged birds were covered with down and weighed 0.4–2.1 kg, and were thus estimated to be 1–8 weeks old

Fig. 1 Motu Nui location in relation to the South Pacific Ocean (a) and Rapa Nui (b), showing chlorophyll-a concentration



(Priddel et al. 2005). Eight and 12 of the tracked birds in 2016 and 2017, respectively, were simultaneously equipped with time–depth recorders (TDRs; CEFAS Data Storage Tags G5+, Cefas Technology, UK). Two of the TDR devices had large sensor variations and were excluded from further analyses.

The GPS devices were programmed to record time, latitude, and longitude every 4 min, and the TDRs to record pressure data every second, and temperature every minute at 12 bits. The GPS devices weighed 26 g and the TDR devices weighed 6.5 g; given that masked boobies weighed 1.8–2.6 kg, the total weight was < 3% of the body mass threshold for attached devices (Wilson and McMahon 2006; Vandenabeele et al. 2012). The individuals were captured at their nest using a hand net from approximately 1 m. The loggers were attached on top of the three central tail feathers using waterproof adhesive TESA tape. All individuals were released back to their nest after attaching the devices. Birds were captured between 07:00 and 10:00 h and between 16:00 and 19:00 h to avoid the hottest time of the day. The total handling time during capture and recapture did not exceed 10 min.

Diet samples were collected opportunistically from masked boobies that regurgitated spontaneously as a result of the authors presence in the colony, or during tagging efforts. Eighteen regurgitated samples were collected in 2016 and 15 in 2017. Due to the digested state of the samples and a lack of information on Rapa Nui fish species, fish and squid in regurgitates were identified to family level using a Pacific fish guide (Fischer et al. 1995) and a site-specific

fish guide (Randall and Cea 2010). Notably, although regurgitates provide a useful and non-invasive method for obtaining valuable information about seabird feeding ecology, the presence of different prey items in the diet may vary due to different intrinsic digestion rates (Barrett et al. 2007).

Regarding local environmental predictors, data on CHL, bathymetry, and SST were downloaded from <https://coastwatch.pfeg.noaa.gov/erddap>. CHL and SST data were derived from monthly composites with a resolution of 0.025° (approx. 2.5 km) from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor carried onboard NASA’s Aqua satellite, and bathymetry (BATH) data from ETOPO1, 0.017°. The names and coordinates of the nearby seamounts were obtained from Rodrigo et al. (2014). Average environmental conditions were extracted using the raster data of BATH, CHL, and SST inside a radius of 120 km (maximum range of a masked booby from Rapa Nui with an error threshold) using the function “extract” in the package “raster” (Hijmans 2019a).

Data processing

Tracking and diving data were processed using R 3.5.2 (R Core Team 2018). Foraging trip parameters including maximum foraging trip distance, total distance traveled, and trip duration were calculated after running the function “trip-Split” provided by Lascelles et al. (2016). The maximum foraging trip distance was measured at the most distant point in a straight line from the colony. Total distance traveled was the sum of the distance between consecutive fixes from

departure to return to the colony. Trip duration was the total time between departure and return to the colony. Foraging trips were considered as soon as the bird left a 1.5 km radius from the colony, because flying fish leaving the water and masked boobies foraging in the vicinity of the colony was observed. Although short trips may include birds bathing (Granadeiro et al. 2018), the presence of diving events in the vicinity of the colony demonstrated that these areas were also used as foraging grounds.

Using GPS data at 4 min intervals, foraging behavior during the foraging trips was classified using the speed and turning angle from successive locations with value delimiters of 0.60–3.14 radians (high turn) and 0–12 km h⁻¹ (low speed). Value delimiters for speed and turning angle were based on the Expectation Maximization binary Clustering (EMbC) algorithm (Garriga et al. 2016, 2019) and were within the thresholds used for other sulids (Mendez et al. 2017). Regarding diving data, a zero offset correction was applied for surface drift in the pressure sensor, and only dives deeper than 0.5 m were considered as true dives (Supplementary material 1). It is acknowledged that this threshold may omit shallow dives (Hagihara et al. 2011), but a larger threshold identified 21% more records as dives by including false dives due to noise or activities such as sitting on the water surface. Mean and maximum dive duration (s), mean and maximum diving depth (m), and diving rate (dives h⁻¹) were calculated per individual trip.

Diving and foraging locations are not necessarily the same; dives may reflect attempts to capture prey, whereas foraging locations reflect searching behavior (Bennison et al. 2017). Because of this dissimilarity, foraging and diving activities during the foraging trips were tested for matches in time and space. First, the locations were grouped into “events” considering at least three successive locations (an area-restricted search approach; see Mendez et al. 2017). The locations falling within a 10 min range were then merged and assigned a median latitude and longitude as a central location. Finally, the locations were matched. False positives (foraging locations but no dives) may occur if boobies capture prey on the wing (Weimerskirch et al. 2005), in which case TDRs will fail to record dives, while false negatives (dives not matching foraging locations) may arise from opportunistic foraging events (Montevecchi et al. 2009), in which case the ability of a classification based on speed and turning angles is limited for identifying foraging behavior. Due to the associated error in each technique, foraging and diving events were tested separately. A radius of 10 km around each seamount was created and diving and foraging events within this radius were classified as “close to seamount,” while others were classified as “far from seamount.” Distance from the seamounts was calculated for each dive and each foraging event using the package “geosphere” (Hijmans 2019b).

Statistical analyses

It was tested if seamounts affected masked boobies’ foraging behavior by applying linear mixed-effects models. Diving rate was used as dependent variable; seamount use or not use was used as factors, with the birds’ identity as random factor. It was determined if foraging or diving events were more likely to occur in the immediacies of the seamounts using Chi-square analysis to compare dive and foraging events classified as “close to seamount” vs “far from seamount.” The variability of individuals’ foraging behavior was evaluated by analysis of variance with foraging or diving parameters as dependent variables and the birds’ identity as a fixed factor. Individual consistencies in foraging parameters were further investigated using the individual as a random intercept in the package “rptR” (Stoffel et al. 2017; Grecian et al. 2018). This package calculates variances between and within individuals and produces a value between 0 and 1, with values closer to 1 representing higher consistency and values closer to 0 representing lower consistency (Courbin et al. 2018).

Inter-annual differences in foraging trip parameters were examined using linear mixed-effects models with foraging (maximum foraging range, trip duration, and total distance traveled) and diving parameters (mean diving depth, mean diving duration, and dive rate) as dependent variables, year as a fixed factor, and birds’ identity as a random factor to account for pseudo-replication. The models were fitted using the “lme” function in the package “nlme” (Pinheiro et al. 2019). Model selection was performed using a likelihood ratio test. There was no significant difference in foraging or diving parameters between the sexes ($P > 0.05$), and information for both sexes was therefore pooled (Supplementary material 2). Residuals were plotted against fitted values, and there was no obvious deviation from the assumption of normally distributed and homogeneous residuals. To test if similar areas were used during both years, the Bhattacharyya coefficient (BA) was extracted using the function “overlap” in the package “ctmm” based on the GPS data (Calabrese et al. 2016). The BA is a measure of similarity between two probability distributions, which gives the overlap in the kernel density estimates (Winner et al. 2018). The overlap between years was calculated by analysis of similarity (ANOSIM) with BA using the package “vegan” (Oksanen 2019). The number of prey items by year was compared using Chi-square tests. The results are shown untransformed, and the values for foraging parameters are given as mean \pm standard deviation.

