

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

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4 Running page head: Intra-specific competition on tropical seabird foraging

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22 Abstract

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

40 **Keywords:** central-place foraging, red-footed booby, distributions, Indian Ocean, GPS tracking

## 41 1. Introduction

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

50 Seabirds have informed much of our understanding of colony- and social-effects on foraging behaviour  
51 (Danchin & Wagner 1997, Wakefield et al. 2013, Bolton et al. 2019), but research is biased towards  
52 high latitude seas, where seasonally and spatially persistent productivity favour social information use  
53 (Riotte-Lambert & Matthiopoulos 2020). At lower latitudes, oligotrophy may exacerbate intra-specific  
54 competition (Oppel et al. 2015) and/or render information gathering too costly (Bocedi et al. 2012,

55 Riotte-Lambert & Matthiopoulos 2020). However, recent research is challenging the paradigm that  
56 tropical predators rely on unpredictable resources (Catry et al. 2009, Soanes et al. 2021, Trevail et al.  
57 2023), and so the environment may be constant enough to support information transfer. It is also  
58 unclear whether social interactions work in the same way to maintain at-sea segregation among  
59 tropical seabirds that commonly forage facultatively with subsurface predators (Au & Pitman 1986,  
60 Jaquemet et al. 2004) and where consistent day lengths and short twilight periods close to the equator  
61 may create additional constraints for diurnal foragers (Lewis et al. 2004, Pinet et al. 2011).

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

69 Here we GPS-track red-footed boobies, *Sula sula rubripes* (hereafter RFB), from four neighbouring  
70 colonies in the Chagos Archipelago, central Indian Ocean, comprising ~1,100, 3,300, 3,500 and ~9,200  
71 breeding pairs and test for inter-colony differences in foraging behaviour: spatial (at-sea distribution,  
72 colony-specific segregation, and departure directions), effort (duration, distal point, total distance  
73 travelled) and diel timing (colony departure and arrival). We accounted for the potential effects of  
74 sex, monsoon, and reproductive stage, while controlling for year and individual, to facilitate inter-  
75 colony comparisons. We predict competition within and among colonies to effect foraging but note  
76 that unpredictable resources and facultative foraging may alter the degree of segregation. We expect  
77 temporal differences among monsoon seasons to be smaller than the effect of intra-specific  
78 competition, resulting in segregated foraging ranges that scale with colony size.

## 79 2. Material & Methods

### 80 **2.1. Study system**

81 Research was conducted at four RFB colonies  $\leq 172$ km apart within the Chagos Archipelago Marine  
82 Protected Area (Hays et al. 2020, Carr et al. 2022): two colonies <2km apart within the Diego Garcia  
83 atoll, Barton Point (7.23°S 72.43°E; 9269 breeding pairs) and East Island (7.23°S 72.42°E; 1113  
84 breeding pairs), Nelson's Island (5.68°S 72.32°E; 3300 breeding pairs), and Danger Island (6.39°S  
85 71.24°E; 3500 breeding pairs) during 2016, 2018-19 and 2022-23 (Figure S1).

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

101 Because of the remote nature of the Chagos Archipelago, both logistical and weather challenges  
102 effected our study design. Within the Diego Garcia atoll, tracking occurred at two sub-colonies (Barton  
103 Point: 2016-19, and East Island: 2022, 1.8km apart) because there were very few breeding birds at  
104 Barton Point in 2022 following extreme weather and loss of nesting vegetation; locations are shown  
105 in supplementary material (Fig S1). To explore the scales at which populations differentiate within the  
106 Chagos Archipelago, we treat these two sub-colonies separately in analyses. We have tracking data  
107 for both monsoon seasons at Diego Garcia and Nelson’s Island (Table 1), however we were unable to  
108 access Danger Island during the SE monsoon due to adverse sea conditions.

