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ORIGINAL PAPER

Sub-colony variation in foraging behaviour and at-sea distribution of a breeding tropical seabird and consequences for marine spatial planning

Malcolm A. C. Nicoll[1] · **Audrey Jaeger**[2] · **Aurelie Hector**[3] · **Jake Letori**[3] · **Gerard Rocamora**[3,4] · **Matthieu Le Corre**[2]

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Abstract

Many species of seabirds are threatened and understanding their at-sea distributions during breeding is a priority for their conservation. Recent developments in tracking technology, data analytical frameworks and tools are proving invaluable in the identification of at-sea areas of high use and hence conservation importance, which can be used to inform marine spatial planning. However, the outputs from these frameworks and tools are contingent on the underlying tracking data, which are shaped by the myriad of decisions made when designing and implementing a tracking program. These decisions include breeding colony choice and identification of areas (sub-colonies) within the colony in which to deploy tracking devices. However, our understanding of the consequences of this on the resulting tracking data and hence identification of at-sea priority areas is limited and rarely considered. In April 2022 we tracked 196 foraging trips of 54 breeding red-footed boobies (*Sula sula*) at two sub-colonies (1.5 km apart) on South Island, Farquhar Atoll in south-west Seychelles. We found that foraging trip distance and duration did not differ between the two sub-colonies, but trip orientation did: resulting in sub-colony segregation at sea predominantly to the north and south of the atoll with consequences for the identification of at-sea areas of high use. Our findings indicate that sub-colony variation in at-sea distribution of breeding seabirds may be more commonplace than current research suggests and if our tracking program had involved only one sub-colony then key outputs which could serve towards marine spatial planning efforts may be biased.

Keywords Biologging · Booby · GPS logger · Marine Protected Area · KBA · Seabird · Track2KBA · Within colony

Introduction

Seabirds are widely acknowledged as a highly threatened group of birds (Croxall et al. 2012; BirdLife International 2022, McClure et al. 2023). Seabird populations are impacted by a range of factors both on land and at sea during different life history stages, hence identifying where and when these impacts occur is a priority for mitigation and seabird conservation (Croxall et al. 2012; Dias et al. 2019; Rodríguez et al. 2019; Clark et al. 2023). While identifying and prioritising terrestrial sites (breeding colonies and roosting sites) for conservation is relatively straightforward, the identification of at-sea areas is more complex due to the extremely vagile nature of seabirds during both breeding (Oppel et al. 2018; Phillips et al. 2023) and non-breeding periods (Phillips et al. 2017; Bonnet-Lebrun et al. 2021; Trevail et al. 2023a). However, developments in and the

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✉ Malcolm A. C. Nicoll
malcolm.nicoll@ioz.ac.uk

[1] Institute of Zoology, Zoological Society of London, Regent's Park, London, UK

[2] Écologie marine tropicale des océans Pacifique et Indien, UMR ENTROPIE, Université de la Réunion, Saint Denis, La Réunion, France

[3] Island Conservation Society, Pointe Larue, Mahé, Seychelles

[4] Island Biodiversity and Conservation Centre, University of Seychelles, Anse Royale, Mahé, Seychelles

widespread application of technology to track year-round seabird movements (Burger and Schaffer 2008; Bernard et al. 2021) have opened a wide range of possibilities to use the resulting information to further at-sea conservation actions (Lascelles et al. 2016; Hays et al. 2019, Davies et al. 2021a).

During the breeding season seabirds are central placed foragers, returning frequently to breeding colonies, and therefore relatively accessible for deployment (and where necessary recovery) of tracking devices to document at-sea areas of high use and hence conservation importance, which can then be used to inform marine spatial planning (Ronconi et al. 2012; Delord et al. 2014; Grecian et al. 2016; Soanes et al. 2016; Dias et al. 2017; Davies et al. 2021b). A variety of analytical frameworks and tools have been used to facilitate this through the identification of high-use areas for single and multiple seabird species (Grecian et al. 2012; Lascelles et al. 2012; Krüger et al. 2017; Carneiro et al. 2020; Cleasby et al. 2020). A comparatively recently developed analytical framework and associated open source R package track2KBA (Beal et al. 2021) integrates population census data with tracking data and can be used to identify ecologically important areas that can be assessed against the Key Biodiversity Area (KBA) Standard, a standard which aims to identify sites contributing significantly to the global persistence of biodiversity (IUCN 2016). This is particularly relevant for breeding seabirds as it provides a standardised approach, using tracking data, to identify specific at-sea sites where actions may be required for seabird conservation efforts.