Results

A total of 123 foraging trips were recorded from 23 individual masked boobies (Fig. 2). Nests were monitored every day during the tagging period of 4–6 days and no bird

showed signs of discomfort associated with the devices, such as making frequent contact with the devices or increased preening activities. Individuals performed an average of 1.64 ± 0.48 trips per day. The mean maximum distance from the colony was 31.9 ± 21.5 km, mean foraging trip duration was 3.4 ± 2.1 h, and the mean total distance traveled during a foraging trip was 80.6 ± 54.2 km (Fig. 3). Diving information was obtained from 18 individuals. Most dives occurred at the surface below 2 m (59%) and lasted < 2 s (49%) (Fig. 4). The deepest dive was 6 m and the longest time submerged was 10 s. Dives occurred throughout the foraging trip at a rate of 4.8 ± 4.2 (range 0.2–36.7) dives h^{-1} , and not at specific sites (Fig. 5). Regurgitates contained 3.7 ± 3.2 items from 1.5 ± 0.8 prey families. Considering the total number of prey items collected, flying fish dominated the diet (Fig. 6).

Foraging and dive events ($n=554$) matched in 32% of all events (true positives), while 44% of all foraging events ($n=495$) showed no dives (false positives) and 23% of all dive events ($n=497$) did not match foraging events (false

negatives). Foraging (Chi-square test, $X_{494}=467$, $P=0.80$) and dive events (Chi-square test, $X_{496}=466$, $P=0.82$) were not significantly related to seamounts (Fig. 7). Dive rates (linear mixed-effects model, $F(1, 95)=0.27$, $P=0.60$) did not differ significantly between trips within or outside the immediacies (< 10 km) of seamounts. Only 28 of the 495 foraging events (searching behavior) and 31 of the 497 total dive events (attempts of capturing prey) occurred in the immediacies of seamounts (Fig. 5). Foraging and diving parameters varied between individuals (Fig. 2, Supplementary material 3), with significant inter-individual differences in maximum distance from the colony, trip duration, mean dive duration, dive depth, and diving rate (Table 1). Individuals' dive depths and durations were repeatable, but the maximum distance from the colony, trip duration, and diving rate were not (Table 1).

Within the foraging range of masked boobies, the water depth was 2.9 ± 0.5 km, CHL was of 0.02 ± 0.01 mg m^{-3} in both years, and SST was 22.2 ± 0.4 $^{\circ}\text{C}$ in 2016 and 21.6 ± 0.2 $^{\circ}\text{C}$ in 2017 (Fig. 8). There were no significant differences in foraging and diving parameters between 2016 and 2017 (Table 1), and the areas used by masked boobies overlapped between years (BA range at 50% UD: 0.53–0.99; ANOSIM $R=0.01$, $P=0.10$; BA range at 95% UD: 0.53–0.99; ANOSIM $R=0.01$, $P=0.09$). The main prey items in both years were flying fish, but the birds' diet was more diverse in 2016 than in 2017, with the inclusion of anchovies (Engraulidae), sardines (Clupeidae), and dolphin-fish (Coryphaenidae) (Fig. 6). Sea chubs (Kyphosidae) were more important in 2017, occurring in six regurgitates with 4.6 ± 2.4 prey items, compared with two regurgitates with 1.5 ± 0.7 prey items in 2016. Nevertheless, the prey items in the diet were homogeneous between years (Chi-square test, $X_8=2.50$, $P=0.96$).

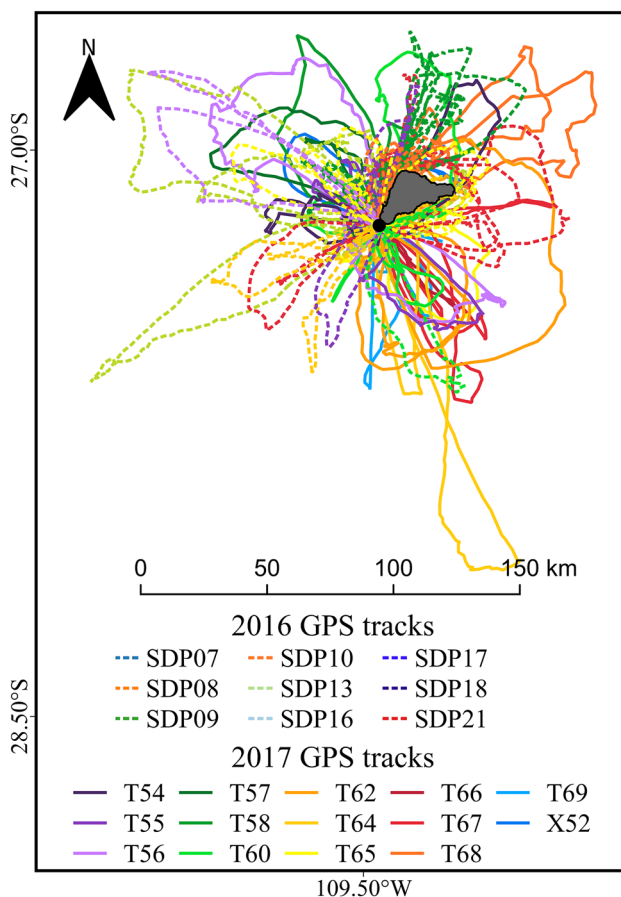


Fig. 2 Foraging trips of individual masked boobies (*Sula dactylatra*) at Rapa Nui during the breeding seasons of 2016 ($n=9$, dashed lines) and 2017 ($n=14$, solid lines). Black dot indicates the location of the masked booby colony

Discussion

The results of this study provide novel information on the foraging behavior of a seabird species in the South Pacific Gyre. The diving parameters were similar to previous reports on diving depths and durations acquired for the species at Clipperton Island (Weimerskirch et al. 2009) and Phillip Island (Sommerfeld et al. 2013). Masked boobies at Rapa Nui made more trips per day (1.6 trips per day) than birds from St. Helena and Ascension Island (0.4–1.0 trips per day; Oppel et al. 2015), possibly related to the fact that foraging trips of masked boobies from Rapa Nui were similar to or shorter than those of masked boobies' from the other colonies. Interestingly, foraging trips of masked boobies would be expected to be shorter in colonies where water productivity was higher, and should thus reflect the possibilities of prey encounter. However, although the CHLs at St.

Fig. 3 Foraging trip parameters for masked boobies (*Sula dactylatra*) at Rapa Nui based on the total number of trips ($n = 123$)