## 109 **2.2. GPS tracking boobies**

110 Shrub-nesting adults with an egg or chick were caught by hand and fitted with a heat-shrink wrapped  
111 GPS logger (iGotU GT-120; 15g, used during 2016, 2018, and 2019; or TechnoSmArt Axy-Trek Marine,  
112 18g, used during 2019 at DG, and 2022-23) on the underside of the central two to four tail feathers,  
113 depending on moult condition, using marine Tesa (4651) tape. Geolocators and immersion loggers  
114 (Intigeo C330, Migrate technology, Cambridge, UK; 3.3g) were attached to a plastic leg ring, but these  
115 data were not analysed in this study. Handling time lasted approximately 10-minutes and included  
116 feather sampling for genetic sexing (Carr et al. 2021), biometric measurements (maximum wing chord,  
117 bill to feathering, bill depth and tarsus, all in mm), mass (g) and colour marking (Ritchey Super  
118 Sprayline Stock Marker). Birds at East Island and Danger Island were tracked during chick-rearing only.

119 Post-deployment nest attendance was monitored daily, and individuals were recaptured after at least  
120 one complete foraging trip when GPS devices were removed (84% recovery across all colonies and  
121 years). Genetic sexing was carried out at the Institute of Zoology, Zoological Society of London during  
122 2016 and 2018 (Carr et al. 2021), by the University of Reunion as part of a collaboration on genetic  
123 connectivity during 2019 (unpublished), and commercially by Avian Biotech during 2022-23.

### 124 **2.3. Processing GPS data**

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

### 131 **2.4. Spatial foraging behaviour**

132 We mapped colony-specific utilisation distributions (UDs), for which 95 and 75% contours indicate  
133 home range areas, and 50 and 25% contours indicate core areas. We measured inter-colony  
134 segregation using Bhattacharya's affinity (BA; Fieberg & Kochanny 2005); an index of spatial similarity  
135 ranging from 0 (distinct UD) to 1 (identical UD). UD calculations were derived across a 1km grid using  
136 default smoothing parameters in the R package *adehabitatHR* (Calenge 2006). We also mapped UD  
137 and calculated overlap during 2019, when we have tracking data for three colonies (Barton Point,  
138 Danger Island, and Nelson's Island) during the same year. We calculated departure angle for each  
139 colony as the beeline angle from the nest to the distal point of the foraging trip, and along a range of  
140 vectors to different distances to the colony; 1km, 5km, 10km & 25km.

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

### 145 **2.5. Foraging effort**

146 To quantify whether foraging effort varied among the four focal colonies, we used mixed effect models  
147 of trip duration, total distance travelled and maximum distance from the colony on complete trips,  
148 only. We used lognormal regression to account for positive skew (lower Akaike's Information Criterion

149 (AIC) compared to modelling Gamma distributions on non-transformed data). We included monsoon  
150 season, sex, and breeding stage as fixed effects to test their effects on trip metrics. We included year  
151 (as a factor) and individual ID as random effects to account for the hierarchical structure of the  
152 data. We present effect significance from the full model using the R packages *lmerTest* (Kuznetsova et  
153 al. 2017). We extracted parameter estimates of significant effects using *ggemmeans()* within the  
154 *ggeffects* R package (Lüdecke 2018) to marginalise over non-focal effects.

## 155 **2.6 Foraging timing**

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

167

## 168 **3. Results**

### 169 **3.1. Tracking data**

170 We tracked 207 birds across four colonies (99 at Barton Point, 8 at East Island, 27 at Danger Island,  
171 and 73 at Nelson's Island), generating 509 foraging trips in total across 5 years (Table 1, Figure S2).  
172 Colonies were not tracked simultaneously, but data were collected during the same calendar year  
173 from multiple colonies in 2018 (Barton Point and Nelson's Island) and 2019 (Barton Point, Danger  
174 Island, and Nelson's Island; Figure S2). Birds travelled to deeper waters east and west of the  
175 archipelago, avoiding shallow waters in the Great Chagos Bank (Fig. 1). At-sea distributions of all  
176 colonies were predominantly contained within the Chagos Archipelago Marine Protected Area (Fig.  
177 1).

