

Resource partitioning by species but not sex in sympatric boobies in the central Pacific Ocean

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ABSTRACT: Sympatric species with similar ecological requirements and differences in body size would be expected to partition resources to facilitate coexistence. For sexually dimorphic species, we may expect resource partitioning by gender as well as by species identity. However, it is difficult to document species and sexual resource partitioning in marine ecosystems, given the intractability of these systems and the vagility of many marine animals. Here, we examined differences in the foraging behavior and prey selection of 2 congeneric and coexisting seabird species—masked boobies *Sula dactylatra* and red-footed boobies *Sula sula*—on Palmyra Atoll in the equatorial Pacific Ocean. These seabirds exhibit substantial size dimorphism between species and also have reverse sexual dimorphism within species. Pronounced interspecific differences in foraging patterns were observed with high-resolution GPS tracking devices, where smaller red-footed boobies conducted longer foraging trips (in both time and distance). Red-footed boobies also had more frequent landings on the sea surface, slower mean and maximum travel speeds, and more westerly trip azimuths. Stable isotope and diet analyses produced data that complemented returns from electronic tagging. Stable isotope ratios of carbon indicated that masked boobies foraged on prey with a less pelagic $\delta^{13}\text{C}$ signature compared to red-footed boobies. In contrast, no gender differences were identified in any foraging parameters. The mechanisms for maintenance of these pronounced differences in niche partitioning across species were not explicitly examined, yet the data suggest physiological variation across species may be a more plausible mechanism than competitive interactions.

KEY WORDS: Resource partitioning · Reverse sexual dimorphism · Foraging ecology · GPS tracking · *Sula sula* · *S. dactylatra*

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INTRODUCTION

Resource partitioning, whether by habitat or diet, is one of the principle factors that permits multiple species to cohabit the same environment (Pianka 1981, Martin 1996, McKane et al. 2002). Partitioning of resources also occurs between sexes of the same species (Selander 1966, Andersson & Norberg 1981, Belk et al. 1988). In many cases, body size plays a role in facilitating the partitioning that occurs within a species, as well as across species. In order to meaningfully exam-

ine patterns of intra- and interspecific resource partitioning, it is necessary to collect high-resolution information on the patterns of space and resource use of subject taxa.

Previous studies of space and resource use in seabirds indicate that sympatric species partition resources temporally (Croxall & Prince 1980, Harrison 1990), spatially (Weimerskirch et al. 1986, Anderson & Ricklefs 1987, Mori & Boyd 2004), and by type of prey (González-Solís et al. 2000a, Catry et al. 2009). In tropical oceanic environments dominated by oligotrophic conditions, larger

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species, which have higher flight costs but greater competitive ability, often dominate the areas where productivity and prey are somewhat elevated (e.g. upwelling zones) (Ballance et al. 1997, Jaquemet et al. 2005). Sexually dimorphic seabird species tend also to significantly partition resources between sexes, with the larger sex generally foraging closer to the colony and taking larger prey (Selander 1966, Gilardi 1992, González-Solís et al. 2000a, Spear et al. 2007). The origin of these inter- and intraspecific patterns of partitioning may occur as a direct result of differentiation evolved to maximize forage yields, or as an indirect outcome of the influence of morphologies selected upon for other reasons that affect flight performance, habitat selection, and diet (Ballance et al. 1997, Shaffer et al. 2001, Lewis et al. 2002).

Tropical seabirds face unique foraging challenges because productivity in tropical marine ecosystems typically is low, prey are patchily distributed, and thermal stresses are high (Ashmole 1971, Longhurst & Pauly 1987). These factors presumably expose tropical seabirds to intense selection for improving foraging efficiency (Ainley 1977, Au & Pitman 1986, Weimerskirch et al. 2008) and may thus exert strong selection pressure for the maintenance of body size differences in tropical seabird species (Lewis et al. 2002, Weimerskirch et al. 2005, 2006). These tropical conditions provide an appropriate setting in which to investigate patterns of niche differentiation in marine ecosystems.

Two of the most common species of tropical boobies (Sulidae) in the central Pacific are the masked *Sula dactylatra* and the red-footed booby *Sula sula*. Ranges of these species overlap, and they often cohabitate the same breeding colonies. These 2 booby species differ significantly in size where masked boobies weigh nearly twice that of red-footed boobies (present study). Both species also exhibit reversed sexual dimorphism, where masked booby (MB) females are from 8 to 27% heavier than males, and red-footed booby (RF) females are approximately 15% heavier than males (Fairbairn & Shine 1993, Lormée et al. 2005). Both species have been shown to exhibit spatial resource partitioning by sex, with females foraging further and for longer periods away from the colony (Weimerskirch et al. 2005, 2006, 2009a,b). The birds also likely have different flight costs (based on wing loading calculations and measured costs of flight), with RFs having substantially lower flight costs than MBs (Ballance et al. 1997, Brewer & Hertel 2007). Colony surveys show that both species have similar nest-attendance patterns (Anderson & Ricklefs 1992, Lormée et al. 2005), and at-sea surveys suggest similarity in foraging behavior and co-occurrence in mixed species flocks (Ballance et al. 1997, Spear et al. 2007). No studies have compared foraging behavior of these bird species in the same location.

