



Foraging behaviour and diet of Brown boobies *Sula leucogaster* from Tinhosas Islands, Gulf of Guinea

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Abstract

Seabirds are a highly threatened group, yet the foraging ecology of several species remains poorly understood. Brown boobies breed in all oceans in the tropical region and are common across their range. In Tinhosa Grande (São Tomé and Príncipe), this species breeds in one of the largest colonies of seabirds in the east tropical Atlantic. We studied the foraging ecology of Brown boobies from this colony during the chick-rearing period. Thirty-three birds were tracked with GPS loggers and their diet was analysed from 11 regurgitations, using traditional and DNA barcoding techniques for prey identification. A total of 127 completed foraging trips were identified, 89% of which lasted less than 24 h. Females performed significantly longer trips and both sexes foraged preferentially over deep oceanic waters. The diet of Brown boobies included juvenile fish and squid (*Sthenoteuthis pteropus*), comprising mostly fish species whose juvenile phases live in the pelagic environment, and only migrate to coastal waters when adults. The most frequent of those prey found was Flying gurnard (*Dactylopterus volitans*). The relevance of such prey shows that Brown booby conservation depends not only on the management of their foraging areas and breeding sites but also on the correct management of the coastal adjacent areas that support the adult individuals of some of their prey. Our results suggest that the areas closest to the colony do not have available resources for these birds to feed on and that Brown boobies may be associate with subsurface marine predators or with sargassum patches to forage.

Introduction

Seabird populations are declining worldwide (BirdLife International 2018) mostly due to direct mortality, changes in food resources and marine ecosystem functioning and breeding habitat lost. Population declines are mainly attributed to invasive alien species and human disturbance on land, bycatch and overfishing at sea, and by climate change

and severe weather (Croxall et al 2012; Dias et al 2019). In tropical regions, seabirds remain generally poorly studied (Weimerskirch 2007; Sydeman et al. 2012), and identifying and characterising their at-sea distribution (e.g. as provided by tracking data), is key to support area-based management measures such as the creation of marine protected areas (Handley et al. 2020).

Sulidae, the family of seabirds comprising gannets and boobies, range from cold temperate seas to the tropics breeding mostly in offshore islands (Brown et al. 1983, Hoyo et al. 1996). Most of the sulids forage in interspecific flocks, on pelagic fish and squid, which can be captured underwater, after plunge diving (Hoyo et al. 1996). During the breeding season, different species can forage in coastal waters or offshore, ranging from a few km to more than 500 km from the nesting sites (e.g. Hamer et al. 2000; Ludynia et al. 2010). Within Sulidae, there are three species of boobies that are pantropical, Brown booby (*Sula leucogaster*), Masked booby (*Sula dactylatra*) and Red-footed booby (*Sula sula*). These pantropical sulid species live in broadly similar environments and have comparable distributions (Hoyo et al. 1996).

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The Brown booby breeds in all oceans in the tropical region and is highly abundant across this region (Brown et al. 1983; Hoyo et al. 1996). This makes Brown booby an interesting species for comparative studies and large-scale environmental monitoring, but such potential is largely yet to be explored. For some populations of this species, particularly in the East Atlantic, the diet and foraging distribution are still poorly known. Brown boobies feed mostly by performing shallow plunge-dives (usually up to 2 m depth; Hoyo et al. 1996; Castillo-Guerrero et al. 2016) and forage mainly on fish and squid and to a lesser extent on crustaceans in shallow coastal waters or offshore (Mellink et al. 2001; Branco et al. 2005; Bunce 2015; Miller et al. 2018). During the breeding season, Brown boobies may show differences between sexes in foraging distribution and in time spent at the colony, due to their strong (reversed) sexual size dimorphism (Lewis et al. 2005; Miller et al. 2018). Populations of Brown booby have been decreasing in several areas (BirdLife International 2020) and the populations of the east Atlantic are particularly under-studied (Schreiber and Norton 2020).

The Tinhosas islands, located ca. 20 km south of Príncipe Island in the Democratic Republic of São Tomé and Príncipe (hereafter STP), host one of the largest colonies of seabirds in the east tropical Atlantic (Bollen et al. 2018). Here an estimate of 738 pairs of Brown boobies nest among over than 140 000 breeding pairs of Sooty terns (*Onychoprion fuscatus*), and smaller numbers of Brown noddies (*Anous stolidus*), and Black noddies (*A. minutus*; Bollen et al. 2018). Brown boobies have declined by 60% over the last 20 years, most likely due to human persecution of birds in the colony, for consumption and trade (Valle et al. 2016; Bollen et al. 2018) and virtually nothing is known on the foraging ecology of this population.

In this study, we investigated the foraging movements of Brown boobies during the breeding season in Tinhosa Grande (Príncipe Autonomous Region) using GPS tracking, testing for differences between sexes in foraging parameters and space use. We also characterise the general environmental conditions in the foraging areas (sea-surface temperature, wind and depth). Finally, we briefly describe their diet, by examining a set of spontaneous regurgitations, and identifying prey using morphological characteristics and DNA barcoding.

Methods

Foraging trips

Fieldwork was carried out on Tinhosa Grande (1°20'31.7"N; 7°17'30.7"E; STP, Gulf of Guinea), one of the three rocky islands that are part of the Tinhosas islands, classified as

Important Bird and Biodiversity Areas and also as a Ramsar Site. A total of 33 adult Brown boobies were captured between 26 and 28 February 2020, while rearing small chicks (ca. 2–4 weeks old). Birds were captured during the day in their nests using a hook fixed to a long. All birds were ringed, weighed (to the nearest 5 g), and the length of the wing (flattened maximum chord, to the nearest millimetre) and culmen (to nearest 0.1 mm) were measured. Birds were sexed by the colour of the bill and the skin around the eye (Brown et al. 1983; Schreiber and Norton 2020). Following measurements and sexing, individuals were fitted with GPS loggers (I-gotU gt120) under the four central tail feathers attached with Tesa® tape. The total weight of the GPS loggers including the waterproofing and tape was 17 g corresponding to 1.4 to 2.5% of the body mass of birds tagged (which ranged from 690 to 1220 g). We did not test the effect of handling and of the GPS deployment on the foraging behaviour of the tracked birds but published evidence suggest that no strong effects are to be expected (e.g. Cleasby et al. 2015). The loggers were set to record a position every 5 min. All GPS devices were retrieved between 4 and 5 March 2020, and it was possible to obtain data from 28 individuals (five devices did not provide data).

