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

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

Alice M Trevail1 \*

Hannah Wood2 \*

Peter Carr2

Ruth Dunn 3,4

Malcolm A Nicoll2

Stephen C Votier3

Robin Freeman2

1 Environment & Sustainability Institute, University of Exeter, Penryn Campus, Cornwall 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, United Kingdom

4 Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, UK

\* Joint first authors: these authors contributed equally to this work

Corresponding author email address: [a.trevail@exeter.ac.uk](mailto:a.trevail@exeter.ac.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 track 207 breeding red-footed boobies (RFB; *Sula sula rubripes*) from four 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 (max distance mean ± s.e.: 112.9 ± 3.7 km; total distance: 298.4 ± 6.2 km) over one to five days (18.5 ± 1.6 hrs). 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.

**Keywords:** central-place foraging, 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 (Thiebault et al. 2014, Buckley 2015), 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 effect 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-track red-footed boobies, *Sula sula rubripes* (hereafter RFB), from four neighbouring colonies in the Chagos Archipelago, central Indian Ocean, comprising ~1,100, 3,300, 3,500 and ~9,200 breeding pairs and test 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 predict competition within and among colonies to effect foraging but note that unpredictable resources and facultative foraging may alter the degree of segregation. We expect 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. Material & Methods

**2.1. Study system**

Research was conducted at four RFB colonies ≤ 172km apart within the Chagos Archipelago Marine Protected Area (Hays et al. 2020, Carr et al. 2022): two colonies <2km apart within the Diego Garcia atoll, 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, 2018-19 and 2022-23 (Figure S1).

Climatology in the Indian Ocean is dominated by two 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). RFB breed asynchronously in the Chagos Archipelago, with two peaks per year coinciding with the two 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 (Orúe et al. 2020, Curnick 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 effected our study design. Within the Diego Garcia atoll, tracking occurred at two sub-colonies (Barton Point: 2016-19, and East Island: 2022, 1.8km 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 supplementary material (Fig S1). To explore the scales at which populations differentiate within the Chagos Archipelago, we treat these two sub-colonies separately in 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 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; 15g, used during 2016, 2018, and 2019; or TechnoSmArt Axy-Trek Marine, 18g, used during 2019 at DG, and 2022-23) on the underside of the central two to four tail feathers, depending on moult condition, using marine Tesa (4651) tape. Geolocators and immersion loggers (Intigeo C330, Migrate technology, Cambridge, UK; 3.3g) were attached to a plastic leg ring, but these data were not analysed in this study. Handling time lasted approximately 10-minutes 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 one 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 during 2022-23.

**2.3. Processing GPS data**

Loggers recorded a GPS fix every five minutes. Once downloaded, fixes outside the deployment period were removed. Foraging trips were defined as > 1km from the colony and > 30 minutes in duration (Carr et al. 2022). From these data we extracted two indices of spatial foraging behaviour: (1) utilisation distributions, and (2) departure angles; three measures of foraging effort: (3) trip duration (hours), (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 utilisation distributions (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 1km grid using default smoothing parameters in the R package *adehabitatHR* (Calenge 2006). We also mapped UDs and calculated overlap during 2019, when we have tracking data for three 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; 1km, 5km, 10km & 25km.

