

JOURNAL OF AVIAN BIOLOGY

Research article

Geolocation and immersion loggers reveal year-round residency and facilitate nutrient deposition rate estimation of adult red-footed boobies in the Chagos Archipelago, tropical Indian Ocean

Stephen C. Votier¹✉, Grace Corcoran², Pete Carr³, Ruth E. Dunn^{1,4}, Robin Freeman³, Malcolm A. C. Nicoll³, Hannah Wood³ and Alice M. Trevail^{1,2}

¹The Lyell Centre, Heriot-Watt University, Edinburgh, UK

²Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Penryn Campus, Penryn, Cornwall, UK

³Institute of Zoology, Zoological Society of London, Regents Park, London, UK

⁴Lancaster Environment Centre, Lancaster University, Lancaster, UK

Correspondence: Stephen C. Votier (s.votier@hw.ac.uk)

Journal of Avian Biology

2024: e03185

doi: [10.1111/jav.03185](https://doi.org/10.1111/jav.03185)

Subject Editor: Yutaka Watanuki

Editor-in-Chief: Jan-Åke Nilsson

Accepted 16 April 2024



Bio-logging has revealed much about high-latitude seabird migratory strategies, but migratory behaviour in tropical species may differ, with implications for understanding nutrient deposition. Here we use combined light-level and saltwater immersion loggers to study the year-round movement behaviour of adult red-footed boobies *Sula sula rubripes* from the Chagos Archipelago, tropical Indian Ocean, to assess migratory movements and estimate nutrient deposition rates based on the number of days they spent ashore. Light levels suggest that red-footed boobies are resident in the Chagos Archipelago year-round, although there are large latitudinal errors this close to the equator. Immersion data also indicate residency with tracked birds returning to land every one or two days. Spending an average of 79.86 ± 2.80 days and 280.84 ± 2.64 nights per year on land allows us to estimate that the 21 670 pairs of red-footed boobies deposit 37.34 ± 0.56 tonnes year⁻¹ of guano-derived nitrogen throughout the archipelago. Our findings have implications for tropical seabird conservation and phylogenetics, as well as for assessing the impact of seabird nutrients on coral reef ecosystems.

Keywords: bio-logging, migration, nutrients, seabird

Introduction

Bio-logging has created a paradigm shift in the study of animal movement ecology (Wilmers et al. 2015). This is exemplified by seabird tracking research which has over-turned the once prevalent view of seabirds as primarily dispersive migrants (Newton 2008), revealing instead a great diversity of migratory strategies within (Weimerskirch et al. 2015) and among species (Grecian et al. 2016, Trevail et al.



www.avianbiology.org

© 2024 The Authors. Journal of Avian Biology published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

2023b). Nevertheless, while there is good coverage of seabird tracking in temperate and polar seas, tropical species are much less well-studied both in terms of the number of individuals and the percentage of species tracked (Bernard et al. 2021). Understanding the amount of time tropical seabirds spend on marine migrations or on land is crucial not only to inform our understanding of population differentiation (Friesen et al. 2007), and appropriate scales for spatial protection measures, but also to quantify terrestrial nitrogen deposition via guano, which is important for coral reef function and resilience (Graham et al. 2018, Benkwitt et al. 2023).

In temperate and polar regions, seabirds may move long distances to track seasonally favourable environmental conditions becoming almost entirely maritime during the non-breeding period (Shaffer et al. 2006, Egevang et al. 2010). These same behavioural adjustments in tropical pelagic seabirds are hypothesized to differ somewhat, since oligotrophic waters with low or unpredictable seasonal variation may favour dispersive or short-distance migratory movements (Weimerskirch 2007, Newton 2008, Winkler et al. 2014). Nevertheless, the majority of tracked tropical seabirds are long-distance migrants, with a diversity of longitudinal, latitudinal, or multi-directional movements among taxa (Table 1). Migratory strategies also vary within species. For instance, Bulwer's petrels *Bulweria bulwerii* are leapfrog migrants – temperate and sub-tropical populations travel long distances and over-fly short-distance tropical breeders (Ramos et al. 2015). Nevertheless, strategic tracking of tropical seabird movements has emerged as a conservation priority (Bernard et al. 2021).

Seven of the ten extant species of Sulidae are tropical or sub-tropical occurring across most of the world's tropical seas. The small number of tracking studies on this family indicate a mix of resident and short-distance migrants, but work is limited to two species (Table 1). We studied the movements and activity of red-footed boobies *Sula sula* (hereafter RFB) year-round. This pantropical species is thought to be largely resident, but movements outside the breeding season have been inferred from indirect evidence in the form of ring recoveries and observations (Schreiber et al. 2020). RFBs are composed of three sub-species based on morphological differences (i.e. variation in the frequency of light and dark phenotypes) and high genetic structuring: nominate *sula* (Caribbean and tropical/sub-tropical Atlantic), *rubripes* (Indian and tropical Pacific Oceans) and *websteri* (eastern Central Pacific Ocean). Gene flow among colonies is suggestive of inter-colony dispersal (Morris-Pocock et al. 2010). Therefore, year-round tracking of RFB movements could prove valuable for understanding the formation/persistence of taxa since high gene flow may arise either because of individuals mixing from multiple populations during the non-breeding season (Friesen et al. 2008), or via inter-colony dispersal by immatures (Bicknell et al. 2014). Moreover, their body size (~ 900 g), pan tropical distribution and large global population (~ 1.4 million mature individuals; Birdlife International 2023) make them potentially important nutrient contributors to threatened coral reef ecosystems

(Graham et al. 2018, Benkwitt et al. 2022), although it is not possible to accurately assess this in the absence of year-round behavioural information (i.e. by quantifying the amount of time spent ashore).

Specifically, we studied the migration behaviour of RFBs of the sub-species *rubripes* breeding in the Chagos Archipelago, Central Indian Ocean (07°14'S, 72°26'E). This isolated group of atolls has ~ 21 670 breeding pairs of RFB (Carr et al. 2021b), representing one of the largest aggregations in the Indian Ocean (Danckwerts et al. 2014). It is also within a 640 000 km² Marine Protected Area (MPA), which protects the world's largest coral atoll and some of the healthiest reefs (Hays et al. 2020).

Our objective is to understand more about RFB movement ecology and its consequences in terms of nutrient deposition throughout the annual cycle using combined geolocation and saltwater immersion loggers deployed on adults. First, we estimate twice daily locations from variation in day length (which covaries with latitude) and the timing of midday/midnight relative to Greenwich Mean Time (indicating longitude), although errors may be considerable so close to the equator (i.e. latitudinal errors of 347 ± 462 km at 03°50'S, 32°25'W; Roy et al. 2021). Second, we use saltwater immersion data to quantify the proportion of time the logger was immersed ('logger wet', likely indicating that the bird was resting at the sea surface or foraging at sea) and the proportion of time the logger was dry (indicating the bird was flying or on land) throughout independently determined stages of the birds' annual cycle (pre-breeding, incubation, chick-rearing) based on direct observations during deployment and recovery. Specifically, we calculated the number of nights when the logger was completely dry (dusk to dawn the following day) per month as a measure of terrestrial overnight roosting (perched in trees near nests or nearby islands) since continuous flights at night are highly unlikely (Weimerskirch et al. 2005). Finally, we used immersion logger derived estimates of time spent on land to calculate the year-round nitrogen input from RFB guano.

