



Breeding stage, not sex, affects foraging characteristics in masked boobies at Rapa Nui

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Abstract

Sexual segregation in foraging occurs in some species and populations of boobies (Sulidae), but it is not a general pattern. Sexual segregation in foraging may occur to avoid competition for food, and this competition may intensify during specific stages of breeding. We examined sexual segregation in foraging in relation to breeding stage in masked boobies *Sula dactylatra* at Rapa Nui by tracking simultaneously incubating and chick-rearing birds using GPS recorders ($n = 18$) and collected a total of 11 regurgitate samples. Stable isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of whole blood samples were carried out in 20 birds. There were no differences in foraging trip parameters or diet between females and males. Both sexes traveled farther and for longer while incubating than while rearing chicks. Isotopic niches ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) overlapped to some degree among all groups at all times, but the lowest overlap between sexes occurred during incubation. While preying on ephemeral distributed flying fish, vertical or horizontal competition avoidance may be almost impossible, and thus females and males share their foraging grounds. Since birds were tracked simultaneously, shorter foraging trips of chick-rearing birds must be an effect of the constraints of provisioning the chick. Differences observed in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values between sexes may be caused by subtle differences in their foraging behaviors, or by differences in physiology linked to breeding. Our findings suggest that local oceanography and its inherent food distribution are determinants for sexual segregation in foraging patterns in masked boobies and possibly also other booby species.

Significance statement

In some animals, females and males forage on different areas or prey on different species to avoid competition for food resources. In boobies (*Sula* sp.), some studies show evidence of sexual segregation in foraging and others do not. Here, we tested if sexual segregation in foraging occurred in masked boobies on the Pacific island of Rapa Nui by studying simultaneously incubating and chick-rearing birds. We found no evidence of sexual segregation on foraging behavior or diet. We discuss that the difference between this and other studies in boobies may be an effect of the local prey availability. When the prey community is more diverse and heterogeneously distributed, each sex may access different resources and thus sexual foraging segregation will occur. In contrast, in areas like Rapa Nui where prey resources are distributed ephemerally, sexual segregation in foraging will not be useful and is thus less likely to occur.

Keywords Sexual size dimorphism · Tropical · Seabird · Foraging · Resource partitioning

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Introduction

Sexual segregation in foraging is a widespread behavioral and ecological phenomenon among animal taxa (Wearmouth and Sims 2008). In many bird species, females and males differ in terms of their spatio-temporal distribution, at sea behavior, and feeding ecology (González-Solís et al. 2000; Catry et al. 2005; Forero et al. 2005; Phillips et al. 2011). Such differences in areas used and prey species consumed by sex have been often seen as a response to alleviate competition for food resources (Selander 1966; Phillips et al. 2011). The larger sex may dominate intra-specific interactions close to the colony, forcing the smaller sex, which also has a better flying efficiency (Shaffer et al. 2001), to travel farther away for foraging (González-Solís et al. 2000). Among boobies (*Sula* spp.), females are persistently larger than males (Nelson 1978; van Oordt et al. 2018), and this notable reversed sexual size dimorphism has frequently been associated with differences in foraging behavior and diet within this taxonomic group.

Sex-related foraging differences in boobies may involve the use of different areas for foraging (Weimerskirch et al. 2006; Stauss et al. 2012), or different diving depths (Lewis et al. 2002; Weimerskirch et al. 2006; Zavalaga et al. 2007), diets (Zavalaga et al. 2007; Miller et al. 2018), or trophic levels (Young et al. 2010b; González-Medina et al. 2017). However, contrasting results have been found within the Sulidae, making it difficult to interpret the persistence of sexual segregation in foraging among boobies (Table 1). For example, female brown boobies (*Sula leucogaster*) foraged farther from their colonies than males at Clipperton Island and at Raine Island, while no sexual differences were noted in the same species foraging in the Isla San Jorge. Likewise, female and male brown and blue-footed boobies (*Sula nebouxi*), respectively, had different $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, whereas no sexual differences in isotope levels were found in red-footed (*Sula sula*) or masked boobies (*Sula dactylatra*; Table 1). These contrasting results in terms of foraging ecology among species and colonies of boobies suggest that sexual segregation in foraging do not occur consistently and might reflect changes in competition levels and local food abundance and availability.

In seabirds, the switch from incubating to chick provisioning triggers pronounced changes in foraging behavior (Hipfner et al. 2013; Navarro et al. 2014). Chick-rearing seabirds may perform shorter trips to assure a regular food delivery to prevent reduced growth of their chicks (Shoji et al. 2015), whereas incubating seabirds are free to forage farther. Accordingly, a decrease in trip duration from the incubation to the chick-rearing stage has been observed in several seabird species (Navarro et al. 2009; Ito et al. 2010; Sommerfeld and Hennicke 2010; Hedd et al. 2014), including Sulids (Castillo-Guerrero et al. 2016; Mendez et al. 2016; Poli et al. 2017). Performing shorter foraging trips during chick-rearing in

comparison to incubating birds is likely a strategy that birds use to minimize their time at sea and maximize their food delivery to chicks at short temporal intervals. However, seabirds foraging closer to their colonies may be more severely affected by competition given that the areas closer to the colony must be subject to greater depletion of food resources (Birt et al. 1987; Oppel et al. 2015). Therefore, the apparently conflicting results regarding foraging segregation in Sulids may be a consequence of the fact that previous work has focused mainly on detecting sexual segregation in foraging either during incubation or during chick-rearing, or without considering possible interactions between sex and breeding stage (see Table 1). Indeed, sexual segregation in foraging during discrete breeding stages have been reported in various tropical seabirds in the Mozambique Channel (Cherel et al. 2008) at Christmas Island (Navarro et al. 2014), and even in temperate seabirds such as northern gannets (*Morus bassanus*) (Lewis et al. 2002; Ismar et al. 2017). Sex-related foraging differences may therefore be a result of constraints imposed by breeding, in interaction with local food availability.

