Multi-colony tracking reveals segregation in foraging range, space use, and timing in a tropical seabird

Alice M. Trevail[1],[*],[#], Hannah Wood[2],[#], Peter Carr[2], Ruth E. Dunn[3],[4], Malcolm A. Nicoll[2], Stephen C. Votier[3], Robin Freeman[2]

[1]Environment & Sustainability Institute, University of Exeter, Penryn Campus, Penryn TR10 9FE, UK
[2]Institute of Zoology, Zoological Society of London, Regents Park, London NW1 4RY, UK
[3]The Lyell Centre, Heriot-Watt University, Edinburgh EH14 4AS, UK
[4]Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK

ABSTRACT: Colonial animals experience density-dependent competition for food, which is posited to influence foraging range and lead to inter-colony segregation. However, such patterns are poorly studied in the tropics, where predictable day lengths, oligotrophic conditions, and facultative foraging may alter the relationships between foraging and intra-specific competition. Here, we GPS-tracked 207 breeding red-footed boobies *Sula sula rubripes* (RFB) from 4 neighbouring Chagos Archipelago colonies (~1100 to 9200 breeding pairs) in the central Indian Ocean, to determine how foraging strategies (i.e. effort, segregation, and timing) vary with colony, while accounting for sex, monsoon season, stage of reproduction, year, and individual. During incubation and chick-rearing, RFBs commute to pelagic foraging grounds (maximum distance mean ± SE: 112.9 ± 3.7 km; total distance: 298.4 ± 6.2 km) over 1 to 5 d (18.5 ± 1.6 h). Foraging effort was highest at the largest colony, and greater among females than males. Departure angles varied among colonies, leading to foraging areas that were largely spatially segregated. Timing of departures and arrivals were strongly constrained by daylight hours, although females and birds at the largest colony left earliest. Our study highlights the importance of inter-colony differences in tropical seabird foraging, which may relate to different levels of intra-specific competition. Moreover, links between foraging times and colony size suggest a previously undescribed outcome of density-dependent competition, highlighting the importance of understanding colonial living across multiple dimensions.

KEY WORDS: Central-place foraging · *Sula sula rubripes* · Red-footed booby · Distributions · Indian Ocean · GPS tracking

1. INTRODUCTION

For animals that live in colonies, species interactions govern many aspects of their biology, including foraging (Ashmole 1963, Wakefield et al. 2013, Patterson et al. 2022). For instance, social information can enhance foraging efficiency (Buckley 1997, Thiebault et al. 2014), while intra-specific competition may reduce per capita intake, which in turn increases foraging range and ultimately limits colony size (Ashmole 1963, Lewis et al. 2001). To mitigate intraspecific competition, colonies often use distinct foraging areas (Bolton et al. 2019), reinforced by social information (Wakefield et al. 2013, Ceia & Ramos 2015). Colony size, which determines both intra-specific competition and the availability of social information, can therefore influence foraging strategies and segregation.

Seabirds have informed much of our understanding of colony and social effects on foraging behaviour (Danchin & Wagner 1997, Wakefield et al. 2013, Bolton et al. 2019), but research is biased towards high-latitude seas, where seasonally and spatially persistent productivity favour social information use (Riotte-Lambert & Matthiopoulos 2020). At lower latitudes, oligotrophy may exacerbate intra-specific competition (Oppel et al. 2015) and/or render information gathering too costly (Bocedi et al. 2012, Riotte-Lambert & Matthiopoulos 2020). However, recent research is challenging the paradigm that tropical predators rely on unpredictable resources (Catry et al. 2009, Soanes et al. 2021, Trevail et al. 2023), and so the environment may be constant enough to support information transfer. It is also unclear whether social interactions work in the same way to maintain at-sea segregation among tropical seabirds that commonly forage facultatively with subsurface predators (Au & Pitman 1986, Jaquemet et al. 2004) and where consistent day lengths and short twilight periods close to the equator may create additional constraints for diurnal foragers (Lewis et al. 2004, Pinet et al. 2011).

Local prey availability (Soanes et al. 2021) and conspecific density (Mendez et al. 2017) both affect foraging effort (Austin et al. 2021). The relative importance of intrinsic factors, such as sex (Austin et al. 2019) and breeding stage (Sommerfeld & Hennicke 2010), also varies across species ranges. If intra-specific competition governs behaviour, we can expect segregated foraging ranges that scale with colony size, in line with temperate species (Wakefield et al. 2013). However, multi-colony studies are essential to understand how intra-specific competition, local variability, and intrinsic factors all shape foraging strategies in the tropics (Mendez et al. 2017).

Here we GPS-tracked red-footed boobies *Sula sula rubripes* (RFBs) from 4 neighbouring colonies in the Chagos Archipelago, central Indian Ocean, comprising ~1100, 3300, 3500, and ~9200 breeding pairs and tested for inter-colony differences in foraging behaviour: spatial (at-sea distribution, colony-specific segregation, and departure directions), effort (duration, distal point, total distance travelled), and diel timing (colony departure and arrival). We accounted for the potential effects of sex, monsoon, and reproductive stage, while controlling for year and individual, to facilitate inter-colony comparisons. We predicted competition within and among colonies to affect foraging but noted that unpredictable resources and facultative foraging may alter the degree of segregation. We expected temporal differences among monsoon seasons to be smaller than the effect of intra-specific competition, resulting in segregated foraging ranges that scale with colony size.