Material and methods

Tracking

RFBs were tracked from Barton Point, Diego Garcia, Chagos Archipelago between January 2018 and February 2020. RFB in the Chagos Archipelago breed asynchronously, with two peaks per year occurring during April and December (Carr et al. 2023). Adults were fitted with combined geolocation and immersion loggers (Intigeo C330, Migrate technology, Cambridge, UK; 3.3 g) attached to a multi-layered impact acrylic leg ring (Interrex-rings, Poland). GPS loggers (iGotU GT-120; 15g) were simultaneously deployed and retrieved after ~ 2–3 foraging trips to track at-sea movements during breeding but not analysed here (Trevail et al. 2023b). The lack of seasonal or synchronous breeding among years led to hand-caught adults in various stages of reproduction:

Table 1. Migratory strategies of tracked tropical and sub-tropical seabirds. While the tropics are defined as the latitudes lower than 23°26' we include studies at slightly higher latitudes as they comprise taxa and ecosystems which are typically considered tropical or sub-tropical.

Species	Family	Habitat	Latitude	Migrant?	Strategy	Direction	Ocean	Ref.
Black-naped tern <i>Sterna sumatrana</i>	Laridae	Neritic	26°30'N	Migrant	Long distance	Latitudinal	Pacific	Thiebot et al. (2020)
Brown booby <i>Sula leucogaster</i>	Sulidae	Neritic	24°11'N	Migrant	Variable	Latitudinal	Pacific	Kohno et al. (2019)
Tropic of Cancer 23°26'N								
Boyd's shearwater <i>Puffinus boydi</i>	Procellariidae	Pelagic	16°36'N, 14°58'N	Migrant	Long distance	Longitudinal	Atlantic	Zajková et al. (2017)
Bulwer's petrel <i>Bulweria bulwerii</i>	Procellariidae	Pelagic	14°58'N to 37°42'N	Migrant	Long distance	Multiple	Atlantic	Ramos et al. (2015)
Great frigatebird <i>Fregata minor</i>	Fregatidae	Pelagic	0.3°N	Resident	–	–	Pacific	Weimerskirch et al. (2017)
Equator								
Sooty tern <i>Onychoprion fuscatus</i>	Laridae	Pelagic	03°43'S	Migrant	Long distance	Longitudinal	Indian	Jaeger et al. (2017)
Masked booby <i>Sula dactylatra</i>	Sulidae	Pelagic	03°50'S	Resident	–	–	Atlantic	Roy et al. (2021)
Brown noddy <i>Anous stolidus</i>	Laridae	Pelagic	03°72'S	Migrant	Long distance	Longitudinal	Indian	Le Corre et al. (2012), Trevail et al. (2023a,b)
Lesser noddy <i>Anous tenuirostris</i>	Laridae	Pelagic	03°72'S	Migrant	Long distance	Longitudinal	Indian	Le Corre et al. (2012), Trevail et al. (2023a,b)
Wedge-tailed shearwater <i>Ardenna pacificus</i>	Procellariidae	Pelagic	04°10'S	Migrant	Variable	Longitudinal	Indian	Catry et al. (2009)
Wedge-tailed shearwater <i>Ardenna pacificus</i>	Procellariidae	Pelagic	04°12'S, 04°18'S, 05°24'S	Migrant	Long distance	Multiple	Indian	Le Corre et al. (2012), Trevail et al. (2023a,b)
Tropical shearwater <i>Puffinus bailloni</i>	Procellariidae	Pelagic	04°12'S	Migrant	Long distance	Latitudinal	Indian	Le Corre et al. (2012), Trevail et al. (2023a,b)
White-tailed tropicbird <i>Phaethon lepturus</i>	Phaethontidae	Pelagic	04°18'S, 12°48'S	Migrant	Long distance	Latitudinal	Indian	Le Corre et al. (2012), Trevail et al. (2023a,b)
Red-footed booby <i>Sula sula</i>	Sulidae	Pelagic	07°14'S	Resident	–	–	Indian	This study
Sooty tern <i>Onychoprion fuscatus</i>	Laridae	Pelagic	07°57'S	Migrant	Long distance	Multiple	Atlantic	Reynolds et al. (2021)
Great frigatebird <i>Fregata minor</i>	Fregatidae	Pelagic	09°54'S, 18°30'S, 22°36'S	Migrant	Short distance	Multiple	Pacific	Weimerskirch et al. (2017)
Round Island petrel (<i>Pterodroma</i> sp.)	Procellariidae	Pelagic	19°51'S	Migrant	Long distance	Multiple	Indian	Franklin et al. (2022)
Wedge-tailed shearwater <i>Ardenna pacificus</i>	Procellariidae	Pelagic	19°54'S, 21°6'S	Migrant	Long distance	Multiple	Indian	Le Corre et al. (2012), Trevail et al. (2023a,b)
Red-tailed tropicbird; <i>Phaethon rubricauda</i>	Phaethontidae	Pelagic	19°54'S, 22°24'S, 19°54'	Migrant	Long distance	Multiple	Indian	Le Corre et al. (2012), Trevail et al. (2023a,b)
Trinidad petrel <i>Pterodroma arminjoniana</i>	Procellariidae	Pelagic	20°30'S	Migrant	Long distance	Longitudinal	Atlantic	Leal and Bugoni (2021)
Barau's petrel <i>Pterodroma baraui</i>	Procellariidae	Pelagic	21°04'S	Migrant	Long distance	Longitudinal	Indian	Pinet et al. (2011b)
Gould's petrel <i>Pterodroma leucoptera caledonica</i>	Procellariidae	Pelagic	21°17'S	Migrant	Long distance	Longitudinal	Pacific	Rayner et al. (2016)
Great frigatebird <i>Fregata minor</i>	Fregatidae	Pelagic	22°18'S	Migrant	Long distance	Multiple	Indian	Weimerskirch et al. (2017)
Red-tailed tropicbird; <i>Phaethon rubricauda</i>	Phaethontidae	Pelagic	22°40'S	Migrant	Long distance	Multiple	Indian	Le Corre et al. (2012), Trevail et al. (2023a,b)
Murphy's petrel <i>Pterodroma ultima</i>	Procellariidae	Pelagic	24°22'S	Migrant	Long distance	Multiple	Pacific	Clay et al. (2017)
Wedge-tailed shearwater <i>Ardenna pacificus</i>	Procellariidae	Pelagic	23°26' S	Migrant	Long distance	Latitudinal	Pacific	McDuie and Congdon (2016)
Tropic of Capricorn 23°26'S								
Wedge-tailed shearwater <i>Ardenna pacificus</i>	Procellariidae	Pelagic	20°39'S, 28°56'S	Migrant	Long distance	Multiple	Indian	Surman et al. (2018)
Lesser noddy <i>Anous tenuirostris</i>	Laridae	Neritic	20°39'S, 28°56'S	Resident	–	–	Indian	Surman et al. (2018)
Brown noddy <i>Anous stolidus</i>	Laridae	Pelagic	20°39'S, 28°56'S	Migrant	Short distance	Latitudinal	Indian	Surman et al. (2018)
Bridled tern <i>Onychoprion anaethetus</i>	Laridae	Pelagic	20°39'S, 28°56'S	Migrant	Long distance	Latitudinal	Indian	Surman et al. (2018)
White tern <i>Gygis alba</i>	Laridae	Pelagic	Lord Howe, 31°31'S	Migrant	Long distance	Latitudinal	Pacific	Carille and O'Dwyer (2022)

pre-breeding (n=2), incubation (n=16), or chick rearing (n=7). It was not possible to monitor breeding sites year-round, but devices were recovered after 7–24 months during periodic return visits when individuals were seen breeding (n=6) or roosting (n=19) in the colony. Genetic sexing using feathers was carried out at the Institute of Zoology, Zoological Society of London (Carr et al. 2023).

