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Variability of resource partitioning in sympatric tropical boobies

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ABSTRACT: Inter- and intraspecific competition can lead to resource partitioning in sympatric species, processes likely affected by environmental productivity and population size. We investigated the foraging behaviour and diet of masked (*Sula dactylatra*) and red-footed (*S. sula*) boobies at Tromelin Island, western Indian Ocean, to examine the role of resource partitioning in the foraging strategies of these sympatric species in an extreme oligotrophic environment. We compared our results to published studies with differing environmental conditions or population sizes. We used GPS loggers and Argos transmitters to track foraging movements and used time–depth recorders to estimate dive depths. Masked boobies travelled further and at faster rates than red-footed boobies, and sexes did not differ in foraging behaviour. Based on randomization tests, the foraging range of each species (95 % utilization distribution; UD) overlapped significantly. However, at core foraging areas (50 % and 25 % UD), interspecific segregation was greater than expected by chance alone. No intraspecific spatial segregation was detected between sexes. Environmental characteristics of area-restricted search zones differed between species, but not sexes; masked boobies utilized warmer, deeper, and less windy oceanic environments than red-footed boobies. Masked boobies attained greater diving depths than red-footed boobies and consumed primarily flying fish, whereas red-footed boobies consumed mostly squid. Red-footed and masked boobies breeding in the extreme oligotrophic environment near Tromelin demonstrated greater dietary partitioning differences in foraging ranges compared to a less oligotrophic environment. This suggests that environmental productivity may play a role in processes of resource partitioning in these sympatric species.

KEY WORDS: Resource partitioning · GPS · Satellite tracking · Area-restricted search · Diet · *Sula dactylatra* · *Sula sula*

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INTRODUCTION

Competition for resources can lead to niche partitioning, either spatially, temporally, or morphologically (Schoener 1974), between closely related species and thus drive the evolution of sympatric species (Hutchinson 1959, Schoener 1983). Since the processes that drive resource partitioning may differ among locations due to variation in environmental productivity or numbers of inter- and intraspecific competitors, comparative studies can help inform our understanding of these processes. Seabirds are ideal subjects for investigating geographic patterns of for-

aging and resource partitioning because they typically form discrete breeding colonies of varying sizes on coastal and oceanic islands with differing local conditions.

Broad mechanisms of resource partitioning within seabird communities have been well established since the pioneering work of Ashmole & Ashmole (1967), Harris (1970), Croxall & Prince (1980), Diamond (1983), Harrison et al. (1983), and Ainley & Boekelheide (1990), and several well-defined ecological guilds have been identified in most oceanic habitats. However, comparisons of the detailed foraging ecology of closely related species within a foraging

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guild have produced contradictory results. In most cases, ecological segregation occurs by spatial separation of the foraging habitats as inferred from direct observation, diet analysis, stable isotope analysis, satellite telemetry, or a combination of these methods. This has been demonstrated in giant petrels (González-Solís et al. 2000), diving petrels (Bocher et al. 2000), albatrosses (Cherel et al. 2002b, Hyrenbach et al. 2002, Pinaud & Weimerskirch 2007, Kappes et al. 2010), penguins (Mori & Boyd 2004, Miller et al. 2010, Wilson 2010), and temperate gulls (Kubetzki & Garthe 2003). Conversely, other studies have revealed important overlap in diet or foraging habitats of closely related species (prions; Cherel et al. 2002a, cormorants; Sapoznikow & Quintana 2003), suggesting either non-limiting food resources, active inter-specific competition for resources, or a limited diversity of prey (Diamond 1983). Evidence of interference competition at sea has been reported for several species, especially those that forage in multi-specific flocks (e.g. Shealer & Burger 1993, Arcos et al. 2001, Maniscalco et al. 2001, Rome & Ellis 2004). In such scenarios, one or a few dominant large species may exclude several smaller species (Ballance et al. 1997).

Tens to millions of seabirds may utilize the same nesting colony, all of which are required to forage within a limited range while breeding. As a consequence, food depletion may occur near the colony ('Ashmole's halo'; Ashmole 1963, Birt et al. 1987, Elliott et al. 2009), ultimately leading to density-dependent effects on seabird populations (Furness & Birkhead 1984, Lewis et al. 2001, Forero et al. 2002). Given the variability in seabird colony size, competitive interactions within and among sympatric species are likely to differ depending on the numbers of competitors.

The relative productivity of an environment may also affect competitive interactions of sympatric species (Schoener 1974). Although the vast majority of studies on niche partitioning among closely related seabirds (cited above) have been conducted in sub-antarctic or temperate waters where food is seasonally superabundant, some recent studies of tropical seabirds (see Catry et al. 2009, Young et al. 2010a,b) have sought to investigate these questions for seabirds foraging in epipelagic tropical waters. In such extreme low-resource environments (Longhurst & Pauly 1987), finding a patch of prey is a rare and unpredictable event (Ashmole 1971, Ballance et al. 1997), and interspecific competition may differ compared to temperate or polar marine habitats.

Boobies (*Sula* spp.) breed and forage in a wide range of habitats, from coastal upwelling environ-

ments to a gradient of tropical and subtropical environments. Although all booby species generally have a limited foraging range when breeding (Weimerskirch et al. 2005a, 2008, 2009c, Zavalaga et al. 2008, 2010, Ludynia et al. 2010), tropical boobies are also unable to dive deeper than a few meters (Lewis et al. 2005, Weimerskirch et al. 2005b, 2008). Consequently, tropical boobies rarely have access to their prey, and require subsurface marine predators such as tunas or dolphins to force prey towards the surface to enable capture (Au & Pitman 1986). As tuna and dolphins are fast swimming animals, their occurrence at the surface is an ephemeral event that must be rapidly localized and exploited. In fact, it has been demonstrated that red-footed boobies (*Sula sula*) employ specific strategies to optimize foraging efficiency in obtaining ephemeral prey (Weimerskirch et al. 2005b). Given that boobies also frequently breed sympatrically with other congeners, there is considerable potential for competitive interactions within and between booby species at transitory multi-species foraging aggregations in the tropics.