2. MATERIALS AND METHODS

2.1. Study system

Research was conducted at 4 RFB colonies ≤172 km apart within the Chagos Archipelago Marine Protected Area (Hays et al. 2020, Carr et al. 2022): 2 colonies <2 km apart within the Diego Garcia atoll, namely Barton Point (7.23° S, 72.43° E; 9269 breeding pairs) and East Island (7.23° S, 72.42° E; 1113 breeding pairs); Nelson's Island (5.68° S, 72.32° E; 3300 breeding pairs); and Danger Island (6.39° S, 71.24° E; 3500 breeding pairs) during 2016, 2018–2019, and 2022–2023 (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m724p155_supp.pdf).

Climatology in the Indian Ocean is dominated by 2 wind-driven monsoon seasons (Schott & McCreary 2001, Lévy et al. 2007): (1) May–November and (2) November–May. During May–November, phytoplankton blooms occur along the coasts of the Bay of Bengal, Arabian Sea, and East Africa, with low levels of productivity protruding into the central Indian Ocean (Lévy et al. 2007). During November–May, the central Indian Ocean is largely oligotrophic (Lévy et al. 2007). In the Chagos Archipelago specifically, the November–May monsoon season is characterised by north-westerly winds and slightly warmer temperatures (hereafter referred to as the NW monsoon), whereas May–November is characterised by south-easterly winds and slightly cooler temperatures (hereafter referred to as the SE monsoon) (National Imagery and Mapping Agency 2001). RFBs breed asynchronously in the Chagos Archipelago, with 2 peaks per year coinciding with the 2 monsoon seasons (Carr et al. 2021). We would expect any effect of monsoon season on foraging strategies to be consistent across the archipelago; for example, sea surface temperature can determine the depth range of sub-surface predators and therefore could change the frequency of facultative foraging opportunities (Curnick et al. 2020, Orúe et al. 2020), while wind speed could change energetic costs of foraging trips (Clay et al. 2023).

Because of the remote nature of the Chagos Archipelago, both logistical and weather challenges affected our study design. Within the Diego Garcia atoll, tracking occurred at 2 sub-colonies (Barton Point: 2016–2019, and East Island: 2022, 1.8 km

Table 1. Sample sizes for each colony of red-footed boobies, monsoon season (NW: north-west, SE: south-east), sex, and breeding stage. Note, 2 individuals were tracked across multiple years at Diego Garcia. Unk.: unknown

Colony	Colony size (breeding pairs)	Lat. (°S)	Long. (°E)	Year	Monsoon	No. of ind.	No. of trips	No. ind. by sex			No. ind. by breeding stage			
								Female	Male	Unk.	Pre-egg laying	Incu-bation	Chick-rearing	Unk.
Barton Point	9269	7.23	72.43	2016	NW	11	15	8	3	0	3	8	0	0
					SE	31	71	15	14	2	1	18	12	0
				2018	NW	21	41	0	2	19	1	15	4	1
					SE	30	88	0	1	29	0	10	18	2
				2019	NW	9	17	4	4	1	3	2	4	0
East Island	1113	7.22	72.42	2022	NW	8	30	4	3	1	0	0	8	0
Diego Garcia	10382			All	All	107	262	31	25	51	8	51	45	3
Danger Island	3500	6.39	71.24	2019	NW	27	58	6	12	9	0	0	27	0
				All	All	27	58	6	12	9	0	0	27	0
Nelson's Island	3300	5.68	72.32	2018	SE	36	104	8	13	15	0	0	36	0
				2019	SE	25	39	0	0	25	0	8	17	0
				2023	NW	12	46	6	6	0	0	0	12	0
				All	All	73	189	14	19	40	0	8	65	0
All				All	All	207	509	51	56	100	8	59	137	3

apart), because there were very few breeding birds at Barton Point in 2022 following extreme weather and loss of nesting vegetation; locations are shown in Fig. S1. To explore the scales at which populations differentiate within the Chagos Archipelago, we treated these 2 sub-colonies separately in the analyses. We have tracking data for both monsoon seasons at Diego Garcia and Nelson's Island (Table 1); however, we were unable to access Danger Island during the SE monsoon due to adverse sea conditions.

