

Geolocation and immersion loggers reveal adult red-footed boobies are year-round residents in the tropical Indian Ocean

Abstract

Bio-logging has revealed much about high-latitude seabird migratory strategies, but tropical species are comparatively understudied. Here we use geolocators to study the year-round movement behaviour of breeding red-footed boobies (*Sula sula rubripes*) from the Chagos Archipelago, tropical Indian Ocean. Light levels suggest that red-footed boobies are resident in the archipelago year-round, although there are large latitudinal errors this close to the equator. However, immersion data revealed tracked birds returned to land year-round, with no extended at-sea periods, further indicating this population is non-migratory. Our findings have important implications for seabird conservation and phylogenetics, as well as for assessing the impact of seabird nutrients on coral reef ecosystems.

Key words: seabird, migration, Chagos Archipelago, bio-logging

INTRODUCTION

Bio-logging has created a paradigm shift in the study of animal migration. This is exemplified by seabird tracking research which has over-turned the once prevalent view of seabirds as primarily dispersive, revealing instead a great diversity of migratory strategies within and among species (Newton 2008). Nevertheless, while many temperate and polar species have been tracked, fewer tropical seabirds have been studied. Understanding tropical seabird migration strategies more fully is crucial for their conservation and because their guano enhances coral reef function and resilience (Graham et al. 2018).

In contrast to temperate and polar species, tropical pelagic seabirds typically forage in oligotrophic waters with low or unpredictable seasonal variation (Weimerskirch 2007). Despite these conditions favouring dispersive or short-distance movements (Newton 2008), the majority of tracked tropical seabirds are long-distance goal-orientated migrants, with a diversity of longitudinal or multi-directional movements among species (Table 1). Migratory strategies also vary within species. For instance, Bulwer's petrels *Bulweria bulwerii* are leapfrog migrants - temperate and sub-tropical populations are travel long distances and over-fly short-distance tropical breeders (Ramos et al. 2015). Nevertheless, more work is required to understand tropical seabird migratory behaviour to develop effective conservation programmes, elucidate the mechanisms underlying their phylogenetic relationships (Friesen et al. 2007) and to quantify the ecosystem services they provide via nutrient cycling (Graham et al. 2018).

Seven of the ten extant species of Sulidae are tropical or sub-tropical occurring across most of world's tropical seas. The small number of tracking studies indicate a mix of resident and short-distance migrants, but work is limited to two species (Table 1). Accordingly, here we study the non-breeding distribution of red-footed boobies *Sula sula* (hereafter RFB). This pantropical species is thought to be largely resident, but movements outside the breeding season is based upon indirect evidence of ring recoveries and observations (Schreiber, et al. 2020). RFB is comprised of 3 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). Year-round tracking of RFB movements could prove valuable for understanding the formation/persistence of taxa since high gene flow may arise because of mixing during the non-breeding season (Friesen et al. 2008), or immature dispersal (Bicknell et al. 2014). Moreover, understanding year-round movements will improve our understanding of their potential to transfer nutrients from pelagic waters to threatened coral reef ecosystems (Graham et al. 2018; Benkwitt et al. 2022).

Specifically, we studied the migration behaviour of *rubripes* RFBs breeding in the Chagos Archipelago, Central Indian Ocean. This isolated group of atolls has ~20,000 breeding pairs of RFB (Carr et al 2021), representing one of the largest aggregations in the Indian Ocean (Danckwerts et al. 2014). It is also within a fully protected 640,00 km² Marine Protected Area (MPA) which protects the world's largest coral atoll and some of the healthiest reefs (Hays et al. 2020). We deployed lightweight (3-4g) leg-mounted global location sensors (GLS) that use light curves to estimate location. While this can provide us with an indication of migratory behaviour, geolocation errors can be greater than migration distances for some short-range migrants, particularly in the tropics (e.g., GLS errors of 65 ± 54 km in longitude and 347 ± 462 km in latitude at 03°50' S, 32°25' W; Roy et al. 2021), so we incorporated saltwater immersion to better elucidate our understanding of behaviour across the annual cycle. Thus, light level geolocation allows us to test whether RFBs exhibit any migratory movements across the annual cycle and saltwater immersion to test for extended at-sea periods, which is relevant for understanding migration ecology and nutrient deposition.