The present study used GPS tracking tag technology, diet analyses, and stable isotopes to examine the hypotheses that the 2 boobies in this low-productivity system would demonstrate clear niche partitioning both between species and by sex within species. GPS tags were affixed to breeding seabirds and provided high-resolution location fixes of foraging behavior. Analyzing stable isotope ratios of C and N can provide information on space use and trophic position (respectively), a method which has been used extensively to determine seabird movements and dietary patterns (Inger & Bearhop 2008, Phillips et al. 2009). Values of $\delta^{13}\text{C}$ tend to be more depleted in pelagic waters relative to coastal reef communities, allowing us to track how offshore seabirds are moving to obtain resources, and $\delta^{15}\text{N}$ undergoes trophic enrichment, providing a useful proxy for determining an organism's trophic position (Michener & Kaufman 2007). At-sea locations were also compared to remotely sensed oceanographic data to investigate the relationships between foraging behavior and the environment.

This project represented a first effort to collect data on niche differentiation in masked and red-footed boobies resident at the same colony. The current analysis provides a valuable point of reference for which to compare the foraging patterns of masked and red footed boobies in the Pacific, to populations elsewhere in the tropics.

MATERIALS AND METHODS

This research was conducted on Palmyra Atoll, (5° 52' N, 162° 04' W) in the central Pacific Ocean over a 2 yr period between the periods from 25 May to 15 October 2007 and 15 September to 27 November 2008. Palmyra consists of a ring of coral-derived islets that encircle a central saltwater lagoon system. The islets of Palmyra are generally forested, with occasional grassland areas and bare rock patches that serve as nesting area for colonies of ground nesting *Sula dactylatra* (MBs). *Sula sula* (RFs) nest almost exclusively in trees and shrubs. Both species nest year round, with no apparent synchrony across species in nesting cycles. Nest counts range from 1000 to 2500 pairs for RFs and only 10 to 50 pairs for MBs (Fefer 1987, E. Flint unpubl. data, H. S. Young unpubl. data).

To study their movement patterns, boobies were captured from a variety of locations around the atoll at either dawn or dusk while they were on their nests. All birds in the present study were either incubating eggs or brooding young chicks. On first capture, birds were fitted with a 30 g GPS data logger (Technosmart, GiPSy-2) engineered to record GPS positions (± 10 m accuracy) approximately every 10 s, taped to 3 central

tail feathers. Loggers were left on birds for 24 to 48 h. RFs were tracked in both 2007 and 2008, while MBs were only tracked in 2008. In total, we had 54 tracks from RFs (22 male, 28 female, 4 unsexed; 20 chick nests and 34 egg nests) and 34 tracks from MBs (18 male and 16 female; 25 chick nests and 9 egg nests). Upon second capture, we removed loggers, applied steel identification bands, measured mass with spring balance (± 5 g), and measured culmen, tarsus, and head-bill lengths with calipers (± 1 mm). We also collected blood from a brachial vessel and from 2 to 4 feather samples (underwing covert) from each bird for genetic (blood) and stable isotope analyses (blood and feather). Food samples spontaneously regurgitated during tagging efforts were collected. Feather samples were also obtained from chicks in nearby RF nests (to avoid additional stress to nests of tagged birds). Nest state (with egg[s] or chick) was recorded for every bird studied. Boobies were sexed by vocalization, coloration of fleshy areas near bills, and by body size (determined from measurements); sex identification of all RFs was also confirmed via molecular analysis (not necessary for MBs given more substantial variation in field identification features).

All locations from GPS data sets were filtered using a backward–forward iterative speed filter (McConnell et al. 1992) based on a maximum travel speed of 90 km h^{-1} . Given that tags were based on GPS technology, $<0.5\%$ of location data were removed. Occasionally, data loggers lost satellite acquisition for periods exceeding 10 min, or batteries lost charge before the bird returned. In such cases ($n = 31$), tracks were examined individually; only complete portions of tracks were utilized for analysis, and data on area restricted search (ARS) behavior and total distance travelled were not taken from incomplete tracks.

Boobies plunge dive for prey to depths of up to 2.4 m for an average of 1.8 s (Weimerskirch et al. 2005). Therefore, it was possible to infer foraging activity and/or periods when birds landed on the sea surface by identifying all locations when travel speeds were $<5 \text{ km h}^{-1}$ between successive sampling intervals (locations within 1 km of land were excluded in this analysis) (Weimerskirch et al. 2008). Frequency of landings was determined by the number of landings per hour over an entire trip. Mean and maximum flight speeds were calculated based on travel speeds $>5 \text{ km h}^{-1}$. Trip length was calculated both as distance travelled from nest (km) and as duration of travel (h) between departure and return to nest. ARS behavior (size of ARS and number per trip) was determined by the fractal landscape method (Tremblay et al. 2007). The outbound and inbound azimuths were determined by establishing the angular difference between the nest and the location of the bird when it was 4 km from

the atoll. The maximum azimuth was the angular difference between the nest and the location of the bird at its maximum range from the colony. All analyses were conducted using custom algorithms created in MatLab 2008b (The Mathworks).

Daily ocean surface vector winds from the Seawinds sensor carried aboard NASA's Quikscat spacecraft (e.g. Naderi et al. 1991, Perry 2001) were extracted for an area chosen to encompass the spatial range of the boobies. The wind directions were then averaged for the region and compared with the outbound azimuth provided by the GPS tags. Comparisons were performed using the ANOVA function of the Matlab Statistics toolbox. Average daily chlorophyll *a* concentrations for each flight were obtained from the moderate imaging spectrometer (MODIS) carried aboard NASA's Aqua spacecraft (O'Reilly et al. 2000). Average daily sea-surface temperatures (SST) were derived from the blended microwave/infrared product produced by Remote Sensing Systems Inc. of Santa Rosa, California (Gentemann et al. 2009).