To explore intra-colony differences in spatial foraging behaviour we calculated Bhattacharya’s affinity between pair-wise 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 four 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 packages *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-hour 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 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 four 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, Figure 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; Figure 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 utilisation distributions showed differential at-sea foraging segregation (Fig. 1b). There was near-complete overlap in UDs between East Island and Barton Point, the two colonies in the Diego Garcia atoll (Fig. 1b), with Bhattacharya’s affinity of 0.77. Among all other colonies, there was no overlap of 25 and 50% UDs (Fig. 1b) and Bhattacharya’s affinity was <0.25 in all cases. There was lowest overlap between Danger Island and all other colonies; (BA values and distances between colonies were: Barton Point 0.01, 162km apart; East Island 0.02, 161km apart; Nelson’s Island <0.001, 142km apart). Between Nelson’s Island and the two Diego Garcia colonies, overlap was still low (BA: Barton Point 0.25, East Island 0.13, both 172km apart). When considering foraging areas during 2019 only, when 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 Bhattacharya’s affinity 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 four tracked colonies (Fig. 1c). Breeders on Diego Garcia departed primarily in a north-easterly direction, with a smaller number departing southwest, at Danger Island departures were westerly and at Nelson’s Island north-easterly (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): Bhattacharya’s affinity between monsoon seasons was 0.77 at Barton Point and 0.85 at Nelson’s Island; between females and males 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 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): Bhattacharya’s affinity 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 hours (range 0.5-111.1 hrs), total distance travelled averaged 298.4 ± 6.2 km (range 1.8 – 1,502 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 hours, with decreasing numbers of two-, three-, four- and five-day outings (Fig. 2a).

There were significant effects of colony and sex on trip duration, total distance, and maximum distance (Fig. 2b, Table S1-3). Overall, birds from Barton Point (the largest colony with 9,269 breeding pairs) travelled furthest and for longest (model parameter estimates, 95% confidence intervals; trip duration: 16.7 hours, 11.1-25.1; max distance: 97.4 km, 64.4-147.4; total distance: 247.4 km, 160.4-381.6) followed by Nelson’s Island (3500 breeding pairs; trip duration: 9.4 hours, 6.9-14.6; max distance: 50.9 km, 32.4-80.1; total distance: 137.0 km, 85.4-219.6) and then Danger Island (3300 breeding pairs; trip duration: 7.4 hours, 4.1-13.2; max distance: 38.9 km, 21.4-70.7; total distance: 99.3 km, 53.3-184.7). There was no difference between foraging trip metrics at East Island and any other colony (Table S1-3, p>0.05), where there was also greatest variation around the mean estimates (1,113 breeding pairs; trip duration: 12.8 hours, 5.8-28.1; max distance: 74.0 km, 32.9-166.1; total distance: 171.2 km, 73.7-397.7). From data across all colonies, females travelled further and for longer than males (model parameter estimates, 95% confidence intervals; trip duration: females 12.7 hours, 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, 27.4-67.3; total distance: females 180.4 km, 112.3-289.8, males 109.4 km, 68.6-174.6). This pattern was consistent when limited to single day trips, only (Fig. S6).

**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 then 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, 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 intraspecific 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 79% of 39 multi-colony studies exhibited non-overlapping distributions, although only one was a tropical-breeder – the Laysan Albatross (*Phoebastria immutabilis*) (Young et al. 2009, Orben et al. 2021). Here, we find evidence of different spatial scales of population segregation in the Chagos Archipelago. Two colonies <2km 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 (Figure 1b). Furthermore, birds tended to avoid waters to the north and northwest where there are several other comparatively large RFB colonies (Figure 1b; showing Peros Banhos & 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 (Figure 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) (Weimerskirch et al. 2005a, Jaquemet et al. 2005, 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 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, *Sula 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 SSTs 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 further 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 observe foraging ranges that scale with colony size among neighbouring populations; a pattern that largely holds true across RFB’s breeding range (Mendez et al. 2017). In this study, RFBs undertook foraging trips that were, on average, 18.5 ± 1.6 hours 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; Mendez et al., 2017; Weimerskirch et al., 2006). 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 (Figure 2c-d) leading to a multi-modal distribution of trip durations (Figure 2a). Most departures occurred soon after dawn (Figure 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 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) and our work provides valuable evidence that similar patterns also prevail in the tropics, and that segregation can also drive temporal adjustments of foraging behaviour. How seabirds optimise foraging opportunities within tropical ecosystems remains a priority for future research.

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**References**

Agafonkin V, Thieurmel B (2018) Suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase.