METHODS

Tracking

RFBs were tracked from Barton Point, Diego Garcia, Chagos Archipelago (07°14'S, 72°26'E). Adults were caught by hand during pre-breeding (n=2), incubation (n=16), or chick rearing (n=7) and fitted with geolocator and immersion loggers (Intigeo C330, Migrate technology, Cambridge, UK; 3.3g) attached to a PVMA 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. 2023). Genetic sexing using feathers was carried out at the Institute of Zoology, Zoological Society of London (Carr et al. 2023). Tags were retrieved after 7-24 months when individuals were seen breeding (n=6) or roosting (n=19) in the colony.

Intra-annual variation in spatial distribution

Locations were derived at 12-hour resolution 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 and *Shiny* app (Langley et al. In review) to create a standardised data frame with a speed filter of 20 m/s and a net displacement filter of 3,000 km to remove erroneous locations. All locations 30 days either side of the vernal and autumn equinox were removed, because of proximity to the equator. Daily locations were calculated as the mean latitude and longitude each day, in local time (GMT+6) to reduce longitudinal error (Fig S1). We calculated overall and monthly utilisation distributions (UDs) from daily locations, for which 75% contours indicate home ranges, and 50 and 25% contours indicate core areas. UD calculations were derived across a 10km 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 saltwater immersion data; (1) dry nights, indicative of overnight roosting on land or nest attendance, and (2) dry days, which provide information on use of terrestrial roosts during the day, and/or breeding behaviour, such as incubation, chick-guarding, and nest defence. Immersion data were processed using the ExMove toolkit (Langley et al. In review) 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 day (dawn to dusk), and night (dusk to dawn). Times of nautical dawn and dusk were derived for the tagging location using *suncalc* in R (Agafonkin & Thieurmél 2018). 'Dry' days, and nights were classified when the proportion dry for each period was ≥ 0.95 . Annual distributions of dry time periods for all study years are shown in the supplementary material (Figures S2-3).

To determine annual patterns in dry periods, we used binomial mixed effects models to evaluate the probability of being dry ($1 \geq 95\%$ dry, $0 < 95\%$ dry). Time period (night or day), month (as a factor), breeding stage (when known), and sex were all included as explanatory variables. Time period (night or day) was included in two-way interactions with (1) breeding stage, i.e., whether probability dry differed among breeding stages, and (2) month, i.e., whether annual activity patterns varied between night and day. Because breeding stages were only known during limited months of tag deployment and retrieval (January, February, & June), we do not have sufficient data to understand whether annual patterns of activity vary among breeding stages (i.e., a three-way interaction between time period, 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 AIC comparison (Tables S1 & S2); the most parsimonious model was chosen as the model with $\Delta AIC < 2$. Model performance was assessed using area under the curve (AUC) values and confusion matrix scores, which were all high, suggesting good model fit (AUC = 0.81; Table S3). We extracted parameter estimates using the *ggeffects* package in R (Lüdtke 2018), including *ggemmeans()* to marginalise over non-focal effects and *ggpredict()*.

Our objective is to understand more about RFB behaviour throughout the annual cycle and especially whether they have extended periods at sea or return repeatedly to land. Therefore, we calculated the number of dry nights (dusk to dawn the following day) per month as a measure of overnight roosting on land since continuous flights at night are highly unlikely, and the number of consecutive nights that were not dry ($< 95\%$ dry) as an indicator of multi-day foraging trips (Trevail et al. In Review).

RESULTS

We obtained GLS data for 25 adult RFBs over 7 to 24 months, from 7 females, 10 males, and 8 of unknown sex.

Intra-annual variation in spatial distribution

RFBs likely remained within the Chagos Archipelago MPA throughout the year with latitudinal variation (but not longitudinal variation) likely due to GLS error close to the equator (Figure 1). Moreover, near-continuous dry overnight periods indicate RFBs were rarely far from land (Figure 2)

lending further support for this population being non-migratory and without inter-colony contact from elsewhere in the Indian Ocean (Figure 1).

Intra-annual variation in onshore activity

Individuals spent 23.4 ± 0.2 nights dry (mean \pm standard error) per month tracked (in percent of night per month, this equates to $76.9 \pm 0.7\%$, range = 39.3% - 100%). Across the year, individuals were recorded as not dry (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 (Figure 3). The probability of being dry was lower during non-breeding than chick rearing and incubation phases, both overnight and during the day (Figure 3a). Whilst the probability of dry was high overnight all year-round (>50% predicted), there seemed to be slightly lower probabilities during December-February (Figure 3b). The probability of being dry during the day showed two annual peaks during April and December (Figure 3b), which corresponds to the breeding peaks of this population (Carr et al. 2021). We found no effect of sex on probability dry.