In most study systems in temperate and polar areas, and where most seabird research has been performed (Ballance and Pitman 1999; Reboredo-Segovia et al. 2020), birds breed synchronously and there is only little temporal overlap between incubating and chick-rearing birds (Hamer et al. 2002). Since both stages happen consecutively in such study systems, one can thus never know if differences in foraging area use between incubating and chick-rearing birds are due to temporal shifts in prey availability, prey depletion in areas used during incubation, or due to the need of parents to provision the chicks with food regularly which forced them to forage near colonies (Navarro et al. 2009; Ito et al. 2010; Hedd et al. 2014; Besel et al. 2018). However, some tropical seabirds breed through the year (Reynolds et al. 2014; Tarburton 2018) and thus, incubating and chick-rearing individuals can be tracked simultaneously. By tracking simultaneously incubating and chick-rearing individuals, one can rule out that changes in temporal prey availability created the differences in foraging parameters between birds, and thus, test for sexual segregation in foraging while facing the constraints due to chick provisioning. Understanding the differences between sexes during different stages of breeding is important, because dissimilarities in fitness or survival rates caused by differential exposure of males and females to different conditions or threats may lead to an imbalanced sex ratio, with population dynamic consequences (Phillips et al. 2005; Harrison et al. 2011; García-Tarrasón et al. 2015; Gianuca et al. 2019). Furthermore, understanding the persistence of foraging behaviors among members of a population improves the ability to manage areas in relation to seabird life stages (Oppel et al. 2018).

Masked boobies are an ideal species to test for the effects of sex and breeding stage on foraging behavior and diet because females and males are easy to differentiate: females are bigger

Table 1 Sex-related differences in foraging ecology reported for masked boobies (*Sula dactylatra*), red-footed booby (*Sula sula*), blue-footed booby (*Sula nebouxi*), brown booby (*Sula leucogaster*), Peruvian booby (*Sula variegata*), Abbott's booby (*Papasula abbotti*), and Nazca booby (*Sula granti*)

Booby species & island	Breeding stage	Foraging trip parameters	Diving trip parameters	Isotopic values	References
Masked booby					
Motu Nui	I & R	F = M	F = M	IF ≠ IM	This study
Clarion Island	I	F = M	F = M		Lerma et al. (2020)
Lord Howe Island	R	F = M	F = M		Machovsky-Capuska et al. (2016)
Tromelin Island	R	F = M	F = M		Kappes et al. (2011)
Phillip Island	R	F = M	F > M		Sommerfeld et al. (2013)
Clipperton Island	R	F = M	F > M		Weimerskirch et al. (2009a)
Isla Muertos	I&R	F = M			Poli et al. (2017)
Ascension	I&R	F = M			Oppel et al. (2015)
St. Helena	I&R	F = M			Oppel et al. (2015)
Palmyra Atoll	P	F = M		F = M	Young et al. (2010a, b)
Albrolhos Island	U			F = M	Mancini et al. (2013)
Atol das Rocas	U			F = M	Mancini et al. (2013)
Fernando de Noronha	U			F = M	Mancini et al. (2013)
Pedro Cays	R	U			Wilkinson et al. (2020)
Red-footed booby					
Europa Island	I & R	IF > RF & M	F = M		Weimerskirch et al. (2006)
Johnston Atoll	I	F = M	F = M		Lewis et al. (2005)
Christmas Island	I	F = M			Mendez et al. (2017)
Walpole Island	I	F = M			Mendez et al. (2017)
Genovesa Island	I	F = M			Mendez et al. (2017)
Chesterfield Island	I	F = M			Mendez et al. (2017)
Europa Island	I & R	F = M			Mendez et al. (2016)
Palmyra Atoll	P			F = M	Young et al. (2010b)
Europa Island	P			F ≠ M	Cherel et al. (2008)
Blue-footed booby					
Isla San Ildefonso	R	F > M	F = M	F = M	Weimerskirch et al. (2009b)
Isla El Rancho	R	F = M			González-Medina et al. (2015)
Isla El Rancho	R	F > M			Castillo-Guerrero and Mellink (2011)
Lobos de Tierra	I & R		F > M		Zavalaga et al. (2007)
Isla El Rancho	I			F ≠ M	González-Medina et al. (2017)
Brown booby					
Isla San Jorge	I&R	F = M	F > M		Castillo-Guerrero et al. (2016)
Isla San Ildefonso	R	F > M	F = M	F = M	Weimerskirch et al. (2009b)
Johnston Atoll	R	F < M	F = M		Lewis et al. (2005)
Raine Island	R	F > M			Miller et al. (2018)
Clipperton Island	U	F > M			Gilardi (1992)
Palmyra Atoll	P			F ≠ M	Young et al. (2010b)
Christmas Island	P			F = M	Navarro et al. (2014)
Albrolhos Island	U			F = M	Mancini et al. (2013)
Fernando de Noronha	U			F = M	Mancini et al. (2013)
Atol das Rocas	U			F = M	Mancini et al. (2013)
Peruvian booby					
Isla Pescadores	R	F = M	F = M		Weimerskirch et al. (2012)

Table 1 (continued)

Booby species & island	Breeding stage	Foraging trip parameters	Diving trip parameters	Isotopic values	References
Lobos de Tierra	R	F = M	F > M		Zavalaga et al. (2010)
Lobos de Afuera	R	F = M	F > M		Zavalaga et al. (2010)
Isla Pajaros	R	U			Ludynia et al. (2010)
Abbott's booby					
Christmas Island	R	U			Hennicke and Weimerskirch (2014)
Nazca booby					
Isla Española	R	U			Zavalaga et al. (2012)

Foraging trip parameters refer to duration of trips and/or maximum distance from the colony. Diving parameters refer to diving depth in meters and/or dive duration in seconds. Isotopic values refer to $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Breeding stage: *I*, incubating; *R*, chick-rearing; *P*, incubation and chick-rearing pooled together; *U*, unspecified; *F*, females; *M*, males; *IF*, incubating females; *RF*, chick-rearing females. If $F > M$ for foraging trip parameters, females foraged farther away from the colony and/or their foraging trips were longer than those of males. If $F > M$ for diving parameters, females dived deeper and/or longer than males

and have a rough voice, whereas males are smaller and have a high-pitched voice (Nelson 1978). In addition, in contrast with most temperate areas, where breeding occurs synchronously (Hamer et al. 2002), masked boobies may breed throughout the year (Marin and Caceres 2010; Flores et al. 2014), offering the opportunity to study the foraging behavior and diet of incubating and chick-rearing birds simultaneously. The current study used tracking technology and stable isotope analyses to test the hypothesis that masked boobies display sexual segregation in foraging, and to test if sexual segregation in foraging is related to constraints imposed by breeding. We expected adults of both sexes to travel farther away during incubation than during chick-rearing. We considered that sexual segregation in foraging would occur during periods of increased demands (during chick-rearing), whereas sexual segregation would not occur during incubation. Thus, we expected to find that the larger size of females enables local dominance as suggested to occur in Sulids and other seabirds (Gilardi 1992; González-Solis et al. 2000; Stahl and Sagar 2000) particularly while rearing chicks. Accordingly, we expect that by foraging in different areas and depths, females encounter different prey, and thus expect to find differences in the isotopic signatures between chick-rearing females and males.