Previous studies have shown that sympatric tropical boobies consume similar prey types, especially flying fish (Exocetidae) and squid (especially Ommastrephidae), with larger species eating larger prey (Dorward 1962, Schreiber & Hensley 1976, Harrison et al. 1983, Young et al. 2010b). Given high overlap of prey types, separation of foraging habitats could provide a mechanism for partitioning of resources. Spatial segregation at sea has been demonstrated among sympatric boobies at Palmyra Atoll in the tropical central Pacific Ocean (Young et al. 2010b), however, studies of sympatric boobies breeding in upwelling environments have produced mixed results. In the Gulf of California, Weimerskirch et al. (2009c) found spatial segregation between sexes within a species, but not between sympatric species, while separation of foraging habitats between booby species was apparent in the Galapagos (Anderson & Ricklefs 1987). Species characteristics, population sizes, and oceanic productivity near the breeding colony likely affect the dynamics of competitive interactions within and among booby species (Weimerskirch et al. 2009c, Young et al. 2010b), and comparative studies can help us understand the mechanisms leading to niche partitioning.

In this study, we investigated the foraging behaviour and habitat use of 2 sympatric tropical seabirds, masked (*Sula dactylatra*) and red-footed (*S. sula*) boobies, breeding at Tromelin Island in the western Indian Ocean, and we compared our results to published studies on booby foraging behaviour at

other locations. The oceanic environment surrounding Tromelin is extremely oligotrophic (chlorophyll *a* ranged from 0.03 to 0.13 mg m⁻³ during the study period), an order of magnitude lower than the waters surrounding Palmyra Atoll (0.1 to 0.2 mg m⁻³), where the foraging behaviour of these species have been studied in detail (Young et al. 2010b). We used a combination of high-resolution GPS tracking data, satellite telemetry, time–depth recorders, and diet analysis to examine the degree of spatial, environmental and dietary segregation between species and sexes in this extreme low-resource environment. Given the larger body size of masked boobies compared to red-footed boobies (Young et al. 2010b) and the importance of body size in structuring at-sea competitive interactions (Ballance et al. 1997, González-Solís et al. 2000), we expected to see significant resource partitioning between species at Tromelin Island. Despite the presence of reversed sexual dimorphism in both species (Weimerskirch et al. 2006, 2009b), Young et al. (2010b) did not find evidence of resource partitioning between sexes in either of these species. We therefore sought to investigate whether or not resource partitioning might occur between sexes in a more extreme oligotrophic environment.

MATERIALS AND METHODS

Study area and booby tracking

Field work was conducted between 5 December 2005 and 2 January 2006 at Tromelin Island (15° 33' S, 54° 31' E; Fig. 1), a small and remote coralline island in the western Indian Ocean. Although the island once supported a diverse seabird community (Le Corre 1996), only 2 seabird species have bred there since the late 1990s, red-footed (130 to 180 pairs) and masked boobies (200 to 250 pairs). Breeding of masked boobies is loosely seasonal, with a weak peak in egg-laying between June and November, while red-footed boobies breed more or less year-round (Le Corre 1996). At the time of the study, 129 pairs of red-footed boobies and 224 pairs of masked boobies were breeding, and most pairs were incubating or brooding young chicks.

We used both GPS loggers and Argos transmitters for complementary purposes. GPS loggers (32 g; NewBehavior) were used to investigate fine-scale behaviour and habitat use during single foraging trips, which are generally <12 to 15 h in boobies (Weimerskirch et al. 2005a, 2008). GPS tags were

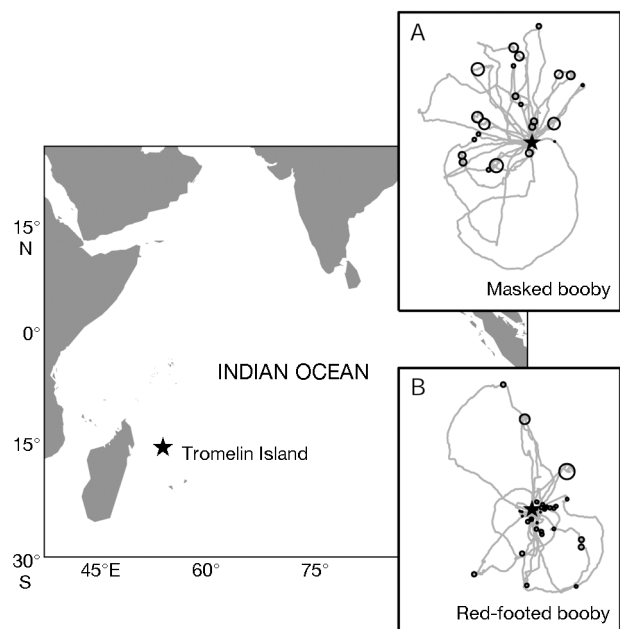


Fig. 1. *Sula dactylatra* and *S. sula*. Map of study area, with foraging trips (grey lines) of (A) masked and (B) red-footed boobies tracked with GPS loggers during the brooding period at Tromelin Island (black star), western Indian Ocean. Area-restricted search zones are indicated by black circles

programmed to record positions every 10 s, which permitted storage of 24 h of location data, and were accurate to ~10 m (Steiner et al. 2000). To study fidelity of individual birds to foraging sites across successive foraging trips, we used Argos transmitters (23 g; PTT 100, Microwave Telemetry), which have a battery life of approx. 40 d and are generally accurate to <10 km (Costa et al. 2010); transmitters provided 6 fixes per day on average. We deployed GPS tags on 17 masked boobies (9 female, 8 male) and 14 red-footed boobies (6 females, 8 males), and PTTs on 8 masked (4 females, 4 males) and 8 red-footed boobies (4 females, 4 males). Tags were attached to the 3 central tail feathers using adhesive tape (Tesa), and represented <3.2% of total bird's body mass in all cases. Each bird was weighed in a bag with a Pesola balance, culmen length was measured using a caliper, and wing length was measured using a ruler. All tracked birds were brooding downy chicks and resumed breeding duties normally after tracking devices were deployed. Argos and GPS deployments occurred during exactly the same period.