DISCUSSION

Location data based on light levels suggest considerable latitudinal movements by RFBs in the Chagos archipelago, which also varied by month, but there was virtually no longitudinal change (Fig. 1). These patterns are probably best explained by the high latitudinal error (347 ± 462) and lower longitudinal error (65 ± 54 km) from light-level geolocation in the tropics (Roy et al. 2021). Also, stationary geolocators in the tropics (unpublished) suggest a similar northerly bias April-August and southerly bias October-February (Fig. 1b). Moreover, saltwater immersion showed near continuous dry periods throughout the year (Fig. 2) so it seems unlikely that birds would be able to fly to the next nearest RFB colony, 1,720km away. Taken together we conclude that RFBs are largely resident in the Chagos archipelago year-round.

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 tracking booby migration using GLS (that we are aware of) show brown boobies (*Sula leucogaster*) at the northernmost extent of their tropical breeding range ($24^{\circ}11'N$) combine long-distance (max 4988km) and short-distance (min 574km) latitudinal movements (Kohn et al. 2019), while masked boobies (*Sula dactylatra*) close to the equator ($03^{\circ}50'S$) were resident year-round (Roy et al. 2021). These results tentatively indicate that birds breeding closer to the equator are likely to be less migratory, but this does not generally 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 show this applies throughout the annual cycle. Roost sites should therefore be protected for this and other tropical species, not just their breeding colonies. GPS and satellite transmitters could be used to identify roosts away from breeding colonies (as has been done for great frigatebirds *Fregata minor*; Weimerskirch et al. 2017), and visits made to gather accurate counts. These roost sites may prove important sources of nutrients for coral reef ecosystems especially since non-breeders can comprise a significant proportion of seabird populations. Quantifying tropical seabird residency patterns from a wide range of species using saltwater immersion would help refine estimates of nutrient input from guano.

The lack of clear non-breeding movements indicates that ongoing gene flow among Indian Ocean RFB populations (Morris-Pocock et al. 2010) are unlikely due to mixing on the wintering grounds. 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 age classes to better understand their conservation and phylogenetic relationships (Votier et al. 2017, Pettex et al. 2019).

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 3.72% of their time in contact with the sea surface year-round and never land on the water at night (Jaeger et al. 2017). This avoidance of the sea surface at night may relate to predation risk from sharks or a foraging tactic (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 that this behaviour is adaptive (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 are unable to sleep on the wing unlike for example, sooty terns *Onychoprion fuscatus* (Jaeger et al. 2017).

The probability of being dry during the day showed two annual peaks during April and December (Figure 3b), which corresponds to the two breeding peaks for this population (Carr et al. 2021). These findings therefore suggest immersion may be useful to better understand breeding phenology in tropical seabirds, which is very poorly understood (Soanes et al. 2021).

RFB's year-round residency and dependence on terrestrial roost sites highlights the value of whole ecosystem management in the tropics. We can now confirm that marine foraging grounds within the Chagos Archipelago MPA are important throughout RFB's annual cycle (Trevail et al. In review). Seabirds are valued indicator species because of their high trophic level, and for tropical species, facultative foraging with sub-surface predators (Veit and Harrison 2017). Therefore, effective MPA enforcement to protect seabird foraging habitats will likely provide year-round benefits to marine species.

Data availability

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 analyses are available via a github repository.

References

- Agafonkin V, Thieurmél B (2018) Suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase.
- Bates D, Mächler M, Bolker BM, Walker SC (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48.
- Benkwitt, C. E., Carr, P., Wilson, S. K., & Graham, N. A. (2022). Seabird diversity and biomass enhance cross-ecosystem nutrient subsidies. Proceedings of the Royal Society B, 289(1974), 20220195.