Laboratory analysis. For isotopic analysis, feather samples were rinsed in deionized water, dried at 60°C , and finely chopped. Blood samples were stored frozen, freeze dried, and powdered. Samples were run at the Stanford Stable Isotope Biogeochemistry Laboratory (SIBL; Thermo Finnegan Delta-Plus XP IRMS), which has an analytical error of $\pm 0.2\%$ for both C and N.

The sex of RF individuals was confirmed for a subset of individuals ($n = 24$) from blood using 2 different molecular methods, each targeting homologous fragments on the Z and W chromosome. One polymerase chain reaction (PCR) used the primers 2550F and 2718R (Fridolfsson & Ellegren 1999), and resulting fragments were run out on 2% agarose gels. A separate PCR made use of primers M2 (Bantock et al. 2008) and P8 (Griffiths et al. 1998). The latter primer was fluorescently labeled, enabling fragment analysis on an automated ABI 3130xl sequencer (Applied Biosystems). The 2 methods yielded identical results and matched with field identification of sex.

For analysis of regurgitated samples, we measured the length of each food item that was sufficiently intact (fish: fork length; squid: mantle length). Since fish were in various states of digestion, we used published length-to-weight conversion factors to estimate their mass (Le Corre et al. 2003). Muscle tissue from the most intact flying fish (Exocetidae, $n = 25$) and squid (Ommastrephidae, $n = 12$) individuals was freeze-dried for isotopic analysis, but was not lipid extracted (C:N ratio was always <3.3 , indicating low lipid levels). Stomach contents were obtained from 34 RFs and 14 MBs (each bird was only sampled once), yielding a total of 91 individual prey items in sufficiently good condition for analysis.

Statistical analyses. We first tested for differences in body size across species and sex within species. Morphological data collected from birds could not be normalized and was thus analyzed using Wilcoxon tests, with sequential Bonferroni corrections. To integrate multiple metrics of body size, the 3 linear measurements (culmen, head-bill, and tarsus) and body mass were analyzed via principal components analysis.

To analyze foraging data, we used mixed-effects ANOVAs to determine if foraging patterns (i.e. distance travelled, trip duration, maximum distance) differed between species and sex (independent fixed factors), with bird number (i.e. individual bird) as a random factor. To analyze effects of species and sex on $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, prey size, and prey composition by diet sample we used fixed-effect ANOVAs (as there was only 1 sample per bird). Prior to each of these analyses, data were analyzed for normality using the Shapiro-Wilk test, and non-normal data were Box-Cox transformed. Within species, we also tested major foraging parameters for differences by nest status and by year (for RFs only). Since no significant differences were found for comparisons involving nest status or year tracked, we did not include these covariates in our final analyses.

All graphs/tables depict untransformed data. All mean (± 1 SD) values are shown untransformed. Statistical analyses on body size, foraging parameters, isotopic analysis, and diet were performed in JMP 7 (SAS Institute).

RESULTS

Body size

There were significant body size differences both between species and between sexes within species (Table 1). Average weights of *Sula dactylatra* were 2 times greater than those of *S. sula* (mean of 1779 and 893 g, respectively), and there was no overlap in body mass between species. In comparison, the differences

in body mass between the sexes (within a species) were smaller, but significant (females were 12 % larger than males for MB and 13 % for RF), with some overlap between sexes.

Results from principal components analysis on body size showed that the first principal component (PC1) explained 95 % of the variance; thus, we used these PC1 values as an index of overall bird size. The differences observed in PC1 between species and sex were similar to those observed using a simple mass metric, although they show less interspecific variation (48 % difference between species) and greater gender variation within a species (29 % difference between sexes for MB, and 15 %, for RF).

Foraging distance and timing

GPS tracking revealed that RFs travelled more than twice as far as MBs per foraging trip, both in terms of total distance travelled and maximum range from the colony (Fig. 1A, Table 2). Mean trip duration was approximately 3 times longer for RFs than for MBs (means of 8.67 and 2.84 h, respectively). The frequency of trip duration, maximum range, and distance flown for MBs were normally distributed compared to values for RFs (Fig. 2). In contrast to MBs, RFs appeared to have 2 distinct peaks in trip length and duration, with a break between long trips and shorter trips at approximately 35 km in distance and 5 h in duration (Fig. 1B,C).

Trip timing also varied by species: MBs left later in the morning (mean of 10:40 local departure for MBs and 08:28 for RFs) and returned earlier in the evening (mean of 13:41 return for MBs and 16:41 for RFs; Table 2, Fig. 2C). For RFs only, trip distance and maximum range were positively linearly related with return time to the colony (trip distance $R^2 = 0.59$, $p < 0.0001$, max range $R^2 = 0.67$, $p < 0.0001$). Starting time for RFs was also correlated with average travel speed ($R^2 = 0.29$, $p = 0.0006$) and maximum travel speed ($R^2 = 0.23$, $p = 0.0001$).