Almeida N, Ramos JA, Rodrigues I, dos Santos I, Pereira JM, Matos DM, Araújo PM, Geraldes P, Melo T, Paiva VH (2021) Year-round at-sea distribution and trophic resources partitioning between two sympatric Sulids in the tropical Atlantic. PLOS ONE 16:e0253095.

Ashmole NP (1963) The regulation of numbers of tropical oceanic birds. Ibis 103 b:458–473.

Au DWK, Pitman RL (1986) Seabird Interactions with Dolphins and Tuna in the Eastern Tropical Pacific. The Condor 88:304–317.

Austin RE, De Pascalis F, Arnould JPY, Haakonsson J, Votier SC, Ebanks-Petrie G, Austin T, Morgan G, Bennett G, Green JA (2019) A sex-influenced flexible foraging strategy in a tropical seabird, the magnificent frigatebird. Marine Ecology Progress Series 611:203–214.

Austin RE, De Pascalis F, Votier SC, Haakonsson J, Arnould JPY, Ebanks-Petrie G, Newton J, Harvey J, Green JA (2021) Interspecific and intraspecific foraging differentiation of neighbouring tropical seabirds. Movement Ecology 9:1–16.

Bocedi G, Heinonen J, Travis JMJ (2012) Uncertainty and the role of information acquisition in the evolution of context-dependent emigration. American Naturalist 179:606–620.

Bolton M, Conolly G, Carroll M, Wakefield ED, Caldow R (2019) A review of the occurrence of inter-colony segregation of seabird foraging areas and the implications for marine environmental impact assessment. Ibis 161:241–259.

Buckley NJ (2015) Spatial‐Concentration Effects and the Importance of Local Enhancement in the Evolution of Colonial Breeding in Seabirds. https://doi.org/101086/286040 149:1091–1112.

Cairns DK (1988) Seabirds as Indicators of Marine Food Supplies. Biological Oceanography 5:261–271.

Calenge C (2006) The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

Carr P (2021) Exploring the benefits of a tropical, large-scale marine protected area for breeding seabirds. University of Exeter

Carr P, Trevail AM, Koldewey HJ, Sherley RB, Wilkinson T, Wood H, Votier SC (2022) Marine Important Bird and Biodiversity Areas in the Chagos Archipelago. Bird Conservation International:1–8.

Carr P, Votier S, Koldewey H, Godley B, Wood H, Nicoll MAC (2021) Status and phenology of breeding seabirds and a review of Important Bird and Biodiversity Areas in the British Indian Ocean Territory. Bird Conservation International 31:14–34.

Catry T, Ramos J, Jaquemet S, Faulquier L, Berlincourt M, Hauselmann A, Pinet P, Le Corre M (2009) Comparative foraging ecology of a tropical seabird community of the Seychelles, western Indian Ocean. Marine Ecology Progress Series 374:259–272.

Ceia FR, Ramos J a. (2015) Individual specialization in the foraging and feeding strategies of seabirds: a review. Marine Biology 162:1923–1938.

Clay TA, Hodum P, Hagen E, Brooke M de L (2023) Adjustment of foraging trips and flight behaviour to own and partner mass and wind conditions by a far-ranging seabird. Animal Behaviour 198:165–179.

Curnick DJ, Andrzejaczek S, Jacoby DMP, Coffey DM, Carlisle AB, Chapple TK, Ferretti F, Schallert RJ, White T, Block BA, Koldewey HJ, Collen B (2020) Behavior and Ecology of Silky Sharks Around the Chagos Archipelago and Evidence of Indian Ocean Wide Movement. Front Mar Sci 7:596619.

Danchin E, Wagner RH (1997) The evolution of coloniality: the emergence of new perspectives. Trends in Ecology & Evolution 12:342–347.