Positions acquired from each deployment were split into discrete at-sea periods by removing locations at the colony; for Argos data, positions were considered to be at the colony if they passed within the average error for the given location quality,

based on stationary trials conducted with tags from the same manufacturer (M. A. Kappes unpubl. data). Data from Argos deployments were further separated into trips if the path between locations intersected a 3 km radius of Tromelin Island; this value was obtained by averaging the location errors of all Argos positions in the data set. This method of defining foraging trips was corroborated with observations of tagged individuals at the nest, when available. An iterative forward/backward averaging speed filter (McConnell et al. 1992) implemented in Matlab (The MathWorks) was applied to remove unlikely locations; we used a maximum speed limit of 95 km h⁻¹, following Weimerskirch et al. (2005a). For GPS data, to distinguish between true foraging trips and short forays close to the colony, only trips that exceeded 30 min were included in analyses of foraging behaviour. On average, short forays lasting 30 min or under ranged only 1.05 km from Tromelin Island; after excluding these points, 97.3% of GPS tracking hours were retained for analysis.

We investigated foraging site fidelity in individuals of each species using Argos data by investigating variability in azimuth to the most distant point. Only individuals with 3 or more successive foraging trips were included in this analysis.

Habitat use

Only complete GPS tracks were included in the analysis of habitat use; in some cases, several foraging trips were recorded for the same individual, so we used the first one to avoid pseudoreplication. This removed 2 trips for masked boobies and 2 trips for red-footed boobies. To determine overall patterns of spatial foraging distribution, we used kernel estimation (Worton 1989) to determine utilization distributions (UD) for each species and for each sex within species. A UD is essentially a probability distribution based on positional data for the location of an individual. Geographic coordinates from GPS tracks were transformed using a Lambert Cylindrical Equal Area projection (Wood et al. 2000), and UD's were estimated with kernel methods (Worton 1989) using the R package *adehabitat* (Calenge 2006). To allow for comparisons between species and sexes, the smoothing factor (h) was set to the mean of the h values calculated from each species or sex, as determined using least-squares cross-validation (LSCV; Silverman 1986). The smoothing factor controls the influence of nearby observations on the density estimate, so that small h values emphasize fine detail,

while large h values demonstrate only prominent features. The LSCV process seeks to achieve a balance by examining multiple bandwidths and selecting the one with the least error (Seaman & Powell 1996). We then employed a randomization analysis to test the null hypotheses that there was no spatial segregation in foraging distributions between species and sexes (Breed et al. 2006). For each comparison, species or sex was randomly assigned to tracks using the same species/sex ratio as the observations, and kernel analysis was applied. The area of overlap divided by the area of the larger polygon was used as the test statistic following Breed et al. (2006), for the 25% (core area), 50% (focal region), and 95% (foraging range) UD's (Hyrenbach et al. 2002). Each test was iterated 500 times, and the p-value determined as the proportion of random overlaps that were smaller than the observed overlap (Breed et al. 2006).

Because marine predators forage on patchy prey resources, it is expected that they will modify their behaviour to search for food at an effective scale to exploit high-density prey patches (Curio 1976, Fauchald & Tveraa 2003). This behaviour, known as area-restricted searching, can be deduced from movement patterns, thus providing a methodology for discerning environmental characteristics where search effort is concentrated (Kareiva & Odell 1987, Fauchald & Tveraa 2003). We used first passage time analysis, a scale-dependent metric of time spent in a given area by an animal (Fauchald & Tveraa 2003) to detect locations where area-restricted search (ARS) effort was concentrated (Kareiva & Odell 1987, Fauchald & Tveraa 2003, Pinaud 2008) for each species. We calculated first passage time at every location along each GPS track for radii ranging from 100 to 5000 m, at 100 m increments, using a custom-built program in Matlab (Robinson et al. 2007). The 'ARS scale' was defined as the circle radius associated with the peak log(variance) in first passage time (Fauchald & Tveraa 2003). For each track, the multimodal distribution of first passage times at the ARS scale was used to delineate 'ARS zones'. Locations corresponding to the mode of higher first passage time values were defined as ARS zones, following Pinaud & Weimerskirch (2007).

Environmental variables were extracted according to the location of ARS zones. To minimize the influence of potential outliers and the effect of differences in ARS scales, we used median values of environmental variables within each ARS zone. Because the number of ARS zones differed per track, we summarized environmental data by taking the median value from all ARS zones for each track. We used sea sur-

face temperature (SST; °C), primary productivity (PP; $\text{mg C m}^{-2} \text{ day}^{-1}$), wind speed (m s^{-1}), and bathymetry (m) to characterize the environmental characteristics of ARS zones. Environmental data were obtained by querying the NOAA OceanWatch Live Access Server using Matlab and ERDDAP (<http://coastwatch.pfeg.noaa.gov/erddap/>).

We used a blended product of SST derived from both microwave and infrared sensors carried on multiple platforms at a spatial resolution of 0.1° and as a 5-d temporal composite (Powell et al. 2008). Measurements were gathered by Japan's Advanced Microwave Scanning Radiometer (AMSR-E) instrument, a passive radiance sensor carried aboard NASA's Aqua spacecraft, NOAA's Advanced Very High Resolution Radiometer (AVHRR), NOAA's GOES Imager, and NASA's Moderate Resolution Imaging Spectrometer (MODIS). Monthly PP estimates (Behrenfeld & Falkowski 1997) were derived at a spatial resolution of 0.167° from monthly chlorophyll *a* values and photosynthetically available radiation obtained from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) on the Orbview-2 satellite, and SST values from the AVHRR Pathfinder Oceans Project. Daily composites of wind speed were gathered by the SeaWinds scatterometer aboard NASA's QuikSCAT satellite at a resolution of 0.125° and a reference height of 10 m. Bathymetry was extracted using data from ETOPO2 at a resolution of 0.033° (Smith & Sandwell 1997).

Dive depths

To study dive depths, we used cylindrical time-depth data loggers (M190-D2GT, 12 bit resolution, $60 \times 15 \text{ mm}$, 20 g, Little Leonardo) on a separate group of 12 birds for 1 to 2 trips. The devices monitored depth (every second) and temperature (every minute); relative accuracy for the depth sensor was 0.1 m. Loggers were deployed on 15 masked boobies (6 males and 9 females) and 19 red-footed boobies (11 males and 8 females) and attached to the birds' 3 central tail feathers using Tesa tape.