Table 1. *Sula dactylatra* and *S. sula*. Morphological comparisons of masked and red-footed boobies by sex. Statistics are results of Wilcoxon tests of sex within species. PC1 values are the first principal component scores of the analysis on all other size metrics. Significant results are indicated in **bold**. Values are presented as means \pm SD

Size metric	n	Masked booby				Red-footed booby			
		Female	Male	p	F	Female	Male	p	F
Mass (g)	49	1907 \pm 156	1678 \pm 128	0.0004	3.6	954 \pm 41	839 \pm 44	0.001	4.9
Culmen (mm)	58	10.3 \pm 0.2	10.2 \pm 0.5	0.25	1.2	8.4 \pm 0.2	8.2 \pm 0.4	1.6	0.1
Tarsus (mm)	49	5.9 \pm 0.2	5.8 \pm 0.2	0.17	1.4	3.6 \pm 0.1	3.7 \pm 0.2	0.4	0.8
Head-bill (mm)	49	16.6 \pm 0.6	15.8 \pm 0.6	0.0005	3.5	13.4 \pm 0.4	12.9 \pm 0.4	0.0007	3.4
PC1				0.006	2.8			0.0001	3.9

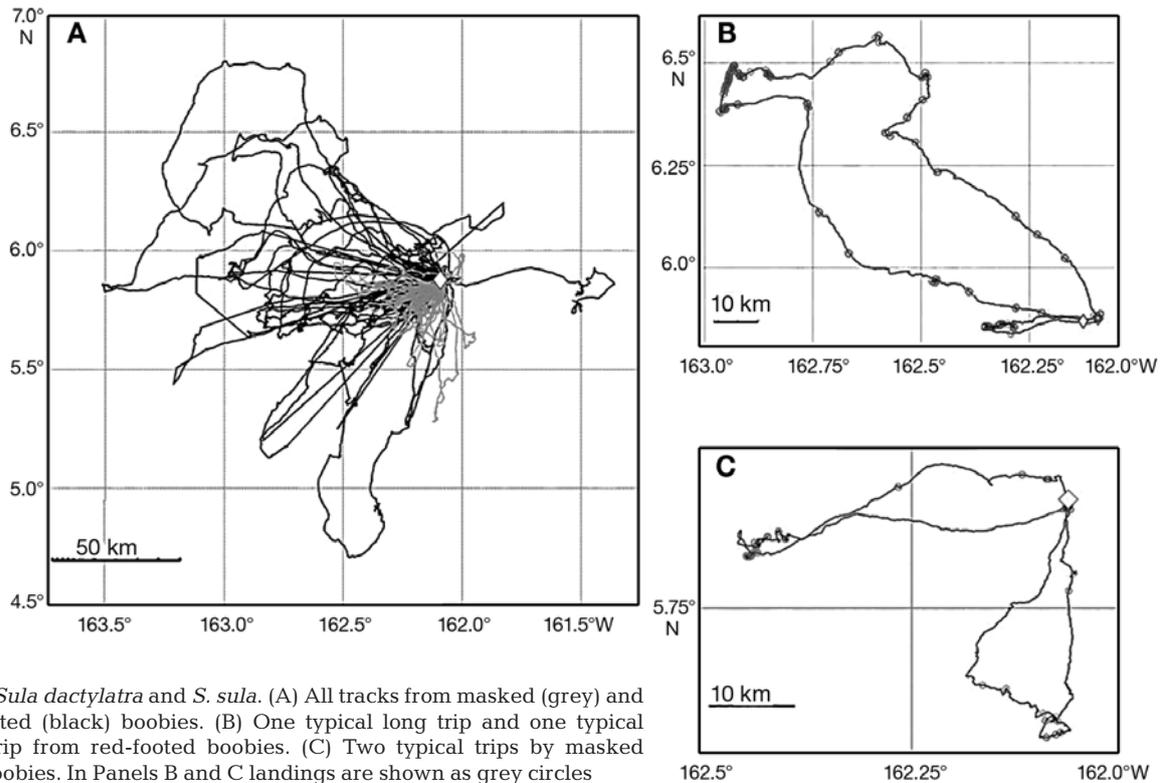


Fig. 1. *Sula dactylatra* and *S. sula*. (A) All tracks from masked (grey) and red-footed (black) boobies. (B) One typical long trip and one typical short trip from red-footed boobies. (C) Two typical trips by masked boobies. In Panels B and C landings are shown as grey circles

Table 2. *Sula dactylatra* and *S. sula*. Foraging parameters of masked (MB) and red-footed (RF) boobies. Values are presented as means \pm SD. Mixed-effects ANOVA models are used to compare whether attributes differ by species and sex (within species), with bird identity as a random factor. Significant results are indicated in **bold**. ARS: area restricted search zone

