

Homing navigation is optimized to diurnal constraints in a tropical seabird, the red-footed booby

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When navigating homewards, central-place foragers can use landmarks and sun angle to adjust their return movement behaviour. However, for tropical oceanic species foraging from low-lying atolls, the effectiveness of their homing journeys on their time returns remains unclear. Thus, in this study, the navigation behaviour of red-footed boobies, *Sula sula rubripes*, in the Chagos Archipelago, central Indian Ocean, was investigated. Using GPS tracking data from 207 breeding adults across four colonies, the homing duration, bearing and trajectory straightness during central-place foraging were explored to elucidate the navigational constraints and temporal dynamics. Return distances and orientations were modelled in relation to the time of day and distance to the colony to assess whether birds adjust their homing behaviour to return before dusk. We found that red-footed boobies navigated efficiently back to their colony on fast, straight and direct flights and adjusted their homing behaviour to arrive at the colony around dusk: the closer to the evening twilight they start their homing journey, the shorter, faster and more direct their routes become. These findings provide a comprehensive understanding of seabird navigation in tropical environments, as well as insights into the adaptive mechanism underlying successful navigation over expansive oceanic territories.

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Navigating animals have access to their location based on olfaction (Papi et al., 1974; Steele et al., 2023), landmarks (T. S. Collett & Collett, 2002; Mather, 1991) and time via information from the sun (Schmidt-Koenig, 1961). During the breeding season, some of these animals, such as insects (Andersson, 1981; Bell, 1990), burrowing mammals (Bakker et al., 2005; Kramer & Nowell, 1980) and parenting birds (Carlson & Moreno, 1981; Martindale, 1982), make round-trips between their breeding site and exploited foraging patches (i.e. central-place foraging). In determining the length of the return journey, central-place foragers rely primarily on visual cues and learned experiences i.e. path integration (Mittelstaedt & Mittelstaedt, 1982). For example, ants compare their current view to nest-oriented views acquired during

initial learning walks (Pyke & Starr, 2021). By regularly updating their position relative to the start of their trip, which is due to the integration of direction and speed information (i.e. path integration; M. Collett & Collett, 2000), they can navigate effectively (Pyke & Starr, 2021). Similarly, honeybees encode spatial relationships among landmarks and celestial cues to determine their position relative to the nest (Dyer, 1996). Furthermore, mammals plan their return route through vector information derived from visual cues (Etienne et al., 1996).

Seabirds, particularly pelagic species, often travel long distances compared with other central-place foragers (Weimerskirch et al., 1994). Their extensive journeys are primarily influenced by colony size, with larger colonies selecting for traits favouring larger foraging ranges, which might be due to selective pressure (Jovani et al., 2016). Furthermore, when prey density is low and sparsely distributed, seabirds forage farther to find suitable prey

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concentrations (Burke & Montevecchi, 2009). Despite the long distances they have to cover, temperate seabirds return to their colony efficiently, flying quickly and directly from the prey patches to the colony (Benhamou, Bonadonna, & Jouventin, 2003; Padget et al., 2019; Pollonara et al., 2015). They use solar angles and odour maps to orient themselves and to navigate back to the colony (Gagliardo et al., 2013; Padget et al., 2018, 2019; Pollonara et al., 2015; Reynolds et al., 2015). In addition, temperate seabirds rely on familiar coastlines as a navigational aid (Goto et al., 2017; Padget et al., 2017; Shiomi et al., 2019). At a larger scale, they use microbarom infrasound to detect areas with preferential wind conditions or coastal areas for homing (Gillies et al., 2023; den Ouden et al., 2022; Smets, 2018). Moreover, some species use the time of day to time their journeys home accordingly as they tend to initiate a homing journey only if they can reach the colony or coastline within a specific time frame (Padget et al., 2019; Shiomi et al., 2012, 2019).

Research on seabird navigation has been primarily conducted at high latitudes (Mendez et al., 2015). However, in the tropics, low-lying islands may reduce access to landmarks, which influence navigational decisions. Moreover, in tropical waters, the low abundance and variable distribution of prey compared with temperate and polar waters (Longhurst & Pauly, 1987; Weimerskirch, 2007) reduce predictable journey times. Many foraging trips of seabirds are constrained by dawn (i.e. end of morning twilight) and dusk (i.e. start of evening twilight; Shiomi et al., 2012, 2019; Padget et al., 2019). In tropical waters, daylength is consistent throughout the year, and diurnal foragers face short twilight periods (Lewis et al., 2004; Pinet et al., 2011). This consistency indicates their arrival times, which is contrary to the variable day lengths experienced in temperate and polar regions. Consequently, tropical seabirds are particularly expected to rely on the time of day for effective navigation back to the colony.