In some trips, a few fixes were occasionally missing and therefore data were interpolated linearly at 5 min intervals to fill in the gaps. Data collected for each bird were then split into individual trips, using the function *tripSplit* from package *Track2KBA* (Beal et al. 2020) running in R software (R Core Team 2020). Flights made within 3 km from the colony or lasting less than 1 h (that could have arisen from our own disturbance) were not considered as a trip and were excluded from any analysis.

The average number of trips per bird was 4.4 during the tracking period, ranging from 1 to 8, and we present the trips statistics including all trips obtained in the study period. However, to avoid any effect due to pseudo-replication, we tested for differences between sexes with linear mixed models (LMM), setting the individual as a random factor, and using package *lme4* (Bates et al. 2015) and *lmerTest* (Kuznetsova et al. 2017). The time of arrival and departure from the colony between one trip to the following one were concentrated in a relatively narrow period of the day, as is often the case in mostly diurnal foragers. The distribution of these variables (as well as the residuals of the models) did not depart from a normal distribution and, therefore, they were not treated as circular variables in LMM's. We also compared the interval between successive trips of males and females using an ANOVA.

We calculated the utilization distribution of each individual using kernel Utilization Distribution using the package *adehabitatHR* (Calenge 2006), setting the value of *h* at 5000 m (calculated by the ad-hoc method, rounded to the nearest thousand). The 50% kernel of each individual

was then intersected with a bathymetry layer obtained from ETOPO1 Global Relief Model (1 arc-minute resolution, <https://www.ngdc.noaa.gov/mgg/global>) to estimate the mean depth of the water in the foraging area of each individual, using the *raster* package (Hijmans 2020). To test whether birds showed any selectivity in relation to the foraging depths, we followed a percentile bootstrap approach, which include the following steps: (1) we defined a circular area around the colony with a radius that comprised 90% of all bird positions (121 km); (2) we then identified (and counted) all pixels used by foraging birds and computed the corresponding average depth; (3) we calculated the mean depths of a sample with the same number of pixels, randomly selected (with reposition) from the available area defined in (1), repeating the procedure 10,000 times. Finally (4) we compared the rank of the value obtained at the bird positions, within the distribution of depths obtained in the random locations, reporting the probability as the number of values in the distribution above the observed value.

We downloaded Seasonal forecast daily grids of sea surface temperature (SST) and 10 m u- and v-component (and intensity) of wind for the study region, at 0.25° resolution (from <https://cds.climate.copernicus.eu/cdsapp#!home>). The spatial resolution of these data is too low to enable any analysis at the level of individual trips. Therefore, we just characterised the wind intensity and SST of the areas used by Brown boobies, by averaging the grid values contained by the minimum convex polygon of 95% of all Brown boobies fixes, during the study period (26 February to 5 March, see Online resource 1). To quantify the overlap in the distributions of males and females, we gathered all positions from both sexes and calculated their home ranges. We then calculated the overlap distribution of both sexes, using the Utilization Distribution Overlap Index in *adehabitatHR* (Fiedberg and Kochanny 2005).

Diet

We collected 11 regurgitations from Brown boobies, who spontaneously regurgitated when handled. These corresponded mostly to individuals that were not tracked. Food items from these samples were identified to the lowest possible taxonomic level. All prey were counted, measured (to the nearest 0.1 mm) and weighed (to the nearest 0.01 g) when intact or nearly intact. To describe the presence and importance of each prey taxon in the diet we calculated the frequency of occurrence (FO %) as the number of regurgitations with a given prey taxon, in relation to the total number of regurgitations, and the numerical frequency (N %) as the number of individuals of a given taxon in relation to the total number of prey items.

In some cases, morphological identification was confirmed with DNA barcoding identification. Total genomic

DNA was extracted from muscle samples of 28 different prey items (24 fish and 4 cephalopod) using REDEExtract-N-Amp Kit (Sigma-Aldrich) according to the manufacturers' instructions. The same kit was used for the amplification of the cytochrome c oxidase subunit I using COI-F1 (5'-TCAACC ACCACAAAGACATTGGCAC-3') and COI-R2 primers (5'-ACTTCAGGGTGACCGAAGAATCAGAA-3'; Ward et al. 2005) for fish samples and LCO1490 (5'-GGTCAA CAAATCATAAAGATATTGG-3') and HCO2198 (5'-TAA ACTTCAGGGTGACCAAAAAATCA-3'; Folmer et al. 1994) for the cephalopod samples. PCR cycling conditions for COI-F1/COI-R2 and LCO1490/HCO2198, respectively, consisted of 2 min initial denaturation at 95 °C, followed by 35 cycles of denaturing at 94 °C for 30 s, annealing at 52 °C for 30 s, extension at 72 °C for 1 min, and final extension of 10 min at 72 °C; and of 3 min initial denaturation at 94 °C, followed by 40 cycles of denaturing at 94 °C for 40 s, annealing at 50 °C for 40 s, extension at 72 °C for 1 min, and final extension of 10 min at 72 °C. PCR products were purified and sequenced in STABVIDA (Sanger sequencing, <https://www.stabvida.net/>) and resulting sequences were aligned and edited with Codon Code Aligner (Codon Code Corporation, <https://www.codoncode.com/index.htm>). Using BLAST (Basic Local Alignment Search Tool) in NCBI through Codon Code Aligner, every sequence was compared with sequences available in GenBank to obtain the most likely identity. Genetic identification was considered to the species level for sequence similarity superior to 98% (e.g. Machida et al. 2009; Leray et al. 2013).

Results

Females of Brown boobies sampled had on average 5% longer wing length, 5% longer culmen length and were 22% heavier than males (Table 1).