Daunt F, Afanasyev V, Silk JRD, Wanless S (2006) Extrinsic and intrinsic determinants of winter foraging and breeding phenology in a temperate seabird. Behavioral Ecology and Sociobiology 59:381–388.

Dunn N, Curnick D (2019) Using historical fisheries data to predict tuna distribution within the British Indian Ocean Territory Marine Protected Area, and implications for its management. Aquatic Conservation: Marine and Freshwater Ecosystems 29:2057–2070.

Fieberg J, Kochanny CO (2005) Quantifying home-range overlap: the importance of the utilization distribution. Journal of Wildlife Management 69:1346–1359.

Gilmour ME, Castillo-Guerrero JA, Fleishman AB, Hernández-Vázquez S, Young HS, Shaffer SA (2018) Plasticity of foraging behaviors in response to diverse environmental conditions. Ecosphere 9:e02301.

Hays GC, Koldewey HJ, Andrzejaczek S, Attrill MJ, Barley S, Bayley DTI, Benkwitt CE, Block B, Schallert RJ, Carlisle AB, Carr P, Chapple TK, Collins C, Diaz C, Dunn N, Dunbar RB, Eager DS, Engel J, Embling CB, Esteban N, Ferretti F, Foster NL, Freeman R, Gollock M, Graham NAJ, Harris JL, Head CEI, Hosegood P, Howell KL, Hussey NE, Jacoby DMP, Jones R, Sannassy Pilly S, Lange ID, Letessier TB, Levy E, Lindhart M, McDevitt-Irwin JM, Meekan M, Meeuwig JJ, Micheli F, Mogg AOM, Mortimer JA, Mucciarone DA, Nicoll MA, Nuno A, Perry CT, Preston SG, Rattray AJ, Robinson E, Roche RC, Schiele M, Sheehan EV, Sheppard A, Sheppard C, Smith AL, Soule B, Spalding M, Stevens GMW, Steyaert M, Stiffel S, Taylor BM, Tickler D, Trevail AM, Trueba P, Turner J, Votier S, Wilson B, Williams GJ, Williamson BJ, Williamson MJ, Wood H, Curnick DJ (2020) A review of a decade of lessons from one of the world’s largest MPAs: conservation gains and key challenges. Marine Biology 167:159.

Jaquemet S, Le Corre M, Marsac F, Potier M, Weimerskirch H (2005) Foraging habitats of the seabird community of Europa Island (Mozambique Channel). Marine Biology 147:573–582.

Jaquemet S, Le Corre M, Weimerskirch H (2004) Seabird community structure in a coastal tropical environment: importance of natural factors and fish aggregating devices (FADs). Marine Ecology Progress Series 268:281–292.

Kappes MA, Weimerskirch H, Pinaud D, Le Corre M (2011) Variability of resource partitioning in sympatric tropical boobies. Marine Ecology Progress Series 441:281–294.

Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest Package: Tests in Linear Mixed Effects Models. Journal of Statistical Software 82:1–26.

Le Corre M, Jouventin P (1997) Kleptoparasitism in Tropical Seabirds: Vulnerability and Avoidance Responses of a Host Species, the Red-Footed Booby. The Condor 99:162–168.

Lévy M, Shankar D, André JM, Shenoi SSC, Durand F, de Boyer Montégut C (2007) Basin-wide seasonal evolution of the Indian Ocean’s phytoplankton blooms. Journal of Geophysical Research: Oceans 112:C12014.

Lewis S, Schreiber EA, Daunt F, Schenk GA, Orr K, Adams A, Wanless S, Hamer KC (2005) Sex-specific foraging behaviour in tropical boobies: does size matter? Ibis 147:408–414.

Lewis S, Schreiber EA, Daunt F, Schenk GA, Wanless S, Hamer KC (2004) Flexible foraging patterns under different time constraints in tropical boobies. Animal Behaviour 68:1331–1337.

Lewis S, Sherratt TN, Hamer KC, Wanless S (2001) Evidence of intra-specific competition for food in a pelagic seabird. Nature 412:816–819.