While analytical tools and well-structured processes are available to analyse tracking data and identify and characterise ecologically relevant important at-sea areas, the process of collecting tracking data is by comparison less structured. For example, when designing these tracking studies numerous decisions are made by the research team relating to the choice of tag technology, deployment methods, when to deploy tags, the number of individuals to tag, which colonies to deploy tags at and where to select individuals from within a colony or across sub-colonies. While prior research, reviews, preliminary analyses and species-specific knowledge can objectively inform tag choice and deployment methods while minimising welfare impacts (Bodey et al. 2018; Geen et al. 2019; Nicoll et al. 2022; Lopez et al. 2023), and when to deploy tags and how many individuals to tag (Soanes et al. 2013; Thaxter et al. 2017; Silva et al. 2023) the last two decisions are often subjective and influenced by logistics and accessibility. These in turn are strongly influenced by seasonal weather patterns, local weather and sea conditions on the day. All of these can influence where birds are tagged in the colony but the decision of which individuals to tag within a colony is likely to bias estimates of colony at-sea distributions. The only study to explicitly examine variation in forging behaviours between sub-colonies found no clear differences among seven Northern gannet (*Morus bassanus*) sub-colonies within the same breeding island (Waggitt et al. 2014) Given the lack of investigation across colonies and species, it is therefore unclear to what extent sub-colony variation is a phenomenon that needs to be considered when identifying important sites for conservation. Here we explore the potential differences in at-sea distributions of birds from sub-colonies using tracking data from a breeding colony (> 9000 breeding pairs) of red-footed boobies (RFB) (*Sula sula*) tagged at two locations (hereafter referred to as sub-colonies) within a colony in south-west Seychelles, Indian Ocean.

In Seychelles, *Sulidae* populations are recovering in response to island restoration activities including cessation of harvesting, eradication of invasive species and habitat restoration (Feare 1978, 1984; Rocamora 2019). These include RFB populations in the south-western atolls (Fig. 1). While RFBs breeding colonies benefit from protected status (e.g., National Park), nothing is known about their at-sea distribution and hence what at-sea areas are important for the recovering populations and how any priority areas could be factored into a Seychelles marine spatial planning assessment. In April 2022 we tracked the movements of 54 individual chick-rearing RFBs at two sub-colonies (1.5 km apart) in the breeding colony at Farquhar Atoll in south-west Seychelles; a globally recognised site important for conservation of several seabird species (Key Biodiversity Areas Partnership 2024). We used the resulting data on 196 foraging trips to (i) quantify foraging trip metrics, document the at-sea distribution and identify potential marine areas for assessment against the KBA Standard, and (ii) show how our sampling strategy across the two sub-colonies can influence our findings and the implications for marine spatial planning.

Methods

Study system

Farquhar Atoll is in south-west Seychelles, around 300 km to the north-east of Madagascar and comprised of 11 named islands (Fig. 1). Historically, RFB breeding colonies were found on many of the islands in the atoll (Feare 1978), but are now restricted to the southern tip of North Island, South Island and the three small Manahas Islands in between (Fig. 1b). South Island, a designated National Park, is 5.7 km long, 0.6–0.9 km wide, 3,900 ha and composed of dunes (up to 20 m high), a sandy ridge on the lagoon side and three tidal inlets known as barachois (Stoddart and Poore 1970). Dominant vegetation types are; planted