2.2. GPS tracking of boobies

Shrub-nesting adults with an egg or chick were caught by hand and fitted with a heat-shrink-wrapped GPS logger (iGotU GT-120; 15 g, used during 2016, 2018, and 2019; or TechnoSmArt Axy-Trek Marine, 18 g, used during 2019 at Diego Garcia, and in 2022–2023) on the underside of the central 2 to 4 tail feathers, depending on moult condition, using marine Tesa (4651) tape. Geolocators and immersion loggers (Intigeo C330, Migrate Technology, 3.3 g) were attached to a plastic leg ring, but these data were not analysed in this study. Handling time lasted approximately 10 min and included feather sampling for genetic sexing (Carr et al. 2021), biometric measurements (maximum wing chord, bill to feathering, bill depth, and tarsus, all in mm), mass (g), and colour marking (Ritchey Super Sprayline Stock Marker). Birds at East Island and Danger Island were tracked during chick-rearing only. Post-deployment nest

attendance was monitored daily, and individuals were recaptured after at least 1 complete foraging trip when GPS devices were removed (84 % recovery across all colonies and years). Genetic sexing was carried out at the Institute of Zoology, Zoological Society of London, during 2016 and 2018 (Carr et al. 2021), by the University of Reunion as part of a collaboration on genetic connectivity during 2019 (unpublished), and commercially by Avian Biotech (https://animalgenetics.com/) during 2022–2023.

2.3. Processing GPS data

Loggers recorded a GPS fix every 5 min. Once downloaded, fixes outside the deployment period were removed. Foraging trips were defined as >1 km from the colony and >30 min in duration (Carr et al. 2022). From these data, we extracted 2 indices of spatial foraging behaviour: (1) utilisation distributions (UDs) and (2) departure angles; 3 measures of foraging effort: (3) trip duration (h), (4) total distance travelled (km), and (5) maximum distance from the colony (km); and timings of (6) departure and (7) arrival.

2.4. Spatial foraging behaviour

We mapped colony-specific UDs, for which 95 and 75 % contours indicate home range areas, and 50 and 25 % contours indicate core areas. We measured

inter-colony segregation using Bhattacharya's affinity (BA; Fieberg & Kochanny 2005), an index of spatial similarity ranging from 0 (distinct UDs) to 1 (identical UDs). UD calculations were derived across a 1 km grid using default smoothing parameters in the R package 'adehabitatHR' (Calenge 2006). We also mapped UDs and calculated overlap during 2019, when we had tracking data for 3 colonies (Barton Point, Danger Island, and Nelson's Island) during the same year. We calculated departure angle for each colony as the beeline angle from the nest to the distal point of the foraging trip, and along a range of vectors to different distances to the colony: 1, 5, 10, and 25 km.

To explore intra-colony differences in spatial foraging behaviour, we calculated BA between pairwise comparisons at each colony: (1) NW and SE monsoon seasons (Barton Point and Nelson's Island), (2) females and males, (3) chick-rearing and incubation (Barton Point and Nelson's Island), and (4) single- and multi-day trips. We mapped tracks for each distinct study period.

2.5. Foraging effort

To quantify whether foraging effort varied among the 4 focal colonies, we used mixed effect models of trip duration, total distance travelled, and maximum distance from the colony on complete trips only. We used lognormal regression to account for positive skew (lower Akaike's information criterion, AIC, compared to modelling gamma distributions on non-transformed data). We included monsoon season, sex, and breeding stage as fixed effects to test their effects on trip metrics. We included year (as a factor) and individual ID as random effects to account for the hierarchical structure of the data. We present effect significance from the full model using the R package 'lmerTest' (Kuznetsova et al. 2017). We extracted parameter estimates of significant effects using 'ggemmeans()' within the 'ggeffects' R package (Lüdecke 2018) to marginalise over non-focal effects.

2.6. Foraging timing

Timing of departure and arrival (time of 24 h day) was quantified from the time an individual left or re-entered a circle of radius 1 km around each colony, respectively, for complete trips only. To model intra- and inter-colony differences in departure and arrival times as continuous variables (rather than limited to 00:00–24:00 h or circular) we calculated departure times relative to nautical dawn and arrival times relative to nautical dusk, in hours using 'suncalc' in R (Agafonkin & Thieurmel 2018). As with foraging effort, we ran mixed effect models of departure/ arrival time on complete trips only. We included monsoon season, sex, and breeding stage as fixed effects, and year (as a factor) and individual ID as random effects. To further explore the relationship between foraging effort and trip timings, we tested whether undertaking a multi-day trip (rather than a single-day trip) was linked to trip timings by also including multi-day or single-day as a factor. We present effect significance from the full model, and extracted marginalised parameter estimates of significant effects.

3. RESULTS

3.1. Tracking data

We tracked 207 birds across 4 colonies (99 at Barton Point, 8 at East Island, 27 at Danger Island, and 73 at Nelson's Island), generating 509 foraging trips in total across 5 years (Table 1; Fig. S2). Colonies were not tracked simultaneously, but data were collected during the same calendar year from multiple colonies in 2018 (Barton Point and Nelson's Island) and 2019 (Barton Point, Danger Island, and Nelson's Island; Fig. S2). Birds travelled to deeper waters east and west of the archipelago, avoiding shallow waters in the Great Chagos Bank (Fig. 1). At-sea distributions of all colonies were predominantly contained within the Chagos Archipelago Marine Protected Area (Fig. 1).