Effective homing strategies have been described in temperate environments (Gagliardo et al., 2013; Gillies et al., 2023; Padget et al., 2019; Pollonara et al., 2015; Reynolds et al., 2015; Shiomi et al., 2019), but whether tropical seabirds can efficiently navigate back to their breeding colonies on low-lying coral reef atolls (the islands of the Chagos Archipelago being ~2 m high) and rely on the time of day to time their homing path remains to be investigated. This study used GPS tracking data from 207 breeding red-footed boobies (RFBs), *Sula sula rubripes*, from four neighbouring colonies in the Chagos Archipelago, central Indian Ocean, to identify navigation behaviour during central-place foraging trips. Their homing duration, bearing and straightness from their final foraging location to their breeding colony were also investigated to explore the mechanism by which they may be constrained by the time of day.

METHODS

Ethical Note

The sampling, care and experimental use of birds were in accordance with institutional guidelines, and the necessary approvals were obtained. In 2016, 2018 and 2019, the capture and handling methods were reviewed by the Zoological Society of London Ethics Committee and were approved by the British Trust for Ornithology special method panel. In 2022 and 2023, data were collected under ethics approval from the University of Exeter ethics committee (ID 493558). Furthermore, the special methods were approved by the British Trust for Ornithology. This research was conducted under permit numbers 0005SE18, 0000SE19, 0006SE19, 0001SE20, 0003SE22 and 0011SE22. Fieldwork was conducted during the cooler parts of the day, either early in the morning or

late in the afternoon. In reducing the likelihood of stress, birds were captured and handled as quickly and efficiently as possible. Birds were captured by hand at the nest, and device deployment lasted between 8 and 15 min. Once captured, they were held in a cloth bag with their heads covered, except when measuring the bill and head. If a bird showed signs of stress during handling, then the process was paused and the bird remained in the cloth bag until all signs of stress subsided. Then, it was released on the ground or returned to its nest site as necessary. The loggers weighed 15 g (iGotU GT-120; Mobile Action Technology, New Taipei City, Taiwan) or 18 g (TechnoSmArt Axy-Trek Marine; <https://www.technosmart.eu/>), which account for 1.6% or 2% of the body mass, respectively (the mean adult weight in this population is 900 g). Loggers were attached to 2–4 central tail feathers using TESA tape (<https://www.tesa.com/>). The recovery rate was 84% across all colonies and years.

Study System and Device Deployments

In 2016, 2018–2019 and 2022–2023, breeding adult RFBs were tracked from four colonies in the Chagos Archipelago, including Nelsons Island (colony size = 3300 breeding pairs; 5.68°S, 72.32°E), Danger Island (3500 breeding pairs; 6.39°S, 71.24°E) and two colonies within the Diego Garcia atoll (known as Barton Point; 9269 breeding pairs; 7.23°S, 72.43°E) and East Island (1113 breeding pairs; 7.23°S, 72.42°E; Fig. S1; Carr et al., 2021). A total of 207 individuals were tracked using archival GPS loggers (heat-shrink wrapped iGotU GT-120 [15 g during 2016, 2018 and 2019] or TechnoSmArt Axy-Trek Marine [18 g during 2019] at Diego Garcia and throughout 2022–2023). The location error around iGotU GPS units is <10 m, which is less than 0.01% of the maximum foraging distance by RFBs; therefore, this error has no effect on our results. Fourteen individuals from Barton Point and East Island colonies, which were caught in 2019 and 2022, were equipped with geolocation and immersion loggers (Intigeo C330, Migrate Technology, 3.3 g; <https://www.migratetech.co.uk/>; Dunn et al., 2024; Trevail et al., 2023). Overall, RFBs in the Chagos Archipelago primarily departed for foraging trips during daylight and returned to the colony around dusk, with most of their trips occurring within a single day (Trevail et al., 2023). Their foraging trips lasted an average of 18.5 ± 1.6 h (SE; range 0.5–111.1 h), with a maximum distance from the colony of 112.9 ± 3.7 km (SE; range 1.4–424.4 km; Trevail et al., 2023).

Identifying Homing Movements

The homing component of the foraging trip was defined as the section between the last foraging location and the colony (Padget et al., 2019). In identifying foraging locations, hidden Markov models (HMMs) equipped with the R package moveHMM v.1.7 (Michelot et al., 2016) were used to identify resting, foraging and transiting behavioural states based on step lengths and turning angles. The data recorded at 5 min intervals were interpolated to 120 s intervals using the function 'redistraj' in adehabitatLT (Calenge, 2006) to refine the resolution, thereby increasing the accuracy of the identification of RFB movement. Then, a gamma distribution and a von Mises distribution were used to characterize step lengths and describe turning angles, respectively (Michelot et al., 2016). During a central-place foraging trip, seabirds would spend time resting on the sea surface (Boyd et al., 2014; Miller et al., 2018; Trevail et al., 2024), fly slowly and tortuously when foraging at sea (Miller et al., 2018; Oppel et al., 2015; Trevail et al., 2024) and spend time transiting, which is characterized by a directed and fast flight from and to the central-place location (Miller et al., 2018; Trevail et al., 2024). Notably, this three-state movement behaviour has been found in boobies (Boyd et al., 2014; Miller et al., 2018).

HMMs were calibrated using three states and the initial parameters used in brown boobies, *Sula leucogaster* from the same location (Table S1; Trevail et al., 2024). The Viterbi algorithm was used to estimate the most likely sequence of movement states derived from the fitted HMM.