	n	Mean \pm SD		Species effect		Sex effect	
		MB	RF	p	F	p	F
Trip duration (h)	61	2.84 \pm 1.52	8.67 \pm 5.30	0.0001	33	0.52	0.7
Total distance travelled (km)	57	89.41 \pm 38.39	195.59 \pm 125.44	0.003	10	0.85	0.2
Maximum foraging range (km)	61	29.35 \pm 11.50	67.52 \pm 44.17	0.0001	19	0.96	0.03
Azimuth at max. range	60	229.99 \pm 8.42	241.17 \pm 11.01	0.004	9.1	0.59	0.7
Outbound azimuth	80	213.56 \pm 41.98	241.61 \pm 70.12	0.003	9.6	0.22	1.5
Inbound azimuth	55	222.63 \pm 48.99	214.39 \pm 99.59	0.67	0.2	0.66	0.4
Travel rate (km h ⁻¹)	82	43.17 \pm 3.68	36.37 \pm 7.58	0.05	3.9	0.87	0.1
Max travel rate (km h ⁻¹)	88	84.12 \pm 3.82	73.82 \pm 13.57	0.001	18.1	0.94	0.1
Time to first landing (min)	74	23.36 \pm 14.73	48.40 \pm 93.86	0.02	6.2	0.76	0.3
Time to last landing (min)	54	11.71 \pm 14.72	94.42 \pm 140.06	0.001	23.7	0.84	0.2
Mean start time (time of day)	54	10:40 \pm 2:09	8:28 \pm 2:79	0.001	18.7	0.18	0.8
Mean end time (time of day)	72	13:41 \pm 2:46	16:41 \pm 4:84	0.007	8.1	0.59	0.6
Landings h ⁻¹	71	15.41 \pm 10.31	28.12 \pm 34.84	0.04	4.5	0.02	4.0
Number of ARS (trip ⁻¹)	30	4.06 \pm 2.38	5.75 \pm 2.67	0.56	2.3	0.87	1.2
Number of ARS (h ⁻¹)	28	1.42 \pm 0.59	0.95 \pm 0.29	0.04	5.0	0.94	0.1
Size of ARS (km)	138	0.84 \pm 0.54	0.69 \pm 0.65	0.16	2.0	0.14	1.9

Flight speed and activity patterns

MBs had higher mean and maximum flight speeds, by approximately 15%, than those of RFs (Table 2). MBs also had shorter distances and times from last landing (or plunge) while enroute to the colony com-

pared to RFs. There were no significant differences by sex or species in frequency of landings, distance to first landing, or mean distance to landing.

There were no significant differences in the size of ARS zones (Table 2) by either species or sex. Likewise, there was no difference in the absolute number of ARS

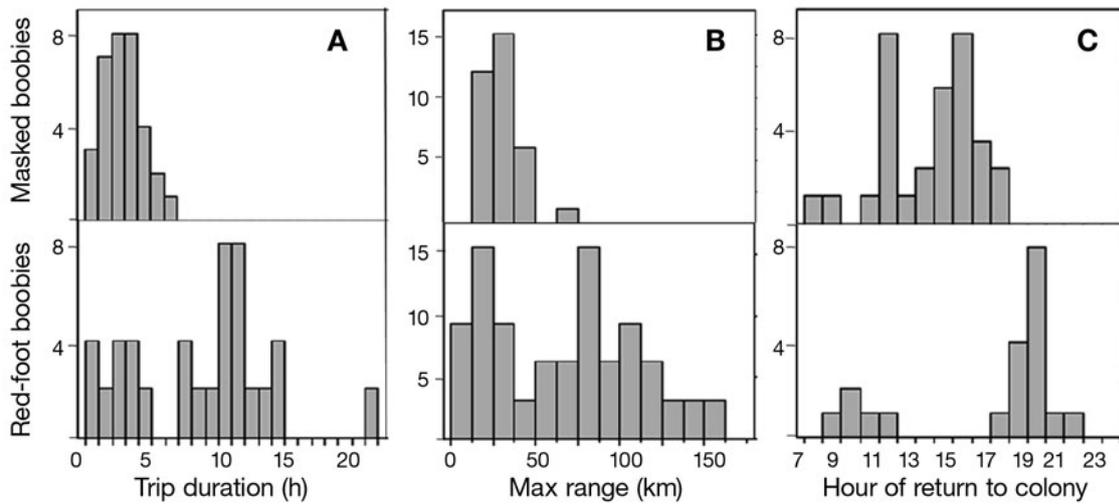


Fig. 2. *Sula dactylatra* and *S. sula*. Histograms of number of trips by (A) trip duration, (B) maximum range, and (C) return time, for masked and red-footed boobies showing 2 distinct peaks in distribution of trips for red-footed boobies and only 1 peak in trip distribution for masked boobies

periods per trip. However, because RF trips were so much longer in duration than MB trips, the frequency of ARS activity was significantly higher for MBs than for RFs.

Foraging habitat and environmental factors

Both bird species flew primarily in a western direction from the atoll. However, MBs had slightly more

southerly outbound and maximum azimuths (Fig. 3: rose plots). There were no differences between species for inbound azimuths (Table 2). There were no significant differences in any measurements of trip azimuth by sex within species either.

SST during foraging trips ranged from 25.5 to 29.0°C; annual average SST was slightly higher to the west of the atoll. Primary productivity in the region was low; chlorophyll *a* ranged from 0.1 to 0.2 mg m⁻³ and was slightly higher to the south than to the north of the atoll,