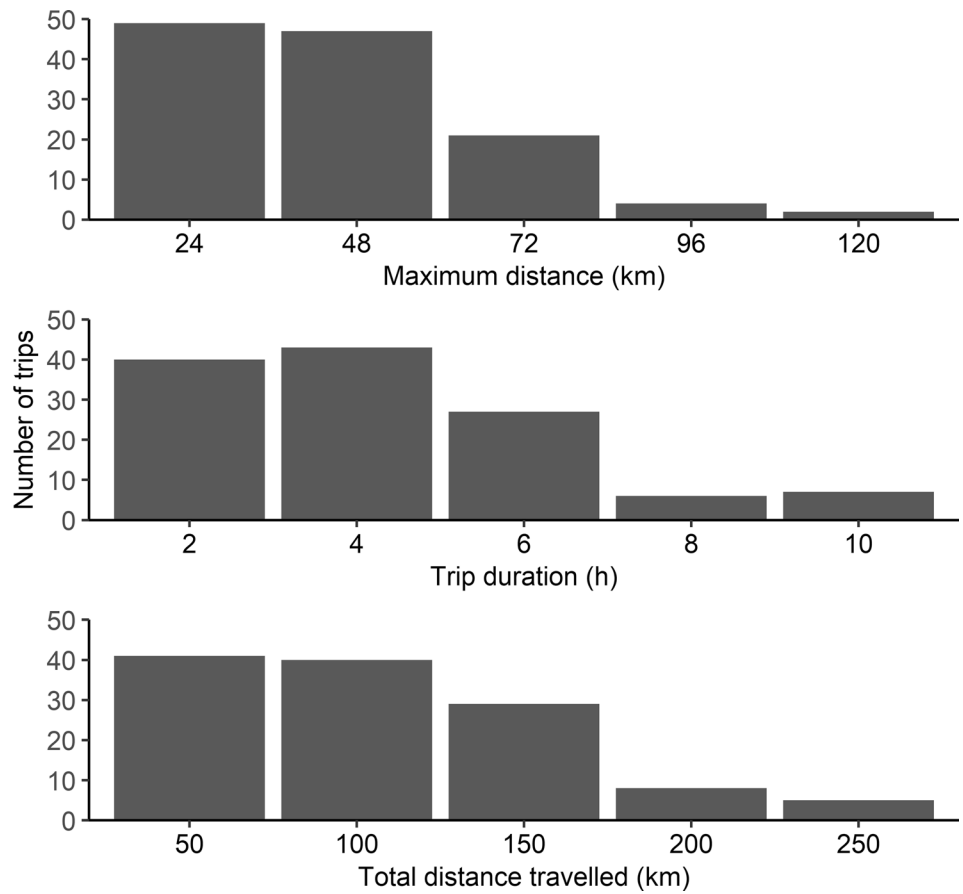
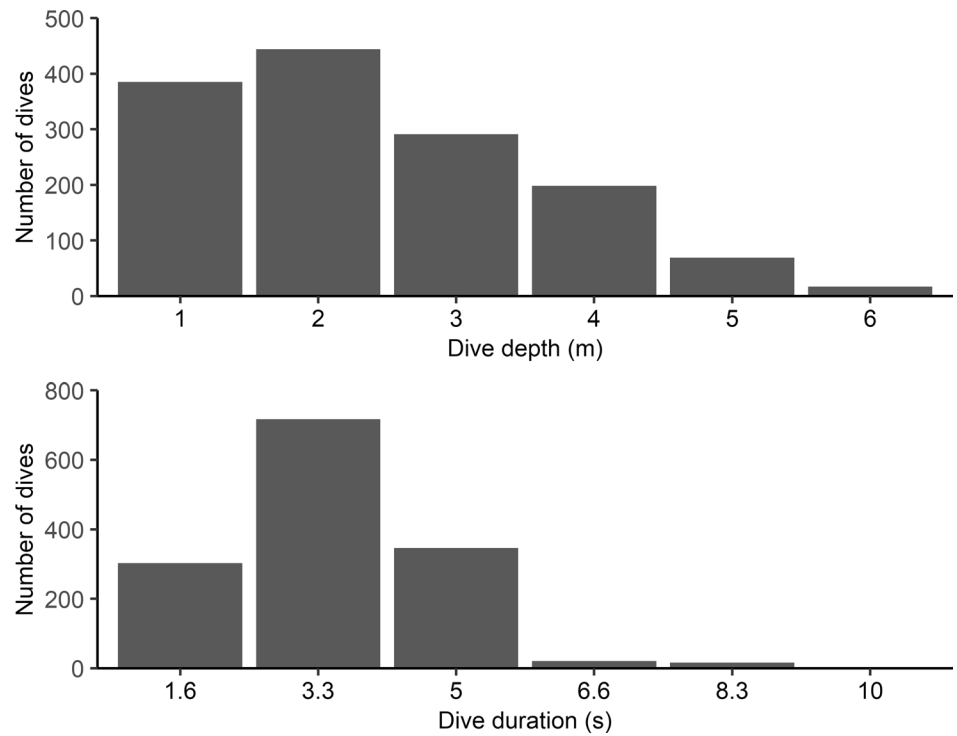


Fig. 4 Dive parameters for masked boobies (*Sula dactylatra*) at Rapa Nui based on the total number of dives ($n = 1404$)



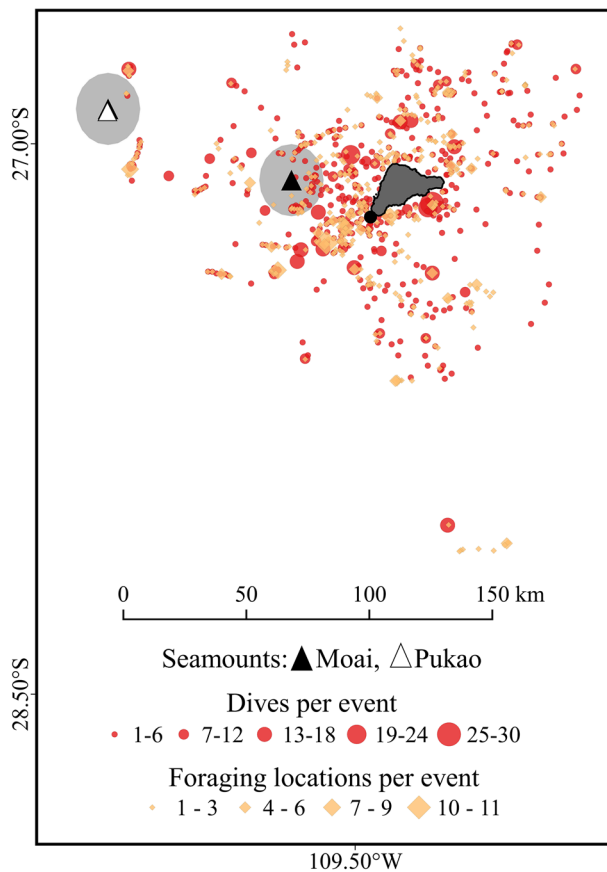


Fig. 5 Diving ($n=497$, red circles) and foraging events ($n=495$, yellow diamonds) of tracked masked boobies (*Sula dactylatra*) at Rapa Nui. Triangles indicate the seamounts; grey circles indicate the area of influence of the seamounts; size of the symbol indicates the number of dives or foraging locations per event; black dot indicates the colony

Helena and Ascension Island were 0.07 and 0.08 mg m^{-3} , respectively (Oppel et al. 2015), foraging trips were similar to or longer (3.4 and 11.4 h) and farther (41 and 78 km) than those at Rapa Nui, where the CHL was 0.02 mg m^{-3} . Similarly, masked boobies on Clipperton Island performed further and longer foraging trips on average (103 km and 8.9 h) in waters that were 10 times more productive (CHL 0.20 mg m^{-3}) (Weimerskirch et al. 2008) than at Rapa Nui.

The larger foraging ranges reported in other studies could be related to greater inter- or intra-specific competition at other sites. Masked boobies in the South Atlantic foraged closer to smaller colonies compared with more densely populated colonies (Oppel et al. 2015). Accordingly, masked booby colonies on St. Helena (500 individuals), Ascension (4600 individuals) (Oppel et al. 2015), and Clipperton Island (120 000 individuals) (Weimerskirch et al. 2008) were larger, supporting the idea that larger colonies might experience high levels of intra-specific competition, resulting in

longer foraging ranges (Lewis et al. 2001). Similar to land deserts, Rapa Nui supports small populations of generalist predators (Ashmole 1963; Cook 1997; Ayal 2007). The masked booby colony was ~ 70 breeding pairs, and no other large plunge divers, except tropicbirds, occur regularly in the area. The shorter foraging trips of masked boobies from Rapa Nui may thus reflect the low level of competition that occurs in small colonies.