Given the bimodal distribution of foraging distances to the colony, which can lead to potential bias in the assignment of foraging behaviour (Fig. S2), and in excluding colony-specific behaviours such as rafting (Carter et al., 2016; Richards et al., 2019) and frigatebird kleptoparasitism (Austin et al., 2019; Osorno et al., 1992), the last foraging location was identified outside a 10 km range around each island to account for the average kleptoparasitism range (10.5 ± 2.4 km; Austin et al., 2019). In 2019, the number of frigatebirds nesting within the Chagos Archipelago was estimated at over 700 individuals (*Fregata ariel* 70 individuals and *Fregata minor* 640 individuals; Carr et al., 2021). In frigatebirds, females likely practise kleptoparasitism (Osorno et al., 1992). However, data on the extent of their kleptoparasitic behaviour in the Chagos were lacking; thus, the female activity range from a related species, *Fregata magnificens*, was used (Austin et al., 2019).

Of the 431 trips studied (2.08% of the data), nine birds did not return directly to the colony, but they spent the night on another islet before returning to the colony the following day (Fig. S3). All these birds nested at Diego Garcia (eight at Barton Point and one at East Island). Given the bias that would have been introduced into homing metrics data, these nine trips were removed from the analyses.

In identifying the start of homing, the last foraging locations were compared with the last dive locations extracted from the immersion logger data (Dunn et al., 2024). The last dives were extracted from each trip ($N = 28$ trips) of 14 birds breeding on Diego Garcia (Fig. 1a and S4). In addition, the outbound segment of the central-place foraging trip was determined (i.e. flight from the colony to the first foraging location) to validate the homing path and differentiate homing from other movements. The first foraging location for each one of the trips was identified the same way as the last foraging location but without any buffer (Fig. S5). The total distance travelled, total duration, straightness and speed from the start of the central-place foraging trip to the first foraging location and start of homing (i.e. the last foraging location) were calculated for each trip the same way as the homing metrics were computed.

Measuring Homing Metrics: Duration, Initial Bearings and Distances

The distance between each GPS point was calculated using the package 'sf' (E. J. Pebesma, 2018; E. Pebesma & Bivand, 2023). For each homing path, various metrics were extracted, including beeline distance (i.e. distance [km] between the last foraging location and the central-place location), homing distance (i.e. total distance [km] travelled by each bird from the last foraging location to the central place) and a straightness index, which is computed as the ratio between beeline distance and homing distance (Benhamou, 2004). With regard to bearings, a beeline orientation (i.e. bearing [degrees] towards the central-place location) and a homing orientation (i.e. bearing [degrees] towards the halfway point between the last foraging location and the central-place location, which is defined as track point corresponding to the value closest to the median of the distance remaining to reach the colony from the last foraging location) were calculated. Given this homing orientation, two additional bearings were measured towards the lower and upper quartile points between the last foraging location and the central-place location (i.e. track point corresponding to the value closest to the lower/upper quartile of the distance remaining to reach the colony from the last foraging location) to ensure that the results do not vary by the point selected. A deflection index (Padget et al., 2019) was computed

between each of these three homing orientations and the central-place location. This index served as the absolute difference between beeline orientation and median/lower/upper quartile orientation. Time was formatted in UTC + 06:00 (local time within the Chagos Archipelago), and different time metrics were computed from following values: total duration of the homing path (h) and time remaining before dusk at the last foraging location (i.e. time interval between the local dusk time of the day of the arrival and the local time of homing departure) using 'sunalc' in R (Thieurmél et al., 2019). The speed of the homing path (km/h), from the last foraging location to the colony, was also calculated.

Statistical Analyses

Metrics were initially compared among homing and outbound paths and the rest of the trip. Then, the effect of the time of day on homing duration, speed, straightness and deflection was tested using linear mixed-effect models, which were fitted using restricted maximum likelihoods to account for biased variance estimates. The response variables, namely, homing duration and deflection, were Poisson distributed; thus, they were \log_{10} transformed. In addition, straightness, a continuous variable bounded by zero and one, was logit transformed. The time remaining before dusk, colony, sex, breeding stage and trip length (multi- or single-day trip) were included as fixed effects to test the influence of each of these parameters on homing metrics (Mendez et al., 2015; Trevail et al., 2023). The effect of the beeline distance on the time remaining before dusk was also tested. Considering that some birds foraged for several days while others completed their trips within a day, an interaction between the length of the trip and the time remaining before dusk was included for each model to test whether the constraint of dusk on homing behaviour differed between single-day and multiday trips. As seabird navigation is likely to be influenced by the beeline distance from the colony (Padget et al., 2019), this metric was added to all the models except for straightness, which is computed by dividing the beeline distance by the homing distance, which would introduce a bias. Year and individual ID were included as random effects to account for temporal and individual variability. Considering the singularity issues, year was excluded from the model with homing duration as the response variable. Effect significance was analysed using the R package 'lmerTest' (Kuznetsova et al., 2017), and models were selected in accordance with a lower Akaike information criterion. In addition, effect significance was extracted from the full model, and parameter estimates of significant effects were extracted using 'ggemmeans()' within the 'ggeffects' R package (Lüdtke, 2018) to marginalize over nonfocal effects (Trevail et al., 2023).