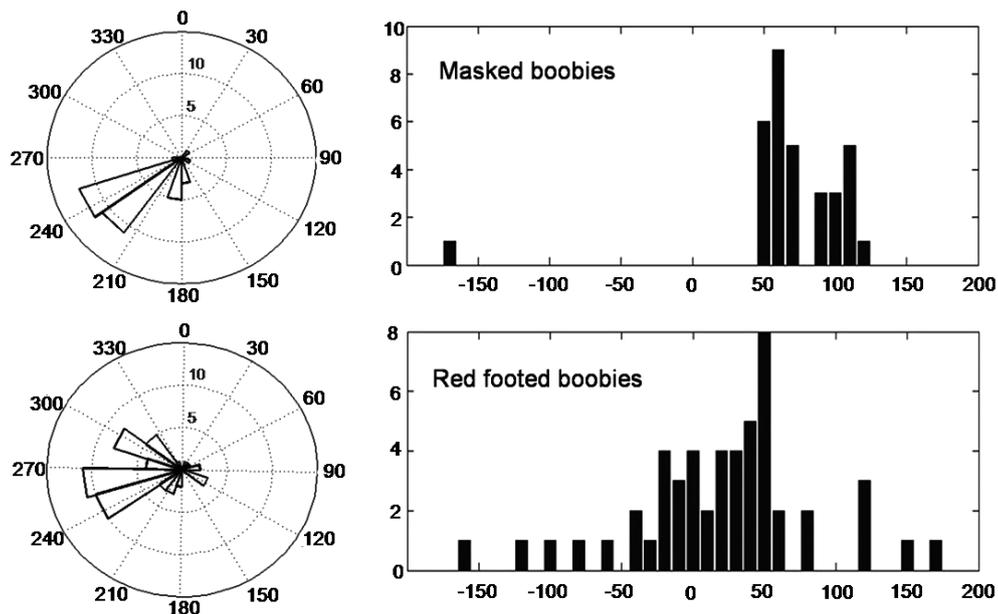


Fig. 3. *Sula dactylatra* and *S. sula*. Left panels depict rose plots of all outbound trip azimuths for masked (top) and red-footed (bottom) boobies. Right panels are histograms of the differences between wind direction and outbound azimuth for each trip for both species. Red-footed boobies head more directly west and keep the wind more directly behind their rear-quarters on outbound trips as compared to masked boobies

with hotspots directly north of the Palmyra Atoll and neighboring Kingman Atoll. However, all variations in SST and chlorophyll *a* over the period of the present study were small in the region delimited by maximum flight ranges of all birds, and the resolution of data available was too coarse given the small travel distances of these birds. Thus, no attempt was made to analyze differences among genders and species by these 2 variables.

Analysis of wind patterns in the region showed wind direction to be quite variable over the course of the year, oscillating in an annual cycle from northeasterly to southeasterly as the Intertropical Convergence Zone moved northward and southward over the atoll. For all trips, the wind strength was always >10 knots; maximum wind speed during a single trip was 15 knots. The difference between outbound azimuth and average wind direction for each trip was significantly different between species ($F = 14$, $p < 0.001$), but not between sexes within species.

Prey type

The diet of both species was numerically dominated by flying fish (predominantly Exocoetidae), composing 94 % of diet samples for MBs and 70 % of diet samples for RFs. The remainder of the diet was composed of squid (predominantly Ommastrephidae). By biomass, flying fish appeared to comprise an even more significant component of the diet; approximately 99 % of the diet by mass for MBs and 92 % for RFs. For samples composed of flying fish, the average prey size was significantly larger for MBs (means: 245 ± 136 g and 26.6 ± 6.4 cm) compared to RFs (means: 134 ± 91 g and 20.6 ± 4.0 cm) (length: $p = 0.01$, $t = 3.3$; mass: $p = 0.01$, $t = 2.8$). The size and weight of fish did not differ significantly between sexes within a species. There was an insufficient number of squid samples for MBs to compare size of squid by species or by sex within booby species.

Isotopic differences

Feather tissue for MBs ($n = 16$) was slightly, but significantly more depleted in $\delta^{13}\text{C}$ than values obtained from RFs ($n = 55$) ($p = 0.001$, $t = 3.50$; Fig. 4). Blood samples showed similar small but significant results; although the difference was very small, there was no overlap in $\delta^{13}\text{C}$ values between species in blood samples (MB: $n = 9$; RF: $n = 11$; $p = 0.01$, $t = 3.7$; Fig. 4). Feathers from RF chicks ($n = 10$) were not significantly different in $\delta^{13}\text{C}$ from adult RFs. There were no significant differences in mean $\delta^{15}\text{N}$ between species or age classes for either feathers or blood. There were no sig-

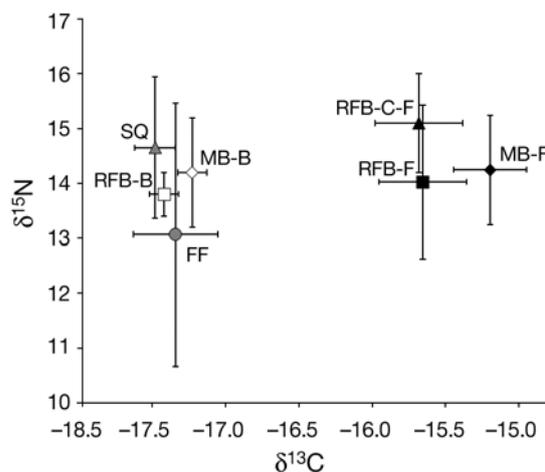


Fig. 4. *Sula dactylatra* (masked booby, MB) and *S. sula* (red-footed booby, RFB). Isotopic carbon and nitrogen values of feathers (-F, black symbols) and blood (-B, white symbols) of adult *S. dactylatra*, the masked booby (MB), and adults. Values are also shown for feathers of red-footed booby chicks (RFB-C), and for muscle (grey symbols) of the common prey items squid (SQ) and flying fish (FF). Error bars = SD

nificant sex differences in isotopic values for either RFs or MBs. Values for both species were consistent with a diet composed largely of flying fish and squid.