Intra-annual variation in spatial distribution

Location estimates were derived at 12-hour intervals from light levels using R package 'SGAT' (Wotherspoon et al. 2013), following methods described in Franklin et al. (2022). Location data were then processed using the 'ExMove' toolkit (Langley et al. 2023) to create a standardised data frame with a speed filter of 20 m s⁻¹ and a net displacement filter of 3000 km to remove erroneous locations. All locations 30 days either side of the vernal and autumn equinox were removed, because day length similarities render geolocation inaccurate (Trevail et al. 2023a). Daily locations for the remaining data were calculated as the mean latitude and longitude each day from the two geolocation estimates, in local time (GMT +6) to reduce longitudinal error (Supporting information). We calculated overall and monthly utilisation distributions (UDs) from daily locations, excluding equinox periods, for which 75% contours indicate home ranges, and 50 and 25% contours indicate core areas. UD calculations were derived across a 10 km grid using default smoothing parameters in the R package 'adehabitatHR' (Calenge 2006). At-sea distributions were mapped alongside Indian Ocean breeding colonies (Authors knowledge of RFB colonies in the western Indian Ocean, BirdLife International and Handbook of the Birds of the World 2020).

Intra-annual variation in onshore activity

To understand year-round activity, we derived two metrics from the bird-borne saltwater immersion data; 1) daytime on land, when the immersion logger was dry during ≥ 0.95% of daylight hours indicative roosting on land or nest attendance (although it is possible birds might spend extended periods flying, this seems unlikely to be ≥ 0.95%) and 2) nighttime on land, where the logger was ≥ 0.95% dry overnight (although we cannot exclude some nighttime flying or resting on floating debris at-sea).

Immersion data were processed using the 'ExMove' toolkit in R (Langley et al. 2023) to create a standardised data frame. We calculated the proportion of time the logger was dry (immersion=0 over a 10-minute period) separately for local daytime (dawn to dusk), and nighttime (dusk to dawn). Times of nautical dawn and dusk were derived for the tagging location (Barton Point, Diego Garcia) using 'suncalc' in R (Agafonkin and Thieurmel 2018).

To determine factors influencing extended dry logger periods and hence most likely time spent on land, we used binomial mixed effects models (i.e. 1 ≥ 95% dry, 0 < 95% dry). Time period (night or day), month (as a factor), breeding

stage (when known: pre-breeding, chick-rearing, incubation, and non-breeding, e.g. when previously tagged breeding birds were seen roosting away from their inactive nest site), and sex (as females have longer foraging trips compared with males; Trevail et al. 2023b) were all included as explanatory variables. Time period (night or day) was included in two-way interactions with 1) breeding stage, i.e. whether the probability of the logger being dry differed among breeding stages and the non-breeding period and 2) month, i.e. whether diurnal and nocturnal activity patterns varied annually. Because breeding stages were only known during limited months of tag deployment and retrieval (January, February and June), and this population breeds asynchronously, we do not have sufficient data to understand whether patterns of activity vary among breeding stages year-round (i.e. a three-way interaction between day/night, month, and breeding stage). Individual ID was included as a random effect. We did not include year because of problems with model convergence and predictive power. We ran GLMMs using 'lme4' in R (Bates et al. 2015), and based model selection on comparison of Akaike's Information Criteria (AIC; Supporting information); the most parsimonious model was chosen as the model with delta AIC < 2. Model performance was assessed using area under the curve (AUC) values (Zweig and Campbell 1993, Trevail et al. 2019) and confusion matrix scores, which were all high, suggesting good model fit (AUC = 0.81; Supporting information). We extracted parameter estimates using the 'ggeffects' package in R (Lüdecke 2018), including 'ggemmeans()' to marginalise over non-focal effects and 'ggpredict()'.

Nitrogen deposition rates

We estimated the annual nitrogen input from RFB guano deposition per hectare per year (NI) for each island (j) throughout the Chagos Archipelago by using immersion data and the approach in Graham et al. (2018):

$$NI_j = \frac{N \times Dr \times Res \times Bd_j}{IsArea_j}$$

where N is the nitrogen content of guano, Dr is the defecation rate, Res is the number of days per year that individuals are resident at the breeding colony, Bd is the number of individuals on each island per residency day, and IsArea is the area of the island.

The nitrogen content of RFB guano (N) was assumed to be 18.1% and their defecation rate (Dr) was assumed to be 26.4 g day⁻¹, assuming no daily change in defecation rate, based on data from the same species at Palmyra Atoll in the Pacific Ocean (Young et al. 2010).

Initially, we estimated RFB residency (Res) based on breeding season length (336 days; Schreiber et al. 2020). We estimated the number of individuals on the island during each of these days (Bd) by multiplying the numbers of apparently occupied nests (AONs) reported in Carr et al. (2021b) by 1.5. We therefore accounted for 1) one bird per pair

making daytime foraging trips whilst the other stayed at the nest (i.e. attendance per AON = 0.5), and 2) both birds being at the colony at nighttime (i.e. attendance per AON = 1; as in [Graham et al. 2018](#)).

We then repeated this calculation, deriving archipelago-specific residency estimates from immersion data instead of species-wide breeding season length estimates. From our immersion data, we therefore calculated the mean number of daytime roosts and nighttime roosts per month, per individual. To account for variability in tracking duration and unknown breeding status for most months, we multiplied monthly day and night attendance by 12 to average across a year (Res). To transform our individual year-round colony attendance estimates to estimates of attendance per pair per year, we divided both the number of year-round dry days and the number of dry nights by 2, to account for each of these periods being half of the entire 24-hour period and calculated the sum of these values. We then multiplied this value by 2 and the number of AONs at each island (Bd; [Carr et al. 2021b](#)), to account for the presence of both individuals within the pair.

Results

We obtained GLS data for 25 adult RFBs over 7–24 months, from 7 females, 10 males, and 8 of unknown sex (Supporting information).

Intra-annual variation in spatial distribution

RFBs showed very limited longitudinal movement throughout the year with utilization distributions close to or within the longitudinal bounds of the Chagos MPA ([Fig. 1](#)). Location estimates varied latitudinally with apparent northward movements during April–August and southward movements during October–February but still not close to other RFB colonies ([Fig. 1](#)).

There was monthly variation in latitude (consistent with GLS error close to the equator) but no obvious longitudinal change indicating that birds probably remained within the Chagos Archipelago MPA throughout the year ([Fig. 1](#)). Moreover, near-continuous dry overnight periods indicate RFBs were rarely far from land ([Fig. 2](#)) lending further support for this population being non-migratory and without inter-colony contact from elsewhere in the Indian Ocean ([Fig. 1](#)).

Intra-annual variation in onshore activity

Birds spent on average 23.4 ± 0.2 nights on land (mean \pm SE) per month tracked (in percentage of nights per month, this equates to $76.9 \pm 0.7\%$, range = 39.3–100%). Across the year, individuals were recorded as wet (i.e. proportion dry < 0.95, away from a terrestrial roost site) for 1.72 ± 0.3 consecutive nights on average (range 1–8). Overall, dry periods were more likely overnight than during the day ([Fig. 3](#)). During chick-rearing and incubation phases, loggers had a higher probability

of being dry compared to non-breeding (i.e. birds roosting at the colony), both overnight and during the day ([Fig. 3a](#)). Whilst the probability of loggers being dry was high overnight all year-round (> 50% predicted), there seemed to be slightly lower probabilities during December–February ([Fig. 3b](#)). The probability of loggers being dry during the day showed two annual peaks during April and December ([Fig. 3b](#), Supporting information), which corresponds to the breeding peaks of this population ([Carr et al. 2021b](#)). There was a lower probability of continuous dry logger periods during July–October ([Fig. 3](#)), possibly indicating non-breeding. We found no effect of sex on the probability of dry logger periods.