Lüdecke D (2018) Ggeffects: Tidy Data Frames of Marginal Effects from Regression Models. Journal of Open Source Software 3:772.

Mendez L, Borsa P, Cruz S, De Grissac S, Hennicke J, Lallemand J, Prudor A, Weimerskirch H, Grissac SD, Hennicke J, Lallemand J, Prudor A, Weimerskirch H (2017) Geographical variation in the foraging behaviour of the pantropical red-footed booby. Marine Ecology Progress Series 568:217–230.

Miller MGR, Carlile N, Phillips JS, McDuie F, Congdon BC (2018) Importance of tropical tuna for seabird foraging over a marine productivity gradient. Marine Ecology Progress Series 586:233–249.

National Imagery and Mapping Agency (2001) Atlas of Pilot Charts Indian Ocean; Fourth Edition. https://msi.nga.mil/Publications/APC

Oppel S, Beard A, Fox D, Mackley E, Leat E, Henry L, Clingham E, Fowler N, Sim J, Sommerfeld J, Weber N, Weber S, Bolton M (2015) Foraging distribution of a tropical seabird supports Ashmole’s hypothesis of population regulation. Behavioral Ecology and Sociobiology 69:915–926.

Orben RA, Adams J, Hester M, Shaffer SA, Suryan RM, Deguchi T, Ozaki K, Sato F, Young LC, Clatterbuck C, Conners MG, Kroodsma DA, Torres LG (2021) Across borders: External factors and prior behaviour influence North Pacific albatross associations with fishing vessels. Journal of Applied Ecology 58:1272–1283.

Orúe B, Pennino MG, Lopez J, Moreno G, Santiago J, Ramos L, Murua H (2020) Seasonal Distribution of Tuna and Non-tuna Species Associated With Drifting Fish Aggregating Devices (DFADs) in the Western Indian Ocean Using Fishery-Independent Data. Frontiers in Marine Science 7:441.

Patterson A, Gilchrist HG, Benjaminsen S, Bolton M, Bonnet-Lebrun AS, Davoren GK, Descamps S, Erikstad KE, Frederiksen M, Gaston AJ, Gulka J, Hentati-Sundberg J, Huffeldt NP, Johansen KL, Labansen AL, Linnebjerg JF, Love OP, Mallory ML, Merkel FR, Montevecchi WA, Mosbech A, Olsson O, Owen E, Ratcliffe N, Regular PM, Reiertsen TK, Ropert-Coudert Y, Strøm H, Thórarinsson TL, Elliott KH (2022) Foraging range scales with colony size in high-latitude seabirds. Current Biology 0.

Perez-Correa J, Carr P, Meeuwig JJ, Koldewey HJ, Letessier TB (2020) Climate oscillation and the invasion of alien species influence the oceanic distribution of seabirds. Ecology and Evolution 10:9339–9357.

Phillips JA, Guilford T, Fayet AL (2023) How do resource distribution and taxonomy affect the use of dual foraging in seabirds? A review. Behavioral Ecology:arad052.

Pinet P, Jaeger A, Cordier E, Potin G, Le Corre M (2011) Celestial Moderation of Tropical Seabird Behavior. PLOS ONE 6:e27663.

Riotte-Lambert L, Matthiopoulos J (2020) Environmental Predictability as a Cause and Consequence of Animal Movement. Trends in Ecology & Evolution 35:163–174.

Rishworth GM, Tremblay Y, Green DB, Connan M, Pistorius PA (2014) Drivers of Time-Activity Budget Variability during Breeding in a Pelagic Seabird. PLOS ONE 9:e116544.

Schott FA, McCreary JP (2001) The monsoon circulation of the Indian Ocean. Progress in Oceanography 51:1–123.

Shi W, Wang M (2021) A biological Indian Ocean Dipole event in 2019. Scientific Reports 2021 11:1 11:1–8.