DISCUSSION

In the present study, we demonstrated that booby species (*Sula dactylatra*, *S. sula*) nesting at Palmyra Atoll do partition resources by species — both in spatial and temporal domains and in prey type; however, they do not show evidence of sexual partitioning of resources. The large body size differences between the species and the documented effects of size on foraging patterns may explain the large species niche partitioning (González-Solís et al. 2000b, Shaffer et al. 2001). However, the observed magnitude of the distinction in habitat utilization at Palmyra between these 2 species was surprising, given that previous tracking work did not suggest widely disparate foraging patterns between these species at other locations (Weimerskirch et al. 2006, 2008).

One of the salient findings of our study is that we did not find support for resource partitioning between sexes within species. This result is in direct contrast to recent findings from a similar comparison of 2 sexually dimorphic sulid species in the Gulf of California, Mexico, where foraging differences were seen between sexes, but not between species (Weimerskirch et al. 2009a). However, in contrast to the oligotrophic waters around Palmyra Atoll, the study in Mexico took place

in a higher productivity system, with nearby coastal upwelling, such that prey would be reliably available to these birds in closer proximity to their breeding colony. Thus, it is likely that birds have greater physiological capacity at the breeding colony in Mexico and, as a consequence, experience less pressure from interspecific competition in foraging compared to the tropical species we studied. Breeding in a higher productivity regime may also permit greater flexibility in parental roles when provisioning young compared to species that breed in a nutrient-poor tropical environment, which could manifest in intersexual differences observed in the former study (Weimerskirch et al. 2009a) and not the latter (the current study).

Niche partitioning

The 2 booby species used markedly different foraging strategies. The larger MBs took shorter trips both in distance and duration than did RFs. This contrasts with results from other GPS tracking studies, which suggested that MBs might forage further offshore than RFs. Incubating MBs at Clipperton Island (10° 18' N, 109° 13' W) frequently foraged an average of 144 km from the colony (and up to 250 km from the colony), while incubating RFs (at Europa Island, 22° 22' S, 40° 21' E) foraged an average of only 67 km from the colony (and up to 148 km from the colony) (Weimerskirch et al. 2005, 2008). However, our results are consistent with general opinion that RFs are more pelagic, based on earlier observations using conventional radio tracking, and with what would be predicted given the lower costs of flight of RFs (Anderson & Ricklefs 1987). Thus, comparison of our results to other tracking studies of the same species suggests that there may be substantial differences in foraging patterns based on geographic location.

Further support of spatial separation between species comes from isotopic differences in $\delta^{13}\text{C}$ in blood, which are consistent with patterns observed in tracking data; the more negative $\delta^{13}\text{C}$ values of RFs suggest more pelagic feeding patterns (Fig. 4). Similar patterns, but greater variation in $\delta^{13}\text{C}$ of feathers, suggest that these foraging differences between species remain during non-breeding periods and may even be amplified. That RF chick feathers are indistinguishable in $\delta^{13}\text{C}$ from RF adult feathers, suggests that at least for this species at Palmyra there may not be large changes in foraging location between breeding and non-breeding periods. The small magnitude of changes observed in $\delta^{13}\text{C}$ (in both feathers and blood) between species is likely due to small isotopic gradients typical of tropical waters (Cherel et al. 2008). Although differences in $\delta^{13}\text{C}$ across genders have

been observed in other studies of RFs, in which sex-specific foraging behavior was documented (Cherel et al. 2008), none were seen here.

We also observed distinct trip types and durations between species. Notably, RFs appeared to have 2 distinct trip modes, a less frequent 'short' trip, similar to the typical MB trip, and a more frequent 'long' trip. The alternation of long and short trips has been observed in a variety of other species, including wandering albatross *Diomedea exulans* (Weimerskirch et al. 1997), blue petrels *Halobaena caerulea* (Chaurand & Weimerskirch 1994), and masked boobies at Clipperton (Weimerskirch et al. 2008). It seems that, at Palmyra, RFs, but not MBs, may exhibit this same pattern. However, further research is needed to document the mechanism driving this pattern and to understand why RFs, but not MBs, would exhibit trip alternations.

Consistent with their generally longer trips, RFs also departed earlier in the morning and returned later at night; many RFs did not return until well past dusk. While this is statistically true even if both short and long trips are pooled for RFs, the difference is most relevant for RFs on long trips (those >35 km and 5 h in length). These birds left an average of 2.5 h earlier in the morning and returned 5.5 h later in the evening. These differences are probably largely driven by differences in trip length, possibly due to RFs targeting more distant foraging locations. The differences may also be facilitated by the comparatively larger eyes of RFs, which allow for greater crepuscular vision, although probably not for night foraging (Ashmole & Ashmole 1967). This would then allow for temporal partitioning of resources, which may play a role in diet differences observed across species.

Higher flight speeds were also observed for MBs, as is consistent with studies showing MBs to have wing loading about 2-fold that of RFs (Hertel & Ballance 1999). This higher wing loading likely explains the faster flight speeds of MBs, but it also likely increases the cost of flight (thus favoring faster, shorter trips for MBs).

Diet samples indicate that there is differentiation by species in the types of prey taken, with RFs taking smaller prey and consuming a greater proportion of squid. These interspecific differences in prey type and prey size are consistent with the differences that have been seen in other studies, although a greater proportion of squid by volume was identified for both species in other studies (Fefer et al. 1984, Asseid et al. 2006, Spear et al. 2007). Our sampling method (using only largely intact animals) may have disproportionately biased against squid and smaller prey, since they may be digested more quickly, potentially explaining the lower proportion of squid found in our study. However, the lower abundance of squid in MB diets compared to

RF diet samples may also be partially explained by the earlier departure and later return of RFs, leading to higher activity in crepuscular hours when squid are more likely to be found (Roe 1974). The higher mass of individual fish prey items in MB diet samples may be related to the larger mass and higher wing loading of this booby species, allowing them to swallow and carry larger items. The lack of isotopic difference in $\delta^{15}\text{N}$ suggests that there were no significant differences in trophic position of prey consumed, as might be expected considering that both booby species feed on the same 2 prey types in an oligotrophic area. The high variability in $\delta^{15}\text{N}$ is likely due to the high variability in $\delta^{15}\text{N}$ seen in flying fish prey.