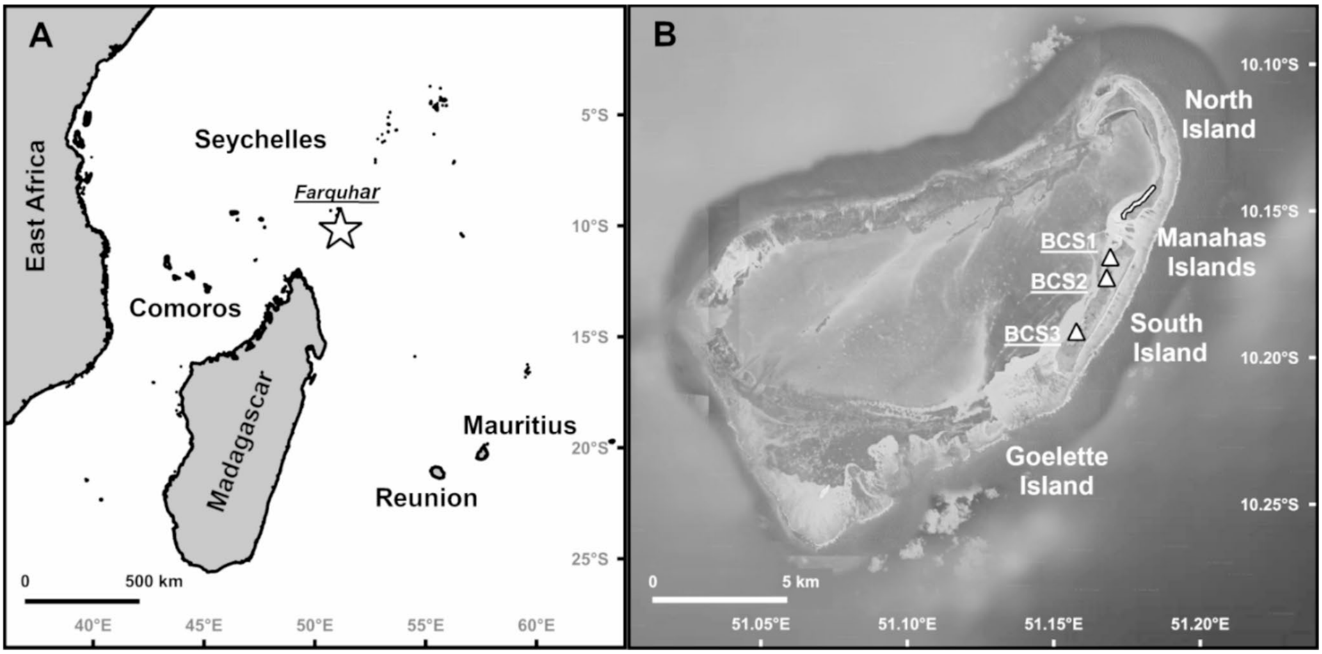

Fig. 1 Maps showing the location of (**A**) Farquhar Atoll (white star) in south-west Seychelles and (**B**) the study barachois (BCS2 and BCS3) on South Island, Farquhar Atoll. The red-footed booby nesting colony on Farquhar Atoll covers South Island, the three Manahas Islands and the lagoon beach head along the southern tip of North Island. The latter is delimited by the thick white line

coconut (*Cocos nucifera*) originally as part of copra plantations, dense stands of *Scaevola taccada* and *Heliotropium arboretum* on the dunes and beach headlands and *Pemphis acidula* (a typical scrub mangrove of the region) in the tidal areas of the barachois (Stoddart and Poore 1970). Recently, the breeding population has increased from < 50 pairs in 1970s (Feare 1978) to an estimated > 9,000 pairs (authors unpublished data). On South Island RFB are found breeding primarily in the two barachois; BCS2 (1801 pairs) and BCS3 (7311 pairs) (Fig. 1b) and along the coastal vegetation between them on the lagoon side of the atoll. Typically, RFB nest in low-lying vegetation composed of *Scaevola taccada*, *Heliotropium arboretum* and *Pemphis acidula.*

Tag deployment

BCS2 (4.46 ha) and BCS3 (14.0 ha) were our studied subcolonies for GPS logger deployment due to their relative accessibility under the tidal range during the study period and the numbers of accessible, active RFB nests with young chicks aged 5–30 days. BSC2 is closer to the field station (on North Island) and access to and mobility around is less restricted by tidal range than BCS3. Breeding RFB were caught on the nest, with a chick, using a hand net or by hand. GPS loggers were fixed to 4 central tail feathers, on the underside of the tail, using marine-stable tape (Tesa 4651, Beiersdorf AG). Two types of loggers were deployed: 39 catlog Gen2 (18 g, Perthold Engineering LLC) and 15 Axytrek (18 g, Technosmart, Italy). Catlog Gen2 tags were set to record a GPS location every 5 min and Axytrek tags recorded a burst of 15 fixes (1 s apart) every 5 min. 54 GPS loggers were deployed between 31/03/2022 and 05/04/2022; 18 in BCS2 and 36 in BCS3. All tagged birds were ringed with an incoloy numbered ring, and for a sub-set of 30 birds, geolocators (GLS) (C330, 2.8 g Migrate Technology, UK), set to record immersion data, were cable tied to these rings. GLS were deployed as part of a separate study and hence data are not included in this study. Total weight of loggers, GLS and rings were < 22 g, which is < 2.4% of the mean weight (930 g) of RFB in this study. A set of morphometric measurements were taken from each tagged adult RFB (wing length, exposed culmen and tarsus (mm) and weight (g)) and from each chick (wing length (mm) and weight (g)). The latter allowed us to age the chicks using a growth curve obtained on the same subspecies of RFB at Tromelin Island (authors unpublished data). All tagged RFB were marked with blue stock marker spray (short-term quick dry sheep marker, Agrihealth, UK) at the base of the neck on the upper breast to aid identification when tags were due to be recovered.

GPS loggers (and GLS) were recovered after 4–9 days deployment between 06/04/2022 and 11/04/2022. Two tags not recovered during this period were recovered on 17/05/2022 and 27/05/2022.

Foraging trip metrics

Data from all recovered GPS loggers were successfully downloaded. We removed locations on land and identified the individual foraging trips with the tripSplit function of the track2KBA package (Beal et al. 2021). For each complete foraging trip, the maximum straight line distance travelled from the colony (km), the total trip distance (km), the average travelling speed (km/h), the trip duration (h), and the direction (in degrees measured from origin to furthest point of trip) were calculated with track2KBA package (Beal et al. 2021). For foraging trip direction mean and standard deviations were estimated, and comparison between sub-colonies were performed using circular statistics with the R package circular (Agostinelli and Lund 2023) (Table 1). For all other foraging trip metrics comparisons between sub-colonies were performed using LMM with individual identity as a random factor in R package nlme (Pinheiro and Bates 2022) (Table 1) and mean ± standard deviation and range were estimated. We also calculated the direction (degrees) between successive fixes (only for locations from origin to furthest locations of each trip) (Fig. 2).