Nitrogen deposition rates

Individuals spent, on average, 6.65 ± 0.23 days (mean \pm SE), and 23.40 ± 0.22 nights on land per month. This equates to 79.86 ± 2.80 days and 280.84 ± 2.64 nights per year. During this time spent on land, we estimate that the 21 670 pairs of breeding RFBs in the Chagos Archipelago could input 37.34 ± 0.56 tonnes year⁻¹ of guano-derived nitrogen, with the 8600 pairs at Diego Garcia depositing 13.91 ± 0.21 tonnes year⁻¹, equating to 5.11 ± 0.07 kg ha year⁻¹.

Discussion

Based on light-level geolocation estimates and behaviour inferred from saltwater immersion loggers, we conclude that RFBs are largely resident in the Chagos Archipelago year-round. Geolocation position estimates suggest virtually no longitudinal movement during the year and while there were variable latitudinal estimates ([Fig. 1](#)), these results are consistent with latitudinal errors from GLS-derived location estimates, notably in the tropics (e.g. latitudinal error (347 ± 462) and longitudinal error (65 ± 54 km) from light-level geolocation at similar latitudes, [Roy et al. 2021](#)). Moreover, a stationary geolocator deployed in Mauritius (Round Island; $19^{\circ}50'S$, $57^{\circ}47'E$; Supporting information) suggests similar northerly bias during April–August and southerly bias during October–February to that observed in the Chagos RFBs ([Fig. 1b](#)). Saltwater immersion loggers showed a high frequency of continuously dry periods overnight throughout the annual cycle ([Fig. 2](#)), indicative of roosting on floating debris, overnighting on land or continuous nocturnal flights ([Jaeger et al. 2017](#)). The latter seems unlikely as GPS tracking shows RFBs rarely spend the night at sea ([Weimerskirch et al. 2005](#), [Trevail et al. 2023b](#)) and while we cannot completely exclude roosting on debris, we think it most likely they return to land.

Sulids are generally thought to be resident or short-distance migrants in the tropics, but there are relatively few year-round tracking studies. The only studies which tracked booby migration using geolocation loggers (that we are aware of) show brown boobies *Sula leucogaster* at the northernmost extent of their tropical breeding range in Japan ($24^{\circ}11'N$) combined long-distance (max 4988 km) and short-distance

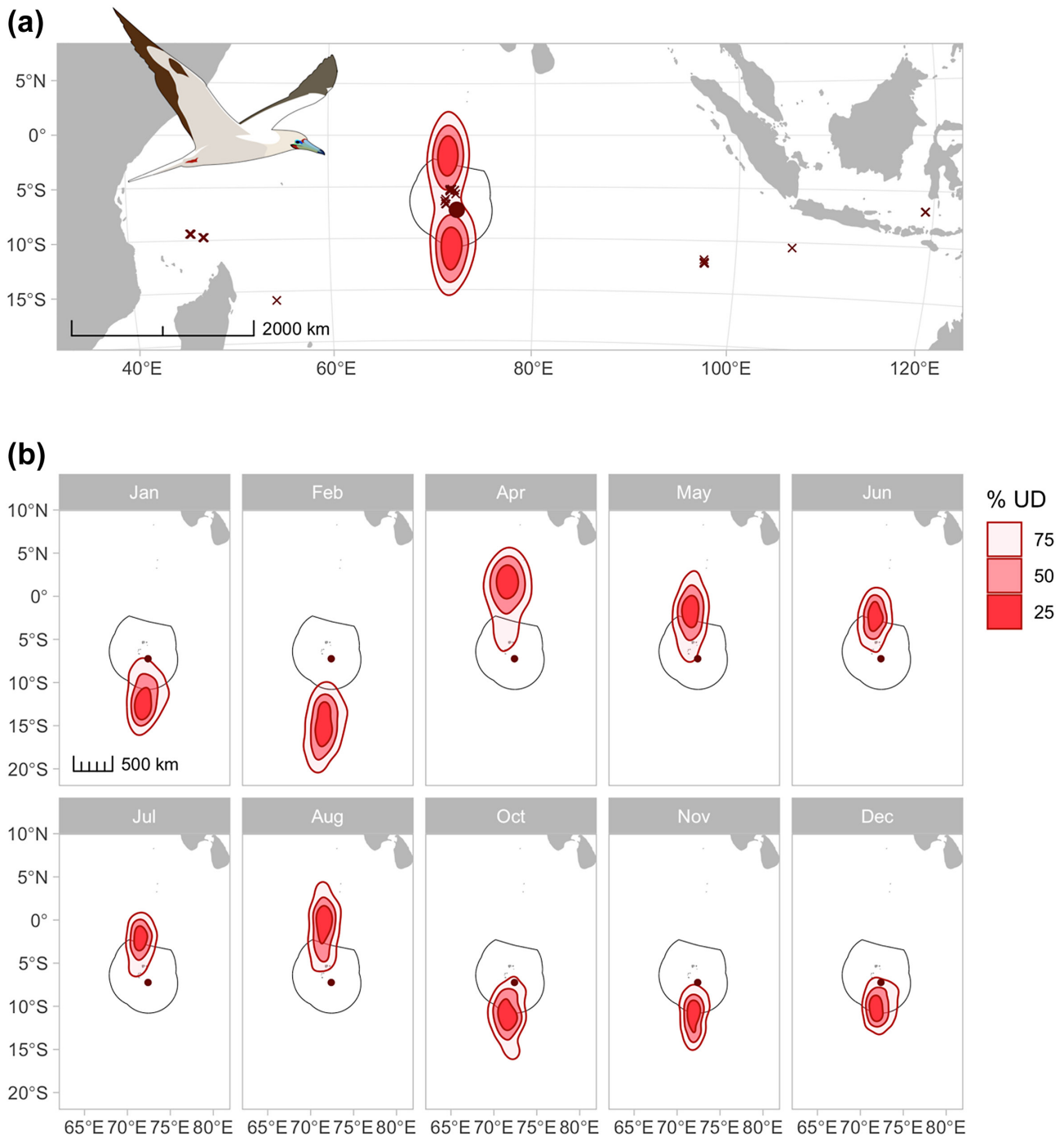


Figure 1. Year-round movements of adult red-footed boobies ($n=25$) from the Chagos Archipelago. Shown here are 75, 50 and 25% utilization distributions based on light-level geolocation for (a) all the data (using a Lambert azimuthal equal-area projection centred on the Chagos Archipelago), and (b) by calendar month. March and September are excluded because of the equinox. Solid point is the location of Diego Garcia, Chagos Archipelago and thin line shows the extent of the Chagos Archipelago Marine Protected Area. Limited longitudinal movements and latitudinal movements fluctuating either side of the equinox are consistent with geolocator error this close to the equator. We therefore conclude that red-footed boobies are resident in the Chagos Archipelago throughout the year and their at-sea distribution does not overlap with that of other populations elsewhere in the Indian Ocean (indicated by crosses on map panel a, based on authors knowledge of RFB colonies in the western Indian Ocean and [BirdLife International and Handbook of the Birds of the World 2020](#)).