Diet analysis

Food samples were opportunistically collected from breeding adults upon return from a foraging trip. Food samples were frozen for analysis at the ECOMAR laboratory, Réunion Island, where each whole sample was weighed, then separated for fur-

ther analysis of individual prey items. Identification of prey was conducted using Smith & Heemstra (1986) for fishes, Clarke (1986) and Nesis (1987) for squids, and our own reference collection. We measured fork length (to the nearest 0.1 mm), caudal length and fresh mass (to the nearest 0.1 g) of all intact fish, and dorsal mantle length, lower rostral length (to the nearest 0.01 mm) and fresh mass of all intact squids. We used allometric relationships (Le Corre et al. 2003) to reconstitute mass and length of partially digested items of the 3 main prey types (Exocetid and Hemiramphid fishes, and Ommastrephid squids).

Statistical analysis

Two-sample *t*-tests were used to investigate size and mass differences between sexes of each species. Rayleigh tests were used to test uniformity in destination bearings for all individuals using the CircStat toolbox in Matlab (Berens 2009); angular deviation, equivalent to standard deviation in linear data (Batschelet 1981), was also calculated for each individual. We used circular-circular correlation to examine if destination bearings were related to wind direction at departure in each species.

We used mixed-effects analysis of variance (ANOVA) to test for differences in trip characteristics and diving behaviour between species and sexes, based on complete GPS tracks or time-depth records, with individual as a random factor. Trip duration, maximum distance reached, total distance travelled and ARS spatial scale were log-transformed to meet normality assumptions; average travel speed did not require transformation. We tested for differences in destination bearings between species and sexes using a 2-way ANOVA for circular data ('Harrison-Kanji test') in the CircStat toolbox in Matlab (Berens 2009), after ensuring data followed the von Mises distribution. Because it was not possible to include a random term in this test, we only included the first trip of each individual.

We used multivariate analysis of variance (MANOVA) to test for species and sex differences in environmental characteristics of ARS zones. Due to unequal group covariance matrices, a permutational MANOVA in the R package *vegan* (Oksanen et al. 2010) was implemented. We used backward stepwise selection for quadratic discriminant analysis using the R package *klaR* (Weihs et al. 2005) to arrive at the final set of discriminating variables between groups.

Table 1. *Sula dactylatra* and *S. sula*. Mass and morphometric measurements (mean \pm SD) of tracked masked and red-footed boobies breeding at Tromelin Island (n = number sampled)

	n	Culmen length (mm)	Wing length (mm)	Mass at capture (g)
Masked booby				
Males	11	102 \pm 1.95	432 \pm 5.95	1584 \pm 74.4
Females	9	101 \pm 1.99	445 \pm 10.6	1836 \pm 133
All	20	102 \pm 1.94	439 \pm 10.7	1730 \pm 151
Red-footed booby				
Males	10	82.5 \pm 3.46	380 \pm 6.04	920 \pm 71.6
Females	11	86.1 \pm 1.86	386 \pm 9.27	1054 \pm 46.2
All	21	84.2 \pm 3.30	383 \pm 8.09	984 \pm 90.7

We used 2-way ANOVA to investigate differences between species and sexes in food load size, the number of prey items per food load, prey size and diet composition. Food load mass, prey item mass and prey item length were log-transformed and percent mass fish (versus squid) was arcsine transformed. The proportion of fish by number was compared between species using a chi-squared test.

All statistical analyses were conducted in the program R (R Development Core Team 2010) unless otherwise noted. All averages are reported as mean \pm SD in the text.

RESULTS

Females of each species weighed significantly more than males (masked boobies: $t_{17} = 4.84$, $p = 0.0002$; red-footed boobies: $t_{19} = 5.04$, $p < 0.0001$; Table 1). Culmen length was significantly longer in red-footed booby females, as compared to males ($t_{19} = 2.90$, $p = 0.009$), but not in masked boobies ($t_{18} = -0.61$, $p = 0.55$). Conversely, wing length was

significantly longer in masked booby females, as compared to males ($t_{18} = 3.13$, $p = 0.006$), but not in red-footed boobies ($t_{19} = 1.70$, $p = 0.11$).

We successfully obtained complete GPS tracks from 13 masked boobies and 13 red-footed boobies (Table 2). We obtained 3 or more successive foraging tracks using Argos transmitters for 7 masked boobies and 8 red-footed boobies, totalling 73 foraging trips (38 masked booby trips, 35 red-footed booby trips). Up to 7 successive foraging trips were recorded for masked boobies (5.43 \pm 1.51 trips per bird) and up to 10 successive foraging trips were recorded for red-footed boobies (4.38 \pm 2.33 trips per bird).

Individuals of both species demonstrated a high degree of variation in heading between consecutive trips; mean angular deviation was 58.3° (range: 26.0 to 74.2) for masked boobies and 60.5° (range: 34.1 to 75.8) for red-footed boobies. Successive destination bearings of individuals were uniformly distributed for both masked boobies (Rayleigh tests, $p > 0.08$ for all individuals) and red-footed boobies (Rayleigh tests, $p > 0.13$ for all individuals). Destination bearings were not correlated with wind direction at departure in either masked ($r_{cc} = 0.17$, $p = 0.30$) or red-footed boobies ($r_{cc} = 0.23$, $p = 0.20$).

Masked boobies reached greater maximum distances while foraging than did red-footed boobies, travelled at faster average speeds, and demonstrated moderate evidence of foraging at larger ARS scales (Table 2). There were no significant differences between species in average trip duration or total distance travelled (Table 2); departure times also did not differ between species (Wilcoxon rank-sum test, $Z = 0.41$, $p = 0.68$). Destination bearings based on GPS data differed between species, but not sexes (Harrison-Kanji test, $\chi^2_2 = 0.38$, $p = 0.83$). GPS-tracked masked boobies headed to foraging sites to the north-west of the colony, while red-footed boobies headed to the south on average (Table 2, Fig. 1). There were no differences between sexes of either species in trip duration, maximum distance reached, total distance travelled, average travel speed, or ARS scale ($p > 0.2$ in all cases).