At-sea distribution

GPS sampling intervals across the two GPS tag types varied, hence track locations were re-interpolated at regular time intervals (5 min) to meet the requirement for density estimation using adehabitatLT (Calenge 2006). Kernel density estimations were then implemented using the adehabitatHR package (Calenge 2006) and the reference bandwidth following Mendez et al. (2017). Kernel density distributions were plotted for each colony using 90% contour (Fig. 2). The overlap between 90% kernels of BCS2 and BCS3 was determined by the Bhattacharyya's affinity index (Fieberg and Kochanny 2005), with a range of 0 (no overlap) to 1 (complete overlap). A randomized kernel overlap score was calculated using Bhattacharyya's affinity index, applied to 90% kernels where foraging trips were randomly assigned to a colony. This randomization was repeated 1000 times, and an average Bhattacharyya's affinity index was computed. The sample sizes were the same as original data.

Important marine site identification

Important marine sites, which could be assessed against the KBA Standard, were identified using the track2KBA package (Beal et al. 2021) following BirdLife International procedure and analyses were run at the scale of each sub-colony and all foraging trips, i.e., for three data sets. 50% isopleth utilisation distributions (UD) were calculated (i.e., core area) for each individual trip with a smoothing factor corresponding to the scale of the area-restricted search (ARS) determined from first passage time analysis following protocols outlined in the track2KBA package. We verified that the representativeness thresholds (proportion of unsampled data located within each UD of subsampled data after running 100 iterations) for each dataset were higher than 70%; a requirement to demonstrate that the area identified following the track2KBA protocol sufficiently represents the overall distribution of the source population. When representativeness is less than 70% this can indicate that birds have a more dispersed distribution and so specific site-based conservation actions may be harder to implement. A 1 km2 grid cell was overlaid on the entire range of core areas, the number of core areas overlapping with each cell of this grid was calculated and all cells were multiplied by the population sizes (BCS2 3602 breeding adults, BCS3 14622 breeding adults, both 18224 breeding adults). Potential marine KBAs were then delineated by grouping together grid cells

Table 1 A summary of red-footed booby foraging trip numbers and trip metrics, in combination (colony level) and between barachois 2 (BCS2; 1801 breeding pairs) and 3 (BCS3; 7311 breeding pairs). Mean values are shown with standard deviations and data range

	BCS2	BCS3	Colony
Number of tracked birds	18	36	54
Number of foraging trips	67	131	198
Number of complete foraging trips	67	129	196
Maximum foraging range (km)	85.9 ± 43.0 [15.3–166.0]	78.6 ± 55.1 [10.3–279.8]	81.1 ± 51.3 [10.3–279.8]
Total trip distance (km)	221.7 ± 107.5 [37.5–500.2]	211.2 ± 149.4 [34.3–824.6]	214.2 ± 136.4 [34.3–824.6]
Travelling speed (kmh)	12.1 ± 6.0 [2.0–29.1]	12.8 ± 6.8 [1.7–33.9]	12.6 ± 6.5 [1.7–33.9]
Trip duration (hours)	21.2 ± 10.7 [2.5–47.9]	19.7 ± 14.7 [1.2–90.3]	20.2 ± 13.4 [1.2–90.3]
Direction (degrees)	69.5 ± 0.9* [1.1–351.1]	354.8 ± 1.6* [3.8–355.3]	178.3 ± 2.0 [1.1–355.3]

*Significant Watson-Williams test, F = 219.47, $P < 0.001$

used by a threshold percentage based on degree of representativeness of source population tracking data. Maximum numbers of RFB using the core-use area were calculated and divided by the global population size. The global population is estimated at 1.4 million mature individuals (IUCN 2020). We verified if the potential marine KBA delineated met KBA criteria D1a (Demographic aggregations), i.e., the site is known or thought to hold aggregations of ≥ 1% of the global population. To explore how our selection of RFB for tagging across the two barachois might influence important site identification we generated outputs for tagged birds from each barachois and for both barachois combined. The overlap between the important site identified for all tracked birds and the important sites identified from tracking data from individual barachois were determined by measuring the different marine sites (e.g., all colony site versus BCS2 only site or all colony versus BCS3 only site). All spatial analyses were conducted using R (R Core Team 2021) and maps generated in QGIS (www.qgis.org).