The main prey item of masked boobies was flying fish, coinciding with results throughout their distributional range (Nelson 1978; Asseid et al. 2006; Weimerskirch et al. 2009; Young et al. 2010; Kappes et al. 2011). The diet of masked boobies at Rapa Nui included species, such as anchovies and sea chubs, which were not reported in previous studies. The difference in supplementary prey species included in the diet of masked boobies must reflect the fact that geographically separated populations of seabirds are exposed to different environmental and ecological conditions (Garthe et al. 2007; Castillo-Guerrero et al. 2016).

Foraging strategy

It was hypothesized that seamounts may attract foraging seabirds at Rapa Nui because of their increased food supply (Morato et al. 2010); however, contrary to these expectations, masked boobies did not appear to use seamounts. Similarly, red-footed boobies (*Sula sula*) did not preferentially forage over seamounts in the Mozambique Channel (Weimerskirch et al. 2005), though the use of seamounts appears to differ among seabird species (Pitcher et al. 2007; Clay et al. 2017). Masked boobies do not feed on primary producers, and there is a natural delay between the primary producers and fish (Suryan et al. 2012). Seamounts may thus not concentrate the prey items that boobies are searching for, and may even have the opposite effect, given that flying fish are offshore specialist species that prefer low-productivity waters (Churnside et al. 2017; Lewallen et al. 2018).

In contrast, the foraging behavior of masked boobies in the hyper-oligotrophic waters of Rapa Nui showed that their prey was not predictably distributed or associated with static environmental features. This was demonstrated by the fact that foraging parameters differed both between and within individuals. It was also found that an individual bird might make several trips on the same day following different behaviors and traveling to different places, in accordance with previous findings that showed low foraging-site fidelity in tropical seabirds (Weimerskirch 2007; Kappes et al. 2011; Hennicke and Weimerskirch 2014; Soanes et al. 2016; Oppel et al. 2017). Flying fish shoals are highly unpredictable (Oxenford et al. 1995); traveling to the same area is thus of limited value to masked boobies, and it may be more efficient to search in different locations. Other animals facing unpredictable resources move without any specific direction

Fig. 6 Prey species in regurgitates from masked boobies (*Sula dactylatra*) at Rapa Nui during the breeding seasons of 2016 (18 regurgitates, 56 prey items) and 2017 (15 regurgitates, 67 prey items). Families identified include Exocoetidae (flying fish), Kyphosidae (sea chub), Engraulidae (anchovy), Hemiramphidae (halfbeaks), Clupeidae (sardines), Omnastrephidae (squid), Carangidae (jacks), and Coryphaenidae (dolphinfish). A number of regurgitates that contained the prey item are presented above the bars and correspond to regurgitates of 2016/2017

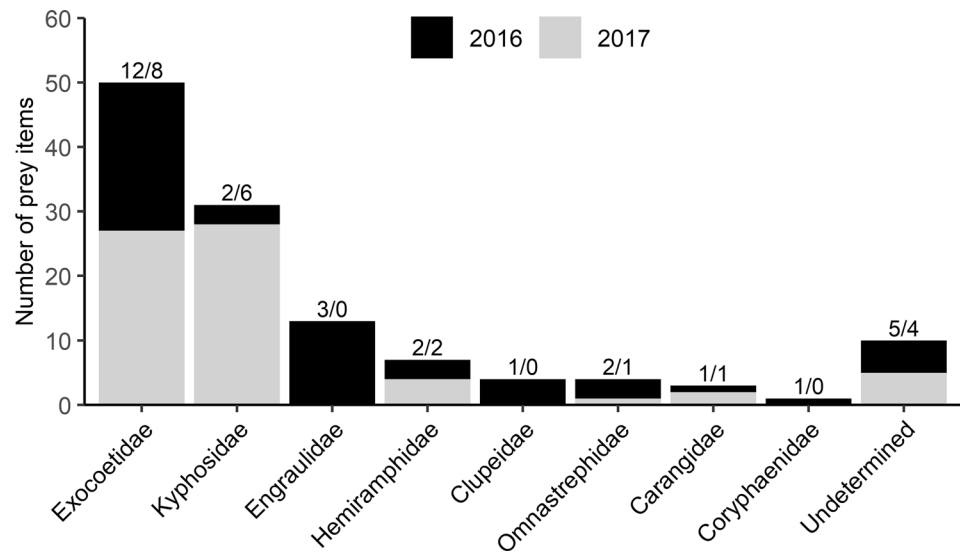
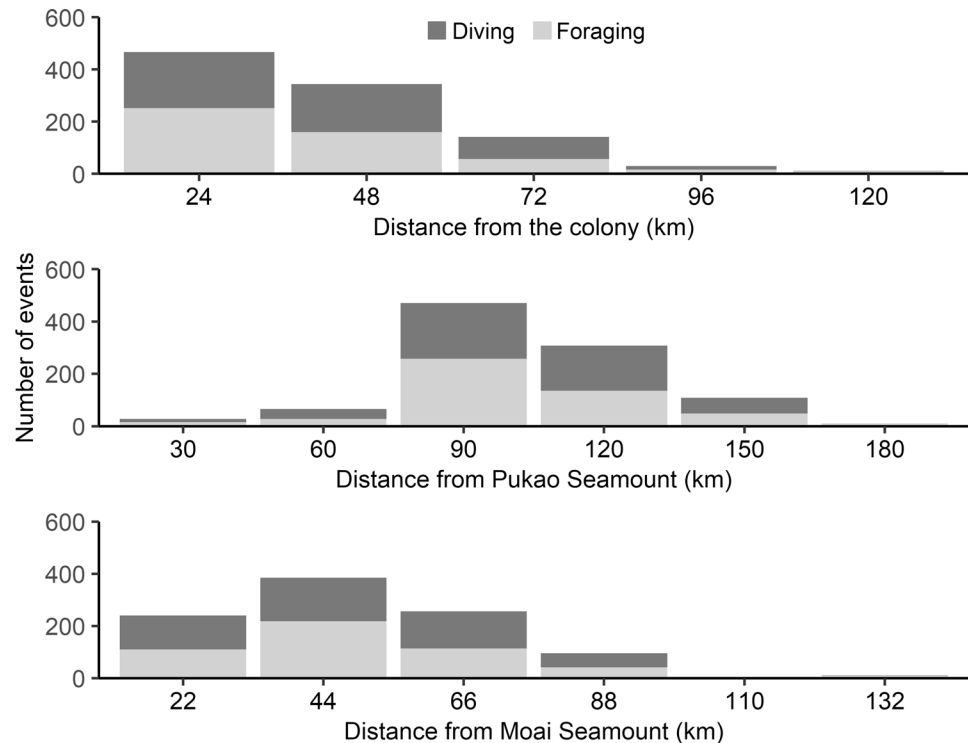


Fig. 7 Diving ($n=497$) and foraging events ($n=495$) of masked boobies (*Sula dactylatra*) in relation to distance to the colony and to the Pukao and Moai Seamounds



but then travel directly when they see something of interest (Venter et al. 2017). This seems to reflect the behavior of masked boobies searching for a prey patch, subsurface predators, or conspecifics. The ephemeral distributions of flying fish are further supported by the techniques used by fishermen, who change locations both within and between days to catch flying fish in the Caribbean (Oxenford et al.

1995) and at Rapa Nui (Pau Hito, Rapa Nui fishermen, pers. comm.). Exploring new areas benefited fishermen facing stochastic systems (O'Farrell et al. 2019). Similarly, an explorative approach may be the dominant searching strategy used by seabirds in oligotrophic waters like Rapa Nui and may allow the masked booby population to maintain a foraging range < 110 km radius.