- Bicknell, A.W., 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. *Diversity and Distributions*, 20(2):160-168.
- BirdLife International and Handbook of the Birds of the World (2020) Bird species distribution maps of the world, Version 2020.1. <http://datazone.birdlife.org/species/requestdis>
- Bonnet-Lebrun, A.-S., M. P. Dias, R. A. Phillips, J. P. Granadeiro, M. d. L. Brooke, O. Chastel, T. A. Clay, A. L. Fayet, O. Gilg, J. González-Solís, T. Guilford, S. A. Hanssen, A. Hedd, A. Jaeger, J. Krietsch, J. Lang, M. Le Corre, T. Militão, B. Moe, W. A. Montevecchi, H.-U. Peter, P. Pinet, M. J. Rayner, T. Reid, J. M. Reyes-González, P. G. Ryan, P. M. Sagar, N. M. Schmidt, D. R. Thompson, R. van Bemmelen, Y. Watanuki, H. Weimerskirch, T. Yamamoto and P. Catry (2021). Seabird Migration Strategies: Flight Budgets, Diel Activity Patterns, and Lunar Influence. *Frontiers in Marine Science* 8(1543).
- 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.
- Carr, P., Trevail, A., Bárrios, S., Clubbe, C., Freeman, R., Koldewey, H. J., ... & Nicoll, M. A. C. (2021). Potential benefits to breeding seabirds of converting abandoned coconut plantations to native habitats after invasive predator eradication. *Restoration Ecology*, 29(5): e13386.
- Carr, P., Votier, S. C, Koldewey, H. J., Godley, B., Wood, H., & Nicoll, M. A. C. (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.
- Carr, P., Trevail, A. M., Koldewey, H. J., Sherley, R. B., Wilkinson, T., Wood, H., & Votier, S. C. (2023). Marine Important Bird and Biodiversity Areas in the Chagos Archipelago. *Bird Conservation International*, 33: e29.
- Catry, T, Ramos J. A., Le Corre M, 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 HA, Brooke MdeL (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., & Jaquemet, S. (2014). Biomass consumption by breeding seabirds in the western Indian Ocean: indirect interactions with fisheries and implications for management. *ICES Journal of Marine Science*, 71(9):’ 2589-2598.
- Dunn, R. E., Wanless, S., Daunt, F., Harris, M. P., & Green, J. A. (2020). A year in the life of a North Atlantic seabird: behavioural and energetic adjustments during the annual cycle. *Scientific Reports*, 10(1), 1-11.
- Franklin, K. A., Norris, K., Gill, J. A., Ratcliffe, N., Bonnet-Lebrun, A. S., Butler, S. J., ... & Nicoll, M. A. C. (2022). Individual consistency in migration strategies of a tropical seabird, the Round Island petrel. *Movement ecology*, 10(1): 1-14.
- Friesen, V.L., Burg, T.M. and McCoy, K.D., 2007. Mechanisms of population differentiation in seabirds. *Molecular Ecology*, 16(9):1765-1785.
- Graham, N.A.J., Wilson, S.K., Carr, P. et al. (2018) Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. *Nature* 559: 250–253