3.2. Foraging distribution

Individual tracks and colony-specific UDs showed differential at-sea foraging segregation (Fig. 1b). There was near-complete overlap in UDs between East Island and Barton Point, the 2 colonies in the Diego Garcia atoll (Fig. 1b), with a BA of 0.77. Among all other colonies, there was no overlap of 25 and 50% UDs (Fig. 1b), and BA was <0.25 in all cases. The lowest overlap was observed between Danger Island and all other colonies (BA values and distances between colonies were: Barton Point 0.01, 162 km apart; East Island 0.02, 161 km apart; Nelson's Island <0.001, 142 km apart). Between Nelson's Island and the 2 Diego Garcia colonies, overlap was
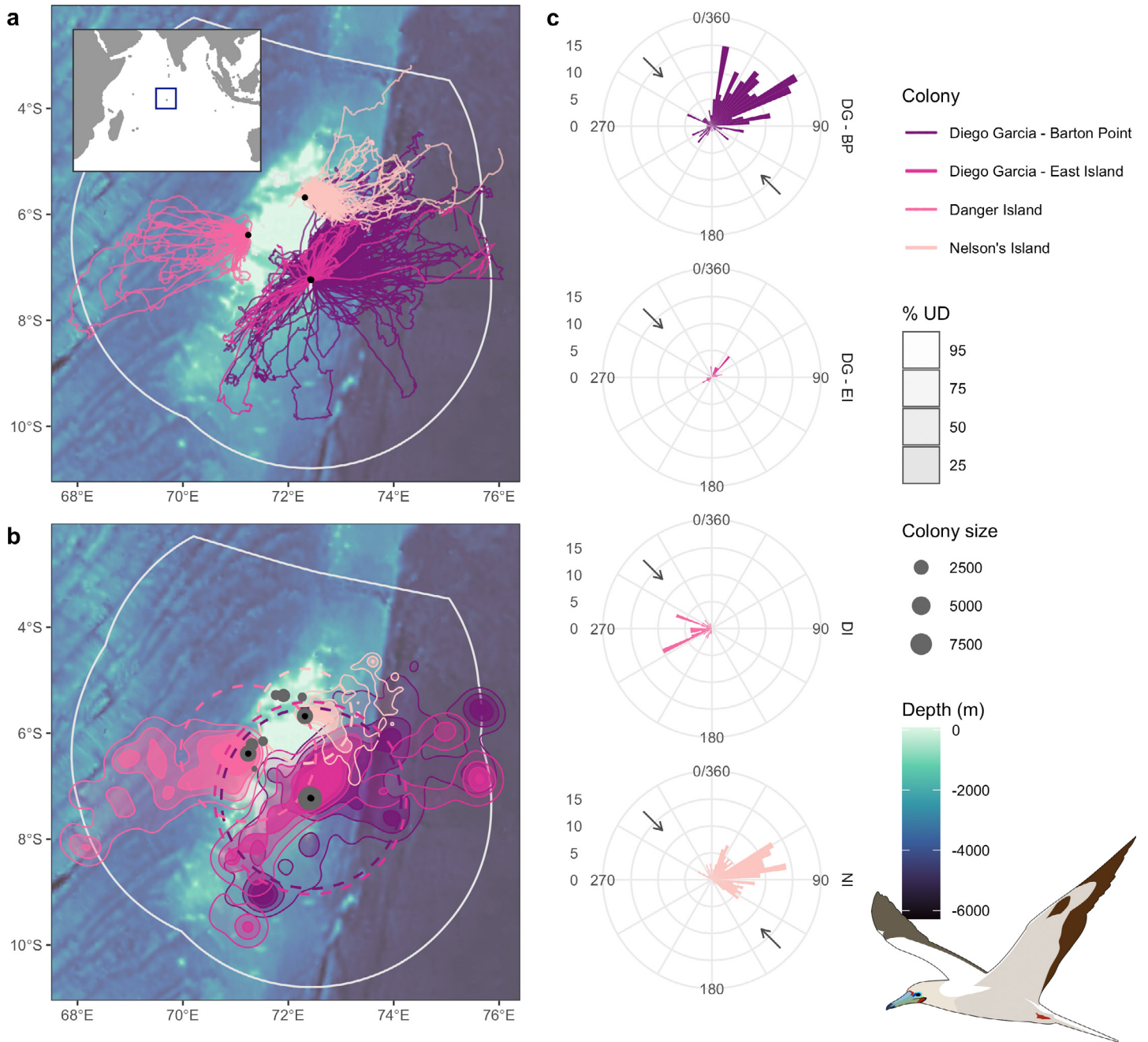
Fig. 1. Red-footed booby foraging area use in the Chagos Archipelago, central Indian Ocean (inset panel); n = 207 total individuals from 4 colonies; 2 in the Diego Garcia Atoll: Barton Point (n = 99) and East Island (n = 8); Danger Island (n = 27); and Nelson's Island (n = 73). (a) Tracked birds mostly remained within the marine protected area (light grey outline) during the breeding season. (b) Birds from the Diego Garcia atoll foraged in very similar areas but were largely segregated at sea from both Danger Island and Nelson's Island; there was no overlap between any 25 and 50 % utilisation distributions (UDs) even though mean foraging ranges overlap (dashed lines). (c) Departure angles to the distal points were directed away from the shallow, central Great Chagos Bank and most commonly perpendicular to the prevailing winds during tracking (black arrows). In panels (a) and (b), black circles indicate tracked colony locations. Grey circles in panel (b) show all red-footed booby colonies in the archipelago, sized proportionally to colony size (number of breeding pairs)

still low (BA: Barton Point 0.25, East Island 0.13, both 172 km apart). When considering foraging areas during 2019 only, for which we have tracking data from

all colonies, colony foraging areas were still largely distinct (Fig. S3); there was no overlap among 25 and 50 % core areas, and BA among colonies was < 0.25