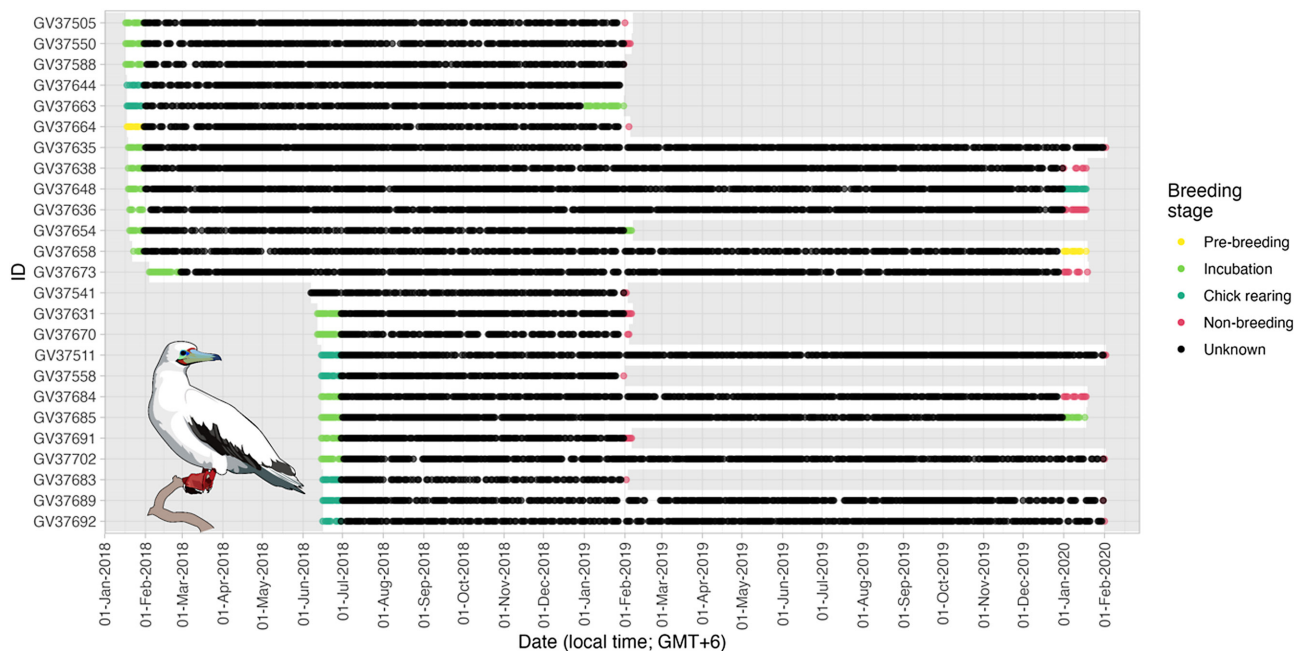


Figure 2. Red-footed boobies showed near-continuous patterns of dry immersion loggers overnight throughout the year (2018–2020, $n=25$) in the Chagos Archipelago, tropical Indian Ocean. Solid points represent overnight on land, classified as such when immersion loggers were ≥ 0.95 dry from dusk to dawn the following day. Blanks are when this criterion was not met. Circles are colour coded according to breeding stage. Grey shading denotes times outside of the geolocator deployment period. Breeding stage was unknown outside of deployment months.

(min 574 km) latitudinal movements (Kohno et al. 2019), while Atlantic breeding masked boobies *Sula dactylatra* close to the equator in Brazil ($03^{\circ}50'S$) were resident year-round (Roy et al. 2021). These results tentatively indicate that boobies breeding closer to the equator are likely to be less migratory, although this does not appear to be the case among many other tropical seabirds (Table 1).

Breeding RFBs regularly roost on land overnight (normally in hardwood trees such as figs; Weimerskirch et al. 2005) and here we suggest this may be the case throughout the annual cycle. For many seabird taxa MPAs may provide at-sea refugia during the non-breeding period (Trevail et al. 2023a) whereas for RFBs terrestrial roost sites may also be especially important for their conservation. GPS and satellite transmitters could be used year-round to accurately pinpoint roosts away from breeding colonies (as has been done for great frigatebirds *Fregata minor*; Weimerskirch et al. 2017), combined with on-site visits to gather counts. Nevertheless, our threshold of $> 95\%$ for the immersion logger being dry likely represents a conservative estimate of time on land overnight because, for example, birds may leave before dawn and return after dusk. Terrestrial roost sites may therefore be even more important than our findings suggest.

Using immersion data to estimate the amount of time adult RFBs spent on land, we suggest that the 21 670 breeding pairs breeding in the Chagos could deposit 37.34 ± 0.56 tonnes year⁻¹ of guano-derived nitrogen throughout the archipelago. This compares with 52.27 tonnes year⁻¹ in

the Chagos archipelago estimated by Graham et al. (2018) who used a RFB breeding season duration of 336 days. These are both likely to be underestimates however since the large numbers of immature birds (RFBs do not breed until they are 3–4 years old; Birdlife International 2023) are not included in these calculations. Further work is required to understand the ecological consequences of differing guano deposition estimates for island and coral reef ecosystems but using tracking data as in our study provides a quantitative approach which could be used to assess nutrient flows and compare the impact of different management scenarios more accurately (Carr et al. 2021a).

The lack of clear non-breeding movements indicates that ongoing gene flow among Indian Ocean RFB populations (Morris-Pocock et al. 2010) are unlikely to be due to mixing during non-breeding periods (Friesen et al. 2007). Instead, therefore, movements by immatures that have not yet recruited is an alternative plausible explanation for colony connectivity. Seabird prospecting is poorly studied however (Votier et al. 2011) and our findings support the drive towards greater research across all age classes and not just adults to better understand their conservation and phylogenetic relationships (Votier et al. 2017).

RFBs rarely spend the night at-sea (Fig. 2) suggesting pressure not to rest on the sea surface during darkness, which is also the case for some other tropical seabirds. For example, sooty terns *Onychoprion fuscatus* only spend 3.7% of their time in contact with the sea surface year-round and never land on the water at night (Jaeger et al. 2017). This