Foraging trips

A total of 127 trips were obtained from 28 birds, of which 14 trips lasted more than 24 h. In those cases, birds spent most of the nocturnal period sitting at sea, as assessed by the relatively fixed GPS positions. Overall, females engaged

Table 1 Measurements of breeding female and male Brown boobies, captured from 26 to 28 February 2020 in Tinhosa Grande for GPS deployment

	Wing length (mm)	Culmen length (mm)	Mass (g)	N
Females	417.9 ± 5.4	98.1 ± 2.2	1082.9 ± 128.6	14
Males	395.7 ± 9.5	93.3 ± 3.5	843.4 ± 79.2	19

N sample size

in significantly longer trips (km), and spent approximately more 2 h out at sea in relation to males, although this difference was not significant (Table 2). However, if we only include single-day trips, females spent significantly more time at sea than males (Females = 9.4 ± 4.0 h, $n=44$ trips of 11 individuals; males = 7.0 ± 3.9 h, $n=69$ trips of 18 individuals, LMM, $t=3.2$, $P=0.0037$). There were no significant differences among sexes in the intervals between consecutive trips (females = 20.4 ± 10.0 h, $n=38$; males = 18.6 ± 10.2 h, $n=60$; ANOVA $F_{1,96}=0.69$, $P=0.408$). The overlap in the utilization distribution of males and females was estimated at 0.62, suggesting some foraging segregation between sexes.

Table 2 Means (\pm SD, range in parenthesis) of the parameters of foraging trips of females ($n=49$) and male ($n=78$) of Brown boobies from Tinhosa Grande, obtained from 26 February to 5 March 2020

Parameter	Females	Males	LMM	<i>P</i>
Total distance (km)	217.9 ± 105.7 (11.6–447.0)	153.1 ± 99.0 (17.7–391.5)	$t=3.0$	0.01
Max. distance (km)	92.7 ± 45.4 (6.0–203.1)	64.4 ± 39.1 (7.9–149.6)	$t=3.1$	0.01
Duration (h)	11.4 ± 7.1 (1.0–32.1)	9.5 ± 8.2 (1.1–33.9)	$t=1.2$	0.26
Time of departure (h)	8.0 ± 3.7 (4.9–15.9)	10.3 ± 3.7 (4.7–16.5)	$t=3.3$	0.001
Time of arrival (h)	17.0 ± 1.9 (10.5–20.4)	17.0 ± 1.8 (9.3–19.3)	$t=0.1$	0.90

Repeated foraging trips from each individual were used for the calculation of statistics, but statistical tests were carried out using linear mixed models (LMM), using the individual as a random factor

Males foraged mostly south-southeast of Tinhosa Grande, while females spread from south-southeast to almost west (Fig. 1). Brown boobies occurred mostly in deep waters, but females foraged in waters significantly deeper than those used by males (2496 ± 697 m, $n=49$ vs. 1965 ± 815 m, $n=78$). A bootstrap sampling of random positions around the colony resulted in mean depths ranging between 2495 and 2406 m (median = 2453 m), while the mean depths at the bird positions was 2520 m (Fig. 2, $P<0.001$).

The average sea surface temperature during the study period in the 95% minimum convex polygon of all location was 30.6 ± 0.30 °C and the wind intensity was 3.4 ± 1.64 m/s, predominantly from the southwest (Online Resource 1).

Diet

Most prey in regurgitations was complete (i.e. with complete vertebral column and skull in the case of fish), which enabled counting and often measuring individuals, even when soft tissues were slightly digested. This also allowed us to identify prey using morphological characteristics (Table 3). The mean number of prey per sample was 25.2 ± 14.4 ($n=11$) and the total number of individuals examined was 277. Genetic analysis allowed the identification of four taxa to species level that were identified to family level based on morphology. It also allowed the identification of two further species from remains which were not possible to identify using morphology, plus the confirmation of morphological identifications. On the other hand, there were two taxa that were identified based on morphology only (Online Resource

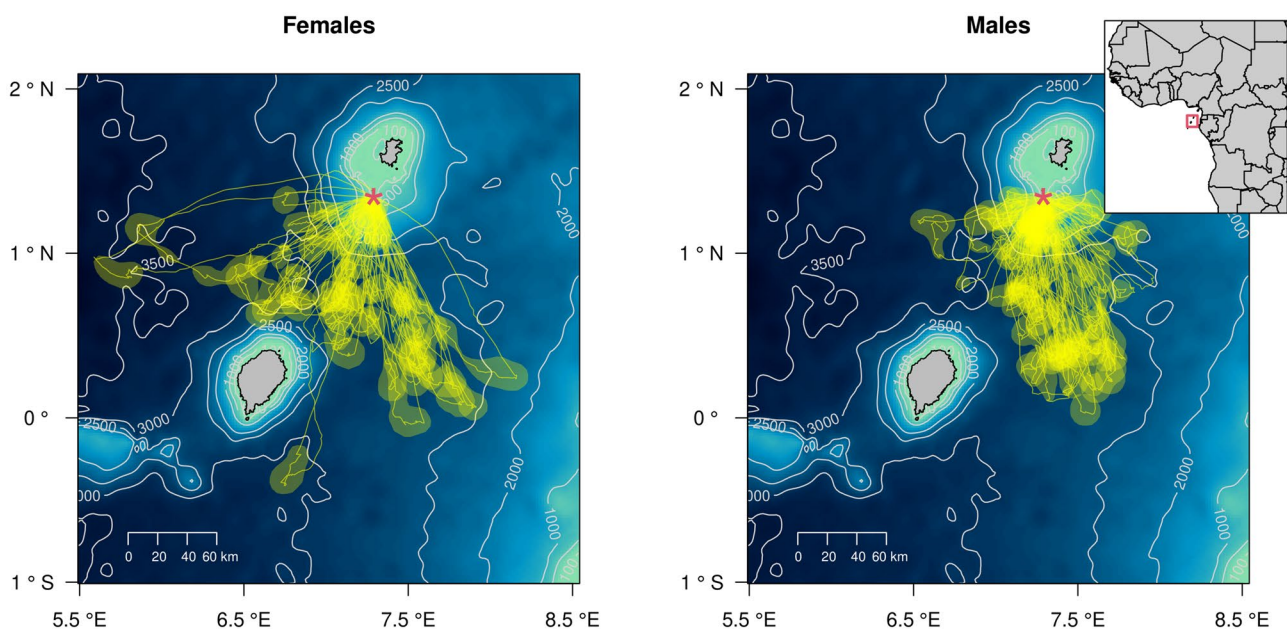


Fig. 1 Foraging trips of male ($n=78$) and female ($n=49$) Brown boobies from Tinhosa Grande performed from 26 February to 5 March 2020 and 50% utilization distribution of each individual; Tinhosa Grande is marked with *, with Príncipe in the north and São Tomé in the south