Methods

Study area

Rapa Nui (also known as Easter Island) is located in the middle of the South Pacific Gyre (Fig. S1). The South Pacific Gyre has oligotrophic waters characterized by low zooplankton biomass and low nutrient concentrations (Reid et al. 1978; Moraga et al. 1999; Morel et al. 2010), which are often associated with low food resources (Longhurst and Pauly 1987).

The fish fauna of Rapa Nui is considered to be extremely impoverished, but with a similar abundance and biomass of fish compared with analogously isolated islands (Randall and Cea 2010; Friedlander et al. 2013). Masked boobies at Rapa Nui breed on Motu Nui (109.4° W, 21.2°S), a small (3.9 ha) rock islet located in the southwest of Rapa Nui. During the breeding season, females lay two eggs which are incubated in turns by both parents for a period of 42 days (Nelson 1978; Priddel et al. 2005). Both eggs may hatch, but only one chick is raised (Nelson 1978; Marchant and Higgins 1990; Priddel et al. 2005). The masked booby colony at Rapa Nui consisted of 56 breeding pairs in 2016, including 32 incubating and 24 chick-rearing pairs.

Data collection

Fieldwork consisted of 4–6-day visits twice a month in October and November 2016. Incubating or chick-rearing individuals were opportunistically selected based on reachability of nest sites and studied simultaneously. It was not possible to record data blind because our study involved focal animals in the field. Focal nests contained one or two eggs, or one chick. A total of 17 eggs were measured by length (L) and breadth (B) using Vernier calipers. Egg volume was calculated using the formula $\text{egg volume} = 0.00051 (\text{LB}^2) + 1.22$ (Clifford and Anderson 2002). Length (64.9 ± 4.2 mm), breadth (43.3 ± 1.5 mm), and egg volume (63.3 ± 6.3 g) were within normal ranges for masked boobies' populations (Priddel et al. 2005). Chicks from tagged birds were covered with down and weighed 0.4–2.1 kg, giving an estimated chick age of 1–8 weeks (Priddel et al. 2005). To deploy the tracking devices, adult birds were captured at their nests by hand or using a hand net from a distance of 1 m. Devices (see below) were attached to the three central rectrix feathers using TESA tape, and retrieved after 3–6 days. During manipulation, the

adults were weighed, measured, and the sex was determined by size and vocalizations. Measurements included bill length (from nasofrontal hinge to the tip) and wing length (from backbone to wing tip). The total manipulation time did not exceed 10 min.

Diet samples were collected opportunistically from masked boobies that regurgitated spontaneously in response to our presence in the colony or during tagging efforts. Regurgitates from four female and three male incubating masked boobies, and one female and three male chick-rearing birds were collected. Fish and squid were identified to family level using a Pacific fish guide (Fischer et al. 1995) and a site-specific fish guide (Randall and Cea 2010).

Whole blood samples were collected from the brachial vein of individual birds during device recovery, using a 25 G needle and non-coated capillary tubes. Stable isotope whole blood samples were collected from four female and six male incubating masked boobies, and four female and six male chick-rearing birds. The samples were placed on glass microscope slides and transported to the lab (Bugoni et al. 2008). Dry whole blood samples (0.2–0.6 mg) from masked boobies were scraped from the slides and placed in tin cups. The isotope signatures of all samples were analyzed at the Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany. The values were expressed in delta notation as the deviation from international standards (in air nitrogen for nitrogen and V-PDB for carbon) according to the equation $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where X is the ^{13}C or ^{15}N and R is the ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$, respectively. The accuracy of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements was better than 0.4 ‰ (one standard deviation (SD)) for laboratory standards. $\delta^{13}\text{C}$ values indicated the foraging regions and feeding preferences, because $\delta^{13}\text{C}$ values are enriched in inshore compared to offshore food webs (Cherel and Hobson 2007) and may reflect differences between plankton and benthic primary productions (Hobson et al. 1994). $\delta^{15}\text{N}$ values provided a useful proxy for determining the trophic position of the organism (Bearhop et al. 2004; Inger and Bearhop 2008), because levels increase by 3–5 ‰ with each successive trophic level (DeNiro and Epstein 1981; Hobson and Clark 1992).

To confirm the low productivity of the waters surrounding Rapa Nui, data on chlorophyll-a concentration (CHL) and sea surface temperature (SST) were downloaded from <http://coastwatch.pfeg.noaa.gov/erddap> from November 2016 with a resolution of 0.025° (approx. 2.5 km) from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor carried onboard NASA's Aqua satellite. Average environmental conditions were extracted using the raster data for CHL and SST within radii of 50 km (core) and 100 km (wider area), using the function “extract” in the package “raster” (Hijmans 2019). CHL and SST were used as they have been proven to be good proxies for seabird prey availability (Kappes et al. 2010; Paiva et al. 2010).

Data processing

GPS loggers (model CatLog-S, weight 26 g, dimensions $3.7 \times 2.2 \times 0.8$ cm) and time-depth recorders (TDRs; weight 6.5 g, model G5+, Cefas Technology, UK) were deployed to record foraging trip parameters. The GPS loggers recorded time, latitude, and longitude every 4 min, and the TDR devices were programmed to record pressure data every 1 s. Masked boobies weighed 1.6–2.6 kg, thus both devices together weighed 2% of the mass of the lightest adult measured and were below the acceptable threshold for seabirds (Vandenabeele et al. 2012). Tracking and diving data were processed in R 3.5.2 (R Core Team 2019). Foraging trip parameters of trip duration, maximum distance from the colony, and total distance were obtained using the function “tripsplit” in the package “marine IBA” provided by Lascelles et al. (2016). The maximum foraging trip distance was measured as the most distant point in a straight line from the colony. Trip duration was the total time between departure and return to the colony. Total distance traveled was the sum of the distance between consecutive fixes from departure to return to the colony. Foraging trips were considered to be trips exceeding a 1.5 km radius from the colony. This threshold was chosen based on observations of flying fish presence and masked boobies foraging in the vicinity of the colony. Regarding the TDR data, a zero offset correction for surface drift was applied, and to correct for noise and potential bathing dives, only dives deeper than 0.5 m were considered as true foraging dives. A total of 20 birds were studied but due to device failure, 18 birds contributed GPS tracks and 11 birds contributed TDR data.