### 178 **3.2. Foraging distribution**

179 Individual tracks and colony specific utilisation distributions showed differential at-sea foraging  
180 segregation (Fig. 1b). There was near-complete overlap in UD<sub>s</sub> between East Island and Barton Point,  
181 the two colonies in the Diego Garcia atoll (Fig. 1b), with Bhattacharya's affinity of 0.77. Among all  
182 other colonies, there was no overlap of 25 and 50% UD<sub>s</sub> (Fig. 1b) and Bhattacharya's affinity was <0.25  
183 in all cases. There was lowest overlap between Danger Island and all other colonies; (BA values and  
184 distances between colonies were: Barton Point 0.01, 162km apart; East Island 0.02, 161km apart;  
185 Nelson's Island <0.001, 142km apart). Between Nelson's Island and the two Diego Garcia colonies,  
186 overlap was still low (BA: Barton Point 0.25, East Island 0.13, both 172km apart). When considering  
187 foraging areas during 2019 only, when we have tracking data from all colonies, colony foraging areas  
188 were still largely distinct (Fig. S3); there was no overlap among 25% and 50% core areas and  
189 Bhattacharya's affinity among colonies was <0.25 (Barton Point – Danger Island 0.02; Barton Point –  
190 Nelson's Island 0.21; Danger Island – Nelson's Island <0.01). Departure angle varied among the four  
191 tracked colonies (Fig. 1c). Breeders on Diego Garcia departed primarily in a north-easterly direction,  
192 with a smaller number departing southwest, at Danger Island departures were westerly and at  
193 Nelson's Island north-easterly (Fig. 1c). Departure angles were consistent among vectors of varying  
194 distances to the colony (Fig. S4) and were primarily perpendicular to the prevailing wind direction.

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

### 203 **3.3. Foraging effort**

204 Foraging trip duration averaged  $18.5 \pm 1.6$  hours (range 0.5-111.1 hrs), total distance travelled  
205 averaged  $298.4 \pm 6.2$  km (range 1.8 – 1,502 km), and maximum distance from the colony averaged  
206  $112.9 \pm 3.7$  km (range 1.4 – 424.4 km; Table 2). Foraging trip duration was also multimodal - most trips  
207 were <24 hours, with decreasing numbers of two-, three-, four- and five-day outings (Fig. 2a).

208 There were significant effects of colony and sex on trip duration, total distance, and maximum  
209 distance (Fig. 2b, Table S1-3). Overall, birds from Barton Point (the largest colony with 9,269 breeding  
210 pairs) travelled furthest and for longest (model parameter estimates, 95% confidence intervals; trip

211 duration: 16.7 hours, 11.1-25.1; max distance: 97.4 km, 64.4-147.4; total distance: 247.4 km, 160.4-  
212 381.6) followed by Nelson's Island (3500 breeding pairs; trip duration: 9.4 hours, 6.9-14.6; max  
213 distance: 50.9 km, 32.4-80.1; total distance: 137.0 km, 85.4-219.6) and then Danger Island (3300  
214 breeding pairs; trip duration: 7.4 hours, 4.1-13.2; max distance: 38.9 km, 21.4-70.7; total distance:  
215 99.3 km, 53.3-184.7). There was no difference between foraging trip metrics at East Island and any  
216 other colony (Table S1-3,  $p>0.05$ ), where there was also greatest variation around the mean estimates  
217 (1,113 breeding pairs; trip duration: 12.8 hours, 5.8-28.1; max distance: 74.0 km, 32.9-166.1; total  
218 distance: 171.2 km, 73.7-397.7). From data across all colonies, females travelled further and for longer  
219 than males (model parameter estimates, 95% confidence intervals; trip duration: females 12.7 hours,  
220 8.2-19.8, males 7.8 hours, 5.0-12.0; max distance: females 72.5 km, 46.0-114.2, males 42.9 hours,  
221 27.4-67.3; total distance: females 180.4 km, 112.3-289.8, males 109.4 km, 68.6-174.6). This pattern  
222 was consistent when limited to single day trips, only (Fig. S6).

### 223 **3.4. Foraging timing**

224 At all colonies, RFB foraging times were constrained by daylight hours; departures started around  
225 dawn and arrivals peaked near dusk (Fig. 2c). Departure times varied by colony, sex, and trip duration  
226 (single/multi-day) (Fig. 2c-e, Table S4). RFBs from Barton Point departed earliest (parameter estimates  
227 in hours after dawn, 95% confidence intervals; 2.7, 1.4-4.1), followed by Nelson's Island (4.6, 3.1-6.1),  
228 and then Danger Island (5.6, 3.5-7.7). There was no difference between departure times at East Island  
229 (2.7, 0.1-5.3) and any other colony (Table S4,  $p = 0.98$ ). Across all colonies, females departed earlier  
230 (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  
231 on single-day trips (4.7, 3.3-6.2). There was no effect of monsoon season or breeding stage on  
232 departure times, and arrival times were consistent across all factors (colony, sex, monsoon season,  
233 breeding stage, and single/multi-day trips; Table S5,  $p>0.05$ ).