Results

Foraging trip metrics

All 54 GPS loggers were recovered, data downloaded successfully and generated a set of 196 complete foraging trips (see Table 1 for details at BCS2 and BCS3). During, the chick-rearing stage, RFB foraging trip lasted 20.2 h (SD 13.4), covered 214.2 km (SD 136.4), at an average speed of 12.6 kmh (SD 6.5) and reached 81.1 km (SD 51.3) from the colony (Table 1). There was no significant difference in any of these metrics between RFB tracked from either BCS2 or BCS3 (LMM, all $P > 0.439$). While RFB from BCS3 travelled in all directions from the colony (0–360°), with a preference for foraging trips to the south (90–270°) (Fig. 2c), RFB from BCS2 travelled almost exclusively to the north of the colony (0–90° and 270–360°) with the majority of trips going to the north-east of the colony (0–90°) (Fig. 2b). This difference in foraging trip bearings was statistically significant (Watson-Williams test, F = 219.47, d.f. = 194, $P < 0.001$) indicating a degree of at-sea segregation between chick-rearing RFB from the two barachois.

At-sea distribution

Foraging trips from each barachois and from both combined are shown in Fig. 2d-f and illustrate how RFB from South Island typically foraged within 200 km of the atoll, with occasional trips up to 280 km from the island. There appeared to be significant at-sea segregation between RFB from the two barachois (Fig. 2e, h and f, i) and 90% kernel distributions for each barachois exhibited low overlap at 24%, with a Bhattacharyya's affinity value of 0.66 compared to kernel overlap when foraging trips were randomly assigned to a colony (Bhattacharyya's affinity value of 0.88).

Important marine site identification

When accounting for tracking data from all birds, we identified an important marine site against KBA criteria D1a (≥ 1% of global population) around Farquhar Atoll of 18,353 km2 (Fig. 3a). In contrast if we had only used foraging trips from BCS2 the area would have been substantially smaller at 8,709 km2, excluded most of the area to the south of Farquhar utilised by RFB from BCS3 (Fig. 3b) and overlapped with the all colony site by 29.6%. Using only tracking data from BCS3 would have resulted in a larger, but spatially similar important marine site of 20,749 km2 overlapping by 78.2% with the all colony site (Fig. 3c).

Discussion

Foraging trips

Compared to other tracked colonies of RFB in the western Indian Ocean, foraging trips of chick-rearing RFB on Farquhar on average lasted longer (duration), travelled a greater distance (trip distance) and reached a greater maximum distance from the colony than at Europa (Mendez et al. 2016, 2017), Nelson's Island (Chagos Archipelago) (Carr et al. 2023) and Tromelin Island (Kappes et al. 2011); were broadly similar to Danger Island (Chagos Archipelago), but less than Diego Garcia (Chagos Archipelago) (Carr et al. 2023). This illustrates subtle variation in foraging strategies between RFB colonies in the region that is likely driven by large-scale regional climatology (e.g., seasonal monsoons (Schott and McCreary Jr 2001), and small-scale variation in ocean productivity (Lévy et al. 2007), bathymetry, subsurface predator distributions (Orúe et al. 2020; Thoya et al. 2022), which combine to shape the distribution of and access to prey resources. In addition colony size, as shown by other studies of RFB, can also influence foraging strategies with larger colonies exhibiting greater foraging effort in terms of range and duration (Mendez et al. 2017; Trevail et al. 2023b), as a consequence of more intense intraspecific competition.

Within the Farquhar colony we found no evidence to suggest that RFB trip metrics (duration and distance) varied between the two barachois (Table 1), but we did find a difference in trip orientation with BCS2 RFB travelling primarily north of the atoll and BCS3 RFB heading predominantly