Habitat use was quantified using the function “kernelUD” in the package “adehabitatHR” based on the GPS locations excluding those < 1.5 km from the colony (Calenge 2006). Kernel estimations of the utilization distribution (UD) in the core (50%) and wider (95%) areas were delimited using the reference bandwidth (0.06–0.11). The Bhattacharyya coefficient (BA) was used to calculate the overlap in areas used according to groups of sex and breeding stage. BA is a measure of similarity between two probability distributions, which reflects the overlap in kernel density estimates and can range from 0 (no overlap) to 1 (identical UD). This method has been proven to be useful for detecting spatial overlap in seabirds (Carneiro et al. 2016; Winner et al. 2018; Dehnhard et al. 2020).

Statistical analyses

The degree of sexual dimorphism among Sulids differs (Nelson 1978; van Oordt et al. 2018), and sexual size dimorphism of masked boobies at Rapa Nui was therefore calculated and compared. For bill and wing length, Welch's t tests were used. First, for testing for potential differences in size

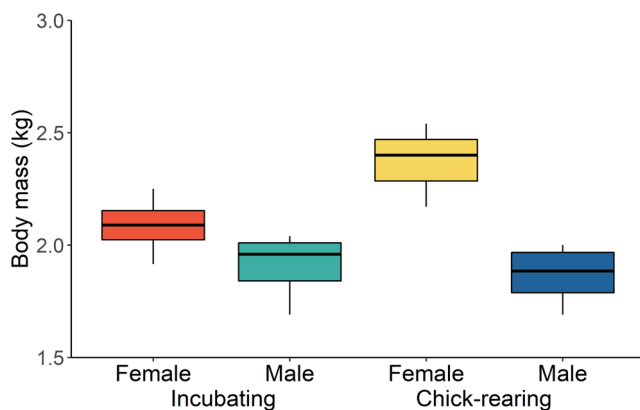


Fig. 1 Body masses of female and male-masked boobies (*Sula dactylatra*) during incubation and chick-rearing at Rapa Nui. Boxes indicate the inter quartile range (IQR), with the central line depicting the median and the whiskers extending to $1.5 \times \text{IQR}$

between incubating and chick-rearing individuals, and later, given that there were no significant differences among breeding stages (all $P > 0.05$), for testing differences between sexes pooling together incubating and chick-rearing individuals. Since body mass is a dynamic variable (Apanius et al. 2008), the effect of sex and breeding stage on body mass were tested using analysis of variance (ANOVA) with body mass as dependent variable, and sex, breeding stage, and the interaction as independent variables. Prior to the analyses, body mass variations with time of the day were tested, but time of the day was not significant ($P > 0.05$) and thus not included in further analyses.

Sexual segregation in foraging was evaluated using generalized linear mixed models fitted using the package “lme4” (Bates et al. 2015). Single models were performed

for each foraging trip parameter (maximum foraging range, trip duration, total distance traveled) and dive parameter (dive depth and dive duration) separately. Models were constructed with the foraging trip parameter or dive parameter as dependent variables; sex, breeding stage, and their interaction were used as fixed effects. Additional models were constructed including sex nested within either body mass, bill, or wing length to account for a possible effect of size following the procedure of Cansee et al. (2020). All models used gamma distribution and included bird ID as a random effect to account for pseudo-replication. An information theoretic approach was adopted to assess the factors influencing the foraging trip parameter and diving parameter. Models were ranked per foraging trip parameter and diving parameter using the Akaike information criterion corrected for small sample sizes (AICc) using the package “MuMIn” (Sutton et al. 2017; Barton 2020). If multiple models were within two AIC units, the model average was calculated. An analysis of similarity (ANOSIM) was run to test if similar areas were used by both sexes and breeding stages, based on the BA using the package “vegan” (Oksanen 2019). The number of prey items by sex and by breeding stage was compared using chi-square tests.

The isotopic values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) were used to calculate the isotopic niche width using the Bayesian framework implemented in the “SIBER” package (Jackson et al. 2011). Standard ellipse areas corrected for small sample sizes were estimated for each sex and breeding stage together with the pairwise overlap percentage value between ellipses (Nunes et al. 2018; Dehnhard et al. 2020). The niche-interaction metrics were calculated between sexes and breeding stages as the

Table 2 Foraging trip parameters, diving parameters, and stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of incubating and chick-rearing female and male-masked boobies (*Sula dactylatra*) at Rapa Nui. Data are presented as mean \pm standard deviation with ranges in parenthesis

	Incubating Female	Male	Chick-rearing Female	Male
Foraging trip parameters				
Sample size	4 (12 trips)	5 (18 trips)	3 (15 trips)	6 (41 trips)
Maximum distance (km)	72 ± 21 (41–104)	47 ± 30 (9–107)	36 ± 27 (5–98)	36 ± 18 (5–83)
Trip duration (h)	6.7 ± 2.5 (3.0–11.3)	4.6 ± 2.9 (1.0–9.9)	3.7 ± 2.6 (0.3–9.6)	3.1 ± 1.7 (0.3–6.4)
Total distance traveled (km)	181 ± 56 (100–276)	122 ± 81 (33–316)	94 ± 60 (14–222)	89 ± 45 (12–175)
Diving parameters				
Sample size	3 (152 dives)	2 (172 dives)	2 (242 dives)	4 (411 dives)
Maximum dive depth (m)	2.0 ± 1.0 (0.5–5.5)	1.7 ± 1.0 (0.5–4.9)	2.0 ± 1.2 (0.5–5.2)	1.6 ± 1.0 (0.5–5.1)
Dive duration (s)	3.2 ± 1.7 (1–10)	2.5 ± 1.2 (1–6)	3.4 ± 1.5 (1–8)	2.6 ± 1.5 (1–10)
Stable isotopes				
Sample size	4	6	4	6
$\delta^{13}\text{C}$ (‰)	-17.3 ± 0.2 (-17.6 – -17.1)	-17.7 ± 0.1 (-17.9 – -17.6)	-17.6 ± 0.3 (-17.9 – -17.3)	-17.5 ± 0.3 (-18.0 – -17.1)
$\delta^{15}\text{N}$ (‰)	16.0 ± 0.6 (15.5–16.9)	15.2 ± 0.4 (14.8–16.0)	16.2 ± 0.6 (15.3–16.7)	15.4 ± 0.7 (14.4–16.2)