## 234 **4. Discussion**

235 Our study shows significant inter-colony differences in RFB foraging behaviour. While, the  
236 neighbouring East Island and Barton Point sub-colonies foraged in similar locations, they were spatially  
237 segregated from the other colonies that had exclusive core foraging areas (Fig. 1). Foraging effort (trip  
238 duration and distance) scaled with colony size (Fig. 2), and birds at the largest colony left earliest.  
239 Females undertook longer trips and departed earlier, although both sexes foraged in the same areas.  
240 There was no effect of monsoon season or reproductive stage on foraging distribution, effort, or  
241 timing. The significant inter-colony differences and at-sea segregation are probably best explained by  
242 intraspecific competition for food, both within and among colonies (Wakefield et al. 2013).



243 Importantly, this effect occurs in oligotrophic waters, where seabirds can be particularly dependent  
244 on facultative foraging with sub-surface, pelagic predators in deeper waters (Au & Pitman 1986).

#### 245 **4.1. Inter-colony segregation**

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

261 The shallow Great Chagos Bank may be unsuitable habitat for RFBs and thus effect colony segregation.  
262 Few tracked RFBs travelled across the centre of the archipelago (Figure 1), where boat-based surveys  
263 have previously observed low seabird abundance (Perez-Correa et al. 2020). This may be because  
264 these shallow waters are unsuitable for facultative species like Skipjack tuna, *Katsuwonus pelamis*  
265 (Jaquemet et al. 2004, Dunn & Curnick 2019), and billfishes (Thoya et al. 2022); and/or pelagic prey  
266 species such as flying fish (Exocoetidae) and flying squid (Ommastrephidae) (Weimerskirch et al.  
267 2005a, Jaquemet et al. 2005, Miller et al. 2018). Furthermore, intra-specific competition with other  
268 sulids breeding in the archipelago could reinforce pelagic distributions via habitat partitioning (Austin  
269 et al. 2021) although these species occur in relatively low numbers so this seems unlikely (924 pairs  
270 of Brown Booby, *Sula leucogaster*, breed on 7 islands, and 164 pairs of Masked Booby, *Sula dactylatra*,  
271 breed on 2 islands; Carr et al. 2021).

#### 272 **4.2. Intra-colony effects.**

273 Foraging effort of RFBs can differ between sexes (Weimerskirch et al. 2006) among breeding stages  
274 (Weimerskirch et al. 2006), and with environmental conditions (Mendez et al. 2017, Gilmour et al.

275 2018), although the extent of these effects varies across the species' range (Lewis et al. 2005, Austin  
276 et al. 2021). RFBs are slightly sexually dimorphic – females are 15% larger and 19% heavier than males  
277 in the Chagos Archipelago (Carr 2021), which corresponds with greater foraging effort by females  
278 (Weimerskirch et al. 2006). As well as undertaking longer foraging trips (Fig. 2b), females left the  
279 colony earlier in the day (Fig. 2d), although both sexes foraged in similar areas at-sea (Fig. S5). Despite  
280 the effect of sex on foraging effort metrics, there was little at-sea segregation between sexes. We  
281 found no evidence for breeding stage differences in foraging trip metrics, which appears to be the  
282 norm in this species (Lewis et al. 2005, Young et al. 2010, Almeida et al. 2021, Austin et al. 2021).

283 Monsoon season did not influence foraging behaviour, despite potential shifts in at-sea foraging  
284 conditions. Cooler SSTs during the SE monsoon season are typically associated with increased tuna  
285 presence, and therefore potentially greater facultative foraging opportunities (Orúe et al. 2020).  
286 However, this effect was not visible in colony foraging effort or distributions. Our models accounted  
287 for annual differences in foraging behaviour, and there was no visible difference in foraging direction  
288 among years (Fig. S2). At Nelson's Island, birds tracked during 2019 travelled further from the colony  
289 (Fig. S2), which could be because the 2019 extreme positive Indian Ocean dipole event caused poor  
290 foraging conditions (Shi & Wang 2021), although this effect was not apparent at Diego Garcia.  
291 Although logistically challenging, more contemporaneous data across multiple colonies would be  
292 needed to robustly test for interannual differences.