Habitat use

Based on randomization tests of spatial overlap, we found that masked and red-footed boobies demonstrated no significant spa-

Table 2. *Sula dactylatra* and *S. sula*. Summary characteristics (mean \pm SD) of masked and red-footed booby foraging trips tracked with GPS at Tromelin Island. Mean \pm angular deviation is given for destination bearing

	Masked booby (13 trips)	Red-footed booby (13 trips)	Statistic	p
Trip duration (h)	5.28 \pm 1.72	4.29 \pm 2.45	$F_{1,23} = 2.46$	0.13
Maximum foraging range (km)	45.8 \pm 16.8	31.0 \pm 21.7	$F_{1,23} = 5.94$	0.02
Total distance travelled (km)	135.5 \pm 62.2	113.7 \pm 72.5	$F_{1,23} = 2.05$	0.17
Travel speed (km h ⁻¹)	42.9 \pm 3.12	37.0 \pm 3.29	$F_{1,23} = 23.68$	0.0001
ARS spatial scale (km)	1.78 \pm 0.99	1.00 \pm 0.63	$F_{1,23} = 4.33$	0.048
Destination bearing (°)	332 \pm 62.1	175 \pm 60.8	$\chi^2_2 = 9.08$	0.01

tial segregation of overall foraging ranges (95 % UD; 54.1 % overlap, $p = 0.15$), however, they did demonstrate lower overlap of focal regions (50 % UD; 24.6 % overlap, $p = 0.010$) and core foraging areas (25 % UD; 22.0 % overlap, $p = 0.008$) than expected by chance alone (Fig. 2). There was no spatial segregation

between sexes in either species in foraging ranges (masked booby: 59.0 % overlap, $p = 0.80$; red-footed booby: 57.1 % overlap, $p = 0.94$), focal regions (masked booby: 25.3 % overlap, $p = 0.59$; red-footed booby: 49.8 % overlap, $p = 0.67$), or core foraging areas (masked booby: 15.4 % overlap, $p = 0.36$; red-footed booby: 50.5 % overlap, $p = 0.65$). Although actual percentage of overlap between sexes in core and focal areas for masked boobies was low, this reflects random variability in foraging destinations among individuals. A single male masked booby had a long foraging trip in an area not used by other individuals, leading to low overlap values. The randomization analysis is specifically designed to be robust against such anomalies, and the corresponding p -values were therefore high.

Environmental characteristics of ARS zones differed significantly between species (permutational MANOVA, $F_{1,23} = 5.59$, $p = 0.02$), but not between sexes ($F_{1,23} = 0.31$, $p = 0.73$). Based on backward stepwise quadratic discriminant analysis, the variables that best discriminated between masked and red-footed booby ARS zones were SST, wind speed and bathymetry. Masked booby ARS zones were generally warmer, deeper and less windy oceanic environments than those of red-footed boobies (Fig. 3).

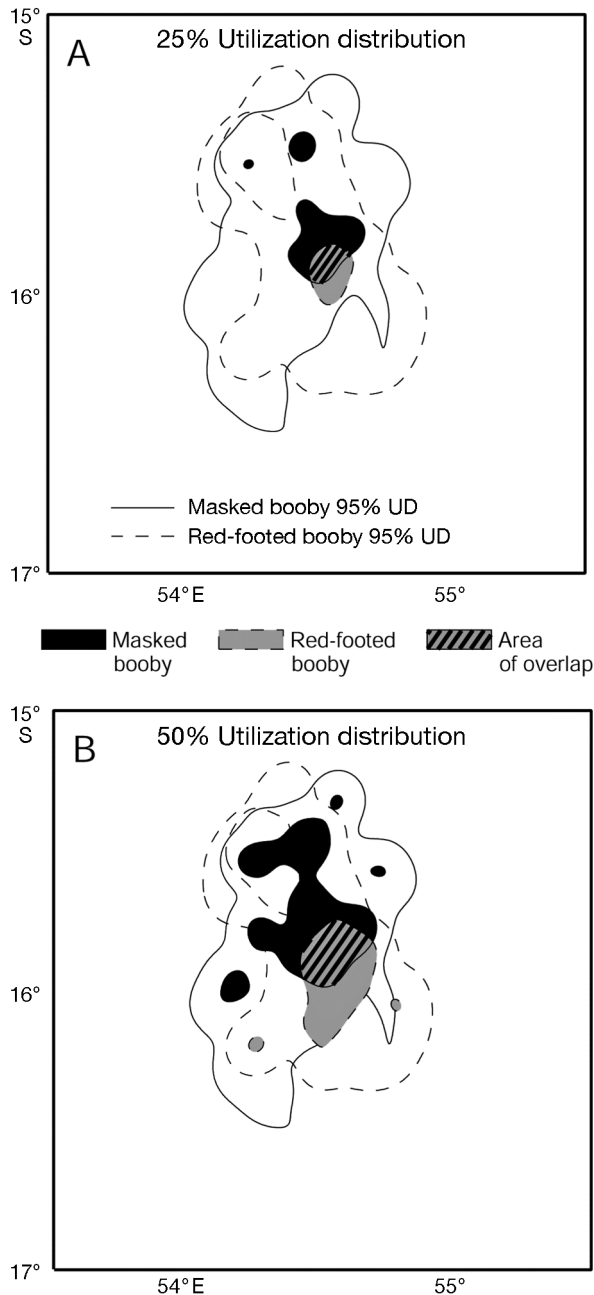


Fig. 2. *Sula dactylatra* and *S. sula*. Spatial overlap of masked and red-footed booby utilization distributions (UD) at core (A; 25 % UD) and focal foraging areas (B; 50 % UD) during the brooding period at Tromelin Island. The overall foraging ranges (95 % UD) are also provided for comparison