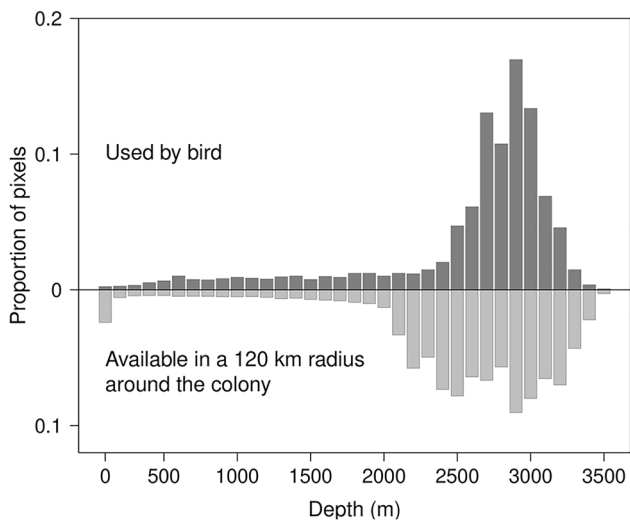


Fig. 2 Distribution of all bathymetric values (in m) within a radius comprising 90% of all positions (121 km, ca. 46,000 km²) of the Brown boobies tracked in Tinhosa Grande (top histogram, light grey) and bathymetric value associated with their GPS positions only (lower histogram, dark grey)

2). Flying gurnard (*Dactylopterus volitans*) was the most abundant prey found in regurgitations, followed by Squirrelfish (*Holocentrus adscensionis*) and False halfbeak (*Oxyporhamphus similis*; Table 3). All prey consisted of juvenile individuals, both from fish and squid species, as assessed from their size.

Discussion

Brown boobies from Tinhosa Grande fed mainly offshore on juvenile fish species, several tens of km from the colony, the vast majority in waters deeper than 2000 m. Some (female) individuals travelled up to almost 450 km in one foraging trip, as far as ca. 200 km off their colony. Birds did not forage on the shelves of the islands, which is particularly large in Príncipe (just north of Tinhosas), highlighting their preference for deep oceanic waters, at least at this time of the season. Furthermore, Brown boobies of Tinhosa Grande foraged for longer, travelling considerably larger distances and using deeper waters, when compared to all other studied populations (Table 4). This suggests that the areas closest to

Table 3 Frequency of occurrence (FO; %) and numeric frequency (NF; %) of prey from 11 regurgitations of Brown boobies (corresponding to 277 individuals)

Prey	FO (%)	NF (%)	Mass (g)	Length (mm)	
Osteichthyes					
Dactylopteridae	Flying gurnard <i>Dactylopterus volitans</i> ³	81.82	61.37	1.76 ± 0.59 (60)	45.99 ± 4.96 (72)
Holocentridae	Squirrelfish <i>Holocentrus adscensionis</i> ¹	36.36	10.83	2.23 ± 0.39 (16)	47.59 ± 2.59 (16)
Hemiramphidae	False halfbeak <i>Oxyporhamphus similis</i> ³	36.36	6.14	21.45 ± 0.83 (2)	128.50 ± 9.19 (2)
Scombridae	Yellowfin tuna <i>Thunnus albacares</i> ²	18.18	0.72	–	–
Carangidae	Blue runner <i>Caranx crysos</i> ²	9.09	0.36	–	–
Exocoetidae	Flyingfish <i>Cheilopogon</i> sp. ³	9.09	0.36	7.77 (1)	83.32 (1)
Nomeidae	Bigeye cigarfish <i>Cubiceps pauciradiatus</i> ²	9.09	15.52	–	52.18 ± 2.84 (3)
	Freckled driftfish <i>Psenes cyanophrys</i> ²	9.09	1.08	5.00 ± 1.61 (2)	57.08 ± 8.72 (2)
	Nomeidae n.i. ¹	9.09	0.36	1.92 (1)	48.34 (1)
Diodontidae	Longspined porcupinefish <i>Diodon holocanthus</i> ³	9.09	0.36	–	31.55 (1)
Monacanthidae	Planehead filefish <i>Stephanolepis hispidus</i> ¹	9.09	0.36	0.86 (1)	27.12 (1)
Cephalopoda	Ommastrephidae				
	Orangeback flying squid <i>Sthenoteuthis pteropus</i> ²	27.27	2.53	–	52.13 ± 5.62 (3)

Prey mean mass ± SD (g), sample size in parenthesis, and mean standard/mantle length ± SD (mm), sample size in parenthesis

Samples from Tinhosa Grande collected in 27 to 28 February 2020; the superscript 1 is used to refer prey identified only by morphology, the superscript 2 is used to refer prey identified only by molecular methods and the superscript 3 is used to refer prey identified by both methods

n.i. not identified, (more detail in Online Resource 2 and Online Resource 3)

Table 4 Mean maximum foraging distance from the colony, trip duration and foraging water depth of Brown boobies during chick rearing from Tinhosa Grande, compared with data from six other colonies

Colony	Year	Mean Maximum foraging distance (km)		Trip duration (h)		Water depth	Reference
		Female	Male	Female	Male		
Tinhosa Grande, São Tomé and Príncipe	2020	92.7	64.4	11.4	9.5	1965–2496 m	This study
Curral Velho, Cape Verde	2014–2015	38.0 (not discriminated by sex)		–	–	–	Oppel et al. (2018)
Swain Reef, Australia	2006	23.9	6.5	9.5	4.9	Shallow	Bunce (2015)
Raine Island, Australia	2014	65.8	50.3	6.2	4.8	~1000–2000 m	Miller et al. (2018)
Isla San Ildefonso, Mexico	2005	39.2	16.6	3.0	2.0	> 500 m	Weimerskirch et al. (2009a, b)
Dog Island, Anguilla	2012	43.8	52.9	5.4	5.8	Shallow	Soanes et al. (2015)
Dog Island, Anguilla	2013	44.8 (not discriminated by sex)		6.7 (not discriminated by sex)		Shallow	Soanes et al. (2016)
Dog Island, Anguilla	2014	39.7 (not discriminated by sex)		5.9 (not discriminated by sex)		Shallow	Soanes et al. (2016)
Sombrero, Anguilla	2014	28.5 (not discriminated by sex)		4.7 (not discriminated by sex)		Shallow	Soanes et al. (2016)
Prickly Pear West, Anguilla	2013	46.2 (not discriminated by sex)		5.5 (not discriminated by sex)		Shallow	Soanes et al. (2016)
Prickly Pear West, Anguilla	2014	30.3 (not discriminated by sex)		4.9 (not discriminated by sex)		Shallow	Soanes et al. (2016)
Saint Peter and Saint Paul Archipelago, Brazil	2015	7.1 (not discriminated by sex)		1.0 (not discriminated by sex)		~500–3500 m	Nunes et al. (2018)
Nakanokamishima Island, Japan	2004	–		2.5	3.8	–	Yoda and Kohno (2008)