Table 3 Generalized linear mixed models comparing foraging and diving trip parameters of masked boobies *Sula dactylatra* at Rapa Nui. Presenting the best five fitted models for each parameter. Shaded cells indicate those variables included in a given model. AICc, Akaike

information criterion; Δ AICc, difference between the model AICc and the lowest AICc for the model set; Weight, the AICc weight of each model. Lower AICc indicates best support models, and Δ AICc < 2 indicates good plausible models and are in indicated in bold

	Variable						Model			
	Sex	Stage	Sex × Stage	Body mass	Wing length	Bill length	df	AICc	Δ AICc	Weight
Maximum distance							4	782.4	0.00	0.596
							6	784.9	2.48	0.172
							4	785.3	2.84	0.144
							7	789.2	6.82	0.020
							7	789.4	6.94	0.019
Trip duration							4	374.4	0.00	0.688
							6	377.9	3.53	0.118
							4	378.1	3.71	0.109
							7	381.3	6.94	0.021
							7	381.3	6.94	0.021
Total distance travelled							4	939.6	0.00	0.624
							6	942.3	2.66	0.165
							4	942.9	3.25	0.123
							7	946.4	6.75	0.021
							7	946.5	6.91	0.020
Maximum dive depth							4	92.1	0.00	0.544
							4	93.1	0.98	0.333
							6	97.1	5.04	0.044
							6	98.3	6.21	0.025
							7	99.9	7.82	0.011
Dive duration							4	113.1	0.00	0.689
							4	115.8	2.74	0.175
							6	118.1	5.05	0.055
							6	120.0	6.91	0.022
							7	120.9	7.82	0.014

Euclidean distance between their positions in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ space (Turner et al. 2010).

Results

Bill lengths of females was on average 1.0% longer than that of males (females mean $10.7 \pm \text{SD } 1.1$ cm, males mean $10.6 \pm \text{SD } 2.1$ cm; Welch's t test, $t = 2.21$, $P = 0.04$). Wing lengths of females was not significantly different from those of males (females mean $46.7 \pm \text{SD } 1.1$ cm, males mean $45.9 \pm \text{SD } 1.3$ cm; Welch's t test, $t = 1.18$, $P = 0.25$). Both incubating and chick-rearing mean body mass differed significantly between females and males, particularly during chick-rearing (interaction sex and breeding stage ANOVA, $F(1,14) = 5.36$, $P = 0.03$). Females were on average 21% heavier than males during chick-rearing and 9% heavier during incubation (Fig. 1).

A total of 30 trips were recorded from incubating birds (12 trips from 4 females, 18 trips from 5 males) and 56 from chick-rearing birds (15 trips from 3 females, 41 trips from 6 males) (Fig. 2). Although females appeared to forage farther and longer than males, the best model comparing foraging parameters retained breeding stage, but not sex, the interaction between breeding stage and sex, or body mass or size of birds (Tables 2 and 3, Fig. 2). On average, birds from both sexes

traveled 59% farther and 66% longer during incubation than during chick-rearing (Table 2), but there were no significant differences in the areas used between females and males during the incubation and chick-rearing periods (50% UD BA 0.68–0.99, ANOSIM $R = 0.10$, $P = 0.15$; 95% UD BA 0.68–0.99 ANOSIM $R = 0.10$, $P = 0.14$) (Fig. 2). The average CHL was $0.02 \pm 0.01 \text{ mg m}^{-3}$ and average SST was $22.2 \pm 0.3 \text{ }^\circ\text{C}$ in both the core (50 km) and wider (100 km) areas (Fig. S1). For dive parameters from incubating (3 female, 2 male) and chick-rearing (2 female, 4 male) masked boobies, the best models retained sex and breeding stage (Table 3), but modeling indicated that neither of these factors had a significant effect on the diving depth or duration (Table 4). Body mass, bill, or wing length were not supported in the models for dive behavior (Table 3).

There was some degree of overlap in the isotopic niche areas ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) among incubating and chick-rearing females and males, but the overlap was lowest between incubating females and males (Table 5, Fig. 3). Furthermore, the Euclidian distance between centroid locations (taking both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values) only differed significantly between males and females during incubation (Table 5). The most frequent prey item in regurgitates from masked boobies was flying fish in both breeding stages and both sexes (Fig. S2). Anchovies only occurred in the diet of incubating birds and sardines only in chick-rearing birds.

Table 4 Parameter estimates of the best supported generalized linear mixed models comparing foraging and diving trip parameters of masked boobies *Sula dactylatra* at Rapa Nui. *R*, rearing; *M*, male. Significant predictor effects ($P < 0.05$) are indicated in italics

	Variable	Estimate	SE	<i>t</i>	<i>P</i>
Maximum distance	Intercept	0.02	0.003	6.00	< 0.01
	Breeding stage (R)	0.01	0.004	2.22	0.03
Trip duration	Intercept	0.21	0.034	6.02	< 0.01
	Breeding stage (R)	0.12	0.048	2.38	0.02
Total distance traveled	Intercept	0.01	0.001	6.26	< 0.01
	Breeding stage (R)	0.004	0.002	2.45	0.01
Maximum dive depth	Intercept	0.52	0.081	6.42	< 0.01
	Sex (M)	0.11	0.101	1.04	0.29
	Breeding stage (R)	0.02	0.101	0.21	0.83
Dive duration	Intercept	0.31	0.039	7.98	< 0.01
	Sex (M)	0.01	0.052	1.91	0.06

Female diet included jacks, while that of males included sardines, dolphinfish, and halfbeaks (Fig. S2). Nevertheless, the prey items were homogeneously distributed between the sexes (chi-square test, $\chi^2_8 = 4.67$, $P = 0.79$) and breeding stages (chi-square test, $\chi^2_8 = 6.00$, $P = 0.64$).

Discussion

In line with our predictions, breeding stage was an important determinant of the foraging behavior: incubating birds consistently traveled farther and for longer periods than chick-rearing individuals. We expected masked boobies to show different foraging strategies between sexes during chick-rearing due to increased competition for areas close to the colony. Instead, females and males showed no significant differences in foraging trip parameters or diving behavior at either breeding stage. Despite a strong overlap in foraging behavior among females and males, the overlap in isotopic niches was lowest between incubating males and females, but not between chick-rearing males and females as we expected.