Table 1 Analyses of foraging and diving parameters of chick-rearing masked boobies (*Sula dactylatra*) breeding at Rapa Nui in 2016 (GPS=9, TDR=6) and 2017 (GPS=14, TDR=12), showing inter-annual, inter-individual, and intra-individual comparisons

Parameter	Inter-annual		Inter-individual		Intra-individual
	Statistic ^a	<i>P</i>	Statistic ^a	<i>P</i>	Statistic ^b
Maximum distance	F1, 21=0.39	0.54	F22, 100=1.78	0.03	0.09±0.07 (0, 0.24)
Trip duration	F1, 21=0.03	0.87	F22, 100=2.22	<0.01	0.17±0.10 (0, 0.37)
Total distance	F1, 21=0.21	0.65	F22, 100=1.70	0.04	0.08±0.07 (0, 0.23)
Dive duration	F1, 16=0.15	0.70	F17, 68=3.04	<0.01	0.43±0.14 (0.14, 0.68)
Diving depth	F1, 16=1.43	0.25	F17, 68=2.88	<0.01	0.41±0.15 (0.09, 0.69)
Diving rate	F1, 16=2.76	0.12	F17, 68=2.43	<0.01	0.13±0.09 (0, 0.32)

^aLinear mixed-effect models with significant differences are indicated in bold

^brepeatability estimations and $r \pm$ standard errors are presented with 95% confidence intervals in parentheses (values close to 0 indicate low consistency; values close to 1 indicate high consistency)

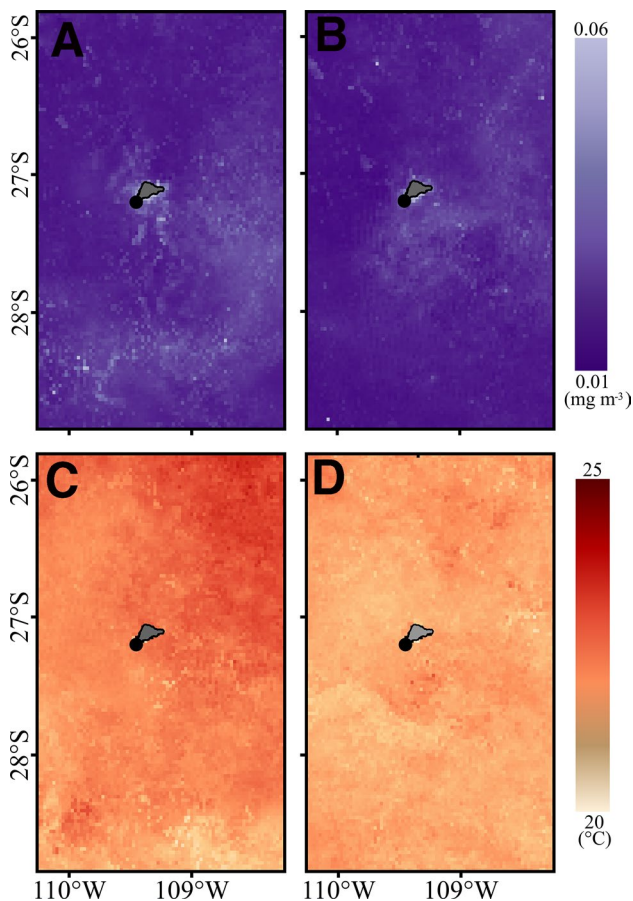


Fig. 8 Chlorophyll-*a* concentrations at Rapa Nui in November 2016 (a) and 2017 (b), and sea surface temperatures in November 2016 (c) and 2017 (d). Black dot indicates the study area

Inter-annual comparisons

There were some differences in the proportion of prey families included in the diet of masked boobies between years. Between-year differences in seabird diets are often associated with environmental conditions that affect prey

distribution and abundance (Burger and Piatt 1990; Croxall et al. 1999). However, the environmental conditions at Rapa Nui were similar during both years. Although the present understanding of prey abundances is limited by a lack of information, the differences in supplementary prey species included in the diets between years may merely be an effect of the birds' opportunistic behavior. Flying fish occur in patchily distributed shoals that are very difficult to predict in space and time (Oxenford et al. 1995), and birds may prevent interruptions to their food supply by opportunistically including other prey species (MacArthur and Pianka 1966; Giraldeau and Dubois 2008). For example, masked boobies included small sea chubs, an inshore fish of which juveniles may occur offshore amongst drifting flotsam and algae (Randall and Cea 2010).

The foraging and diving parameters of the masked boobies were similar in both study years. Similarly, petrels, as other tropical seabird inhabiting the South Pacific Gyre, showed no inter-annual differences in their foraging parameters (Clay et al. 2017). The consistent foraging parameters and relatively stable environmental conditions around Rapa Nui suggest that there was no need for the birds to change their foraging behaviors under these conditions. Flying fish may occur in the region throughout the year because they do not generally make long-distance migrations, and they have short generations (1–2 years) and small home ranges of < 500 km² (Lewallen et al. 2018). Masked boobies form associations with tuna species during foraging (Au and Pitman 1986), and tuna may occur in the area because of the presence of flying fish and because of the suitable sea conditions around Rapa Nui for some tuna species, including moderate SST and low surface CHL (Teo et al. 2007). However, detailed information on the distributions of flying fish and tuna is lacking, largely because data on the quantitative distributions of oceanic pelagic species are difficult and expensive to collect (Oxenford et al. 1995; Churnside et al. 2017; Lewallen et al. 2018). Nonetheless, masked booby foraging parameters suggest that prey availability is regular and stable, otherwise their energy reserves would be depleted

and they would avoid breeding, which is demonstrably not the case. The evidence suggests that masked boobies breed on Rapa Nui throughout the year and have done so since at least 1904 (Marin and Caceres 2010; Flores et al. 2014).

Peaks in productivity are often associated with an increase in food availability, which plays a significant role in the time of breeding for many seabirds (Hamer et al. 2002). However, tropical areas tend to have a weak productivity peak (Weimerskirch 2007). Year-round breeding of several tropical seabirds may thus be due to the stable but short year-round availability of food, which offers multiple breeding opportunities throughout the year, but for only a limited number of breeding pairs (Reynolds et al. 2014; Tarburton 2018). It is therefore worth speculating that the year-round breeding of masked boobies in Rapa Nui may be another adaptation to hyper-oligotrophic conditions, by diluting the peak of food demands and potentially allowing more birds to coexist in the same breeding grounds than if they all bred at the same time.

Conclusions

The current study provides the first description of the foraging ecology of a plunge-diving seabird species in the hyper-oligotrophic waters of the South Pacific Gyre. The results suggest that the foraging strategies of masked boobies were influenced by the distributions of flying fish at a distance < 110 km from the coast. The locations of foraging trips indicated that traveling to a specific location, such as seamounts, may be of little value to masked boobies in Rapa Nui. The stability of the environmental conditions around Rapa Nui means that the birds' foraging behavior remains similar between years, implying similar prey abundances. These results show that masked boobies can adapt to a wide range of oceanographic conditions, including the hyper-oligotrophic waters of the South Pacific Gyre, thus demonstrating the flexible characteristics of this species, which may in turn explain its wide distribution throughout the tropics.

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Data availability Tracking data are archived at Movebank (<https://www.movebank.org>).

Compliance with ethical standards

Conflict of interest All the authors declare that they have no conflict of interest.

Ethical statement This study was conducted according to the regulations of the Servicio Agrícola y Ganadero de la Oficina Sectorial Rapa Nui, certificate nos. 310/2016 and 388/2017, sector Santiago nos. 5343/2016 and 5024/2017 and the Ministerio de Agricultura certificate 04/101/18/0001, in line with the applicable international ethical standards for the care and use of wild animals. Fieldwork and sample collection were supervised and approved by Comisión Nacional Forestal (CONAF-Rapa Nui).