the colony do not provide enough resources for all foraging birds. Yet, the other pantropical boobies (i.e. Masked booby and Red-footed booby) may forage up to 114 km from the colony, during the chick-rearing period, also in deep oceanic waters (Weimerskirch et al. 2005, 2009b; Oppel et al. 2015).

During breeding, as a consequence of the presence of conspecifics or of birds from co-occurring species, food depletion may occur near the colonies, forcing birds to travel further from the colony to forage (Ashmole 1963; Furness and Birkhead 1984). Therefore, inter- and intra-specific competition for food may shape the foraging distribution of populations (e.g. Oppel et al. 2015). Further studies analysing the foraging distribution and diet of the other species breeding of Tinhosas islands (particularly of the super-abundant sooty terns and noddies) are needed to address magnitude of the competition among those species.

Seabirds can rely on subsurface marine predators, such as cetaceans or fish, to locate or capture prey, especially in deep waters when predators force prey to the water surface while feeding (Ballance and Pitman 1999; Correia et al. 2019). These associations often play an important role for foraging success in the tropical regions, where productivity is lower and resources are more patchily distributed

and less predictable than in temperate and polar ones (Longhurst and Pauly 1987; Ballance and Pitman 1999). Brown boobies are known to associate with subsurface marine predators (e.g. Santos et al 2010), which might be an important source of food for birds in Tinhosa Grande. Additionally, some of the prey found in this study, are known to associate with floating macroalgae, such as sargassum (e.g. Blue runner, Flyingfish, Freckled driftfish, Planehead filefish; FAO 2016; Casazza and Ross 2008), which can make them easier to capture by Brown boobies (Haney 1986). However, direct observations of such circumstances are needed to confirm these hypotheses.

Marine fishery discards may represent an important source of food for seabirds (e.g. Granadeiro et al. 2013) and Brown boobies have been observed taking advantage of these discards (Blaber et al. 1995; Hill and Wassenberg 2000; Carniel and Krul 2012). However, our results do not suggest that Brown boobies from Tinhosa Grande are associated with fishery discards, as their diet consisted mostly in pelagic juvenile fish and squid, as opposed by demersal prey usually consumed by seabirds when associated with fisheries discards. Nevertheless, specific information about

discards in our study area is lacking (Kelleher 2005; Zeller et al. 2018).

Differential foraging strategies in seabirds may be related to differences in foraging areas, in foraging behaviour and in prey type (Phillips et al. 2004; Colominas-Ciuró et al. 2018). Around Tinhosa Grande, females performed longer trips and in deeper waters, apparently spreading their foraging areas much more than males, which more consistently targeted areas south-southeast of the island. Such pattern of longer female trips during chick-rearing period has already been observed in Brown boobies (Weimerskirch et al. 2009a; Miller et al. 2018), however, longer trips performed by males have also been found in Johnston Atoll in the central Pacific Ocean, during incubation (Lewis et al. 2005). Sexual segregation in foraging areas during chick rearing can be linked to differences in the type of prey consumed (e.g. Colominas-Ciuró et al. 2018), which was already observed in Brown boobies (Miller et al. 2018). Nevertheless, our opportunistic sampling did not enable any quantification of these differences, since sample sizes were very small. On the other hand, on Tinhosa Grande and in other colonies, males spent more time at the nest than females, which may indicate that males are more prone to engage in territory/chick protection (Gilardi 1992; Weimerskirch et al. 2009a; Miller et al. 2018), or else not able to increase their investment in provisioning (Sommerfeld et al. 2013; Velando and Alonso-Alvarez 2003).

The diet of pantropical boobies includes a variety of epipelagic fish and squid, from which usually flying fishes (Exocoetidae) and flying squids (Ommastrephidae) are the most important prey (e.g. Harrison et al. 1983; Kappes et al. 2011; Donahue et al. 2020). Brown boobies tend to feed mostly on pelagic fish, and at a lower frequency on pelagic squids, both in coastal waters and offshore (Harrison et al. 1983; Mellink et al. 2001; Naves et al. 2002; Weimerskirch et al. 2009a; Miller et al. 2018). Although coastal benthopelagic or demersal prey species have been found before in the diet of Brown boobies, they were linked to foraging in shelf waters (Harrison et al. 1983). In this study, all prey were epipelagic juveniles. Some of them, such as Flying gurnards, Longspined porcupinefish, Planehead filefish and Squirrelfish are known to be brephoepipelagic, i.e., pelagic and occurring offshore in early life stages, but coastal when adults (Allen et al. 2006). Particularly Flying gurnard, the most frequent and numerous prey found, is an abundant coastal fish species in the Democratic Republic of São Tomé and Príncipe (Krakstad et al. 2010) with significant economic importance in adult phases (Maia et al. 2018). Alongside other fish species, Flying gurnard is known to be a frequent prey of offshore pelagic predators (Oxenford and Wayne 1999; Vaske and Lessa 2019), such as marlins, dolphinfishes, tunas and seabirds (Naves et al. 2002; Junior and Lessa 2004; Rooker et al. 2007; Pinheiro et al.

2010). Therefore, our findings suggest that Brown boobies may be feeding in association with such subsurface marine predators.

In this study, we emphasize the importance of combining complementary techniques to obtain more comprehensive information in diet studies. The combination of morphologic and molecular identification seems adequate specially to obtain species-level identifications as well as prey quantification and size (Alonso et al. 2014).