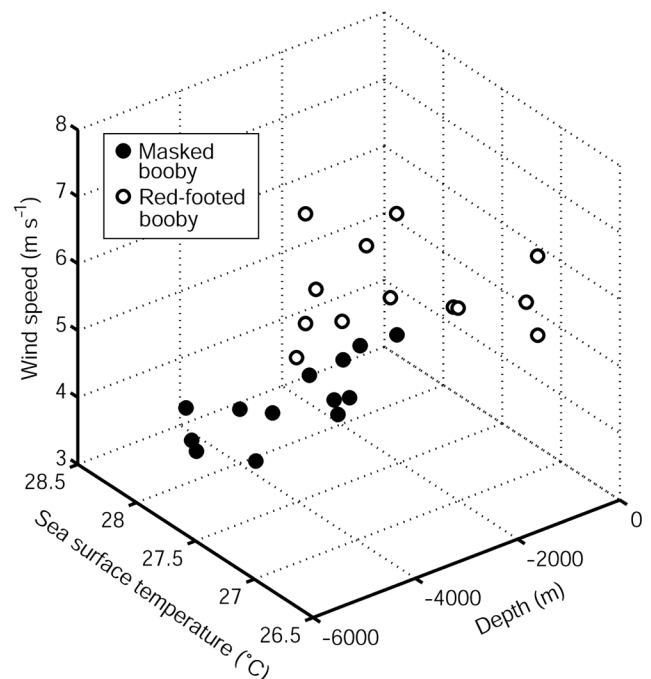


Fig. 3. *Sula dactylatra* and *S. sula*. Environmental characteristics of area-restricted search zones of foraging masked and red-footed boobies breeding at Tromelin Island

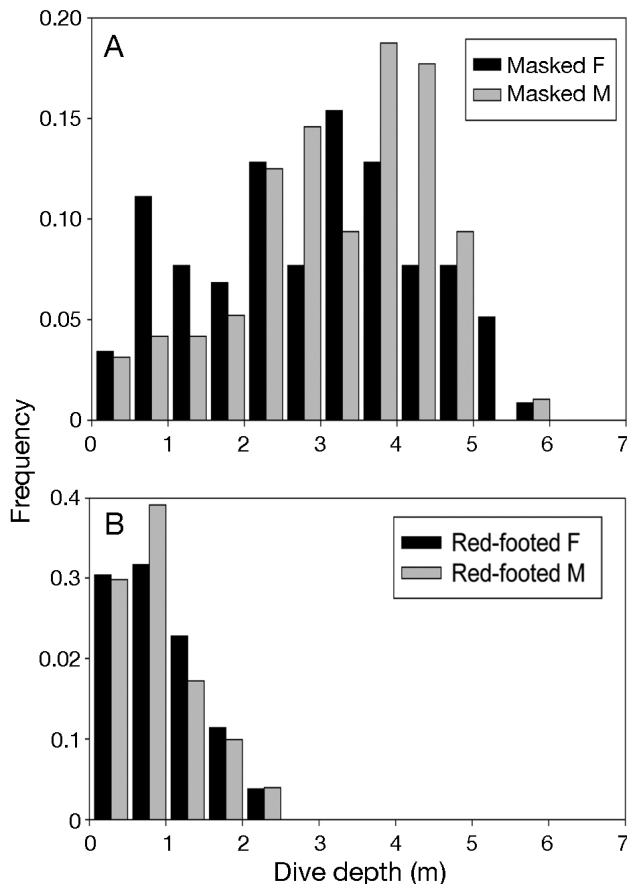


Fig. 4. *Sula dactylatra* and *S. sula*. Frequency distribution of dive depths attained by (A) masked and (B) red-footed boobies breeding at Tromelin Island (F = female and M = male)

Dive depths and diet

Masked boobies dived to greater depths than red-footed boobies ($F_{1,32} = 277$, $p < 0.0001$; Fig. 4), but there were no differences in depths attained between sexes ($F_{1,32} = 1.0$, $p = 0.23$). We collected 25 regurgitates (12 from masked boobies and 13 from red-footed boobies) from tracked adults upon return from foraging. Masked boobies returned from foraging with heavier food loads than red-footed boobies, but the mean number of prey per regurgitate was the same in both species (Table 3). This is because masked boobies returned with heavier and longer

prey items than red-footed boobies (Table 3). There were also interspecific differences in diet composition: the proportion of fish (versus squid) was significantly greater by number and by mass in the diet of masked boobies, as compared to red-footed boobies (Table 3). Almost 66% of prey items recovered from masked boobies were flying fish, whereas only 23% of red-footed booby prey items were flying fish (Table 3). The majority of prey items returned by red-footed boobies were squid, most of which were of the family Ommastrephidae (Table 3). Sexes did not differ in food load size ($F_{1,22} = 0.0034$, $p = 0.95$), number of prey per food load ($F_{1,22} = 3.45$, $p = 0.08$), prey item mass ($F_{1,107} = 0.008$, $p = 0.93$), prey item length ($F_{1,109} = 0.085$, $p = 0.77$), or the proportion of fish in the diet (by mass: $F_{1,22} = 0.416$, $p = 0.53$).

DISCUSSION

Foraging behaviour of boobies nesting at Tromelin Island differed between species, but not between sexes within species. Young et al. (2010b) also found species, but not sex, differences in foraging behaviour of masked and red-footed boobies breeding in sympatry on Palmyra Atoll. Conversely, Weimerkirch et al. (2006) found sex differences in foraging range and trip duration of red-footed boobies nesting on Europa Island during incubation; however, these differences were not present during brooding. Masked boobies nesting on Clipperton Island in the eastern Pacific Ocean also did not demonstrate sex differ-

Table 3. *Sula dactylatra* and *S. sula*. Summary and statistical differences between the diets of masked (12 regurgitates; 91 prey items) and red-footed (13 regurgitates; 94 prey items) boobies at Tromelin Island. Values are mean \pm SD