### 293 **4.3. Foraging effort**

294 Here, we observe foraging ranges that scale with colony size among neighbouring populations; a  
295 pattern that largely holds true across RFB's breeding range (Mendez et al. 2017). In this study, RFBs  
296 undertook foraging trips that were, on average,  $18.5 \pm 1.6$  hours long and reached a maximum of  
297  $112.9 \pm 3.7$  km from the colony. These metrics are similar to RFBs breeding at isolated colonies in the  
298 Pacific (1400 breeding pairs; Lewis et al. 2005, Young et al. 2010) and Caribbean (1000 breeding pairs;  
299 Austin et al., 2021), but are longer than elsewhere in the Indian Ocean, including both Tromelin (129  
300 breeding pairs; (Kappes et al. 2011) and Europa Island, where multi-day trips are rare (2800-3800  
301 breeding pairs; Mendez et al., 2017; Weimerskirch et al., 2006). Our results demonstrate temporal  
302 and spatial partitioning at-sea to mitigate inter-colony competition, which, alongside local resource  
303 landscapes (Cairns 1988, Mendez et al. 2017), may further explain regional variability in foraging  
304 effort.

### 305 **4.4. Foraging times**

306 RFBs tend to forage diurnally with departure times constrained by dawn and arrival times by dusk  
307 (Figure 2c-d) leading to a multi-modal distribution of trip durations (Figure 2a). Most departures  
308 occurred soon after dawn (Figure 2c-d), which may enable individuals to maximise available foraging  
309 time, whilst minimising energetic costs of searching for sufficient prey during limited daylight hours  
310 (Lewis et al. 2004). This diurnal time limit may be compounded in the tropics where day lengths and  
311 twilight periods are relatively short, compared to those experienced by high latitude-breeding  
312 seabirds that do not appear to be so constrained by daylight hours during summer (Daunt et al. 2006).  
313 Returning close to twilight could reduce kleptoparasitism risk by frigatebirds. These birds aggregate  
314 at the colony to attack individuals returning with food (Austin et al. 2019), and have fewer crepuscular  
315 than diurnal chases (Le Corre & Jouventin 1997). Alternatively, RFBs may more commonly undertake  
316 single day trips to avoid over-nighting on the water because of predation risk (Weimerskirch et al.  
317 2005b, Zavalaga et al. 2012), unless undertaking multi-day trips. Temperate breeding Cape gannets,  
318 *Morus capensis*, also forage visually during daylight hours, leading to similar multi-modal trip  
319 distributions (Rishworth et al. 2014). However, departures after dusk appear more common than we  
320 observed here, perhaps because the risks of being at sea overnight are higher in this tropical system.