Final considerations

This is the first study on the foraging ecology of Brown boobies in the Gulf of Guinea. Despite being limited in its temporal scope, this study showed that there were marked differences between sexes in foraging ranges and that birds had a clear preference for foraging over deep oceanic waters, at unusually high distances from the colony. Further sampling will be needed to understand if these patterns and the prey consumed vary within the season and across years, and also to understand why foraging ranges are much larger here than in other studied populations. The dependence of this population on juvenile fish that are coastal in the adult phase such as Flying gurnard shows that Brown booby conservation is not only dependent on the safeguard of their foraging areas and breeding sites, but also on the correct management of the coastal adjacent areas that support the adult individuals of the species consumed by them.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00227-021-03904-0>.

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Data availability The tracking data generated during and/or analysed during the current study are available in BirdLife Seabird Tracking Database (<http://www.seabirdtracking.org/>).

Declarations

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

Ethical approval The tracking was approved by the government of Democratic Republic of São Tomé and Príncipe; bird ringing was performed under the permit 50/2019 (ICNF) and permission to carry out procedures in animals was granted to JPG by Direcção Geral de Alimentação e Veterinária, Portugal (Ref: 0421).

Informed consent All the authors included in this manuscript have agreed to be listed and approve the submitted version of the manuscript.

References

- Allen LG, Pondella DJ, Horn MH (2006) The ecology of marine fishes: California and Adjacent waters. University of California Press, Berkeley
- Alonso H, Granadeiro JP, Waap S, Xavier J, Symondson WOC, Ramos JA, Catry P (2014) An holistic ecological analysis of the diet of Cory's shearwaters using prey morphological characters and DNA barcoding. *Mol Ecol* 23:3719–3733. <https://doi.org/10.1111/mec.12785>
- Ashmole N (1963) The regulation of numbers of tropical oceanic birds. *Ibis* 103:458–473
- Ballance LT, Pitman RL (1999) Foraging ecology of tropical seabirds. In: Adams NJ, Slotow RH (eds) Proc 22 Int Ornithol Congr, Durban. BirdLife South Africa, Johannesburg, pp 2057–2071
- Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effect models using lme4. *J Stat Softw* 67:1–48
- Beal M, Ooppel S, Handley J, Pearmain L, Morera-Pujol V, Miller M, Taylor P, Lascelles B, Dias M. (2020) BirdLifeInternational/track-2kba: First Release (Version 0.5.0). Zenodo
- BirdLife International (2018) State of the World's birds: taking the pulse of the planet. BirdLife International, Cambridge, UK
- BirdLife International (2020) Species factsheet: *Sula leucogaster*. <http://www.birdlife.org>. Accessed 26 Aug 2020
- Blaber SJM, Milton DA, Smith GC, Farmer MJ (1995) Trawl discards in the diets of tropical seabirds of the northern Great Barrier Reef, Australia. *Mar Ecol Prog Ser* 127:1–13. <https://doi.org/10.3354/meps127001>
- Bollen A, Matilde E, Barros N (2018) An update assessment of the seabird populations breeding at Príncipe and Tinhasas. *Ostrich* 89:47–58. <https://doi.org/10.2989/00306525.2017.1380085>
- Branco JO, Fracasso HAA, Machado IF, Bovendorp MS, Verani JR (2005) Diet of *Sula leucogaster* Boddaert, in the Moleques do Sul Island, Florianópolis, Santa Catarina, Brazil. *Rev Bras Zool* 22:1044–1049. <https://doi.org/10.1590/S0101-81752005000400033>
- Brown LH, Urban EX, Newman K (1983) The birds of Africa, vol 1. Academic Press, London
- Bunce A (2015) Foraging behaviour of a declining population of Brown Boobies (*Sula leucogaster*) breeding in the Swain Reefs, Great Barrier Reef. *Emu* 155:368–372. <https://doi.org/10.1071/MU14037>
- Calenge C (2006) The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. *Ecol Model* 197:516–519. <https://doi.org/10.1016/j.ecolmodel.2006.03.017>
- Carniel V, Krul R (2012) Utilisation of discards from small-scale fisheries by seabirds in coastal waters of Paraná State, Brazil. *Seabird* 25:29–38
- Casazza TL, Ross SW (2008) Fishes associated with pelagic Sargassum and open water lacking Sargassum in the Gulf Stream off North Carolina. *Fish Bull* 106:348–363
- Castillo-Guerrero JA, Lerma M, Mellink E, Suazo-Guillén E, Peñaloza-Padilla EA (2016) Environmentally-mediated flexible foraging strategies in Brown Boobies in the Gulf of California. *Ardea* 104:33–47. <https://doi.org/10.5253/arde.v104i1.a3>
- Cleasby IR, Wakefield ED, Bodey TW, Davies RD, Patrick SC, Newton J, Votier SC, Bearhop S, Hamer KC (2015) Sexual segregation in a wide-ranging marine predator is a consequence of habitat selection. *Mar Ecol Prog Ser* 518:1–12
- Colominas-Ciuró R, Santos M, Coria N, Barbosa A (2018) Sex-specific foraging strategies of Adélie penguins (*Pygoscelis adeliae*): females forage further and on more krill than males in the Antarctic Peninsula. *Polar Biol* 41:2635–2641. <https://doi.org/10.1007/s00300-018-2395-1>
- Correia E, Granadeiro JP, Mata VA, Regalla A, Catry P (2019) Trophic interactions between migratory seabirds, predatory fishes and small pelagics in coastal West Africa. *Mar Ecol Prog Ser* 622:177–189. <https://doi.org/10.3354/meps13022>
- Croxall JP, Butchart SHM, Lascelles B, Stattersfield AJ, Sullivan B, Symes A, Taylor P (2012) Seabird conservation status, threats and priority actions: a global assessment. *Bird Conserv Int* 22:1–34. <https://doi.org/10.1017/S0959270912000020>
- Hoyo J del, Elliott A, Sargatal J, Cabot J (1996) Handbook of the birds of the world. Vol. 3 (hoatzin to auks). Barcelona, Lynx Edicions, p 821
- Dias MP, Martin R, Pearmain EJ, Burfield IJ, Small C, Phillips RA, Yates O, Lascelles B, Borboroglu PG, Croxall JP (2019) Threats to seabirds: a global assessment. *Biol Conserv* 237:525–537. <https://doi.org/10.1016/j.biocon.2019.06.033>
- Donahue SE, Adams J, Renshaw MA, Hyrenbach KD (2020) Genetic analysis of the diet of red-footed boobies (*Sula sula*) provisioning chicks at Ulupa'u Crater. O'ahu Aquat Conserv. <https://doi.org/10.1002/aqc.3470>
- FAO (2016) The living marine resources of the Eastern Central Atlantic. Volume 4: Bony fishes part 2 (Perciformes to Tetraodontiformes) and Sea turtles. FAO Species Identification Guide for Fishery Purposes. FAO, Rome
- Fiedberg J, Kochanny CO (2005) Quantifying home-range overlap: the importance of the utilization distribution. *J Wildl Manag* 69:1346–1359
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Mol Mar Biol Biotechnol* 3:294–299
- Furness R, Birkhead T (1984) Seabird colony distributions suggest competition for food supplies during the breeding season. *Nature* 311:655–656
- Gilardi JD (1992) Sex-specific foraging distributions of brown boobies in the Eastern Tropical Pacific. *Col Waterbirds* 15:148–151. <https://doi.org/10.2307/1521367>
- Granadeiro JP, Brickle P, Catry P (2013) Do individual seabirds specialize in fisheries' waste? The case of black-browed albatrosses foraging over the Patagonian Shelf. *Anim Conserv* 17:19–26. <https://doi.org/10.1111/acv.12050>
- Hamer KC, Phillips RA, Wanless S, Harris MP, Wood AG (2000) Foraging ranges, diets and feeding locations of gannets *Morus*