Breeding phase and foraging trip parameters

The observation that masked boobies at Rapa Nui traveled farther and longer during the incubation period matched with the results of other studies of masked boobies (Oppel et al. 2015; Poli et al. 2017) and our expectations. In our study system, since we tracked incubating and chick-rearing birds simultaneously, we can rule out that changes in temporal prey availability created the differences in foraging parameters between incubating and chick-rearing birds, and thus, the differences between incubating and chick-rearing birds might be a reaction to constraints of chick provisioning. Notably, chlorophyll-*a* concentrations and sea surface temperatures

were similar in the core and wider areas at Rapa Nui, indicating that incubating and chick-rearing birds experienced similar environmental conditions. Optimal foraging theory suggests that predators make foraging decisions that optimize energy intake with minimal energy investment (Charnov 1976; Pyke et al. 1977; Louzao et al. 2014), hence the energy investment of traveling farther in incubating birds must have some advantages. Although our interpretations are limited by a lack of information on food abundance, the areas closer to the colony must be subject to greater depletion of food resources by individuals from the colony, creating an Ashmole's halo (Birt et al. 1987; Oppel et al. 2015), while this effect is reduced farther away from the colony. Incubating birds which are more flexible by not having to constantly feed their chick may thus forage farther (Ito et al. 2010; Shoji et al. 2015). More distant areas from the colony, outside of Ashmole's halo may offer less competition for food resources, but only be accessible to incubating individuals or non-breeders.

Sex-specific foraging trip parameters

Against our expectations, we found no differences in the foraging behavior between incubating or chick-rearing females and males. Body mass and body size did not affect foraging behavior either. This is surprising since differences in body mass, found here between both sexes, have previously been associated with differences in foraging behavior in Sulids (Lewis et al. 2005; Weimerskirch et al. 2006; Zavalaga et al. 2007; Sommerfeld et al. 2013). Thus, the larger size of females did not enable local dominance as suggested to occur in Sulids and other seabirds (Gilardi 1992; González-Solís et al. 2000; Stahl and Sagar 2000), and the lighter weight of males cannot account for longer-ranging foraging trips (Shaffer et al. 2001). Sexual size dimorphism alone therefore

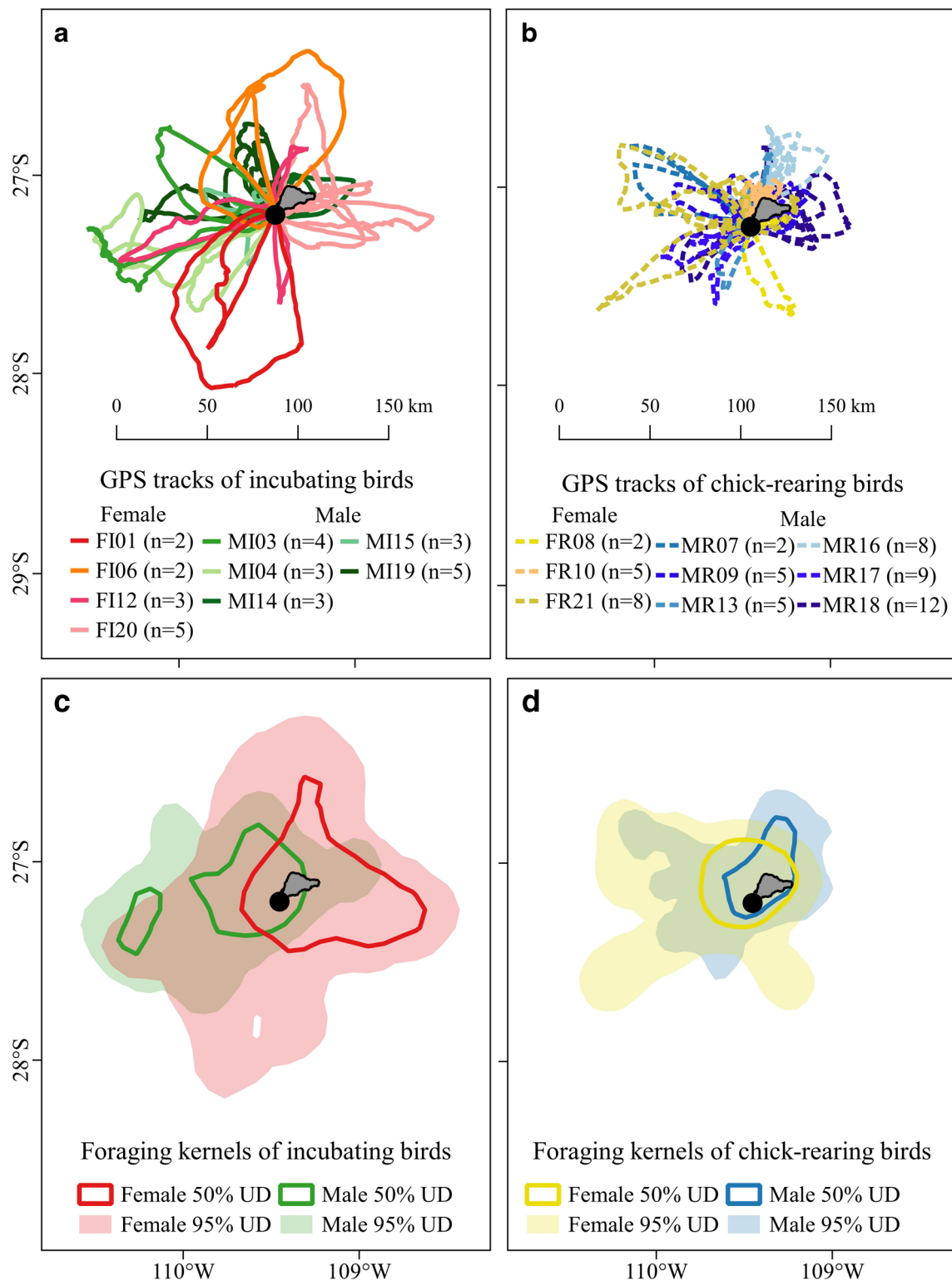


Fig. 2 Masked boobies (*Sula dactylatra*) tracking data for female and male incubating (**a**) and chick-rearing (**b**) birds; and kernel utilization distributions (UD) for female and male incubating (**c**) and chick-rearing (**d**) birds. The black dot shows the location of the masked booby colony

cannot explain the results on sexual segregation in foraging on our study and those of previous studies.