RESULTS

Identifying Foraging Trip Homing Behaviour

For 422 trips, the HMM appropriately identified three behavioural states: resting (step: mean step length \pm standard deviation = 0.231 ± 0.276 km; turn: $\mu = 2.45e-05$, $\kappa = 9.99e+03$), foraging (step: 0.239 ± 0.298 km; turn: $\mu = -2.94e-03$, $\kappa = 2.14$) and transiting (step: 1.27 ± 0.262 km; turn: $\mu = -7.17e-05$, $\kappa = 97.0$; Fig. 1a). For a subsample of birds with dive loggers ($N = 28$ trips), the last foraging location identified from the HMM was 30.15 ± 35.43 km from the last dive, accounting for $12.76\% \pm 9.67\%$ of the total trip length (Fig. 1a and S4).

Homing began 56.86 ± 48.24 km (10.26; 355.98) from the colony. The average duration of their homing path was 1.53 ± 1.26 h; the average deflection from the beeline was $10.44^\circ \pm 17.22^\circ$, and the average time remaining before dusk at the onset of homing was

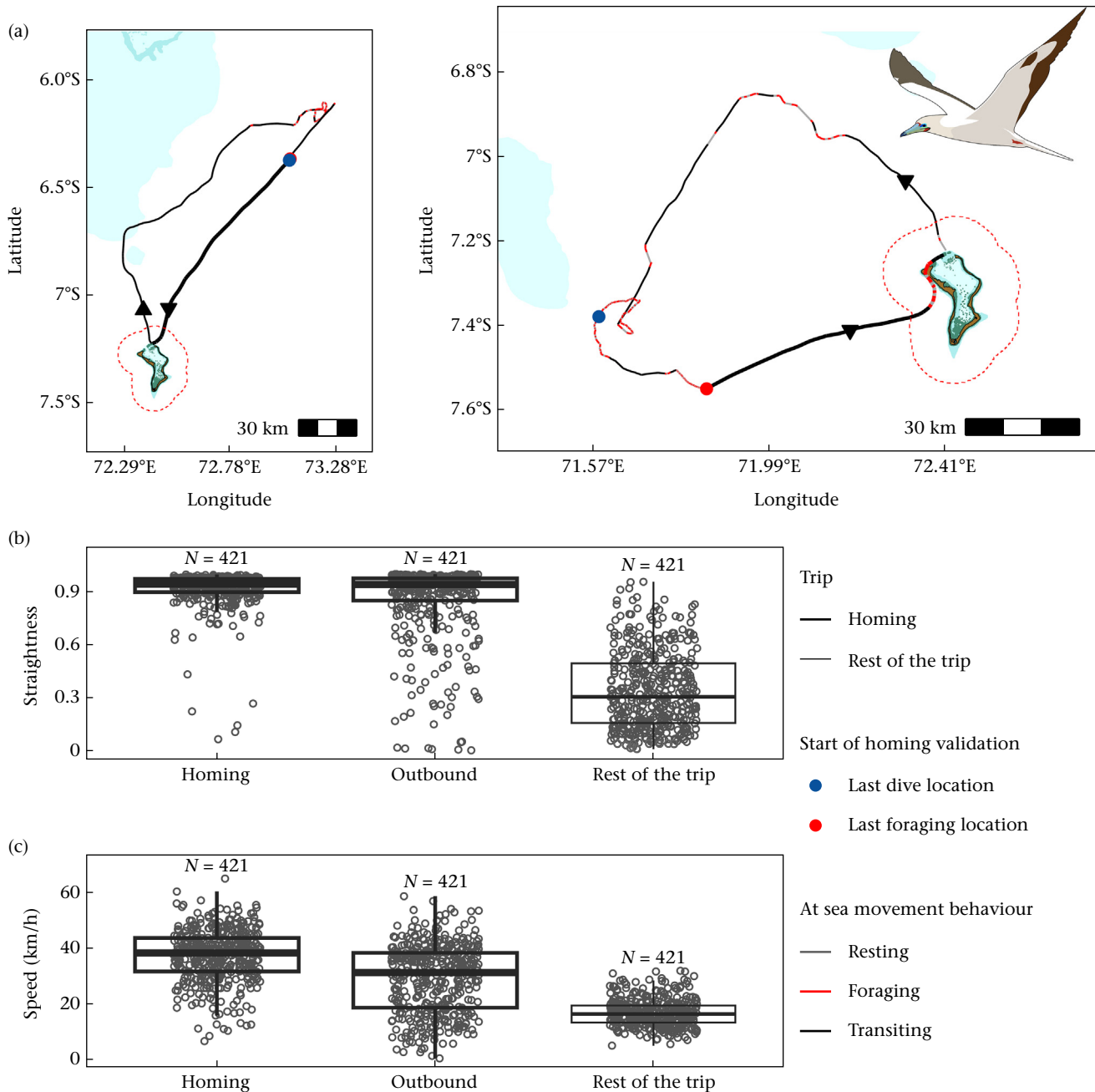


Figure 1. At-sea movement behaviour of 207 RFBs from four colonies in the Chagos Archipelago. (a) Example of 120 s interpolated tracks from two individuals from the Diego Garcia colony. (b) Comparison of flight straightness among the homing trip, the outbound trip and the rest of the central-place foraging trip. (c) Comparison of flight speed (km/h) among the homing trip, the outbound trip and the rest of the central-place foraging trip. In panel a, the red dashed line shows the 10 km buffer used to select the final foraging locations shown in red; blue point is the last dive location (Dunn et al., 2024); black arrows show the direction of the travel; light-blue shading shows water shallower than 100 m. In panels b and c, the internal line is the median; the box represents the IQR (the bottom edge of the box represents the first quartile, which indicates that 25% of the data are below this value; the top edge of the box represents the third quartile, which indicates that 75% of the data are below this value); the whiskers extend to the smallest and largest values within 1.5 times the IQR from the first and third quartiles, respectively; each value of the data is shown by a small circle. In panels b and c, the outbound trip is shown in boldface in respect to Fig. S4.