- bassanus* in the North Sea: evidence from satellite telemetry. *Mar Ecol Prog Ser* 200:257–264. <https://doi.org/10.3354/meps200257>
- Handley JM, Pearmain EJ, Opper S, Carneiro APB, Hazin C, Phillips RA, Ratcliffe N, Staniland IJ, Clay TA, Hall J, Scheffer A, Fedak M, Boehme L, Pütz K, Belchier M, Boyd IL, Trathan PN, Dias MP (2020) Evaluating the effectiveness of a large multi-use MPA in protecting Key Biodiversity Areas for marine predators. *Divers Distrib* 26:715–729. <https://doi.org/10.1111/ddi.13041>
- Haney JC (1986) Seabird patchiness in tropical oceanic waters: the influence of Sargassum “reefs.” *Auk* 103:141–151. <https://doi.org/10.1093/auk/103.1.141>
- Harrison CS, Hida TS, Seki MP (1983) Hawaiian seabird feeding ecology. *Wildl Monogr* 85:3–71
- Hijmans RJ (2020) raster: Geographic Data Analysis and Modeling. R package version 3.4–5. <https://CRAN.R-project.org/package=raster>
- Hill BJ, Wassenberg TJ (2000) The probable fate of discards from prawn trawlers fishing near coral reefs. *Fis Res* 48:277–286. [https://doi.org/10.1016/S0165-7836\(00\)00185-5](https://doi.org/10.1016/S0165-7836(00)00185-5)
- Junior TV, Lessa RP (2004) Feeding habits of the Common dolphinfish *Coryphaena hippurus*, in northeastern Brazil’s Exclusive Economic Zone. *Arquivos de Ciências do Mar* 37:131–138
- 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>
- Kelleher K (2005) Discards in the world’s marine fisheries. An update. FAO Fisheries Technical Paper. No. 470. FAO, Rome
- Krakstad J-O, Alvheim O, Lopes, JDS, Iwamoto T (2010) Survey of the demersal resources 10 May– 20 May 2010. Bergen. Institute of Marine Research
- Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest package: tests in linear mixed effects models. *J Statist Softw* 82:1–26
- Leray M, Yang JY, Meyer CP, Mills SC, Agudelo N, Ranwez V, Boehm JT, Machida RJ (2013) A new versatile primer set targeting a short fragment of the mitochondrial COI region for metabarcoding metazoan diversity: application for characterizing coral reef fish gut contents. *Front Zool* 10:34. <https://doi.org/10.1186/1742-9994-10-34>
- Lewis S, Schreiber EA, Daunt F, Schenk GA, Orr K, Adams A, Wanless S, Hamer KC (2005) Sex-specific foraging behaviour in tropical boobies: does size matter? *Ibis* 147:408–414. <https://doi.org/10.1111/j.1474-919x.2005.00428.x>
- Longhurst AR, Pauly D (1987) Ecology of tropical oceans. Academic Press, San Diego, CA
- Ludynia K, Garthe S, Luna-Jorquera G (2010) Distribution and foraging behaviour of the Peruvian Booby (*Sula variegata*) off northern Chile. *J Ornithol* 151:103–111. <https://doi.org/10.1007/s10336-009-0431-1>
- Machida RJ, Hashiguchi Y, Nishida M, Nishida S (2009) Zooplankton diversity analysis through single-gene sequencing of a community sample. *BMC Genomics* 10:438. <https://doi.org/10.1186/1471-2164-10-438>
- Maia HA, Morais RA, Siqueira AC, Hanazaki N, Floeter SR, Bender MG (2018) Shifting baselines among traditional fishers in São Tomé and Príncipe islands, Gulf of Guinea. *Ocean Coast Manag* 154:133–142. <https://doi.org/10.1016/j.ocecoaman.2018.01.006>
- Mellink E, Domínguez J, Luévano J (2001) Diet of Eastern Pacific Brown Boobies *Sula leucogaster brewsteri* on Isla San Jorge, north-eastern Gulf of California, and an April comparison with diets in the middle Gulf of California. *Mar Ornithol* 29:23–28
- Miller MGR, Silva FRO, Machovsky-Capuska GE, Congdon BC (2018) Sexual segregation in tropical seabirds: drivers of sex-specific foraging in the Brown Booby *Sula leucogaster*. *J Ornithol* 159:425–437. <https://doi.org/10.1007/s10336-017-1512-1>
- Naves LC, Brusque LF, Vooren CM (2002) Feeding ecology of *Sula leucogaster*, *Anous stolidus* and *Anous minutus* at Saint Peter and Saint Paul’s Rocks, Brazil. *Ararajuba* 10:21–30
- Nunes GT, Bertrand S, Bugoni L (2018) Seabirds fighting for land: phenotypic consequences of breeding area constraints at a small remote archipelago. *Sci Rep* 8:665. <https://doi.org/10.1038/s41598-017-18808-7>
- Opper 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>
- Opper S, Bolton M, Carneiro APB, Dias MP, Green JA, Masello JF, Phillips RA, Owen E, Quillfeldt P, Beard A, Bertrand S, Blackburn J, Boersma PD, Borges A, Broderick AC, Catry P, Cleasby I, Clingham E, Creuwels J, Crofts S, Cuthbert RJ, Dallmeijer H, Davies D, Davies R, Dilley BJ, Dinis HA, Dossa J, Dunn MJ, Efe MA, Fayet AL, Figueiredo L, Frederico AP, Gjerdrum C, Godley BJ, Granadeiro JP, Guilford T, Hamer KC, Hazin C, Hedd A, Henry L, Hernández-Montero M, Hinke J, Kokubun N, Leat E, Tranquilla LM, Metzger B, Militão T, Montrond G, Mullié W, Padgett O, Pearmain EJ, Pollet IL, Pütz K, Quintana F, Ratcliffe N, Ronconi RA, Ryan PG, Saldanha S, Shoji A, Sim J, Small C, Soanes L, Takahashi A, Trathan P, Trivelpiece W, Veen J, Wakefield E, Weber N, Weber S, Zango L, Daunt F, Ito M, Harris MP, Newell MA, Wanless S, González-Solís J, Croxall J (2018) Spatial scales of marine conservation management for breeding seabirds. *Mar Policy* 98:37–46. <https://doi.org/10.1016/j.marpol.2018.08.024>