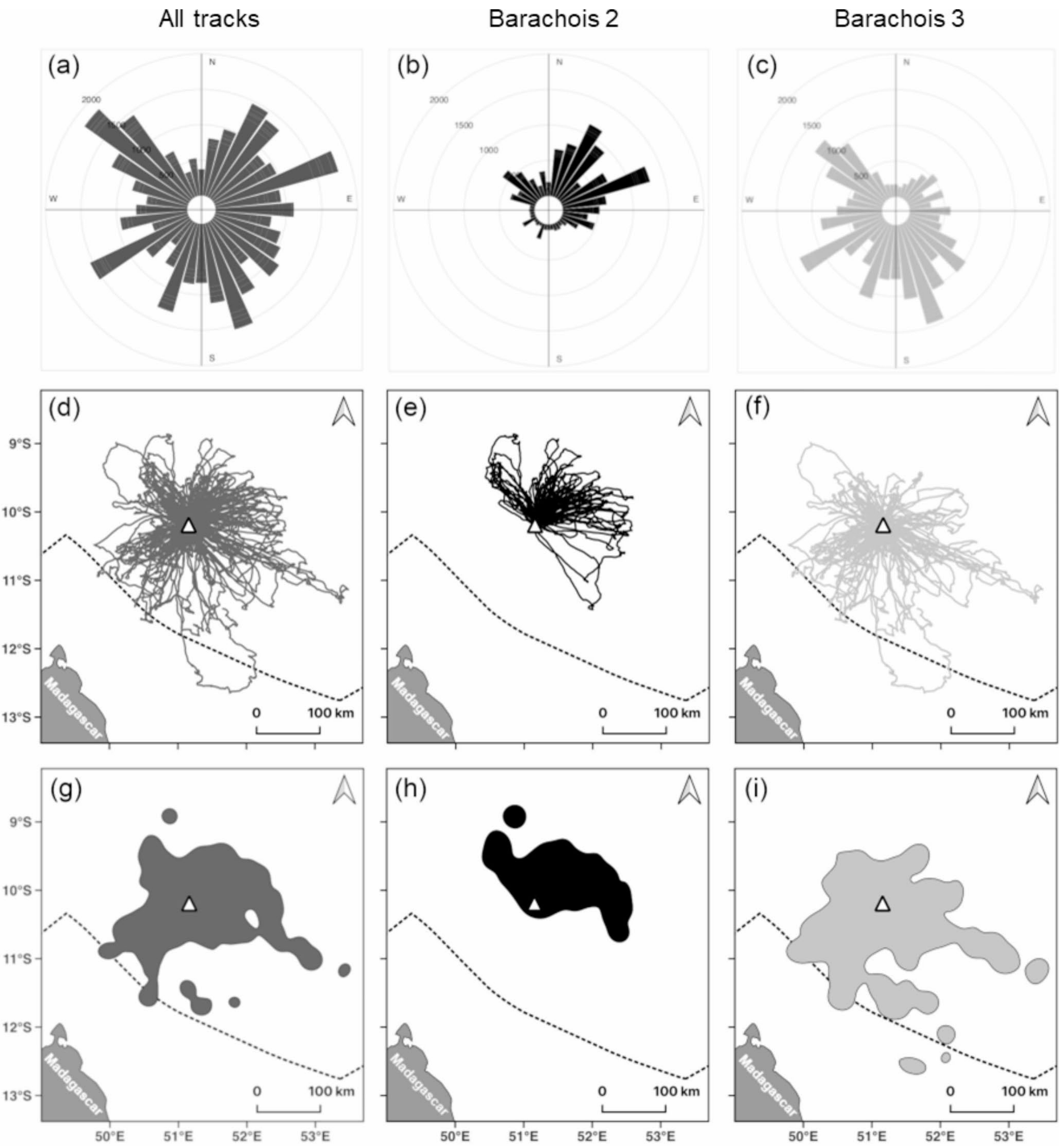

Fig. 2 Foraging trip directions, flight paths and 90% kernel distributions for 54 breeding red-footed booby from South Island, Farquhar Atoll (white triangle): (**a**) flight direction of all foraging trips from their starting point to the furthest point of their trip, (**b**) flight direction of foraging trips from barachois 2, (**c**) flight direction of foraging trips from barachois 3, (**d**) all 196 foraging trips, (**e**) 67 foraging trips from barachois 2, (**f**) 129 foraging trips from barachois 3, (**g**) 90% contour for all foraging trips, (**h**) 90% contour for foraging trips from barachois 2, and (**i**) 90% contour for foraging trips from barachois 3. Values on the circular plot lines in a-c indicate the number of locations in each segment. The dashed line represents the Exclusive Economic Zone of Seychelles

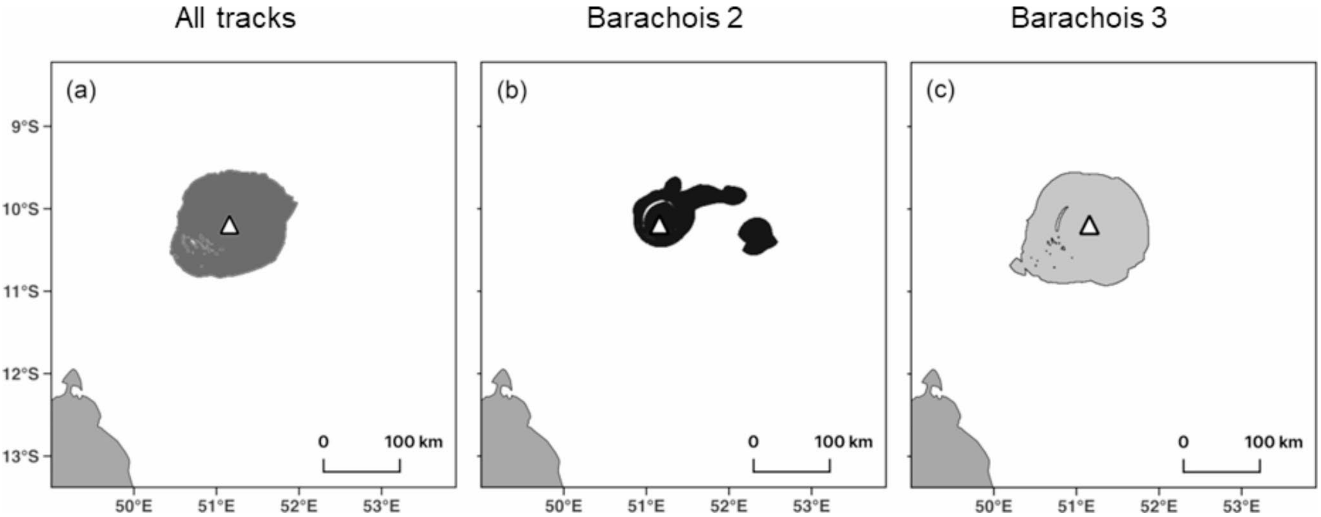

Fig. 3 Potential marine areas for assessment against the KBA Standards for the red-footed booby colony at South Island, Farquhar Atoll (white triangle). (**a**) based on all (196) foraging trips, (**b**) based on 67 foraging trips from barachois 2 and (**c**) based on 129 foraging trips from barachois 3. For all scenarios, the representativeness score was > 70% facilitating identification of an important site which can be assessed against the KBA Standard