	Masked booby	Red-footed booby	Statistic	p
Food load mass (g)	216.3 \pm 94.6	121.9 \pm 61.0	$F_{1,22} = 8.16$	0.009
Number of prey per food load	7.6 \pm 1.7	7.2 \pm 2.6	$F_{1,22} = 0.174$	0.68
Mass of prey items (g)	42.4 \pm 25.6	21.4 \pm 23.0	$F_{1,107} = 30.3$	<0.0001
Length of prey items (mm)	168.0 \pm 55.9	100.3 \pm 57.7	$F_{1,109} = 50.1$	<0.0001
Fish (by number,%)	76.9	35.1	$\chi^2_1 = 32.8$	<0.0001
Fish (by mass,%)	87.5	54.9	$F_{1,22} = 6.64$	0.017
Squid (by number,%)	23.1	64.9		
Squid (by mass,%)	12.5	45.1		
Prey families by number (%) and rank (in brackets) for each species				
Exocetidae (flying fish)	65.9 [1]	23.4 [2]		
Hemiramphidae (half-beaks)	4.4 [5]	–		
Other fish families	–	4.2 [5]		
Unidentified fish	6.6 [4]	7.4 [4]		
Ommastrephidae (flying squid)	14.3 [2]	53.2 [1]		
Unidentified squids	8.8 [3]	11.7 [3]		

ences in foraging range and trip duration (Weimerskirch et al. 2009b), but other differences in foraging activity were evident. A study of sympatric blue-footed (*Sula nebouxii*) and brown (*S. leucogaster brewsteri*) boobies in the Gulf of California (Weimerskirch et al. 2009c), however, demonstrated greater sex-specific than species-specific differences in foraging behaviour. It has been suggested that the presence of superabundant prey in this high-productivity upwelling environment could reduce competitive pressure between species, leading to a lack of niche differentiation (Weimerskirch et al. 2009c). High prey availability might also allow greater flexibility in parental roles. Weimerskirch et al. (2009c) found that females of blue-footed and brown boobies spent more time at sea foraging than males and less time at the nest guarding the chick(s). Therefore, sex-specific differences in foraging behaviour may reflect a division of labour only possible in a high-productivity environment (Young et al. 2010b). The relative importance of species versus sex differences in the foraging behaviour of boobies breeding in productive, upwelling systems compared to those breeding in oligotrophic tropical waters may therefore be attributable to environmental effects.

Masked and red-footed boobies at Tromelin Island demonstrated a low degree of fidelity in successive foraging trips, a strategy that likely reflects the dynamic, unpredictable nature of prey patches associated with sub-surface marine predators (Weimerskirch 2007). High fidelity to foraging sites has been demonstrated in Peruvian boobies (*Sula variegata*; Zavalaga et al. 2010) and other marine predators (Baduini et al. 2006, Baylis et al. 2008, Call et al. 2008, Pettex et al. 2010). However, these studies were all conducted in high productivity environments. In a study of northern gannets (*Morus bassanus*; Hamer et al. 2001), differences in foraging site fidelity at 2 different breeding colonies were attributed to differences in prey predictability in local foraging areas. Low foraging site fidelity in tropical boobies (Anderson & Ricklefs 1987, Weimerskirch et al. 2005a) suggests that they must constantly adjust foraging trajectories to track ephemeral prey patches.

At Tromelin Island, masked boobies travelled further from the colony when foraging than red-footed boobies did. Conversely, at Palmyra Atoll, where masked and red-footed boobies also breed in sympatry, Young et al. (2010b) found that red-footed boobies travelled further than masked boobies to reach foraging sites for both brooding and incubating adults. Young et al. (2010b) suggested that the greater range of red-footed boobies reflected its more pelagic nature

(Nelson 1978, Schreiber et al. 1996) and more efficient flight abilities (Weimerskirch et al. 2005b), and may have been driven by intraspecific competition due to the large colony size (1000 to 2500 breeding pairs) of red-footed boobies on Palmyra. Masked boobies breed in smaller numbers (10 to 50 breeding pairs) at Palmyra, suggesting that lower levels of intraspecific competition might allow masked boobies to remain close to the colony when foraging (Young et al. 2010b).

Masked boobies at Tromelin Island (224 breeding pairs) had longer trip durations and greater maximum foraging ranges than at Palmyra Atoll (Young et al. 2010b) but smaller maximum ranges than at Clipperton Island (Weimerskirch et al. 2009b), the largest masked booby colony in the world (60 000 breeding pairs; Weimerskirch et al. 2009a). Differences in intraspecific competition due to colony size could account for differences in maximum ranges of masked boobies observed at these 3 sites. Alternatively, environmental differences may have influenced patterns of prey distribution at these sites. Because tracking of masked boobies at Clipperton Island occurred when adults were rearing large chicks, the later stage of breeding may also have influenced the greater foraging ranges seen at Clipperton. Red-footed boobies at Tromelin Island (129 pairs) had shorter trip durations and maximum ranges than at Palmyra Atoll (Young et al. 2010b), as well as compared to incubating and brooding red-footed boobies on Europa Island (2800 to 3800 breeding pairs; Weimerskirch et al. 2006). Maximum ranges of brooding birds were greater at Palmyra than at Europa, despite larger numbers of red-footed boobies nesting at Europa. Further comparative study would be necessary to determine whether colony size (Ashmole 1963, Ainley et al. 2003), environmental conditions (Huettmann & Diamond 2001), or both (Grémillet et al. 2004), account for observed variability in foraging range.

Masked boobies travelled at a faster rate than red-footed boobies, both at Tromelin Island and at Palmyra Atoll (present study and Young et al. 2010b, respectively), and this is likely related to differences in wing loading between species (Hertel & Ballance 1999). Greater wing loading in masked boobies could account for faster flight speeds, but also may increase the cost of flight (Hertel & Ballance 1999 and Young et al. 2010b). Given a higher cost of flight, and the presumed advantage of the larger masked booby when directly competing for prey with the smaller red-footed booby (Table 1; Ballance et al. 1997, González-Solís et al. 2000), it might be expected that

red-footed boobies would range farther than masked boobies when breeding in sympatry (Young et al. 2010b). Alternatively, overall foraging range may be affected more by intraspecific effects or environmental conditions.

Resource partitioning

We found differences in foraging distribution, habitat use, dive depths and diet between species, but not sexes, of boobies breeding at Tromelin Island. This evidence of spatial, environmental and dietary resource partitioning suggests that interspecific competition may have shaped foraging strategies of these sympatric species (Young et al. 2010a,b). However, given the current small population sizes at Tromelin, it is unclear how frequently competitive interactions occur between species at sea. A lack of sex-specific differences suggests that size-related differences between sexes do not lead to resource partitioning through competition, even in an extreme oligotrophic environment where prey resources are scarce and unpredictable (Longhurst & Pauly 1987). This lends further support to the notion that sex-specific differences in booby foraging behaviour may arise only in high productivity environments where superabundant prey allows greater flexibility in parental roles (Weimerskirch et al. 2009c, Young et al. 2010b). In this case, differences in foraging behaviour between sexes are related to breeding involvement, rather than influenced by competitive interactions for resources. This is consistent with previous research on masked and red-footed boobies in low-productivity environments; no sex-related differences in diet were found for masked boobies at Clipperton Island (Weimerskirch et al. 2009b) and Palmyra Atoll (Young et al. 2010b), or for red-footed boobies at Europa Island (Weimerskirch et al. 2006) and Palmyra Atoll (Young et al. 2010b).