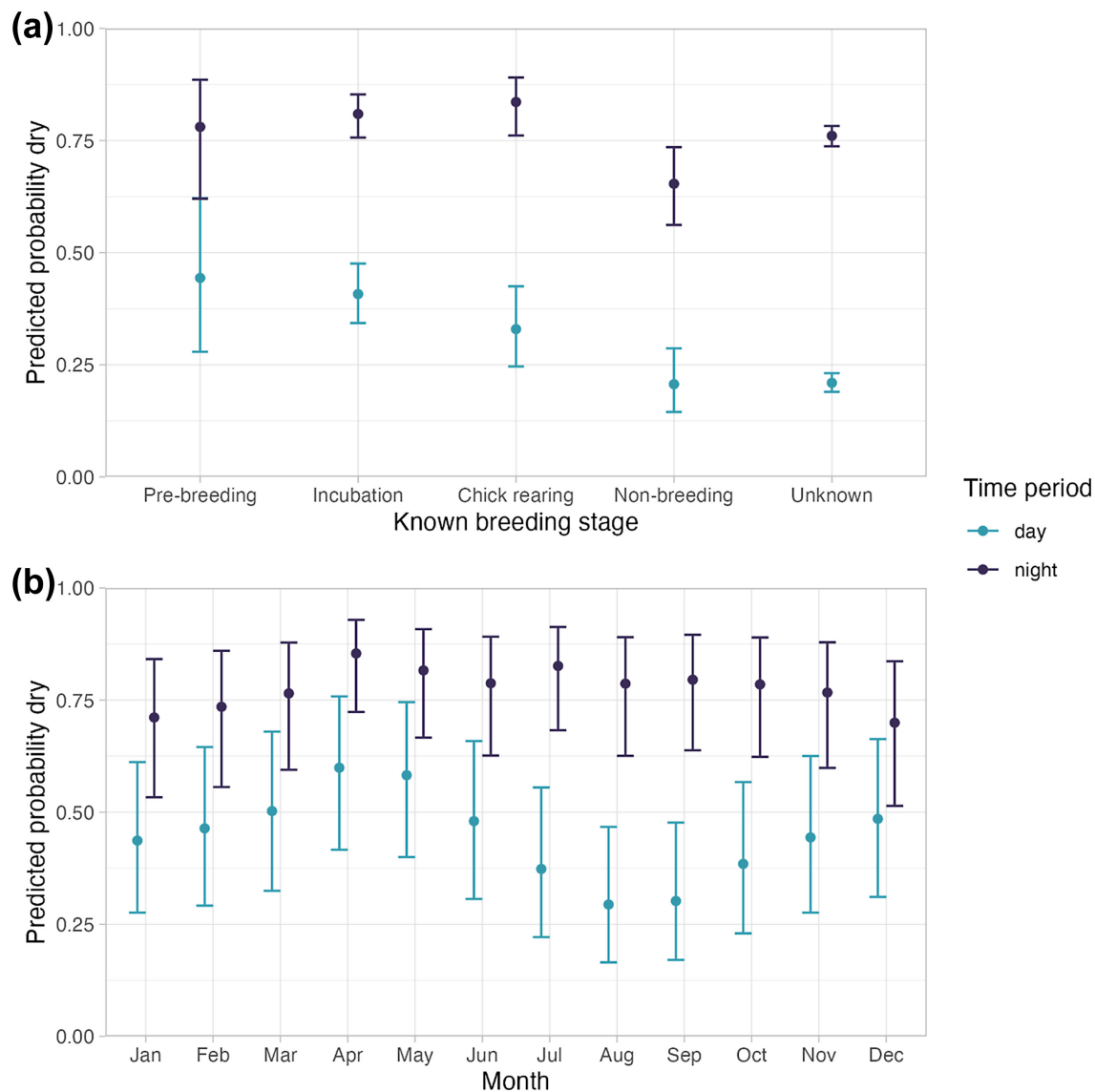


Figure 3. Predicted probability of daytime on land and nighttime on land from model outputs, indicative of terrestrial roosting or nest attendance (2018–2020), varies among (a) known breeding stages and (b) months. In all cases, probability of the logger being dry is higher over-night (sunset to sunrise the following day) than during the day (sunrise to sunset). Parameter estimates are marginalised over all levels of non-focal effects, i.e. (a) month and individual ID, and (b) known breeding stage (pre-breeding, incubation, chick-rearing and non-breeding, i.e. roosting, were all based on observations at tag deployment; breeding stage was unknown outside of deployment months) and individual ID. Error bars represent 95% confidence intervals. Parameter estimates and individual data are shown in Supporting information.

avoidance of the sea at night may relate to predation risk from sharks, foraging tactics, or both (Weimerskirch et al. 2005) and contrasts with temperate and polar seabirds which frequently rest on the water overnight throughout the annual cycle (Dunn et al. 2020). Nevertheless, many seabird species (including some tropical taxa) modulate their at-sea activity in relation to the lunar cycle indicating some behavioural flexibility (Pinet et al. 2011a, Bonnet-Lebrun et al. 2021). It is possible therefore that nocturnal avoidance of the sea surface (in tandem with the lunar cycle) limits the migratory ability of species with high flight costs, such as RFBs, which do not appear to sleep on the wing but instead generally head for land at night (Trevail et al.

2023b). Some non-tropical seabirds also tend not to range far outside the breeding season because of spending most nights at the colony, which is also possibly due to predation risk (Tanton et al. 2004).

The probability of immersion loggers with extended dry periods during daylight hours (which could be explained by breeding behaviour) showed two peaks during April and December (Fig. 3b), corresponding to the two breeding peaks for this RFB population (Carr et al. 2021b). These findings therefore suggest immersion may be useful to better understand poorly understood tropical seabird breeding phenology (Soanes et al. 2021). Nevertheless, this would only be effective when collected alongside detailed direct observations of

breeding chronology in colonies to interpret/validate immersion patterns.

RFB's migratory residency and dependence on terrestrial roost sites year-round contrasts with many seabird species which have distinct maritime non-breeding seasons (Table 1) highlighting the value of a whole ecosystem perspective (i.e. marine and terrestrial habitats) in the tropics. Seabirds are valuable indicators of marine food supplies and global change because of their high trophic level, and, for tropical species, facultative foraging with sub-surface predators (Veit and Harrison 2017). However, our study reveals that effective seabird monitoring and management should not only incorporate a detailed understanding of their marine but also their terrestrial behaviours year-round.

Acknowledgements – We thank Kirsty Franklin for help processing the light data. We also thank the British Indian Ocean Territory Administration and Royal Marines for help in the field. We also grateful to two reviewers and the handling editor, whose comments have helped to improve the manuscript.

Funding – This work was funded by the Bertarelli Foundation for Marine Science.

Permits – Permission to conduct research on seabirds in the Chagos Archipelago was granted by the British Indian Ocean Territory Administration.

Author contributions

Stephen C. Votier: Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (equal); Writing – original draft (equal). **Grace Corcoran:** Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Pete Carr:** Conceptualization (equal); Data curation (equal); Investigation (equal); Writing – review and editing (equal); **Ruth E. Dunn:** Methodology (equal); Writing – review and editing (equal). **Robin Freeman:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Malcolm A. C. Nicoll:** Conceptualization (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (equal); Writing – review and editing (equal). **Hannah Wood:** Data curation (equal); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Alice M. Trevail:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/jav.03185>.

Data availability statement

Tracking data are available on the seabird tracking data base (www.seabirdtracking.org, Dataset ID = 2026). Immersion data will be archived online at time of publication. Code for all data import, processing, analyses, and visualisations are available via a github repository: <https://github.com/AliceTrevail/RFB-long-term-GLS.git>.