The food resources around Rapa Nui may be scarce (Randall and Cea 2010; Friedlander et al. 2013), but prey may be

distributed in a way that sexual segregation in area use or depth does not reduce competition for food among the sexes. Flying fish, the most frequent prey item of masked boobies in this study, is distributed ephemerally, thus showing high spatio-temporal

Table 5 Stable ellipse areas (50% and 95%) for small sample sizes of female (F) and male (M) incubating (I) and chick-rearing (R) masked boobies at Rapa Nui. Raw overlap is the overlap among groups calculated as percent. Niche area overlap reflects the shared niche space calculated as [area of overlapping region]/([area of ellipse 1] + [area of ellipse 2] - [area of the overlapping region]). The Euclidian distance refers to the distance between centroids between groups. *P* values were generated based on a residual permutation procedure

	Incubating F-M	Chick-rearing F-M	Female I-R	Male I-R
50%				
Area 1	0.59	0.59	0.59	0.25
Area 2	0.25	0.89	0.59	0.89
Raw overlap (%)	< 0.01	0.12	0.09	0.18
Niche area overlap	< 0.01	0.09	0.08	0.19
95%				
Area 1	2.56	2.55	2.56	1.08
Area 2	1.08	3.86	2.55	3.86
Raw overlap (%)	0.67	1.80	1.42	0.99
Niche area overlap	0.23	0.39	0.39	0.25
Euclidian distance				
Mean distance to centroid	0.17	0.12	0.01	0.30
<i>P</i> value	< 0.01	0.07	0.07	0.23

variation in its occurrence (Oxenford et al. 1995). In addition, boobies may catch flying fish and squid in the surface waters or above the water (Au and Pitman 1986; Davenport 1994; Weimerskirch and Le Corre 2005). Consequently, avoidance of competition for catching this kind of prey may be almost impossible. This agrees with a study by Mancini et al. (2013), which found that in general, tropical seabirds showed less isotopic differences among sexes compared to polar and temperate species, likely since foraging segregation is limited by the low food abundance and patchy distribution of prey at tropical regions (Longhurst and Pauly 1987; Ballance and Pitman 1999; Weimerskirch 2007). However, other tropical seabird species did show sexual segregation in foraging behavior (see Table 1 and Mancini et al. 2013). Possibly, the inconsistency in finding sexual segregation in foraging in Sulids is an effect of the distribution of their prey resources according to the geography (Garthe et al. 2007; Tait et al. 2014; Castillo-Guerrero et al. 2016), and time of the study (Hamer et al. 2007; Harding et al. 2007; Garthe et al. 2011).

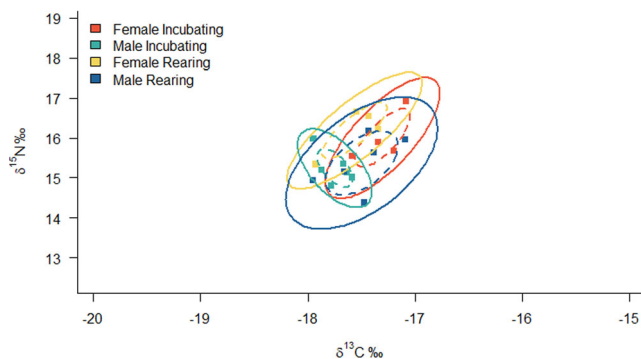


Fig. 3 Sex-specific isotopic niches ($\delta^{13}\text{C}$ & $\delta^{15}\text{N}$) in incubating and chick-rearing masked boobies (*Sula dactylatra*) at Rapa Nui. Squares represent the individual measurements in whole blood. Standard ellipses of 40% are depicted as dotted and 95% as complete ellipses

Boobies primarily prey on epipelagic fish (Nelson 1978), and epipelagic fish communities are more diverse and heterogeneously distributed in coastal than in oceanic habitats (Hunt Jr. 1990; Angel 1993; Reese et al. 2011; Lewallen et al. 2017). In addition, prey species vary in their nutritional content (water-lipid-protein ratio) (Machovsky-Capuska et al. 2016; Miller et al. 2018; Machovsky-Capuska and Raubenheimer 2020). Female and male seabirds may react to the nutritional content of the available prey by foraging differently to cover their sex-specific nutritional requirements (Lewis et al. 2002; Machovsky-Capuska et al. 2016). The more complex prey community, heterogeneous distribution, and different nutritional content of prey items in coastal habitats may thus promote foraging segregation, whereas oceanic areas, which have a less diverse and more ephemerally distributed prey community, may prevent this (Ashmole 1971). Indeed, booby species such as blue-footed boobies and brown boobies which have a more diverse diet (Mellink et al. 2001; Ancona et al. 2012; Castillo-Guerrero et al. 2016; González-Medina et al. 2018; Miller et al. 2018) were more likely to exhibit sexual segregation in foraging (see Table 1). This contrasts to pelagic species such as red-footed boobies and masked boobies, which rely mostly on flying fish and squid (Schreiber and Hensley 1976; Young et al. 2010a). Therefore, in less diverse homogeneous environments such as Rapa Nui, sexual segregation in foraging would be expected to be weak. A comparative study focusing on prey communities and their nutritional content would be needed to further explore if these are the main causes for sexual segregation in foraging between booby species and colonies.

Sex-specific isotopic niches

Sexual segregation in isotopic niches of incubating birds contrasts with previous studies which found no sex-related

differences in isotopic signatures in masked boobies (Young et al. 2010a; Mancini et al. 2013). The aforementioned studies, however, did not separate between the breeding stages of the individuals (see Table 1).

It is important to draw attention to the fact that stable isotopes in whole blood reflect the diet assimilated over a period of 3–4 weeks before blood sampling (Vander Zanden et al. 2015). Our stable isotope results therefore integrate a longer period of time, which does not fully match our tracking data. There may be a residual influence of the pre-laying period for incubating birds and of the incubation period for chick-rearing birds. Non-breeding boobies may move over larger distances (Kohno et al. 2019), and during the pre-laying period, males perform shorter foraging trips to expend more time defending a territory and to avoid extra-pair paternity (Osorio-Beristain and Drummond 2001), whereas females are not fixed to the nest yet. Therefore, females and males may exploit different food webs and isoscapes previous to the incubating period. Nevertheless, it is likely that masked boobies from Rapa Nui during the pre-laying period stayed within the same oligotrophic food web. Firstly, the high degree of isolation of Rapa Nui (Flores et al. 2014) makes it unlikely for boobies from Rapa Nui to travel very far away, even during the pre-laying period. Secondly, the Gyre covers an area of 37 million square kilometers (Reintjes et al. 2019), so even when located on one of the neighboring islands, the food web will be similarly oligotrophic. Finally, the pre-laying period lasts about 30 days in Sulids (Osorio-Beristain and Drummond 1998), during which birds occupying nest sites are therefore restrained in their movements. Hence, the studied birds were very likely, already foraging in the homogeneous, oligotrophic waters of Rapa Nui during the pre-laying period, and thus in an area where segregation in foraging behavior between females and males should not occur.