- Oxenford HA, Wayne H (1999) Feeding habits of the dolphinfish (*Coryphaena hippurus*) in the eastern Caribbean. *Sci Mar* 63:303–315. <https://doi.org/10.3989/scimar.1999.63n3-4317>
- Phillips RA, Silk JRD, Phalan B, Catry P, Croxall JP (2004) Seasonal sexual segregation in two Thalassarche albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? *Proc R Soc Lond B* 271:1283–1291. <https://doi.org/10.1098/rspb.2004.2718>
- Pinheiro PB, Travassos P, Tolotti MT, Barbosa TM (2010) Diet of the white marlin (*Tetrapturus albidus*) from the southwestern equatorial Atlantic Ocean. *Collect Vol Sci Pap ICCAT* 65:1843–1850
- R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Rooker JR, Bremer JRA, Block BA, Dewar H, De Metrio G, Corriero A, Kraus RT, Prince ED, Rodríguez-Maín E, Secor DH (2007) Life history and stock structure of atlantic bluefin tuna (*Thunnus thynnus*). *Rev Fish Sci* 15:265–310. <https://doi.org/10.1080/10641260701484135>
- Santos COM, Oshima JEF, Pacifico ES, Silva E (2010) Feeding associations between Guiana dolphins, *Sotalia guianensis* (Van Bénèden, 1864) and seabirds in the Lagamar estuary, Brazil. *Braz J Biol* 70:9–17. <https://doi.org/10.1590/S1519-6984201000010004>
- Schreiber EA, Norton RL (2020) Brown Booby (*Sula leucogaster*), version 1.0. In *Birds of the World* (S. M. Billerman, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA
- Soanes LM, Bright JA, Bolton M, Millet J, Mukhida F, Green JA (2015) Foraging behaviour of Brown Boobies *Sula leucogaster* in Anguilla, Lesser Antilles: preliminary identification of at-sea distribution using a time-in-area approach. *Bird Conserv Int* 25:87–96. <https://doi.org/10.1017/S095927091400001X>
- 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 Policy* 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
- Sydeman WJ, Thompson SA, Kitaysky A (2012) Seabirds and climate change: roadmap for the future. *Mar Ecol Progr Ser* 454:107–117. <https://doi.org/10.3354/meps09806>
- Valle S, Barros N, Ramírez I, Wanless RM (2016) Population estimates of the breeding birds of the Tinhosas islands (Gulf of Guinea), the only major seabird colony of the eastern tropical Atlantic. *Ostrich* 87:209–215. <https://doi.org/10.2989/00306525.2016.1207720>
- Vaske Jr T, Lessa, TR (2019) Occurrence of brephoepipelagic fishes in the stomach contents of large pelagic predators in the south-western equatorial Atlantic Ocean. *Cah Biol Mar* 60: 235–241
- Velando A, Alonso-Alvarez C (2003) Differential body condition regulation by males and females in response to experimental manipulations of brood size and parental effort in the blue-footed booby. *J Anim Ecol* 72:846–856. <https://doi.org/10.1046/j.1365-2656.2003.00756.x>
- Ward RD, Zemlak TS, Innes BH, Last PR, Hebert PDN (2005) DNA barcoding Australia's fish species. *Phil Trans R Soc B* 360:1847–1857. <https://doi.org/10.1098/rstb.2005.1716>
- Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? *Deep Sea Res Part II: Top Stud Oceanogr* 54:211–223
- Weimerskirch H, Corre ML, Jaquemet S, Marsac F (2005) Foraging strategy of a tropical seabird, the Red-footed booby, in a dynamic marine environment *Mar Ecol Progr Ser* 288:251–261. <https://doi.org/10.3354/meps288251>
- Weimerskirch H, Shaffer SA, Tremblay Y, Costa DP, Gadenne H, Kato A, Ropert-Coudert Y, Sato K, Aurioules D (2009a) Species- and sex-specific differences in foraging behaviour and foraging zones in Blue-footed and Brown Boobies in the Gulf of California. *Mar Ecol Progr Ser* 391:267–278. <https://doi.org/10.3354/meps07981>
- Weimerskirch H, Le Corre M, Gadenne H, Pinaud D, Kato A, Ropert-Coudert Y, Bost CA (2009b) Relationship between reversed sexual dimorphism, breeding investment and foraging ecology in a pelagic seabird, the masked booby. *Oecologia* 16:637–649. <https://doi.org/10.1007/s00442-009-1397-7>
- Yoda K, Kohno H (2008) Plunging behaviour in chick-rearing Brown Boobies. *Ornithol Sci* 7:5–13
- Zeller D, Cashion T, Palomares M, Pauly D (2018) Global marine fisheries discards: a synthesis of reconstructed data. *Fish Fish* 19:30–39. <https://doi.org/10.1111/faf.12233>

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