3.43 ± 3.65 h (Table 1). The section of the trip after the last foraging location had straighter flight trajectories (mean straightness \pm standard deviation = 0.92 ± 0.11 ; Table 1) than the section of the rest of the trip (0.34 ± 0.22 ; permutation t test: 999 runs, $N = 422$, $P < 0.001$; Fig. 1b) and that from the colony to the first foraging location (0.85 ± 0.21 ; permutation t test: 999 runs, $N = 422$, $P < 0.001$; Fig. 1b and S5). They also flew faster during the final leg (37.60 ± 9.32 km/h; Table 1) compared with the rest of the trip (16.94 ± 4.86 km/h; permutation t test: 999 runs, $N = 422$, $P <$

0.001 ; Fig. 1c) and the outbound path (22.36 ± 12.16 km/h; permutation t test: 999 runs, $N = 422$, $P < 0.001$; Fig. 1c and S5).

Homing Efficiency and Influence of Time of Day

The time remaining before dusk was positively correlated with homing duration (parameter estimate in log-hours = 0.010, P values < 0.0001 ; Table S2; Fig. 2a) and negatively correlated with flight speed (parameter estimate in km/h = -0.284 , $P = 0.010$;

Table 1
Homing trip metrics extracted from 422 trips of 207 RFBs from four colonies in the Chagos Archipelago

Metric	Barton Point	East Island	Danger Island	Nelson's Island	All
Beeline distance (km)	73.98 ± 52.67	69.43 ± 35.48	34.39 ± 29.71	30.77 ± 22.98	54.27 ± 46.06
Homing distance (km)	78.37 ± 53.95	72.16 ± 36.83	37.53 ± 32.30	36.47 ± 30.32	58.86 ± 48.24
Straightness	0.93 ± 0.06	0.96 ± 0.03	0.91 ± 0.09	0.90 ± 0.16	0.92 ± 0.11
Homing duration (h)	1.93 ± 1.25	1.87 ± 0.97	1.04 ± 0.74	1.07 ± 1.26	1.53 ± 1.26
Homing speed (km/h)	38.99 ± 8.20	38.44 ± 7.35	33.19 ± 7.78	37.03 ± 11.01	37.60 ± 9.32
Beeline orientation (d°)	215.21 ± 64.38	170.71 ± 71.56	88.48 ± 58.51	240.20 ± 43.07	206.09 ± 73.92
Homing orientation (d°)	214.07 ± 64.88	170.78 ± 71.06	83.89 ± 58.73	238.79 ± 51.96	204.52 ± 76.60
Deflection (d°)	8.27 ± 11.21	6.53 ± 5.19	10.87 ± 9.58	14.03 ± 25.25	10.44 ± 17.22
Time remaining before dusk (h)	3.81 ± 4.32	3.81 ± 4.07	2.08 ± 2.71	3.31 ± 2.58	3.43 ± 3.65
Number of trips	203	25	50	144	422