- Hays, G. C., Koldewey, H. J., Andrzejaczek, S., Attrill, M. J., Barley, S., Bayley, D. T., ... & Curnick, D. J. (2020). A review of a decade of lessons from one of the world's largest MPAs: conservation gains and key challenges. *Marine Biology*, 167: 1-22.
- Jaeger, A., Feare, C. J., Summers, R. W., Lebarbenchon, C., Larose, C. S., & Le Corre, M. (2017). Geolocation reveals year-round at-sea distribution and activity of a superabundant tropical seabird, the sooty tern *Onychoprion fuscatus*. *Frontiers in Marine Science*, 4: 394.
- Kohno, H., Mizutani, A., Yoda, K., & Yamamoto, T. (2019). Movements and activity characteristics of the brown booby *Sula leucogaster* during the non-breeding period. *Marine Ornithology*, 47:169-174.
- Leal, G. R., & Bugoni, L. (2021). Individual variability in habitat, migration routes and niche used by Trindade petrels, *Pterodroma arminjoniana*. *Marine Biology*, 168(8): 134.
- Lüdtke D (2018) Ggeffects: Tidy Data Frames of Marginal Effects from Regression Models. *J Open Source Softw* 3:772.
- McDuie, F., & Congdon, B. C. (2016). Trans-equatorial migration and non-breeding habitat of tropical shearwaters: implications for modelling pelagic Important Bird Areas. *Marine Ecology Progress Series*, 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. *Molecular Phylogenetics and Evolution*, 54(3):883-896.
- Newton, I. (2008). *The migration ecology of birds*. Elsevier.
- Pinet, P., A. Jaeger, E. Cordier, G. I. Potin and M. Le Corre (2011a). "Celestial Moderation of Tropical Seabird Behavior." *PLoS ONE* 6(11): e27663.
- Pinet P, Jaquemet S, Pinaud D, Weimerskirch H, Phillips RA, Le Corre M (2011b) Migration, wintering distribution and habitat use of an endangered tropical seabird, Barau's petrel *Pterodroma barau*. *Mar Ecol Prog Ser* 423:291-302.
- Ramos, R., Sanz, V., Militão, T., Bried, J., Neves, V. C., Biscoito, M., ... & González-Solís, J. (2015). Leapfrog migration and habitat preferences of a small oceanic seabird, Bulwer's petrel (*Bulweria bulwerii*). *Journal of Biogeography*, 42(9):1651-1664.
- Rayner MJ, Carlile N, Priddel D, Bretagnolle V and others (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., ... & Paiva, V. H. (2021). Year-Round Movements of Sooty Terns (*Onychoprion fuscatus*) Nesting Within One of the Atlantic's Largest Marine Protected Areas. *Frontiers in Marine Science*, 1755.
- Roy, A., Delord, K., Nunes, G. T., Barbraud, C., Bugoni, L., & Lanco-Bertrand, S. (2021). Did the animal move? A cross-wavelet approach to geolocation data reveals year-round whereabouts of a resident seabird. *Marine Biology*, 168(7): 114.
- Schreiber, E. A., R. W. Schreiber, and G. A. Schenk (2020). Red-footed Booby (*Sula sula*), version 1.0. In *Birds of the World* (S. M. Billerman, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bow.refboo.01>

- Soanes, L. M., Green, J. A., Bolton, M., Milligan, G., Mukhida, F., & Halsey, L. G. (2021). Linking foraging and breeding strategies in tropical seabirds. *Journal of Avian Biology*, 52(7): e02670
- Sumner MD, Wotherspoon SJ, Hindell MA (2009) Bayesian Estimation of Animal Movement from Archival and Satellite Tags. *PLoS One* 4: e7324.
- Surman, C. A., Nicholson, L. W., & Phillips, R. A. (2018). Distribution and patterns of migration of a tropical seabird community in the Eastern Indian Ocean. *Journal of Ornithology*, 159(3):867-877.
- Thiebot J, Pinaud D (2010) Quantitative method to estimate species habitat use from light-based geolocation data. *Endanger Species Res* 10:341–353.
- Veit, R. R., & Harrison, N. M. (2017). Positive interactions among foraging seabirds, marine mammals and fishes and implications for their conservation. *Frontiers in Ecology and Evolution*, 5:121.
- Votier, S. C., Grecian, W. J., Patrick, S., & 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. *Marine biology*, 158: 355-362.
- Votier, S. C., Fayet, A. L., Bearhop, S., Bodey, T. W., Clark, B. L., Grecian, J., ... & Patrick, S. C. (2017). Effects of age and reproductive status on individual foraging site fidelity in a long-lived marine predator. *Proceedings of the Royal Society B: Biological Sciences*, 284: 20171068.
- Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources?. *Deep Sea Research Part II: Topical Studies in Oceanography*. 54: 211-223.
- Weimerskirch, H., Borsa, P., Cruz, S., de Grissac, S., Gardes, L., Lallemand, J., ... & Prudor, A. (2017). Diversity of migration strategies among great frigatebirds populations. *Journal of Avian Biology*, 48(1):103-113.
- Wotherspoon SJ, Sumner MD, Lisovski S. R package SGAT: solar/satellite geolocation for animal tracking. GitHub Repository; 2013. <http://github.com/swotherspoon/sgat>
- Zajková, Z., Militão, T., & González-Solís, J. (2017). Year-round movements of a small seabird and oceanic isotopic gradient in the tropical Atlantic. *Marine Ecology Progress Series*, 579:169-183.