(Barton Point–Danger Island 0.02; Barton Point–Nelson's Island 0.21; Danger Island–Nelson's Island <0.01). Departure angle varied among the 4 tracked colonies (Fig. 1c). Breeders on Diego Garcia departed primarily in a north-easterly direction, with a smaller number departing south-west; departures were westerly at Danger Island and north-easterly at Nelson's Island (Fig. 1c). Departure angles were consistent among vectors of varying distances to the colony (Fig. S4) and were primarily perpendicular to the prevailing wind direction.

Spatial overlap among intra-colony effects was high (Fig. S5): BA between monsoon seasons was 0.77 at Barton Point and 0.85 at Nelson's Island; between females and males, BA was 0.74 at Barton Point, 0.56 at East Island, 0.86 at Danger Island, and 0.78 at Nelson's Island; between chick-rearing and incubation, BA was 0.78 at Barton Point and 0.77 at Nelson's Island. Overlap was lower between single- and multi-day trips, reflecting a difference in travel distance (Fig. S5): BA was 0.53 at Barton Point, 0.33 at East Island, 0.40 at Danger Island, and 0.63 at Nelson's Island. Tracked RFBs foraged in similar directions each year, across monsoon seasons (Fig. S5).

3.3. Foraging effort

Foraging trip duration averaged 18.5 ± 1.6 h (SE; range 0.5–111.1 h), total distance travelled averaged 298.4 ± 6.2 km (range 1.8–1502 km), and maximum distance from the colony averaged 112.9 ± 3.7 km (range 1.4–424.4 km; Table 2). Foraging trip duration

was also multimodal; most trips were <24 h, with decreasing numbers of 2, 3, 4, and 5 d outings (Fig. 2a).

There were significant effects of colony and sex on trip duration, total distance, and maximum distance (Fig. 2b; Tables S1–S3). Overall, birds from Barton Point (the largest colony with 9269 breeding pairs) travelled farthest and for longest (model parameter estimates, 95% confidence intervals; trip duration: 16.7 h, 11.1–25.1 h; max. distance: 97.4 km, 64.4–147.4 km; total distance: 247.4 km, 160.4–381.6 km), followed by Nelson's Island (3500 breeding pairs; trip duration: 9.4 h, 6.9–14.6 h; max. distance: 50.9 km, 32.4–80.1 km; total distance: 137.0 km, 85.4–219.6 km) and Danger Island (3300 breeding pairs; trip duration: 7.4 h, 4.1–13.2 h; max. distance: 38.9 km, 21.4–70.7 km; total distance: 99.3 km, 53.3–184.7 km). There was no difference between foraging trip metrics atF East Island and any other colony (Tables S1–S3, p > 0.05), where there was also greatest variation around the mean estimates (1113 breeding pairs; trip duration: 12.8 h, 5.8–28.1 h; max. distance: 74.0 km, 32.9–166.1 km; total distance: 171.2 km, 73.7–397.7 km). From data across all colonies, females travelled farther and for longer than males (model parameter estimates, 95% confidence intervals; trip duration: females 12.7 h, 8.2–19.8 h, males 7.8 h, 5.0–12.0 h; max. distance: females 72.5 km, 46.0–114.2 km, males 42.9 h, 27.4–67.3 h; total distance: females 180.4 km, 112.3–289.8 km, males 109.4 km, 68.6–174.6 km). This pattern was consistent when limited to single-day trips only (Fig. S6).

Table 2. Foraging trip metrics across the Chagos Archipelago for each red-footed booby colony and monsoon period (NW: north-west, SE: south-east) included in this study