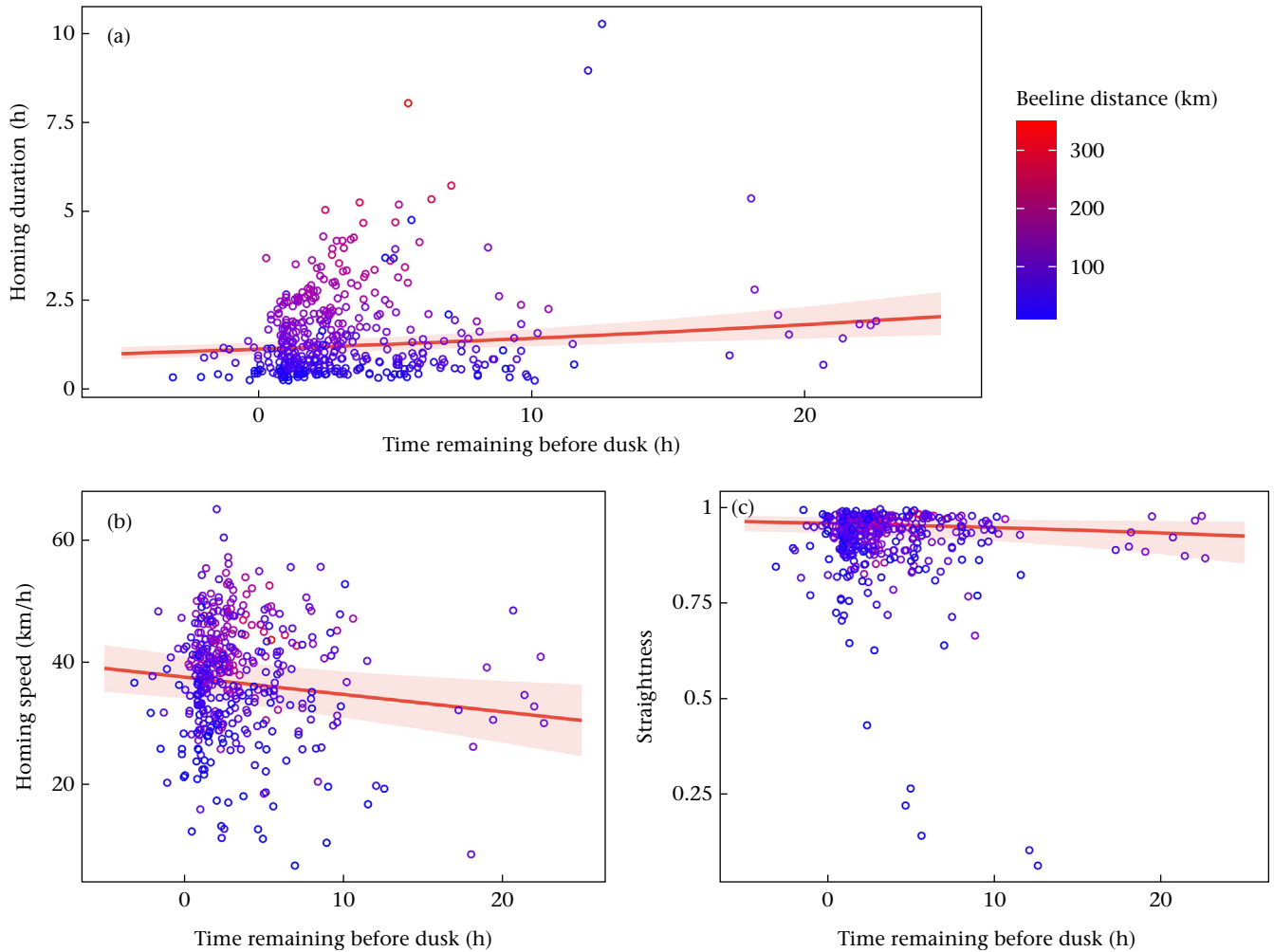


Figure 2. Trip timing adjustment of 207 RFBs from four colonies in the Chagos Archipelago ($N = 422$ trips). (a) Homing duration decreases as dusk approached. (b) Homing birds become fast as dusk approached. (c) Homing path becomes straighter as dusk approached. The red line (with 95% CI) indicates the predicted estimates extracted from the respective linear mixed models. The black dashed line is dusk time. Coloured shading indicates beeline distances.

Table S3; Fig. 2b) and straightness (parameter estimate in logit value = -0.026 , $P = 0.042$; Table S4; Fig. 2c). The time remaining before dusk showed no effect on deflection from the beeline, when considering all deflection values computed from the halfway, upper and lower quartiles of the distance travelled to the colony (all P values > 0.05 ; Tables S5–7).

The beeline distance showed a significant effect on homing duration ($P < 0.0001$; Table S2) and speed ($P < 0.0001$; Table S3) with the homing path being shorter and slower when getting closer

to the colony. The beeline distance to the colony had no effect on the time remaining before dusk (parameter estimate = -0.431 km, $P = 0.666$).

Variability in the Homing Behaviour of RFBs

Trip length showed a significant effect on homing speed and duration, with multiday trips showing faster homing flights (38.24, 34.49–41.99; $P = 0.008$; Table S3) and shorter homing durations

(1.15, 0.977–1.35; $P = 0.047$; [Table S2](#)) than single-day trips (speed estimate = 35.21, 31.75–38.67; duration estimate = 1.29, 1.12–1.51). The interaction tested between the trip length and the time remaining before dusk was not supported by the models, that is, the time of day placed the same constraints on homing behaviour across single- and multiday trips. Trip length showed no significant effect on homing straightness and deflection (all P values > 0.1).

In addition, colony showed a significant effect on homing speed and duration, with birds from Danger Island showing slower homing flights (33.19, 27.78–37.23; $P = 0.031$; [Table S3](#)) and birds from Nelsons Island showing shorter homing durations (1.07, 0.933–1.29; $P = 0.035$; [Table S2](#)) than those from other colonies. Evidence of birds from Nelsons Island being more tortuous while homing (0.90, 0.91–0.97; $P = 0.058$; [Table S4](#)) than the birds from the other colonies is lacking. The colony showed no significant effect on deflection (all P values > 0.1).