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

#### 332 **4.5. Conclusions**

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

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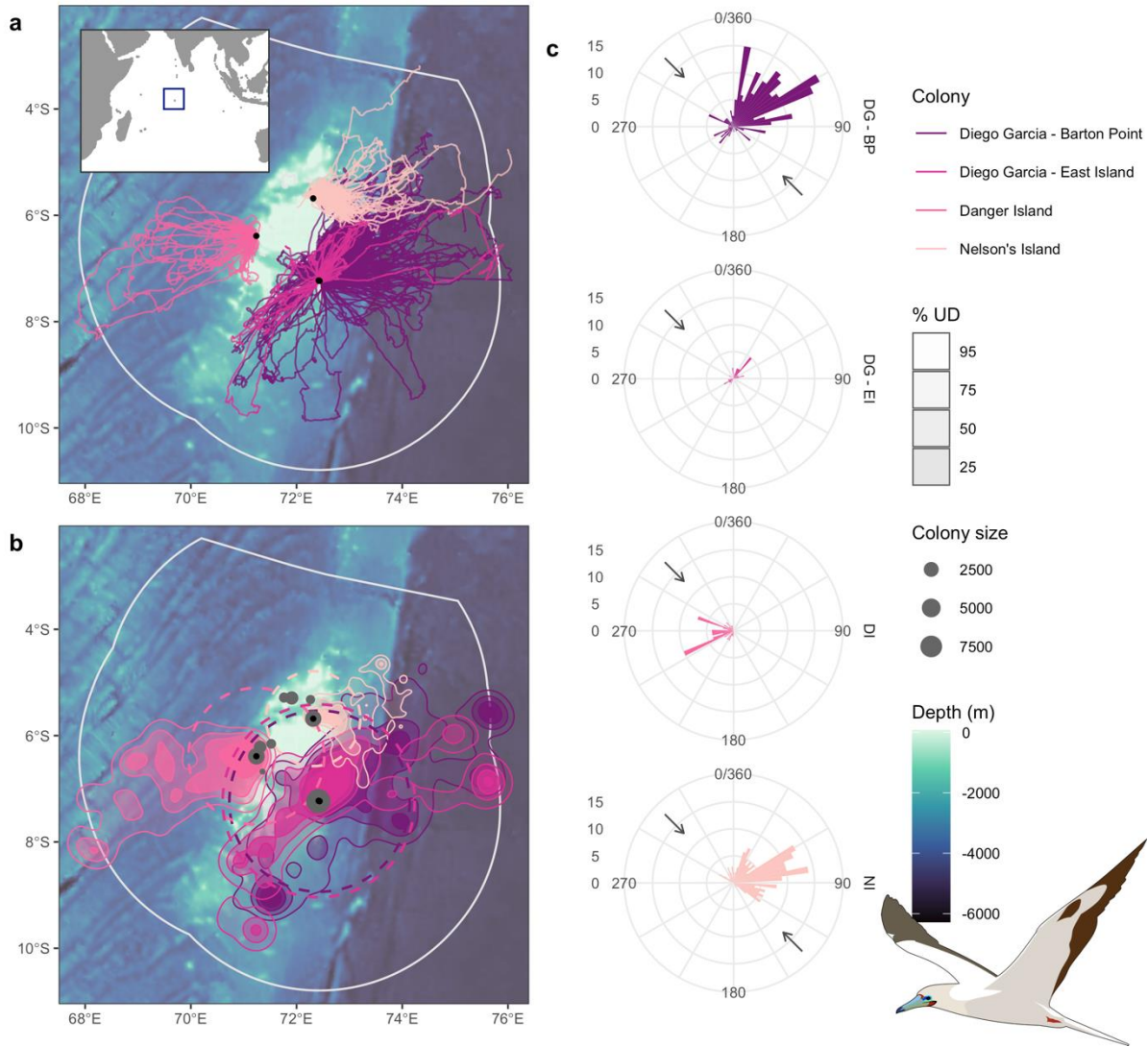
**Table 1.** Sample sizes for each colony, monsoon season (NW: North West, SE: South East), sex, and breeding stage. Note, 2 individuals were tracked across multiple years at Diego Garcia.

Colony	Colony size (br. pairs)	Latitude (°N)	Longitude (°E)	Year	Monsoon	No. individuals	No. trips	No. individuals by Sex			No. individuals by Breeding Stage			
								Female	Male	Unkown	Pre-egg laying	Incubation	Chick rearing	Unkown
ALL				ALL	ALL	207	509	51	56	100	8	59	137	3
Barton Point	9,269	-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	1,113	-7.22	72.42	2022	NW	8	30	4	3	1	0	0	8	0
Diego Garcia	10,382			ALL	ALL	107	262	31	25	51	8	51	45	3
Danger Island	3,500	-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
Nelson's Island	3,300	-5.68	72.32	2018	SE	36	104	8	13	15	0	0	36	0
					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