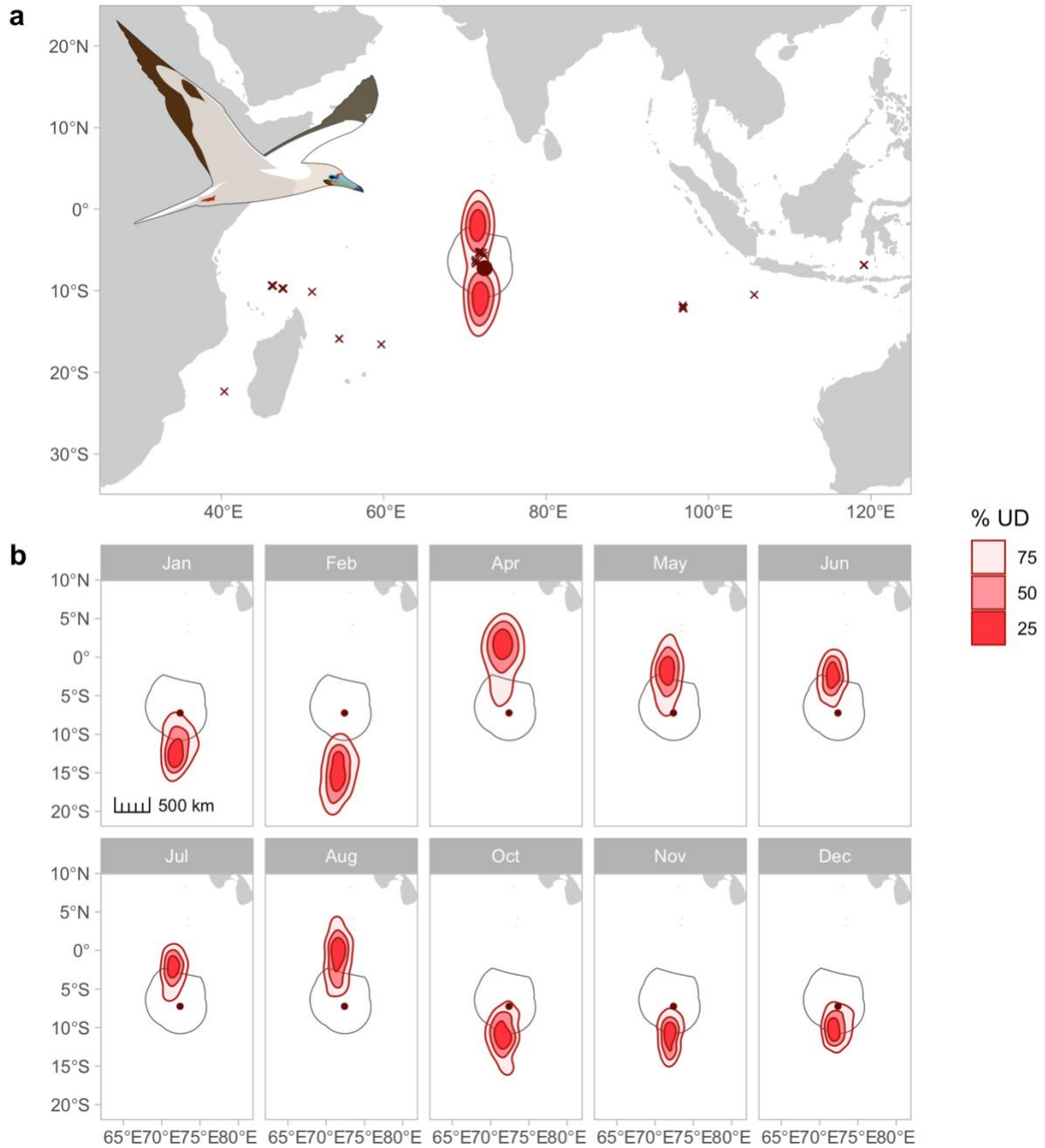


Fig. 1. Year-round movements of adult red-footed boobies from the Chagos Archipelago. Shown here are 75, 50 and 25% utilization distributions based on light-level geolocation by (a) year, and (b) calendar month. March and September are excluded because of the equinox. Solid point is the location of Diego Garcia and thin line shows the extent of the Chagos Archipelago MPA. Limited longitudinal movements and latitudinal movements fluctuating either side of the equinox is 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 therefore do not overlap with breeding colonies (indicated by X on map A) elsewhere in the Indian Ocean (Authors knowledge of RFB colonies in the western Indian Ocean, BirdLife International and Handbook of the Birds of the World; 2020).