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References

- Ashmole NP (1963) The regulation of numbers of tropical oceanic birds. *Ibis* 103:458–473. <https://doi.org/10.1111/j.1474-919X.1963.tb06766.x>
- Ashmole NP (1971) Seabird ecology and the marine environment. Avian Biology. Academic Press, New York
- Assali C, Bez N, Tremblay Y (2017) Seabird distribution patterns observed with fishing vessel's radar reveal previously undescribed sub-meso-scale clusters. *Sci Rep* 7:1–10. <https://doi.org/10.1038/s41598-017-07480-6>
- Asseid BS, Drapeau L, Crawford RJM, Dyer BM, Hija A, Mwinyi AA, Shinula P, Upfold L (2006) The food of three seabirds at Latham Island, Tanzania, with observations on foraging by masked boobies *Sula dactylatra*. *Afr J Mar Sci* 28:109–114. <https://doi.org/10.2989/18142320609504138>
- Au DWK, Pitman RL (1986) Seabird interaction with dolphins and tuna in the Eastern Tropical Pacific. *Condor* 88:304–317. <https://doi.org/10.2307/1368877>
- Ayal Y (2007) Trophic structure and the role of predation in shaping hot desert communities. *J Arid Environ* 57:171–187. <https://doi.org/10.1016/j.jaridenv.2006.05.013>
- Ballance LT, Pitman RL, Fiedler PC (2006) Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: a review. *Prog Oceanogr* 69:360–390. <https://doi.org/10.1016/j.pcean.2006.03.013>
- Ballance LT, Pitman RL, Reilly SB (1997) Seabird community structure along a productivity gradient: importance of competition and energetic constraint. *Ecology* 78:1502–1518. <https://doi.org/10.2307/2266144>

- Barrett RT, Camphuysen CK, Anker-Nielssen T, Chardine JW, Furness RW, Garthe S, Hüppop O, Leopold MF, Montevecchi WA, Veit RR (2007) Diet studies in seabirds: a review and recommendations. *ICES* 64:1675–1691
- Bennison A, Bearhop S, Bodey TW, Votier SC, Grecian WJ, Wakefield ED, Hamer KC, Jessopp M (2017) Search and foraging behaviors from movement data: a comparison of methods. *Ecol Evol* 8:13–24. <https://doi.org/10.1002/ece3.3593>
- Burger AE, Piatt JF (1990) Flexible time budgets in breeding common murre: buffers against variable prey abundance. *Stud Avian Biol* 14:71–83
- Calabrese JM, Fleming CH, Gurarie E (2016) Ctm: an R package for analyzing animal relocation data as a continuous-time stochastic process. *Methods Ecol Evol* 7:1124–1132. <https://doi.org/10.1111/2041-210X.12559>
- Castillo-Guerrero JA, Lerma M, Mellink E, Suazo-Guillen E, Peñaloza-Padilla EA (2016) Environmentally-mediated flexible foraging strategies in Brown Boobies in the Gulf of California. *Ardea*. <https://doi.org/10.5253/arde.v104i1.a3>
- Charnov EL (1976) Optimal foraging, the marginal value theorem. *Theor Popul Biol* 9:129–136. [https://doi.org/10.1016/0040-5809\(76\)90040-X](https://doi.org/10.1016/0040-5809(76)90040-X)
- Churnside JH, Wells RJD, Boswell KM, Quinlan JA, Marchbanks RD, Mccarty BJ, Sutton TT (2017) Surveying the distribution and abundance of flying fishes and other epipelagic in the northern Gulf of Mexico using airborne lidar. *Bull Mar Sci* 93:591–609. <https://doi.org/10.5343/bms.2016.1039>
- Claustre H, Sciandra A, Vaultot D (2008) Introduction to the special section bio-optical and biogeochemical conditions in the South East Pacific in late 2004: the BIOSOPE program. *Biogeochemistry* 5:679–691. <https://doi.org/10.5194/bg-5-679-2008>
- Clark MR, Rowden AA, Schlacher T, Williams A, Consalvey M, Stocks KI, Rogers AD, O'Hara TD, White M, Shank TM, Hall-Spencer JM (2010) The ecology of seamounts: structure, function and human impacts. *Annu Rev Mar Sci* 2:253–278. <https://doi.org/10.1146/annurev-marine-120308-081109>
- Clay TA, Phillips RA, Manica A, Jackson HA, Brooke MDL (2017) Escaping the oligotrophic gyre? The year-round movements, foraging behaviour and habitat preferences of Murphy's petrels. *Mar Ecol Prog Ser* 579:139–155. <https://doi.org/10.3354/meps12244>
- Courbin N, Besnard A, Péron C, Saraux C, Fort J, Perret S, Tornos J, Grémillet D (2018) Short-term prey field lability constrains individual specialisation in resource selection and foraging site fidelity in a marine predator. *Ecol Lett* 21:1043–1054. <https://doi.org/10.1111/ele.12970>
- Cook WE (1997) Avian desert predators. In: Cloudsley-Thompson JL (ed) *Adaptations of desert organisms*. Springer, Berlin, p 129. <https://doi.org/10.1007/978-3-642-60353-2>
- Croxall JP, Reid K, Prince PA (1999) Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. *Mar Ecol Prog Ser* 177:115–131. <https://doi.org/10.3354/meps177115>
- Fischer W, Krupp F, Schneider W, Sommer C, Carpenter KE, Niem VH (1995) *Guía FAO para la identificación de especies para los fines de la pesca. Pacífico, centro-oriental*. FAO, Rome
- Friedlander AM, Ballesteros E, Beets J, Berkenpas E, Gaymer CF, Gorny M, Sala E (2013) Effects of isolation and fishing on the marine ecosystem of Easter Island and Salas y Gomez, Chile. *Aquat Conserv Mar Freshw Ecosyst* 23:515–531. <https://doi.org/10.1002/aqc.2333>
- Flores MA, Schlatter RP, Hucke-Gaete R (2014) Seabirds of Easter Island, Salas y Gomez Island and Desventuradas Islands, south-eastern Pacific Ocean. *Lat Am J Aquat Res* 42:752–759
- Garriga J, Palmer JRB, Oltra A, Bartumeus F (2016) Expectation-maximization binary clustering for behavioural annotation. *PLoS ONE* 11:1–12. <https://doi.org/10.1371/journal.pone.0151984>
- Garriga J, Palmer JRB, Oltra A, Bartumeus F (2019). EMbC: expectation-maximization binary clustering. R package version 2.0.3. <https://www.cran.r-project.org/package=EMbC>. Accessed Jan 2019
- Garthe S, Montevecchi WA, Chapdelaine G, Rail J-F, Hedd A (2007) Contrasting foraging tactics by northern gannets (*Sula bassana*) breeding in different oceanographic domains with different prey fields. *Mar Biol* 151:687–694. <https://doi.org/10.1007/s00227-006-0523-x>
- Giraldeau L-A, Dubois F (2008) Social foraging and the study of exploitative behavior. *Adv Study Behav* 38:59–104. [https://doi.org/10.1016/S0065-3454\(08\)00002-8](https://doi.org/10.1016/S0065-3454(08)00002-8)
- Granadeiro JO, Campioni L, Catry P (2018) Albatrosses bathe before departing on a foraging trip: implications for risk assessments and marine spatial planning. *Bird Conserv Int* 28:208–215. <https://doi.org/10.1017/S0959270916000459>
- Grecian WJ, Lane JV, Michelot T, Wade HM, Hamer KC (2018) Understanding the ontogeny of foraging behaviour: insights from combining marine predator bio-logging with satellite-derived oceanography in hidden Markov models. *J R Soc Interface* 15:20180084. <https://doi.org/10.1098/rsif.2018.0084>
- Guillemette M, Grégoire F, Bouillet D, Rail JF, Bolduc F, Caron A, Pelletier D (2018) Breeding failure of seabirds in relation to fish depletion: is there one universal threshold of food abundance? *Mar Ecol Prog Ser* 587:235–245. <https://doi.org/10.3354/meps12442>
- Hagihara R, Jones Rem Sheppard JK, Hodgson AJ, Marsh H (2011) Minimizing errors in the analysis of dive recording from shallow-diving animals. *JEMBE* 399:173–181. <https://doi.org/10.1016/j.jembe.2011.01.001>
- Hamer KC, Schreiber EA, Burger J (2002) Breeding biology, life histories, and life history–environment interactions in seabirds. In: Schreiber EA, Burger J (eds) *Biology of marine birds*. CRC Press, New York
- Harding A, Piatt J, Schmutz J, Shultz M, Van Pelt T, Kettle A, Speckman S (2007) Prey density and the behavioral flexibility of a marine predator: the common murre (*Uria aalge*). *Ecology* 88:2024–2033. <https://doi.org/10.1890/06-1695.1>
- Hennicke JC, Weimerskirch H (2014) Coping with variable and oligotrophic tropical waters: foraging behavior and flexibility of the Abbott's booby *Papadula abbotii*. *Mar Ecol Prog Ser* 499:259–273
- Hijmans RJ (2019a) Introduction to the 'raster' package. <https://www.cran.r-project.org/web/packages/raster/vignettes/Raster.pdf>. Accessed Jan 2019
- Hijmans RJ (2019b) Introduction to the 'geosphere' package. <https://www.cran.r-project.org/web/packages/geosphere/geosphere.pdf>. Accessed Jan 2019
- Jaquemet S, Le Corre M, Marsac F, Potier M, Weimerskirch H (2005) Foraging habitats of the seabird community of Europa Island (Mozambique Channel). *Mar Biol* 147:573–582. <https://doi.org/10.1007/s00227-005-1610-0>
- Jaramillo A, Johnson MTJ, Rothfels CJ, Johnson RA (2008) The native and exotic avifauna of Easter Island: then and now. *Bol Chil Ornitol* 14:8–21
- Kappes MA, Weimerskirch H, Pinaud D, Le Corre M (2011) Variability of resource partitioning in sympatric tropical boobies. *Mar Ecol Prog Ser* 441:281–294. <https://doi.org/10.3354/meps09376>
- Lascelles BG, Taylor PR, Miller MGR, Dias MP, Opiel S, Torres L, Hedd A, Le Corre M, Phillips RA, Scott SA, Weimerskirch H, Small C (2016) Applying global criteria to tracking data to define important areas for marine conservation. *Divers Distrib* 22:422–431. <https://doi.org/10.1111/ddi.12411>