Evidence of females showing shorter homing durations (1.15, 0.977–1.35; $P = 0.056$; [Table S2](#)) than males (1.23, 1.05–1.44) is also limited. Sex showed no significant effect on the other homing metrics (all P values > 0.1). Furthermore, the breeding stage had no significant effect on the homing metrics (all P values > 0.1).

DISCUSSION

In this study, RFBs navigated efficiently back to their colony on fast, straight trajectories that are well aligned to the most direct path. Furthermore, RFBs adjusted their homing behaviour in relation to the time of day, that is, as dusk approached, flights became faster and straighter, which reduced the time between the last foraging location and colony return. RFBs exhibited faster and shorter homing trips when returning from a multiday journey compared with a single-day flight. Collectively, these findings indicate that RFBs can use navigational cues to adjust homing behaviour in a tropical, oceanic environment.

Homing Efficiency

RFBs are efficient when it comes to homing, showing fast and direct flights to get back to the colony. Their homing paths were significantly faster and straighter than the outbound path and the rest of the trip ([Fig. 1b](#) and [c](#)). The deflection from the beeline averaged $10.44^\circ \pm 17.22^\circ$, which is less than that in previously studied species ([Padget et al., 2019](#)), indicating that RFBs accurately estimate the direction of their colony from the start of homing. No increase in deflection with homing duration or sinuosity was found in other species either ([Padget et al., 2019](#)), and the strong directional sense indicated by their remarkably well-oriented and direct flight paths could explain the lack of significant effects of the time of day on flight deflection. Moreover, this reduction in energy and time costs, which are reflected in short and direct homing routes, could optimize the energy expenditure during central-place foraging trips ([Shiomi et al., 2012](#)). Therefore, birds back from multiday trips may compensate for the length of their journeys by optimizing their energy expenditure, performing particularly fast and direct homing routes. This characteristic is particularly important in tropical waters, which have limited food resources compared with temperate and polar waters ([Longhurst & Pauly, 1987](#)) and where the abundance and distribution of seabirds' prey are less predictable ([Weimerskirch, 2007](#)). However, the studies conducted in temperate and arctic environments, which we have cited, primarily use Procellariiformes as models, whereas our study focuses on a species belonging to Suliformes.

Cues for Efficient Navigation Under the Constraint of Dusk

Constrained by dusk, RFBs can decide when to return to the colony and adjust the modalities of their return flight, flying faster and straighter to arrive at the colony before dusk ([Fig. 2](#)). Similar behaviours have been described in temperate species breeding on coastal islands where access to landmarks may enable them to make such adjustments ([Padget et al., 2019](#); [Shiomi et al., 2012, 2019](#)). In these species, RFB homing behaviour, including the time allowed for homing, is strongly influenced by the minimum distance needed to travel to get back to the colony (i.e. beeline distance; [Padget et al., 2019](#)). This finding indicates that RFBs could assess the distance separating them from the colony at the start of their homing path ([Padget et al., 2017, 2019](#); [Shiomi et al., 2012](#)). However, RFBs could adjust routes and speeds rather than start heading earlier when returning from more distant locations because of the fact that the beeline distance to the colony had no influence on the time remaining before dusk. However, oceanic waters and low-lying islands, which characterize the Chagos Archipelago, are unlikely to have similar visual cues. During the transiting phase of their central-place foraging trips, RFBs typically reach altitudes of 20–50 m above the sea, and most of them conclude their trips by ascending to high altitudes, up to 500 m, before rapidly descending back to the colony ([Weimerskirch et al., 2005](#)). This behaviour could help birds to avoid frigatebird attacks ([Le Corre & Jouventin, 1997](#)) or enable them to spot the colony from a greater distance ([Weimerskirch et al., 2005](#)). Theoretically, at sea level, birds would start to see the islands of the Chagos Archipelago from around 5 km, but at an altitude of 500 m, their visual range would extend to ~80 km, which would enable them to locate and reorient towards the colony. However, sighting distance can vary with meteorological conditions and light levels ([Lind et al., 2012](#); [Mitkus et al., 2016](#)). In the tropics, in the absence of long coastlines, diurnal seabirds are spotting the colony directly rather than aiming for the coast and then joining the colony similar to temperate species ([Shiomi et al., 2019](#)). From the onset of their return journey, RFBs can acquire distance information from their vision and time of day from solar angles, possibly using a time-compensated sun compass ([Padget et al., 2018](#)), to estimate the time they have left to return to the colony before dusk ([Padget et al., 2019](#)). Flying back to the colony around dusk might also make orientation easier as the remaining light of the sun clearly indicates where west is depending on the season. With regard to their vision, tropical seabirds could rely on olfactory cues to navigate effectively ([Gagliardo et al., 2013](#); [Pollonara et al., 2015](#); [Reynolds et al., 2015](#)).