Soanes LM, Green JA, Bolton M, Milligan G, Mukhida F, Halsey LG (2021) Linking foraging and breeding strategies in tropical seabirds. Journal of Avian Biology:jav.02670.

Sommerfeld J, Hennicke JC (2010) Comparison of trip duration, activity pattern and diving behaviour by Red-tailed Tropicbirds (Phaethon rubricauda) during incubation and chick-rearing. Emu 110:78–86.

Thiebault A, Mullers R, Pistorius P, Meza-Torres MA, Dubroca L, Green D, Tremblay Y (2014) From colony to first patch: Processes of prey searching and social information in Cape Gannets. Auk 131:595–609.

Thoya P, Kadagi NI, Wambiji N, Williams SM, Pepperell J, Möllmann C, Schiele KS, Maina J (2022) Environmental controls of billfish species in the Indian Ocean and implications for their management and conservation. Diversity and Distributions 28:1554–1567.

Trevail AM, Nicoll MAC, Freeman R, Le Corre M, Schwarz J, Jaeger A, Bretagnolle V, Calabrese L, Feare C, Lebarbenchon C, Norris K, Orlowski S, Pinet P, Plot V, Rocamora G, Shah N, Votier SC (2023) Tracking seabird migration in the tropical Indian Ocean reveals basin-scale conservation need. Current Biology.

Wakefield ED, Bodey TW, Bearhop S, Blackburn J, Colhoun K, Davies R, Dwyer RG, Green JA, Grémillet D, Jackson AL, Jessopp MJ, Kane A, Langston RHW, Lescroël A, Murray S, Le Nuz M, Patrick SC, Péron C, Soanes LM, Wanless S, Votier SC, Hamer KC (2013) Space partitioning without territoriality in gannets. Science 341:68–70.

Weimerskirch H, Corre ML, Ropert-Coudert Y, Kato A, Marsac F (2006) Sex-specific foraging behaviour in a seabird with reversed sexual dimorphism: The red-footed booby. Oecologia 146:681–691.

Weimerskirch H, De Grissac S, Ravache A, Prudor A, Corbeau A, Congdon BC, McDuie F, Bourgeois K, Dromzée S, Butscher J, Menkes C, Allain V, Vidal E, Jaeger A, Borsa P (2020) At-sea movements of wedge-tailed shearwaters during and outside the breeding season from four colonies in New Caledonia. Marine Ecology Progress Series 633:225–238.

Weimerskirch H, Le Corre M, Jaquemet S, Marsac F (2005a) Foraging strategy of a tropical seabird, the red-footed booby, in a dynamic marine environment. Marine Ecology Progress Series 288:251–261.

Weimerskirch H, Le Corre M, Ropert-Coudert Y, Kato A, Marsac F (2005b) The three-dimensional flight of red-footed boobies: adaptations to foraging in a tropical environment? Proceedings Biological sciences 272:53–61.

Young HS, Shaffer SA, McCauley DJ, Foley DG, Dirzo R, Block BA (2010) Resource partitioning by species but not sex in sympatric boobies in the central Pacific Ocean. Marine Ecology Progress Series 403:291–301.

Young LC, Vanderlip C, Duffy DC, Afanasyev V, Shaffer SA (2009) Bringing home the trash: do colony-based differences in foraging distribution lead to increased plastic ingestion in Laysan albatrosses? PloS one 4:e7623.

Zavalaga CB, Emslie SD, Estela FA, Müller MS, Dell’Omo G, Anderson DJ (2012) Overnight foraging trips by chick-rearing Nazca Boobies Sula granti and the risk of attack by predatory fish. Ibis 154:61–73.

**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 | 0 |
| Nelson’s Island | 3,300 | -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 |

**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 |

**A close-up of a map

Description automatically generated**

**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).

A group of graphs and charts

Description automatically generated

**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 ± 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.