- Lewallen EA, Van Wijnen AJ, Bonin CA, Lovejoy NR (2018) Flying-fish (Exocoetidae) species diversity and habitats in the eastern tropical Pacific Ocean. *Mar Biodivers* 48:1755–1765. <https://doi.org/10.1007/s12526-017-0666-7>
- Lewis S, Sherratt TN, Hamer KC, Wanless S (2001) Evidence of intra-specific competition for food in a pelagic seabird. *Nature* 412:816–819. <https://doi.org/10.1038/35090566>
- Luna N, Varela AI, Brokordt K, Luna-Jorquera G (2018) Assessing potential predator risk by introduced predators on unattended eggs in the red-tailed tropicbird, *Phaethon rubricauda*, on Rapa Nui (Easter Island). *TCS* 11:1–8. <https://doi.org/10.1177/1940082918785079>
- Longhurst AR, Pauli D (1987) Ecology of tropical ocean. Academic press, San Diego
- Longhurst A, Sathyendranath S, Platt T, Caverhill C (1995) An estimate of global primary production in the ocean from satellite radiometer data. *J Plankton Res* 17:1245–1271. <https://doi.org/10.1093/plankt/17.6.1245>
- Louzao M, Wiegand T, Bartumeus F, Weimerskirch H (2014) Coupling instantaneous energy-budget models and behavioural mode analysis to estimate optimal foraging strategy: an example with wandering albatrosses. *Mov Ecol* 2:8. <https://doi.org/10.1186/2051-3933-2-8>
- Mannocci L, Catalogna M, Dorémus G, Laran S, Lehodey P, Massart W, Monestiez P, Van Canneyt O, Watremez P, Ridoux V (2014) Predicting cetacean and seabird habitats across a productivity gradient in the South Pacific Gyre. *Prog Oceanogr* 120:383–398. <https://doi.org/10.1016/j.pocean.2013.11.005>
- Marin M, Caceres P (2010) Sobre las aves de isla de Pascua. *Boletín del Mus Nac Hist Nat* 59:75–95
- MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. *Am Nat* 100:603–609
- Mecho A, Easton EE, Sellanes J, Gorny M, Mah C (2019) Unexplored diversity of the mesophotic echinoderm fauna in the Easter Island ecoregion. *Mar Biol* 166:91. <https://doi.org/10.1007/s00227-019-3537-x>
- Mendez L, Borsari P, Cruz S, De Grissac S, Hennicke J, Lallemand J, Prudor A, Weimerskirch H (2017) Geographical variation in the foraging behaviour of the pantropical red-footed booby. *Mar Ecol Prog Ser* 568:217–230. <https://doi.org/10.3354/meps12052>
- Montevicchi W, Benvenuti S, Garthe S, Davoren G, Fifield D (2009) Flexible foraging tactics by a large opportunistic seabird preying on forage- and large pelagic fishes. *Mar Ecol Prog Ser* 385:295–306. <https://doi.org/10.3354/meps08006>
- Morato T, Hoyle SD, Allain V, Nicol SJ, Karl D (2010) Seamounts are hotspots of pelagic biodiversity in the open ocean. *PNAS* 107:9707–9711. <https://doi.org/10.1073/pnas.0910290107>
- Morel A, Claustre H, Gentili B (2010) The most oligotrophic subtropical zones of the global ocean: similarities and differences in terms of chlorophyll and yellow substance. *Biogeosciences* 7:3139–3151. <https://doi.org/10.5194/bg-7-3139-2010>
- Nelson JB (1978) The Sulidae: gannets and boobies. Oxford University Press, Oxford
- O'Farrell S, Sanchirico JN, Spiegel O, Depalle M, Haynie AC, Murawski SA, Perruso L, Strelcheck A (2019) Disturbance modifies payoff in the explore–exploit trade-off. *Nat Commun* 10:3363. <https://doi.org/10.1038/s41467-019-11106-y>
- Oksanen J (2019) Vegan: community ecology package. R version 2.5-5. <https://www.cran.r-project.org/web/packages/vegan/>. Accessed Jan 2019
- Oppel S, Beard A, Fox D, Mackley E, Leat E, Henry L, Clingham E, Fowler N, Sim J, Sommerfeld J, Weber N, Weber S, Bolton M (2015) Foraging distribution of a tropical seabird supports Ashmole's hypothesis of population regulation. *Behav Ecol Sociobiol* 69:915–926. <https://doi.org/10.1007/s00265-015-1903-3>
- Oppel S, Weber S, Weber N, Fox D, Leat E, Sim J, Sommerfeld J, Bolton M, Broderick AC, Godley BJ (2017) Seasonal shifts in foraging distribution due to individual flexibility in a tropical pelagic forager, the Ascension frigatebird. *Mar Ecol Prog Ser* 585:199–212. <https://doi.org/10.3354/meps12377>
- Oxenford HA, Mahon R, Hunte W (1995) Distribution and relative abundance of flyingfish (Exocoetidae) in the eastern Caribbean. I. Adults. *Mar Ecol Prog Ser* 117:11–23. <https://doi.org/10.3354/meps117011>
- Patrick SC, Bearhop S, Grémillet D, Lescoërl A, Grecian WJ, Bodey TW, Hamer KC, Wakefield E, Le Nuz M, Votier SC (2014) Individual differences in searching behavior and spatial foraging consistency in a central place marine predator. *Oikos* 123:33–40. <https://doi.org/10.1111/j.1600-0706.2013.00406.x>
- Péron C, Weimerskirch H, Bost CA (2012) Projected poleward shift of king penguins' (*Aptenodytes patagonicus*) foraging range at the Crozet Islands, southern Indian Ocean. *Proc R Soc B* 279:2515–2523. <https://doi.org/10.1098/rspb.2011.2705>
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2019) Package 'nlme'. <https://www.cran.r-project.org/package=nlme>. Accessed Jan 2019
- Pitcher TJ, Morato T, Hart PJB, Clark MR, Haggan N, Santos RS (2007) Seamounts: ecology, fisheries, and conservation. Blackwell, Oxford
- Priddel D, Olsor S, Wheeler R (2005) Breeding biology of masked boobies (*Sula dactylatra tasmani*) on Lord Howe Island, Australia. *Emu* 105:105–113. <https://doi.org/10.1071/MU04028>
- Pyke GH, Pulliam HR, Charnov E (1977) Optimal foraging: a selective review of theory and tests. *Q Rev Biol* 52:137–154. <https://doi.org/10.1086/409852>
- Quillfeldt P, Masello JF (2013) Impacts of climate variation and potential effects of climate change on South American seabirds—a review. *Mar Biol Res* 9:337–357. <https://doi.org/10.1080/17451000.2012.756982>
- Core Team R (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Randall JE, Cea A (2010) Shore fishes of Easter Island. University of Hawaii Press, Honolulu
- Reintjes G, Tegetmeyer HE, Bürgisser M, Orlic S, Tews I, Zubkov M, Voß D, Zielinski O, Quast C, Glöckner FO, Amann R, Ferdelman TG, Fuchs BM (2019) On site analysis of bacterial communities of the ultra-oligotrophic South Pacific Gyre. *Appl Environ Microbiol*. <https://doi.org/10.1128/aem.00184-19>
- Reynolds SJ, Marin GR, Dawson A, Wearn CP, Hughes BJ (2014) The sub-annual breeding cycle of a tropical seabird. *PLoS ONE* 9:e93582. <https://doi.org/10.1371/journal.pone.0093582>
- Riotte-Lambert L, Matthiopoulos J (2019) Environmental predictability as a cause and consequence of animal movement. *TREE* 35:163–174. <https://doi.org/10.1016/j.tree.2019.09.009>
- Rodrigo C, Díaz J, González-Fernández A (2014) Origin of the easter submarine alignment: morphology and structural lineaments. *Lat Am J Aquat Res* 42:857–870
- Soanes LM, Bright JA, Carter D, Dias MP, Fleming T, Gumbs K, Hughes G, Mukhida F, Green JA (2016) Important foraging areas of seabirds from Anguilla, Caribbean: implications for marine spatial planning. *Mar Pol* 70:85–92. <https://doi.org/10.1016/j.marpol.2016.04.019>
- Sommerfeld J, Kato A, Ropert-Coudert Y, Garthe S, Hindell MA (2013) The individual counts: within sex differences in foraging strategies are as important as sex-specific differences in masked boobies *Sula dactylatra*. *J Avian Biol* 44:531–540. <https://doi.org/10.1111/j.1600-048X.2013.00135.x>
- Sommerfeld J, Kato A, Ropert-Coudert Y, Garthe S, Wilcox C, Hindell MA (2015) Flexible foraging behaviour in a marine predator the masked booby (*Sula dactylatra*), according to foraging locations