Foraging context

Both bird species foraged primarily in the western direction from the atoll. Multiple studies of seabirds in the tropics have used chlorophyll *a* and/or SST levels to explain seabird use of specific areas in tropical oceans (Ballance et al. 1997, Jaquemet et al. 2005, Weimerskirch et al. 2005), and previous work suggests that RFs can adapt foraging patterns to forage in more productive waters (Weimerskirch et al. 2005). However, no major variation in SST or chlorophyll was observed at Palmyra that would explain this pattern. Given the strong easterly currents that surround Palmyra Atoll from the North Equatorial Counter Current, a high productivity eddy not detected by our course level metrics might exist to the west of the atoll (Hamman et al. 2004). It is possible that RFs take advantage of their more efficient flight abilities, to travel further to utilize more productive waters. However, this is not clearly supported by remotely sensed SST and chlorophyll data, and more detailed analysis of water productivity on a trip-by-trip basis would be needed to document any such patterns.

A more likely explanation for the westerly direction of both bird species is the prevailing wind direction. The westerly direction of outbound flight would allow them to fly with winds on their rear-quarters on outbound flights, which should be the most energy-efficient means of travel, and with headwinds on the return flight (Pennycuick 1989). Other studies (Pennycuick 1989, Spear & Ainley 1997) suggest that seabirds, and Pelicaniformes in particular, tend to fly with or across headwinds, in order to cover large distances and maximize prey detection. Flying the return leg into headwinds would be conducive to foraging, as birds would be able to maintain high flight speeds and low ground speeds, to facilitate searching. This is consistent with studies that show that RF increase landing frequency with time of day (Weimerskirch et al. 2005).

Wing loading should also be greater on the return leg, because birds would be returning with payloads of food. Greater wing loading on the return would allow boobies to penetrate headwinds more easily. The cause of significant differences observed in wind direction to flight direction between species is not immediately apparent. It may be that the differences in deflection from wind direction may be an artifact of the birds targeting different foraging zones, rather than a preference by the birds concerning wind direction. Another possible explanation for the identical return azimuth of both species is that it is a strategy to arrive in groups, as this has been documented to make them less vulnerable to kleptoparasitism by frigatebirds, which are common at this site (Le Corre & Jouventin 1997).

CONCLUSIONS

We used high resolution tracking data to examine hypotheses about habitat utilization in 2 species of boobies on Palmyra Atoll. A total of 565 h of high-resolution track data was obtained, and we identified clear species-specific foraging patterns, but no significant patterns of resource partitioning by gender.

It is unclear what maintains species-specific foraging patterns at Palmyra Atoll. Given the low abundance of MBs on the atoll, it seems intuitively unlikely that competitive exclusion of RFs by MBs could maintain these foraging differences. Given the much greater size of MBs it also seems doubtful that the reverse could occur. No aggressive behavior has been observed by the authors between these species at sea, and they nest in extremely close proximity to one another. It seems more likely that much of the differentiation in foraging patterns and resource use (i.e. lower flight speeds, smaller prey size, and later return times for RFs) is caused by physiological variation that evolved over time, which allows the species to partition resources (e.g. mass-related lower wing loading and larger eyes for RFs). There may also be interactions between physiological constraints of the birds (e.g. the size of prey they can carry and the times of day they can forage) and unidentified environmental factors, such as the location of different prey types, which drive these foraging differences. There is little published information on the distribution of the primary prey species of these birds, and no clear reason to predict there would be variation in prey abundance between foraging zones utilized by these 2 species.

If anatomical differences lead to high niche partitioning between species, then intraspecific competition may be more important than interspecific competition in affecting foraging behavior of a given species. This could explain why MB foraging patterns are so

different at Palmyra compared to observations from Clipperton Island (Weimerskirch et al. 2008). The masked booby colonies at Clipperton are extremely large, and the birds may thus be forced to forage further off shore due to intraspecific competition (Lewis et al. 2001). The small colony size and thus low intraspecific competition at Palmyra may allow them to feed closer to the colony. Since RF colonies are large at Palmyra, there would still be strong intraspecific competition in that species.

The lack of support found in the present study for significant partitioning of resources by gender is also notable given the abundance of studies that have demonstrated resource partitioning across a wide variety of sexually dimorphic species, including these and other sulid species (Selander 1966, Gilardi 1992, González-Solís et al. 2000a, Weimerskirch et al. 2009a,b). Yet, some studies have found resource partitioning by sex in monomorphic species (Gray & Hamer 2001, Peck & Congdon 2006), and Weimerskirch et al. (2009a) found partitioning by sex, but not by species, despite the fact that species size differences were greater than sexual size differences. All of these results suggest that factors beyond size may be important in determining sexual partitioning and that sexual partitioning appears to be flexible within species and may be correlated to a variety of complex and local factors. Comparative studies across sites would help to elucidate the variables that lead to the occurrence or absence of resource partitioning by sex.

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