| Colony	Year	Monsoon	Trip duration (h)				Total distance (km)				Max. distance (km)			
			Mean	SE	Min.	Max.	Mean	SE	Min.	Max.	Mean	SE	Min.	Max.
Barton Point	2016	NW	44.0	1.4	0.7	86.2	564.6	4.7	11.9	975.9	250.4	3.1	3.9	406.1
		SE	26.9	0.7	1.4	73.1	412.8	2.6	11.2	867.5	152.6	1.5	6.4	322.8
	2018	NW	26.9	0.9	1.0	80.0	422.7	3.0	1.8	862.4	159.2	1.8	3.9	298.6
		SE	16.6	0.6	1.4	60.2	268.4	2.0	3.2	816.5	103.3	1.1	1.4	236.4
	2019	NW	27.6	1.4	0.8	85.5	524.8	5.6	21.9	1501.9	160.9	2.9	8.9	422.8
East Island	2022	NW	21.7	1.5	0.5	102.5	360.5	5.3	2.2	1379.2	133.9	2.9	1.5	397.2
Diego Garcia	All	All	27.3	1.2	0.5	102.5	425.6	4.2	1.8	1501.9	160.1	2.9	1.4	422.8
Danger Island	2019	NW	16.1	0.8	0.9	111.1	267.6	2.8	13.4	1265.6	98.0	1.7	5.9	421.7
	All	All	16.1		0.9	111.1	267.6		13.4	1265.6	98.0		5.9	421.7
Nelson's Island	2018	SE	5.7	0.2	0.5	12.3	105.1	1.1	8.2	248.0	38.1	0.7	4.4	91.5
	2019	SE	21.4	0.8	1.4	62.6	314.3	2.8	27.8	927.0	136.1	1.7	12.4	424.4
	2023	NW	9.1	0.7	0.6	36.1	186.0	3.1	11.6	680.8	67.7	1.8	4.7	231.4
	All	All	12.1	1.7	0.5	62.6	201.8	5.9	8.2	927.0	80.7	4.1	4.4	424.4
All	All	All	18.5	1.6	0.5	111.1	298.4	6.2	1.8	1501.9	112.9	3.7	1.4	424.4
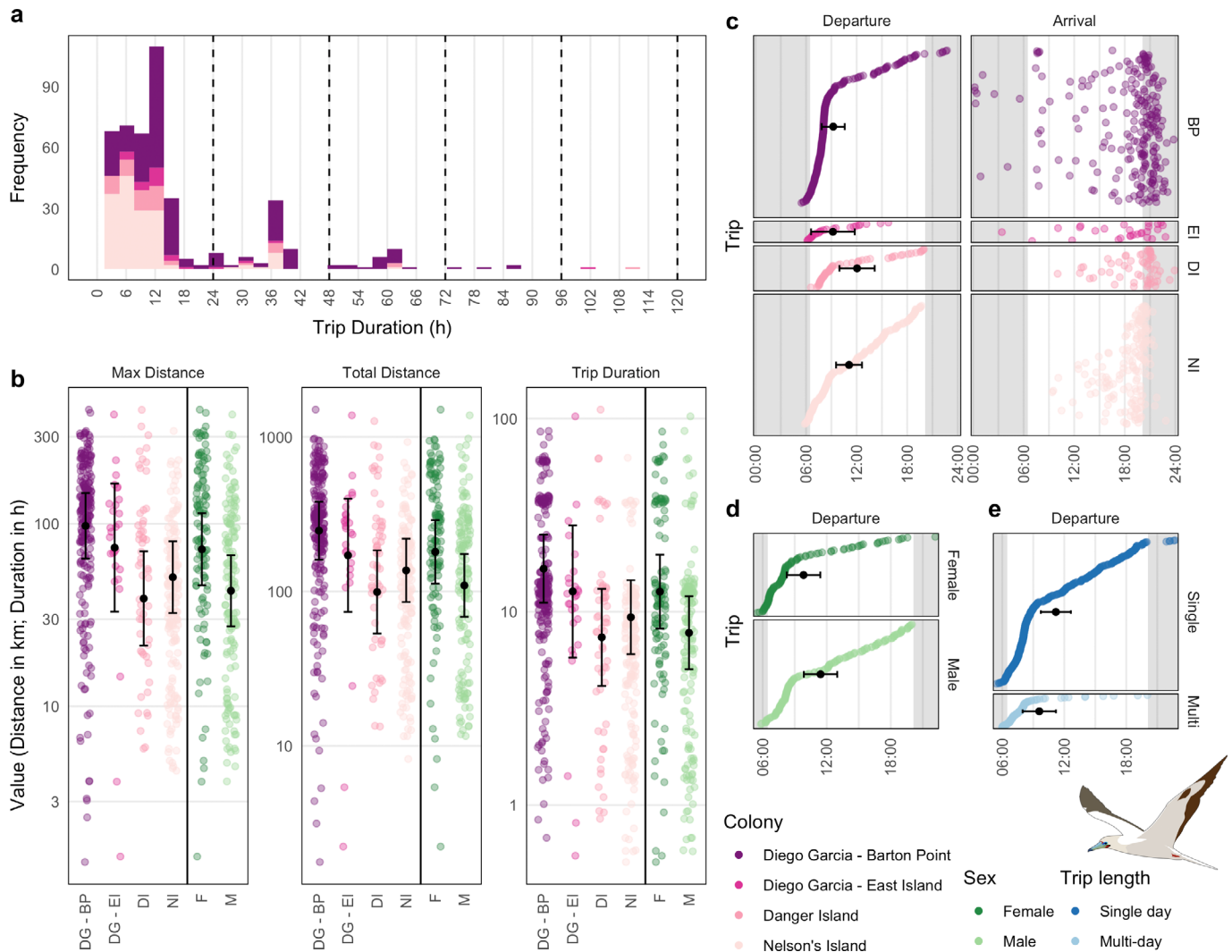
Fig. 2. Red-footed booby foraging effort in the Chagos Archipelago; n = 207 total individuals from 4 colonies (see Fig. 1). At all colonies, (a) most trips were short (<1 d), with decreasing numbers of 2, 3, 4, and 5 d outings. (b) Foraging effort differed between Barton Point (BP) and both Danger Island (DI) and Nelson's Island (NI) in terms of maximum distance from the colony, total distance travelled, and trip duration. (c−e) Departure times during foraging trips (presented along the y-axes) predominantly occurred during daylight hours, and arrival times were concentrated around dusk at all colonies. (c) Both departure and arrival times differed among colonies, (d) females departed earlier than males, and (e) departure times were earlier on multi-day trips than single-day trips. Dashed lines in panel (a) delineate whole days. Error bars in panels (b−e) are model predictions ± 95% confidence intervals from linear mixed effect regressions. Grey shading in panels (c−e) shows night-time hours according to mean nautical dawn and dusk over the study period