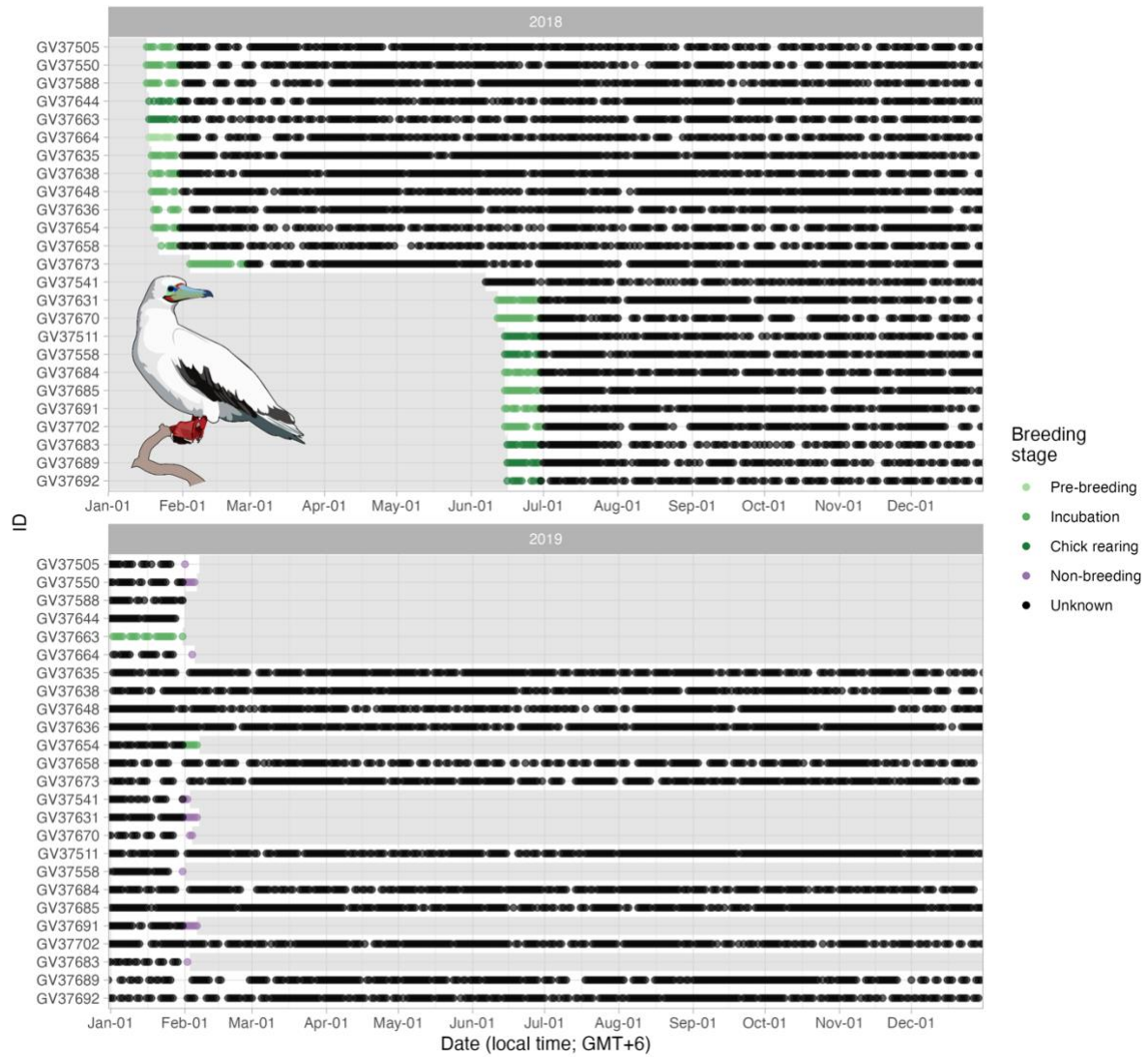


Figure 2. Red-footed boobies showed near-continuous patterns of dry nights throughout the year, indicative of terrestrial overnight roosting or nest attendance. Dry nights were classified when proportion dry from dusk to dawn the following day was ≥ 0.95 . Grey shading denotes times outside of the GLS deployment period. Data here are shown for years with full data, only (2018, top; and 2019, bottom). Data for 2020 are presented in supplementary material (Figure S2).