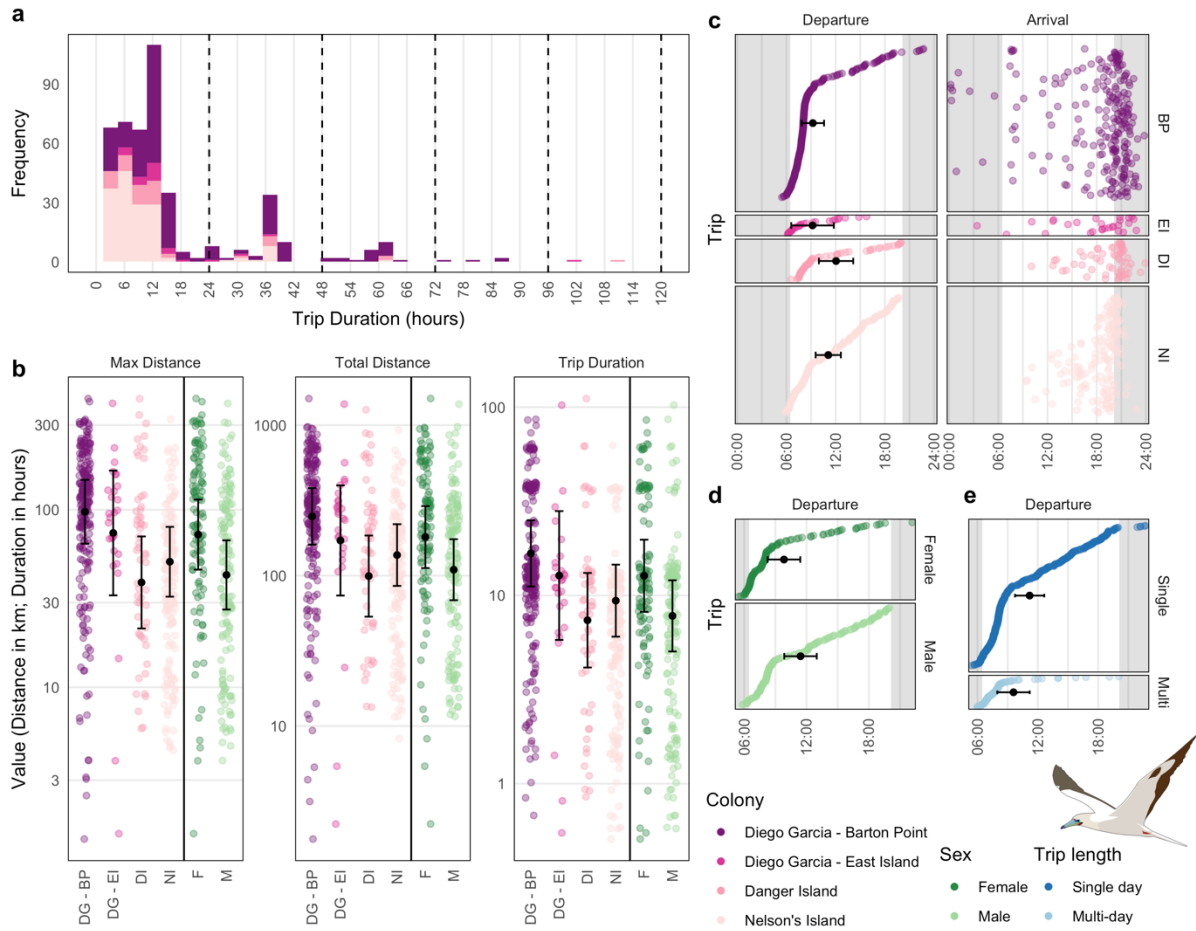


**Table 2.** Foraging trip metrics across the Chagos Archipelago for each colony and monsoon period (NW: North West, SE: South East) included in this study.

Colony	Year	Monsoon	Trip duration (hours)				Total distance (km)				Max distance (km)			
			mean	se	min	max	mean	se	min	max	mean	se	min	max
ALL	ALL	ALL	18.5	1.6	0.5	111.1	298.4	6.2	1.8	1,501.9	112.9	3.7	1.4	424.4
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	1,501.9	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	1,379.2	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	1,501.9	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	1,265.6	98.0	1.7	5.9	421.7
	ALL	ALL	16.1		0.9	111.1	267.6		13.4	1,265.6	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



**Figure 1.** Red-footed booby foraging area use in the Chagos Archipelago, in the central Indian Ocean (inset panel);  $n = 207$  total individuals from four colonies; two 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 MPA (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).



**Figure 2.** Red-footed booby foraging effort in the Chagos Archipelago;  $n = 207$  total individuals from four colonies; two in the Diego Garcia Atoll - Barton Point ( $n = 99$ ) and East Island ( $n = 8$ ), Danger Island ( $n = 27$ ), and Nelson's Island ( $n = 73$ ). At all colonies, (a) most trips were short <one day, with decreasing numbers of two-, three-, four- and five-day outings; although (b) Foraging effort differed between Barton Point and both Danger Island and Nelson's Island 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, although (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 on panel (a) delineate whole days. Error bars on panels (b) - (e) are model predictions  $\pm$  95 % confidence intervals from linear mixed effect regressions. Grey shading on panels (c-e) shows night-time hours according to mean nautical dawn and dusk over the study period.