Variability in Homing Efficiency

Intercolony variability was evident in RFB homing behaviour. Birds from Danger Island flew more slowly on their return to the colony, while those from Nelsons Island exhibited shorter and more tortuous homing flights compared with those from other colonies. Considering that RFB colonies on Nelsons Island and Danger Island (with 3300 and 3500 breeding pairs, respectively; [Carr et al., 2021](#)) are smaller than those on Diego Garcia (11 113 breeding pairs combined; [Carr et al., 2021](#)), these differences could be influenced by colony size. Given the intraspecific competition, colonies segregate at sea with departure angles varying among colonies ([Trevail et al., 2023](#)), and smaller colonies deplete fewer prey resources around the colony, thereby reducing their foraging ranges and trip durations ([Jovani et al., 2016](#); [Lewis et al., 2001](#); [Trevail et al., 2023](#)). Given the high intraspecific competition they face, birds from larger colonies must optimize their energy expenditure with faster and more direct flights compared with those from smaller colonies. In addition, the high density of congeners on the

return journey, as well as the presence of other species such as frigatebirds close to the colony, could provide greater availability of social information by flying in formation with other individuals, enabling them to navigate more efficiently to the colony (Dall et al., 2005; Weimerskirch et al., 2010). However, some RFBs are less efficient in navigating to the colony, as shown by the nine birds resting on another islet before reaching the colony the day after. These birds probably did not estimate the parameters of their return route efficiently enough to get back to their nest before dusk, and they had to rest on another island to wait for the night to pass. This finding is consistent with the limitations that dusk imposes on them, as they seem to prefer to rest elsewhere than at their colony rather than fly after dusk. However, interpreting these results with caution is crucial because of the individual variability observed in data distribution (Fig. 2).

The length of the central-place foraging trips that seabirds undertake during the breeding season varies with the breeding stage (Weimerskirch et al., 2006), being short during brooding and increasingly longer during incubation and fledging (Mendez et al., 2015). However, no significant effect was observed despite the variation in homing behaviour across different breeding stages (Trevail et al., 2023; Weimerskirch et al., 2006). Considering the influence of sexual dimorphism on the central-place foraging behaviour of RFB, where females undertake longer trips and depart earlier (Trevail et al., 2023), because of their large size and heavy weight (Carr, 2021; Weimerskirch et al., 2006), considerable significant evidence of females navigating more efficiently than males to compensate with the length of their trip would have been expected. The importance of breeding stage and sex in the homing behaviour of RFBs might be masked by the constraint of dusk, indicating that the time remaining before dusk might be a main driver of their homing efficiency.

Homing Movement Validation

Distances between the last foraging location and the last dive represented $12.76\% \pm 9.67\%$ of the total trip length. Notably, such differences can be explained by the varied nature of their foraging behaviour, which includes not only dives but also aerial captures of flying preys that would not have been identified when analysing dives (Dunn et al., 2024), but which were shown in RFB (Jaquemet et al., 2005; Weimerskirch et al., 2005), as well as in other boobies (Dorward, 1962; Miller et al., 2018). Given that Exocoetidae flying fishes (e.g. *Exocoetus volitans* and *Cheilopogon furcatus*) and Ommastrephinae flying squid (e.g. *Sthenoteuthis oualaniensis*) account for a large proportion of RFB feed (Weimerskirch et al., 2005), studying the movement of birds to categorize their foraging behaviour represents a more holistic approach than simply determining the last dive as the last foraging point. Therefore, the distances between the last foraging locations and last dives should be considered, and combining this tracking study with other methods such as video or accelerometric analyses could shed light on these differences.

Conclusion

In this study, we found that RFBs adjusted their homing behaviour based on the time of day, flying faster and straighter as dusk approaches to ensure timely colony return, thereby highlighting their efficiency in navigating, even in visually sparse environments with low-lying landmarks. Therefore, in temperate environments (Padget et al., 2019), dusk is a constraint for seabird navigation in the tropics, and seabirds can use dynamic information on time and location. Although we provide evidence that solar and visual information contribute to tropical seabird navigation, the

potential incorporation of olfactory and infrasound cues by tropical seabirds warrants further investigation. Despite a backdrop of growing threats, from bycatch to climate change, investigating how and why organisms relocate, as well as the implications of such movement, remains an important research direction to minimize human disturbance on seabird population connectivity and breeding success.

Author Contributions

Peter Carr: Writing – review & editing, Validation. **Joshua Coste:** Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis. **Ruth E. Dunn:** Writing – review & editing, Validation, Methodology. **Robin Freeman:** Validation, Supervision, Methodology, Conceptualization. **Malcolm A. Nicoll:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization. **Alice M. Trevail:** Writing – review & editing, Visualization, Validation, Supervision, Software, Methodology, Investigation, Data curation, Conceptualization. **Stephen C. Votier:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Funding acquisition. **Hannah Wood:** Validation.

Data Availability

All data are accessible via the BirdLife International Seabird Tracking Database (data set IDs: 1687, 1688 and 1689; <https://www.seabirdtracking.org/>).

Declaration of Interest

The authors have no conflicts of interest to declare.

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Supplementary Material

Supplementary material associated with this article is available at <https://doi.org/10.1016/j.anbehav.2025.123116>.

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