The foraging ranges (95 % UD) of masked and red-footed boobies at Tromelin were not spatially segregated more than expected by chance alone. However, at a fine scale, we observed significant spatial and environmental segregation. The core (25 % UD) and focal (50 % UD) foraging regions of each species did not overlap, and ARS zones of each species could be discriminated by SST, wind speed and bathymetry. This suggests that mechanisms of resource partitioning occurred at the level of microhabitat (segregation of habitat within overlapping ranges), as opposed to geographic separation of foraging ranges (MacArthur 1958, Schoener 1974). Because many

studies of niche partitioning in marine birds have investigated spatial segregation on a large-scale (González-Solís et al. 2000, Hyrenbach et al. 2002, Kappes et al. 2010), the current study highlights the importance of fine-scale partitioning of resources in maintaining niche separation (Wilson 2010). Furthermore, masked boobies attained greater diving depths than red-footed boobies which provided an additional mechanism of resource partitioning between these species. This segregation is likely related to the greater mass of masked boobies, which would allow individuals of this species to reach greater depths when plunge diving (Ropert-Coudert et al. 2004).

Despite the relatively small scale within which Tromelin boobies forage during brooding (Fig. 1) and the coarse resolution of remotely-sensed environmental data investigated (0.033° to 0.167°), we found significant differences in the environmental characteristics of ARS zones of masked and red-footed boobies. Masked booby ARS zones were warmer, less windy and over deeper water than those of red-footed boobies. Masked boobies consumed predominantly flying fish, while red-footed boobies consumed predominantly squid, so the use of different habitats while foraging may be related to prey types consumed. In addition, masked boobies consumed larger prey items, so it is possible that environmental conditions selected by masked boobies allowed for more efficient capture of larger flying fish, as compared to the smaller squid consumed by red-footed boobies. Interspecific differences in diving depth likely also played a role in the size and type of prey available to each species. Our results suggest that dietary partitioning between booby species at Tromelin may remove the need for large-scale spatial partitioning between foraging ranges, whereas observed fine-scale spatial partitioning may reflect distribution of prey or conditions which favour prey capture.

At Palmyra Atoll, where there are greater numbers of breeding red-footed boobies, and fewer breeding masked boobies than at Tromelin, there was greater overlap in diet composition between masked and red-footed boobies (both species' diets were dominated by flying fish; Young et al. 2010b). The more productive, though still oligotrophic, environment near Palmyra may support a greater abundance of flying fish than the highly oligotrophic environment near Tromelin (Jaquemets et al. 2005). At Christmas Island in the Pacific Ocean, in a similar oceanic environment to Palmyra Atoll, masked and red-footed boobies consumed predominantly flying fish (Schreiber & Hensley 1976), whereas red-footed boo-

boobies in the extreme oligotrophic environment near Tromelin and Europa Island (Weimerskirch et al. 2006) consumed predominately squid. Given the higher energy density of fishes compared to squid (Clarke & Prince 1980), tropical boobies may select for flying fishes over squid when foraging. If flying fish are relatively scarce in the environment near Tromelin, the dietary partitioning we observed between species may be indicative of a competitive advantage of the larger masked booby to acquire energy rich prey when foraging at sea.

Overall energy content of prey items consumed by masked boobies was likely greater than that of red-footed boobies, due to greater energy density (Clarke & Prince 1980) and larger size of prey consumed. Masked boobies have greater whole body energetic requirements than red-footed boobies because of their larger body size; this size difference may, however, confer a competitive advantage in acquiring energetically favourable prey. The combination of these factors may account for the fact that masked boobies generally consume proportionately less squid than red-footed boobies (Schreiber & Hensley 1976, Diamond 1983) and other smaller congeners (Weimerskirch et al. 2009a). Masked boobies at Clipper-ton Island, in a moderately oligotrophic environment (average chlorophyll 0.2 mg m^{-3}), eat almost exclusively fishes, especially flying fishes, whereas the smaller brown booby demonstrates a reliance on squid (36% squid in the diet; Weimerskirch et al. 2008, 2009a). Although size-related competitive interactions may influence dietary choices by sympatric boobies, differences in regional oceanographic environments across locations also impact the sizes and species of prey available, which ultimately have important effects on energetic profitability of prey. Future comparative work including additional geographic locations, foraging environments, and combinations of sympatric congeners would help elucidate the processes underlying resource partitioning in boobies.

CONCLUSIONS

The results of this study highlight the importance of investigating resource partitioning at both geographic and fine scales, and across a variety of habitats and locations. The oligotrophic foraging environment surrounding Tromelin Island, as well as breeding population size, has likely shaped observed patterns of resource partitioning between masked and red-footed boobies. We observed interspecific differences in spatial segregation (at a fine scale), uti-

lization of differing environmental conditions, differences in diving depths, and significant dietary separation between species. Although our study covered only a short temporal period (one month during the brooding stage) at a single location, observed patterns of niche differentiation help explain how these 2 pantropical seabirds breed sympatrically on numerous islands throughout their range. Comparison with other study locations suggested a possible relationship between colony size and foraging range in masked and red-footed boobies; however, further study would be necessary to determine how environmental conditions also impact these parameters. Lower dietary overlap at extreme oligotrophic conditions (Tromelin) and differences in patterns of resource partitioning (species versus sex differences) at locations with differing environmental conditions suggest that productivity may influence competitive interactions between sympatric boobies. Given the likely importance of body size, breeding population size and environmental conditions in structuring competitive interactions, studies of booby foraging ecology at additional geographic locations, marine environments and combinations of sympatric congeners could provide further insight into the processes underlying observed patterns of resource partitioning.

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