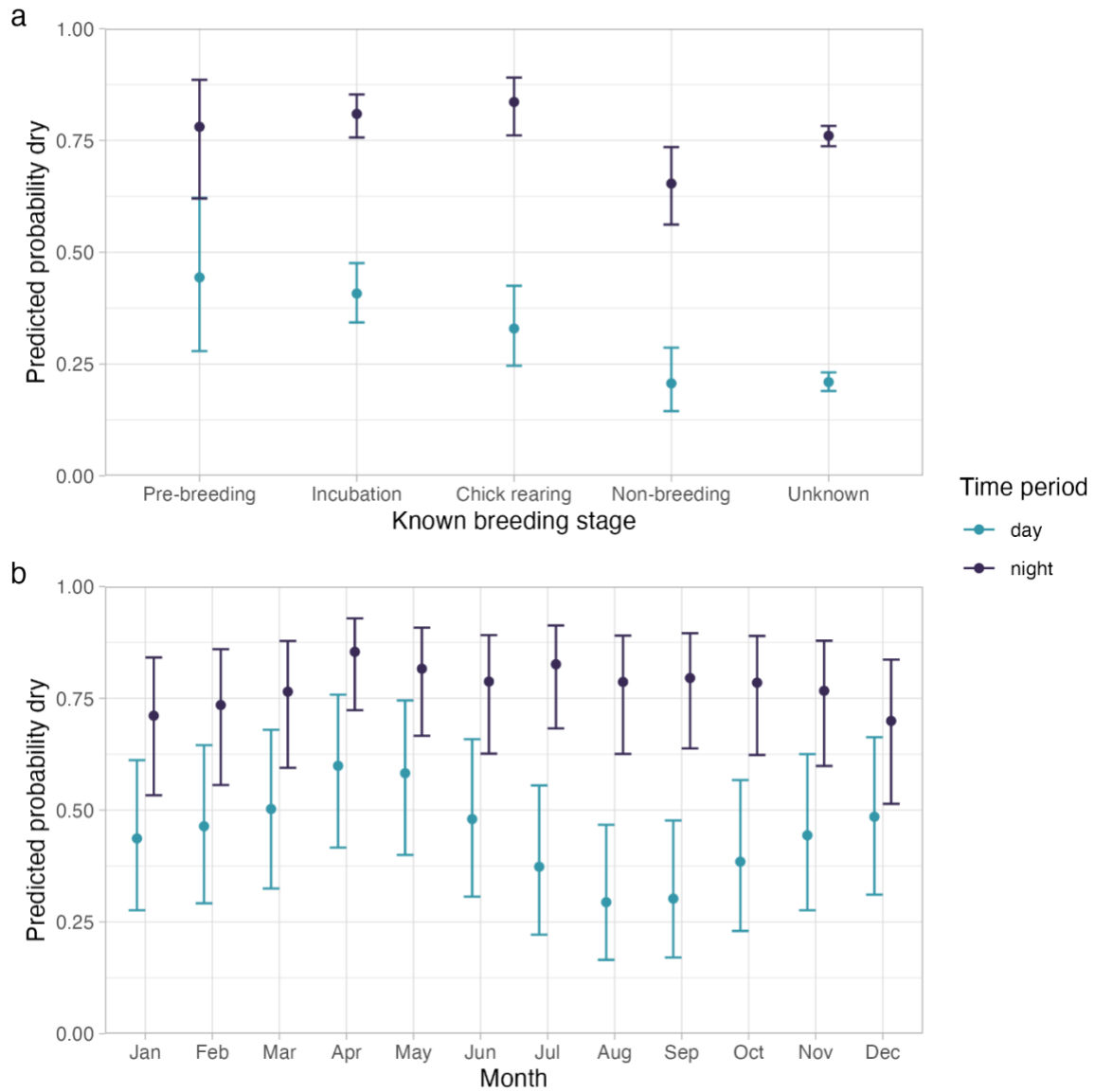


Figure 3. Predicted probability of dry days and nights, indicative of terrestrial roosting or nest attendance, varies among (a) known breeding stages and (b) months. In all cases, probability dry is higher overnight (sunset to sunrise the following day) than during the day (sunrise to sunset). Parameter estimates are marginalised over all levels of non-focal effects, i.e., (a) month and individual ID, and (b) known breeding stage and individual ID. Error bars represent 95% confidence intervals. Parameter estimates are shown in Table 1.