3.4. Foraging timing

At all colonies, RFB foraging times were constrained by daylight hours; departures started around dawn and arrivals peaked near dusk (Fig. 2c). Departure times varied by colony, sex, and trip duration (single-/multi-day) (Fig. 2c−e; Table S4). RFBs from Barton Point departed earliest (parameter estimates in hours after dawn, 95% confidence intervals; 2.7, 1.4−4.1), followed by Nelson's Island (4.6, 3.1−6.1) and Danger Island (5.6, 3.5−7.7).

There was no difference between departure times at East Island (2.7, 0.1−5.3) and any other colony (Table S4, p = 0.98). Across all colonies, females departed earlier (3.4, 1.8−4.9) than males (4.9, 3.4−6.5), and RFBs departed earlier on multi-day trips (3.1, 1.5−4.7) than on single-day trips (4.7, 3.3−6.2). There was no effect of monsoon season or breeding stage on departure times, and arrival times were consistent across all factors (colony, sex, monsoon season, breeding stage, and single-/multi-day trips; Table S5, p > 0.05).

4. DISCUSSION

Our study shows significant inter-colony differences in RFB foraging behaviour. While birds from the neighbouring East Island and Barton Point sub-colonies foraged in similar locations, they were spatially segregated from the other colonies that had exclusive core foraging areas (Fig. 1). Foraging effort (trip duration and distance) scaled with colony size (Fig. 2), and birds at the largest colony left earliest. Females undertook longer trips and departed earlier, although both sexes foraged in the same areas. There was no effect of monsoon season or reproductive stage on foraging distribution, effort, or timing. The significant inter-colony differences and at-sea segregation are probably best explained by intra-specific competition for food, both within and among colonies (Wakefield et al. 2013). Importantly, this effect occurs in oligotrophic waters, where seabirds can be particularly dependent on facultative foraging with sub-surface pelagic predators in deeper waters (Au & Pitman 1986).

4.1. Inter-colony segregation

In a recent review of inter-colony segregation of seabird foraging areas, Bolton et al. (2019) found that 79% of 39 multi-colony studies exhibited non-overlapping distributions, although only 1 species was a tropical breeder: the Laysan albatross *Phoebastria immutabilis* (Young et al. 2009, Orben et al. 2021). Here, we found evidence of different spatial scales of population segregation in the Chagos Archipelago. Two colonies <2 km apart within the Diego Garcia atoll showed overlapping foraging areas and comparable foraging effort, suggesting that they may form a single meta-population. Individuals could move within breeding colonies on East Island and Barton Point on the eastern arm of Diego Garcia (Fig. S1), in response to weather-driven vegetation changes that alter breeding habitat availability throughout the atoll. At a larger spatial scale, despite Danger Island, Nelson's Island, and Diego Garcia being within the foraging range of each other, at-sea foraging areas were either entirely distinct, or showed little overlap (Fig. 1b). Furthermore, birds tended to avoid waters to the north and northwest where there are several other comparatively large RFB colonies (Fig. 1b; showing Peros Banhos and Salomon Islands colonies). This suggests intra-specific competition among colonies, and perhaps that resource landscapes are predictable enough for reliable social information transfer (Bocedi et al. 2012, Riotte-Lambert & Matthiopoulos 2020).

The shallow Great Chagos Bank may be unsuitable habitat for RFBs and thus effect colony segregation. Few tracked RFBs travelled across the centre of the archipelago (Fig. 1), where boat-based surveys have previously observed low seabird abundance (Perez-Correa et al. 2020). This may be because these shallow waters are unsuitable for facultative species like skipjack tuna *Katsuwonus pelamis* (Jaquemet et al. 2004, Dunn & Curnick 2019) and billfishes (Thoya et al. 2022), and/or pelagic prey species such as flying fish (Exocoetidae) and flying squid (Ommastrephidae) (Jaquemet et al. 2005, Weimerskirch et al. 2005a, Miller et al. 2018). Furthermore, intra-specific competition with other sulids breeding in the archipelago could reinforce pelagic distributions via habitat partitioning (Austin et al. 2021), although these other species occur in relatively low numbers, so this seems unlikely (924 pairs of brown booby *Sula leucogaster* breed on 7 islands, and 164 pairs of masked booby *S. dactylatra* breed on 2 islands; Carr et al. 2021).