A possible explanation for the stable isotopic difference between males and females during incubation might be that incubating and/or pre-laying females were consuming different prey while using similar areas as males. This would agree with results on monomorphic Australasian gannets (*Morus serrator*) (Ismar et al. 2017) and dimorphic Magellanic penguins (*Spheniscus magellanicus*) (Raya Rey et al. 2012), species in which males and females segregate in diet but not in their foraging areas. In masked boobies, both sexes require energy to exhibit dynamic traits in the feet color and facial mask during the pre-laying period which signal individual quality (Rull et al. 2016), and for females, the egg formation is a highly energy-demanding period (Nager et al. 2001). Females may thus consume different prey or different proportions of the same prey to meet the nutritional requirements associated with egg production and laying (Lewis et al. 2002; Xavier and Croxall 2006; García-Tarrasón et al. 2015; Connan et al. 2019).

Female-masked boobies at Rapa Nui laid on average two eggs, which may represent up to 6% of the incubating female's body mass, and incubating females had lower body mass than

chick-rearing females. The wing lengths of female and male-masked boobies differed by ~2% at Clipperton (Weimerskirch et al. 2009a), Phillip Island (Sommerfeld et al. 2013), and in the current study. However, in terms of body mass, chick-rearing females were 14% heavier than males at Clipperton, 16% heavier at Phillip Island, and 21% heavier at Rapa Nui. In contrast to chick-rearing birds, the difference in body mass on incubating birds was smaller between males and females, with females being only 9% heavier than males (this study). In sea-birds, high-quality parents may breed earlier in the season (Arnold et al. 2004). Thus, differences in body mass can be an effect of including high-quality females which started breeding earlier in the season. However, in Rapa Nui, there is not a clear temporality in breeding (Marin and Caceres 2010) and thus, we would not expect that there are early or late breeding individuals. However, to formally rule this out, one would need to monitor if the heavier chick-rearing females (higher quality) are able to rear their chick, and the lighter incubating females (lower quality) fail later in incubation or hatching (Arnold et al. 2004). Unfortunately, due to the complicated logistics to reach this island, we did not monitor breeding success. Alternatively, the body mass differences between incubating and chick-rearing females could suggest that chick-rearing females may have recovered from the investment of egg laying. In Sulids, the energetic demands of breeding may particularly affect female body condition (Velando and Alonso-Alvarez 2003; González-Medina et al. 2017). Thus, foraging to meet or recover from the nutritional requirements associated with egg production and laying seems plausible. Our results coincide with patterns of body mass variations of breeding female blue-footed boobies (Lerma 2014) but contrast with the results in Nazca boobies and brown boobies. Nazca boobies showed a decline in parental body mass during the breeding season (Apanius et al. 2008), while body condition in brown boobies was not affected by breeding stage (Dehnhard and Hennicke, 2013). These inconsistencies among species may once more reflect different food availability at different colonies.

Finally, we must consider that the differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values rely on the premise that these measurements are primarily determined by the foraging behavior and diet of the consumers. Although this is largely true (Hobson 1993; Cherel et al. 2008; Parnell et al. 2013), isotope levels may also be affected by physiological and biochemical factors, which are rarely taken into account and tested. Our results on body mass suggest that incubating females were in poorer body condition than males, and rather than indicating sex-related differences in foraging ecology, the different isotopic signatures between the sexes in this study may therefore reflect differences in the physiological states of individuals. For sea-bird species with reversed sexual size dimorphism, physiological condition and energy requirements of the larger sex were also suspected to cause differences in stable isotope levels (Mancini et al. 2013).

Conclusion

Birds of both sexes foraged farther away and for longer periods during incubation compared to chick-rearing as an effect of breeding demands. Although Rapa Nui is an oligotrophic area with potentially low food resources, which could promote foraging segregation, there were no obvious foraging differences between the sexes. We suggest that this occurred as an effect of food resources at Rapa Nui being distributed in a way that sexual segregation in foraging will not be useful to avoid inter-sexual competition for resources. The observed differences in stable isotopes are somewhat inconclusive. Larger sample sizes, an isotope study of the underlying food web and possibly a different study design, including tracking during the pre-laying period or investigating stable isotopes in plasma (which reflects the diet of few days; Vander Zanden et al. 2015), would be needed to understand the reasons for the sex-specific isotopic niches ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) within this population. Overall, sexual size dimorphism in boobies does not seem to be the primary reason for sexual segregation in foraging. Instead, the pattern of sexual segregation in foraging is probably given by local prey distribution and the nutritional needs that each sex has to meet. In this context, when the prey community is more diverse and heterogeneously distributed, sexual segregation in foraging would be useful to meet sex-specific nutritional requirements. However, in environments like around Rapa Nui, where prey resources distribute ephemerally, sexual segregation in foraging can be expected to be weak.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00265-020-02921-1>.

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Data accessibility Tracking data is stored in www.movebank.org

Code availability R scripts to undertake the analyses of stable isotope analyses along with the dataset are attached as supplementary material.

Author contributions ML, GL, and SG experimental design; ML collection and analysis of the data; CCV and ML laboratory work; ML and ND writing of the manuscript; all authors commented and corrected the manuscript.

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Compliance with ethical standards

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

Ethical approval This study complies with the international, national, and institutional guidelines following ethical standards for the care and use of wild animals, and was supervised and approved by the Servicio Agrícola y Ganadero under the permits No. 310/2016 & 388/2017 Oficina Sectorial Rapa Nui, and No. 5343/2016 & 5024/2017 sector Santiago; the Comisión Nacional Forestal (CONAF-Rapa Nui); and the Ministerio de Agricultura certificate 04/101/18/0001.

Informed consent Consent to participate is not applicable.

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