south. This segregation is unusual and not reflected in other studies in the region where RFB have been tagged at multiple locations across breeding colonies (Mendez et al. 2016, 2017; Carr et al. 2023; Trevail et al. 2023b) or elsewhere across their pan-tropical range. Considering other taxa and locations, sub-colony segregation in trip direction is relatively understudied compared to inter-colony variation as reviewed by Bolton et al. (2019) and illustrated by studies on Northern gannets (Dean et al. 2015; Angel et al. 2016). The few studies that have investigated sub-colony segregation found no segregation between Northern gannets tracked across seven sub-colonies within 400 m (Waggitt et al. 2014) or in Cory's shearwater (*Calonectris borealis*) at two colonies 800 m apart on Belenga Island (Pereira et al. 2022). However, segregation was observed in Scopoli's shearwaters (*Calonectris diomedea*) across two sub-colonies 7 km apart (on separate islets) (Morinay et al. 2022), with those breeding in the western islet headed to the southwest while shearwaters from the eastern islet headed to the north and east. For sub-colonies of Cory's shearwater on the same island (2 km apart on different sides of the island) directional segregation was observed (Ceia et al. 2015) and explained by the geography of the colonies in respect of orientation to the sea. On Farquhar Atoll it is unlikely geography is influential as both barachois are on the western side of South Island (Fig. 1) and do not differ in their topography and are hence orientated towards the sea and prevailing weather conditions in the same way. Hence, it is unlikely to be a physical or environmental difference between the two barachois that is driving this segregation in foraging trip direction and is perhaps related to RFB population sizes in the two barachois with foraging to the north by RFB from BCS2 (smaller population) as a means of reducing foraging competition at-sea with RFB from BCS3. This could be facilitated by social cues, which have been shown to positively influence directional choices of foraging opportunities in Australasian gannets (*Morus serrator*) (Jones et al. 2018). However, at BCS2 RFB may be using cues from conspecifics in BCS3 to initiate foraging trips in the opposite direction to avoid competition at sea, potentially leading to the development of cultural foraging strategies within BCS2 (Gremillet et al. 2004). While BCS2 and BCS3 are only ~ 1.5 km apart, RFBs nest along the low-lying vegetation on the beach head between them, hence they would not be precluded from obtaining directional information associated with foraging opportunities from social cues.

At-sea distribution

Foraging trips of chick-rearing RFB from the colony on South Island encompass an area around the colony within a 280 km radius. Within this, RFBs from BCS2 were found typically to the north of the atoll and those for BCS3 were found to the south with some movements to the north (Fig. 2). Hence, 90% utilisation distributions for RFB from the two barachois showed little overlap, indicating a high degree of at-sea segregation in this study. While other studies show inter-colony at-sea segregation in the region in RFB (Trevail et al. 2023b) and in other seabird species elsewhere (Bolton et al. 2019), we believe this is the first study to provide evidence for sub-colony variation in at-sea distribution in a tropical seabird during the breeding season. While our finding is compelling, it is based on our definition of colony and the tracking of movements during a 2-week window in a single breeding season. We assume that RFB nesting across South Island are all part of the same colony, and base this on the observation that while the greatest concentrations of nests are typically found in the two barachois (Fig. 1b) nesting RFB can be found along the beach headland and in suitable vegetation between barachois, suggesting one colony rather than multiple colonies on South Island, the Manahas Islands and the southern tip of North Island. Ideally (as originally planned), we would have conducted tracking of breeding RFB during each of the two monsoons seasons that characterize the climatology of the region (Schott and McCreary Jr 2001). This would have provided a more in-depth insight into breeding RFB foraging areas throughout the year and minimised any biases associated with a single study period. However, this was not possible due to the global coronavirus (COVID-19) pandemic and logistical constraints associated with working in the remote south-western atolls.

Marine important site identification

Using the track2KBA package (Beal et al. 2021) an important site sufficiently representative of the distribution of the sampled RFB population from Farquhar Atoll was identified. The size of this (18,353km^2) is broadly comparable to important marine sites for other RFB colonies in the western Indian Ocean (4,063 km2, 10,574 km2 and 33,369 km2) (Carr et al. 2023) following the same protocols. Given the relatively large size of these sites this is perhaps indicative of the scale required when considering at-sea conservation actions which may be required to support breeding RFBs in the region.