4.2. Intra-colony effects

Foraging effort of RFBs can differ between sexes (Weimerskirch et al. 2006), among breeding stages (Weimerskirch et al. 2006), and with environmental conditions (Mendez et al. 2017, Gilmour et al. 2018), although the extent of these effects varies across the species' range (Lewis et al. 2005, Austin et al. 2021). RFBs are slightly sexually dimorphic; females are 15% larger and 19% heavier than males in the Chagos Archipelago (Carr 2021), which corresponds with greater foraging effort by females (Weimerskirch et al. 2006). As well as undertaking longer foraging trips (Fig. 2b), females left the colony earlier in the day (Fig. 2d), although both sexes foraged in similar areas at-sea (Fig. S5). Despite the effect of sex on foraging effort metrics, there was little at-sea segregation between sexes. We found no evidence for breeding stage differences in foraging trip metrics, which appears to be the norm in this species (Lewis et al. 2005, Young et al. 2010, Almeida et al. 2021, Austin et al. 2021).

Monsoon season did not influence foraging behaviour, despite potential shifts in at-sea foraging conditions. Cooler sea surface temperatures during the SE monsoon season are typically associated with increased tuna presence, and therefore potentially greater facultative foraging opportunities (Orúe et al.

2020). However, this effect was not visible in colony foraging effort or distributions. Our models accounted for annual differences in foraging behaviour, and there was no visible difference in foraging direction among years (Fig. S2). At Nelson's Island, birds tracked during 2019 travelled farther from the colony (Fig. S2), which could be because the 2019 extreme positive Indian Ocean dipole event caused poor foraging conditions (Shi & Wang 2021), although this effect was not apparent at Diego Garcia. Although logistically challenging, more contemporaneous data across multiple colonies would be needed to robustly test for interannual differences.

4.3. Foraging effort

Here, we observed foraging ranges that scale with colony size among neighbouring populations, a pattern that largely holds true across the breeding range of RFBs (Mendez et al. 2017). In this study, RFBs undertook foraging trips that were, on average, 18.5 ± 1.6 h long and reached a maximum of 112.9 ± 3.7 km from the colony. These metrics are similar to RFBs breeding at isolated colonies in the Pacific (1400 breeding pairs; Lewis et al. 2005, Young et al. 2010) and Caribbean (1000 breeding pairs; Austin et al. 2021), but are longer than elsewhere in the Indian Ocean, including both Tromelin (129 breeding pairs; Kappes et al. 2011) and Europa Island, where multi-day trips are rare (2800–3800 breeding pairs; Weimerskirch et al. 2006, Mendez et al. 2017). Our results demonstrate temporal and spatial partitioning at-sea to mitigate inter-colony competition, which, alongside local resource landscapes (Cairns 1988, Mendez et al. 2017), may further explain regional variability in foraging effort.

4.4. Foraging times

RFBs tend to forage diurnally with departure times constrained by dawn and arrival times by dusk (Fig. 2c,d) leading to a multi-modal distribution of trip durations (Fig. 2a). Most departures occurred soon after dawn (Fig. 2c,d), which may enable individuals to maximise available foraging time, whilst minimising energetic costs of searching for sufficient prey during limited daylight hours (Lewis et al. 2004). This diurnal time limit may be compounded in the tropics where day lengths and twilight periods are relatively short, compared to those experienced by high latitude-breeding seabirds that do not appear to be so constrained by daylight hours during summer (Daunt et al. 2006). Returning close to twilight could reduce kleptoparasitism risk by frigatebirds. These birds aggregate at the colony to attack individuals returning with food (Austin et al. 2019), and have fewer crepuscular than diurnal chases (Le Corre & Jouventin 1997). Alternatively, RFBs may more commonly undertake single day trips to avoid overnighting on the water because of predation risk (Weimerskirch et al. 2005b, Zavalaga et al. 2012), unless undertaking multi-day trips. Temperate breeding Cape gannets *Morus capensis* also forage visually during daylight hours, leading to similar multi-modal trip distributions (Rishworth et al. 2014). However, departures after dusk appear more common than we observed here, perhaps because the risks of being at sea overnight are higher in this tropical system.

A key finding was that birds from the largest colony (Barton Point) departed earlier than birds from the smaller colonies, Nelson's Island and Danger Island (Fig. 2c). We propose that these differences relate to a combination of intraspecific competition and diurnal foraging constraints—birds experiencing highest competition are only able to complete a trip by leaving early and returning late. Furthermore, at all colonies, females departed earlier than males, and RFBs departed earlier on multi-day trips than single-day trips. The necessity to undertake a long trip may be known in advance of departure, or there could be a decision process to maximise foraging opportunities that can only be reached on a long trip (Weimerskirch et al. 2020, Phillips et al. 2023). Either way, short day lengths and twilight periods in the tropics may cue foraging decisions. Further research into fine-scale behaviour could answer such questions about how birds locate and prioritise foraging opportunities in these landscapes.

4.5. Conclusions

Our work shows inter-colony differences in RFB foraging behaviour, possibly related to intraspecific food competition within and among colonies. Between-colony segregation is common among high-latitude seabirds (Bolton et al. 2019); our work provides valuable evidence that similar patterns also prevail in the tropics, and that segregation can also drive temporal adjustments in foraging behaviour. How seabirds optimise foraging opportunities within tropical ecosystems remains a priority for future research.

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