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.t4b8gtj8x> (Votier et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Agafonkin, V. and Thieurmél, B. 2018. Suncalc: compute sun position, sunlight phases, moon position and lunar phase. – <https://cran.r-project.org/web/packages/suncalc/suncalc.pdf>.
- Bates, D., Mächler, M., Bolker, B. M. and Walker, S. C. 2015. Fitting linear mixed-effects models using lme4. – *J. Stat. Softw.* 67: 1–48.
- Benkwitt, C. E., Carr, P., Wilson, S. K. and Graham, N. A. J. 2022. Seabird diversity and biomass enhance cross-ecosystem nutrient subsidies. – *Proc. R. Soc. B* 289: 20220195.
- Benkwitt, C. E., D'Angelo, C., Dunn, R. E., Gunn, R. L., Healing, S., Mardones, M. L., Wiedenmann, J., Wilson, S. K. and Graham, N. A. 2023. Seabirds boost coral reef resilience. – *Sci. Adv.* 9: eadj0390.
- Bernard, A., Rodrigues, A. S. L., Cazalis, V. and Grémillet, D. 2021. Toward a global strategy for seabird tracking. – *Conserv. Lett.* 14: e12804.
- Bicknell, A. W. J., Knight, M. E., Bilton, D. T., Campbell, M., Reid, J. B., Newton, J. and Votier, S. C. 2014. Intercolony movement of pre-breeding seabirds over oceanic scales: implications of cryptic age-classes for conservation and metapopulation dynamics. – *Divers. Distrib.* 20: 160–168.
- Birdlife International. 2023. Species factsheet: *Sula sula*. – <http://datazone.birdlife.org/species/red-footedbooby-sula-sula>.
- BirdLife International and Handbook of the Birds of the World. 2020. Bird species distribution maps of the world, ver. 2020.1. – <http://datazone.birdlife.org/species/requestdis>.
- Bonnet-Lebrun, A.-S. et al. 2021. Seabird migration strategies: flight budgets, diel activity patterns, and lunar influence. – *Front. Mar. Sci.* 8: 683071.
- Calenge, C. 2006. The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. – *Ecol. Modell.* 197: 516–519.
- Carlile, N. and O'Dwyer, T. 2022. At-sea movements of the white tern *Gygis alba* in waters off eastern Australia. – *Mar. Ornithol.* 50: 151–158.
- Carr, P., Trevail, A., Bárrios, S., Clubbe, C., Freeman, R., Koldewey, H. J., Votier, S. C., Wilkinson, T. and Nicoll, M. A. C. 2021a. Potential benefits to breeding seabirds of converting abandoned coconut plantations to native habitats after invasive predator eradication. – *Restor. Ecol.* 29: e13386.
- Carr, P., Votier, S. C., Koldewey, H. J., Godley, B., Wood, H. and Nicoll, M. A. C. 2021b. Status and phenology of breeding sea-

- birds and a review of important bird and biodiversity areas in the British Indian Ocean Territory. – *Bird Conserv. Int.* 31: 14–34.
- Carr, P., Trevail, A. M., Koldewey, H. J., Sherley, R. B., Wilkinson, T., Wood, H. and Votier, S. C. 2023. Marine important bird and biodiversity areas in the Chagos Archipelago. – *Bird Conserv. Int.* 33: e29.
- Catry, T., Ramos, J. A., Le Corre, M. and Phillips, R. A. 2009. Movements, at-sea distribution and behaviour of a tropical pelagic seabird: the wedge-tailed shearwater in the western Indian Ocean. – *Mar. Ecol. Prog. Ser.* 391: 231–242.
- Clay, T. A., Phillips, R. A., Manica, A., Jackson, H. A. and Brooke, M. 2017. Escaping the oligotrophic gyre? The year-round movements, foraging behaviour and habitat preferences of Murphy's petrels. – *Mar. Ecol. Prog. Ser.* 579: 139–155.
- Danckwerts, D. K., McQuaid, C. D., Jaeger, A., McGregor, G. K., Dwight, R., Le Corre, M. and Jaquemet, S. 2014. Biomass consumption by breeding seabirds in the western Indian Ocean: indirect interactions with fisheries and implications for management. – *ICES J. Mar. Sci.* 71: 2589–2598.
- Dunn, R. E., Wanless, S., Daunt, F., Harris, M. P. and Green, J. A. 2020. A year in the life of a North Atlantic seabird: behavioural and energetic adjustments during the annual cycle. – *Sci. Rep.* 10: 1–11.
- Egevang, C., Stenhouse, I. J., Phillips, R. A., Petersen, A., Fox, J. W. and Silk, J. R. D. 2010. Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. – *Proc. Natl Acad. Sci. USA* 107: 2078–2081.
- Franklin, K. A., Norris, K., Gill, J. A., Ratcliffe, N., Bonnet-Lebrun, A. S., Butler, S. J., Cole, N. C., Jones, C. G., Lisovski, S., Ruhomaun, K., Tatayah, V. and Nicoll, M. A. C. 2022. Individual consistency in migration strategies of a tropical seabird, the Round Island petrel. – *Movem. Ecol.* 10: 1–14.
- Friesen, V. L., Burg, T. M. and McCoy, K. D. 2007. Mechanisms of population differentiation in seabirds. – *Mol. Ecol.* 16: 1765–1785.
- Graham, N. A. J., Wilson, S. K., Carr, P., Hoey, A. S., Jennings, S. and MacNeil, M. A. 2018. Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. – *Nature* 559: 250–253.
- Grecian, W. J., Witt, M. J., Attrill, M. J., Bearhop, S., Becker, P. H., Egevang, C., Furness, R. W., Godley, B. J., González-Solís, J., Grémillet, D., Kopp, M., Lescroël, A., Matthiopoulos, J., Patrick, S. C., Peter, H. U., Phillips, R. A., Stenhouse, I. J. and Votier, S. C. 2016. Seabird diversity hotspot linked to ocean productivity in the Canary current large marine ecosystem. – *Biol. Lett.* 12: 20160024.
- Hays, G. C. et al. 2020. A review of a decade of lessons from one of the world's largest MPAs: conservation gains and key challenges. – *Mar. Biol.* 167: 1–22.
- Jaeger, A., Feare, C. J., Summers, R. W., Lebarbenchon, C., Larose, C. S. and Le Corre, M. 2017. Geolocation reveals year-round at-sea distribution and activity of a superabundant tropical seabird, the sooty tern *Onychoprion fuscatus*. – *Front. Mar. Sci.* 4: 394.
- Kohn, H., Mizutani, A., Yoda, K. and Yamamoto, T. 2019. Movements and activity characteristics of the brown booby *Sula leucogaster* during the non-breeding period. – *Mar. Ornithol.* 47: 169–174.
- Langley, L. P., Lang, S., Ozsanlav-Harris, L. and Trevail, A. 2023. ExMove: an open-source toolkit for processing and exploring animal tracking data in R.
- Leal, G. R. and Bugoni, L. 2021. Individual variability in habitat, migration routes and niche used by Trindade petrels, *Pterodroma arminjoniana*. – *Mar. Biol.* 168: 134.
- Le Corre, M., Jaeger, A., Pinet, P., Kappes, M. A., Weimerskirch, H., Catry, T., Ramos, J. A., Russell, J. C., Shah, N. and Jaquemet, S. 2012. Tracking seabirds to identify potential Marine Protected Areas in the tropical western Indian Ocean. – *Biol. Conserv.* 156: 83–93.
- Lüdecke, D. 2018. Ggeffects: tidy data frames of marginal effects from regression models. – *J. Open Source Softw.* 3: 772.
- McDuie, F. and Congdon, B. C. 2016. Trans-equatorial migration and non-breeding habitat of tropical shearwaters: implications for modelling pelagic important bird areas. – *Mar. Ecol. Prog. Ser.* 550: 219–234.
- Morris-Pocock, J. A., Steeves, T. E., Estela, F. A., Anderson, D. J. and Friesen, V. L. 2010. Comparative phylogeography of brown (*Sula leucogaster*) and red-footed boobies (*S. sula*): the influence of physical barriers and habitat preference on gene flow in pelagic seabirds. – *Mol. Phylogenet. Evol.* 54: 883–896.
- Newton, I. 2008. The migration ecology of birds. – Elsevier.
- Pinet, P., Jaeger, A., Cordier, E., Potin, G. and Le Corre, M. 2011a. Celestial moderation of tropical seabird behavior. – *PLoS One* 6: e27663.
- Pinet, P., Jaquemet, S., Pinaud, D., Weimerskirch, H., Phillips, R. A. and Le Corre, M. 2011b. Migration, wintering distribution and habitat use of an endangered tropical seabird, Barau's petrel *Pterodroma baraui*. – *Mar. Ecol. Prog. Ser.* 423: 291–302.
- Ramos, R., Sanz, V., Militão, T., Bried, J., Neves, V. C., Bischoito, M., Phillips, R. A., Zino, F. and González-Solís, J. 2015. Leap-frog migration and habitat preferences of a small oceanic seabird, Bulwer's petrel (*Bulweria bulwerii*). – *J. Biogeogr.* 42: 1651–1664.
- Rayner, M. J., Carlile, N., Priddel, D., Bretagnolle, V., Miller, M., Phillips, R., Ranjard, L., Bury, S. and Torres, L. 2016. Niche partitioning by three *Pterodroma* petrel species during non-breeding in the equatorial Pacific Ocean. – *Mar. Ecol. Prog. Ser.* 549: 217–229.
- Reynolds, S. J., Wearn, C. P., Hughes, B. J., Dickey, R. C., Garrett, L. J., Walls, S., Hughes, F. T., Weber, N., Weber, S. B., Leat, E. H. K., Andrews, K., Ramos, J. A. and Paiva, V. H. 2021. Year-round movements of sooty terns (*Onychoprion fuscatus*) nesting within one of the Atlantic's largest marine protected Areas. – *Front. Mar. Sci.* 8: 744506.
- Roy, A., Delord, K., Nunes, G. T., Barbraud, C., Bugoni, L. and Lanco-Bertrand, S. 2021. Did the animal move? A cross-wavelet approach to geolocation data reveals year-round whereabouts of a resident seabird. – *Mar. Biol.* 168: 114.
- Schreiber, E. A., Schreiber, R. W. and Schenk, G. A. 2020. Red-footed booby (*Sula sula*), ver. 1.0. – In: Billerman, S. M. (ed.), *Birds of the World*. Cornell Laboratory of Ornithology.
- Shaffer, S. A., Tremblay, Y., Weimerskirch, H., Scott, D., Thompson, D. R., Sagar, P. M., Moller, H., Taylor, G. A., Foley, D. G., Block, B. A. and Costa, D. P. 2006. Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. – *Proc. Natl Acad. Sci. USA* 103: 12799–12802.
- Soanes, L. M., Green, J. A., Bolton, M., Milligan, G., Mukhida, F. and Halsey, L. G. 2021. Linking foraging and breeding strategies in tropical seabirds. – *J. Avian Biol.* 52: e02670.
- Surman, C. A., Nicholson, L. W. and Phillips, R. A. 2018. Distribution and patterns of migration of a tropical seabird community in the eastern Indian Ocean. – *J. Ornithol.* 159: 867–877.
- Tanton, J. L., Reid, K., Croxall, J. P. and Trathan, P. N. 2004. Winter distribution and behaviour of Gentoo penguins *Pygoscelis papua* at South Georgia. – *Polar Biol.* 27: 299–303.