Underpinning the identification of the important site around Farquhar Atoll are decisions relating to the identification of breeding individuals for tagging. These include decisions prior to arrival at Farquhar Atoll (e.g., South Island as the study colony and targeting chick-rearing individuals) and those made following an initial in-situ assessment of the colony and the two barachois (e.g., nest numbers and accessibility and chick age). As a result of these decisions, we identified BCS2 and BCS3 as our study sites and tagged individuals within these. However, it is clear from our findings that there is a (unexpected) degree of sub-colony variation in at-sea foraging areas with limited overlap between RFBs from these barachois. While we combined tracking data from both sites to identify the important sites this apparent segregation could have resulted in different important sites if we had only tagged birds in one barachois. This is illustrated in Fig. 3 and shows how both the location and size of the important site would differ, particularly if RFB were only tagged in BCS2 where there was a > 50% reduction in size of the important site. If the study had focussed only on BCS2, then at the least it would have provided the best available evidence to identify an initial important marine site meeting KBA standards and inform conservation actions and marine spatial planning. If there was doubt that this was not necessarily representative of RFB at Farquhar Atoll, then further tracking studies would be warranted, particularly of RFB from BCS3. Our approach assumes that the RFB we tagged in each barachois are a representative sample of all RFB in each barachois. Hence, our findings do suggest that if conditions allowed only tagging of breeding RFB at one barachois, then deploying tags in the larger population at BCS3 would results in the identification of an important marine site that was most representative of the colony on South Island.

While we have examined spatial variation in our tagging strategy between sub-colonies, we were not able to consider temporal variation based around stages of the breeding cycle or the environmental conditions associated with the two monsoon seasons at our study site. RFB were strongly synchronised in their breeding across the two barachois and breeding adults were tagged while rearing chicks aged between 5 and 30 days. As mentioned, we would have ideally conducted our tagging program during both monsoon seasons and over multiple years, but this was not possible. Given a longer tagging period and less breeding synchrony in the colony we would have ideally tagged both incubating and chick rearing RFB, particularly as RFBs at-sea distributions are known to vary between breeding stages (Mendez et al. 2016). Inclusion of tracking data accounting for both temporal elements may well have resulted in the identification of a different important site, although a recent study of multiple seabird taxa has shown that one bout of tracking chick-rearing adults is often sufficient to represent at-sea distributions (Beal et al. 2023). Hence, it must be recognised that the important site identified in this study represents the at-sea distribution of only chick-rearing RFB during one monsoon season for the Farquhar Atoll RFB colony.

Conclusions

When designing and conducting field-based tracking studies of colonial nesting seabirds, decisions are made in advance and on the day that can influence the selection of sites where individuals are tagged within a colony. Where the focus is on identification of at-sea distributions and priority foraging grounds the choice of sites within a single colony may (Ceia et al. 2015) or may not (Waggitt et al. 2014) significantly impact the findings, though the extent and ecological drivers of sub-colony variation in foraging distributions among seabirds, remain poorly understood. In our study we show how RFB from two sites within a colony exhibit substantial at-sea segregation of foraging grounds, which if unaccounted for could result in the identification of important sites, which from a conservation and marine spatial planning perspective could be considered misrepresentative. We therefore recommend, where possible, due consideration is given to (i) the selection of tagging sites (where feasible) across a colony to reflect geography, topography and coastal features and (ii) the inclusion of analyses to explore the influence of tagging sites, particularly in tropical species that remain comparatively less well studied than their temperate and high latitude counterparts.

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Author contributions Audrey Jaeger, Matthieu Le Corre, Malcolm Nicoll & Gerard Rocamora contributed to the study conception and design. Data collection was conducted by Aurelie Hector, Jake Letorri, Matthieu Le Corre & Malcolm Nicoll. Analyses were conducted by Audrey Jaeger, Matthieu Le Corre & Malcolm Nicoll. The first draft of the manuscript was written by Malcolm Nicoll and all authors commented on subsequent versions of the manuscript. All authors read and approved the final manuscript.

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Data availability All location data are available on the Birdlife International Seabird Tracking Database https://www.seabirdtracking.org/ (Data set IDs 2187 & 2188).

Declarations

Compliance with ethical standards This study has been approved by the Seychelles Bureau of Standards, Republic of Seychelles (ref. A0157). The banding and tracking operations were undertaken as part of the Personal Program of Matthieu Le Corre ethically and scientifically approved by the Centre de Recherches sur la Biologie des Populations d'Oiseaux (PP616, CRBPO, France).

Competing interests The authors have no relevant financial or non-financial interests to disclose.

Ethics approval This study has been approved by the Seychelles Bureau of Standards, Republic of Seychelles (ref. A0157). The banding and tracking operations were undertaken as part of the Personal Program of Matthieu Le Corre ethically and scientifically approved by the Centre de Recherches sur la Biologie des Populations d'Oiseaux (PP616, CRBPO, France).
Tables.

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