- and environmental conditions. *J Exp Mar Bio Ecol* 463:79–86. <https://doi.org/10.1016/j.jembe.2014.11.005>
- Stoffel MA, Nakagawa S, Schielzeth H (2017) rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods Ecol Evol* 8:1639–1644. <https://doi.org/10.1111/2041-210X.12797>
- Suryan RM, Santora JA, Sydeman WJ (2012) New approach for using remotely sensed chlorophyll a to identify seabird hotspots. *Mar Ecol Prog Ser* 451:213–225. <https://doi.org/10.3354/meps09597>
- Tarburton MK (2018) Evidence of year-round breeding of birds in the Samoan islands, in the context of the Australasian and South Pacific regions. *Notornis* 65:92–108
- Teo SLHH, Boustany AM, Block BA (2007) Oceanographic preferences of Atlantic bluefin tuna, *Thunnus thynnus*, on their Gulf of Mexico breeding grounds. *Mar Biol* 152:1105–1119. <https://doi.org/10.1007/s00227-007-0758-1>
- Testa G (2014) Variabilidad espacio-temporal de clorofila-a superficial e influencia de los montes submarinos en la Eastern Seamount Chain. Bachelor thesis, Universidad Católica de Valencia, Spain
- Vandenabeele SP, Shepard EL, Grogan A, Wilson RP (2012) When three per cent may not be three per cent; device-equipped seabirds experience variable flight constraints. *Mar Biol* 159:1–14. <https://doi.org/10.1007/s00227-011-1784-6>
- Venter JA, Prins HHT, Mashanova A, Slotow R (2017) Ungulates rely less on visual cues, but more on adapting movement behaviour, when searching for forage. *PeerJ* 5:1–15. <https://doi.org/10.7717/peerj.3178>
- Weimerskirch H, Le Corre M, Ropert-Coudert Y, Kato A, Marsac F (2005) The three-dimensional flight of red-footed boobies: adaptations to foraging in a tropical environment? *Proc R Soc B* 272:53–61. <https://doi.org/10.1098/rspb.2004.2918>
- Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? *Deep Sea Res Part II* 54:211–223. <https://doi.org/10.1016/j.dsr2.2006.11.013>
- Weimerskirch H, Le Corre M, Bost CA (2008) Foraging strategy of masked boobies from the largest colony in the world: relationship to environmental conditions and fisheries. *Mar Ecol Prog Ser* 362:291–302. <https://doi.org/10.3354/meps07424>
- Weimerskirch H, Le Corre M, Gadenne H, Pinaud D, Kato A, Ropert-Coudert Y, Bost CA (2009) Relationship between reversed sexual dimorphism, breeding investment and foraging ecology in a pelagic seabird, the masked booby. *Oecologia* 161:637–649. <https://doi.org/10.1007/s00442-009-1397-7>
- Wilson RP, McMahon CR (2006) Measuring devices on wild animals: what constitutes acceptable practice? *Front Ecol Environ* 4:147–154
- Winner K, Noonan MJ, Fleming CH, Olson KA, Mueller T, Sheldon D, Calabrese JM (2018) Statistical inference for home range overlap. *Methods Ecol Evol* 9:1679–1691. <https://doi.org/10.1111/2041-210X.13027>
- Young HS, Shaffer SA, McCauley DJ, Foley DG, Dirzo R, Block BA (2010) Resource partitioning by species but not sex in sympatric boobies in the central Pacific Ocean. *Mar Ecol Prog Ser* 403:291–301. <https://doi.org/10.3354/meps08478>

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