- Thiebot, J. B., Nakamura, N., Toguchi, Y., Tomita, N. and Ozaki, K. 2020. Migration of black-naped terns in contrasted cyclonic conditions. – *Mar. Biol.* 167: 1–12.
- Trevaill, A. M., Green, J. A., Sharples, J., Polton, J. A., Arnould, J. P. Y. and Patrick, S. C. 2019. Environmental heterogeneity amplifies behavioural response to a temporal cycle. – *Oikos* 128: 517–528.
- Trevaill, A. M., Nicoll, M. A. C., Freeman, R., Le Corre, M., Schwarz, J., Jaeger, A., Bretagnolle, V., Calabrese, L., Feare, C., Lebarbenchon, C., Norris, K., Orłowski, S., Pinet, P., Plot, V., Rocamora, G., Shah, N. and Votier, S. C. 2023a. Tracking seabird migration in the tropical Indian Ocean reveals basin-scale conservation need. – *Curr. Biol.* 33: 5247–5256.
- Trevaill, A., Wood, H., Carr, P., Dunn, R. E., Nicoll, M. A. C., Votier, S. and Freeman, R. 2023b. Multi-colony tracking reveals segregation in foraging range, space use, and timing in a tropical seabird. – *Mar. Ecol. Prog. Ser.* 724: 155–165.
- Veit, R. R. and Harrison, N. M. 2017. Positive interactions among foraging seabirds, marine mammals and fishes and implications for their conservation. – *Front. Ecol. Evol.* 5: 121.
- Votier, S. C., Grecian, W. J., Patrick, S. and Newton, J. 2011. Inter-colony movements, at-sea behaviour and foraging in an immature seabird: results from GPS-PPT tracking, radio-tracking and stable isotope analysis. – *Mar. Biol.* 158: 355–362.
- Votier, S. C., Fayet, A. L., Bearhop, S., Bodey, T. W., Clark, B. L., Grecian, J., Guilford, T., Hamer, K. C., Jeglinski, J. W. E., Morgan, G., Wakefield, E. and Patrick, S. C. 2017. Effects of age and reproductive status on individual foraging site fidelity in a long-lived marine predator. – *Proc. R. Soc. B* 284: 20171068.
- Votier, S. C., Corcoran, G., Carr, P., Dunn, R. E., Freeman, R., Nicoll, M. A. C., Wood, H. and Trevaill, A. M. 2024. Data from: Geolocation and immersion loggers reveal year-round residency and consequent nutrient deposition rates of adult red-footed boobies in the Chagos Archipelago, tropical Indian Ocean. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.t4b8gtj8x>.
- Weimerskirch, H., Delord, K., Guitteaud, A., Phillips, R. A. and Pinet, P. 2015. Extreme variation in migration strategies between and within wandering albatross populations during their sabbatical year and their fitness consequences. – *Sci. Rep.* 5: 8853.
- Weimerskirch, H. 2007. Are seabirds foraging for unpredictable resources? – *Deep Sea Res. II* 54: 211–223.
- Weimerskirch, H., Le Corre, M., Ropert-Coudert, Y., Kato, A. and Marsac, F. 2005. The three-dimensional flight of red-footed boobies: adaptations to foraging in a tropical environment? – *Proc. R. Soc. B* 272: 53–61.
- Weimerskirch, H., Borsa, P., Cruz, S., de Grissac, S., Gardes, L., Lallemand, J., Corre, M. L. and Prudor, A. 2017. Diversity of migration strategies among great frigatebirds populations. – *J. Avian Biol.* 48: 103–113.
- Wilmers, C. C., Nickel, B., Bryce, C. M., Smith, J. A., Wheat, R. E. and Yovovich, V. 2015. The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. – *Ecology* 96: 1741–1753.
- Winkler, D. W., Jørgensen, C., Both, C., Houston, A. I., McNamara, J. M., Levey, D. J., Partecke, J., Fudickar, A., Kacelnik, A., Roshier, D. and Piersma, T. 2014. Cues, strategies, and outcomes: how migrating vertebrates track environmental change. – *Movem. Ecol.* 2: 10.
- Wotherspoon, S. J., Sumner, M. D. and Lisovski, S. 2013. R package SGAT: solar/satellite geolocation for animal tracking. GitHub repository. – <http://github.com/swotherspoon/sgat>.
- Zajková, Z., Militão, T. and González-Solís, J. 2017. Year-round movements of a small seabird and oceanic isotopic gradient in the tropical Atlantic. – *Mar. Ecol. Prog. Ser.* 579: 169–183.
- Zweig, M. H. and Campbell, G. 1993. Receiver-operating characteristic (ROC) plots: a fundamental evaluation tool in clinical medicine. – *Clin. Chem.* 39: 561–577.