Differences in foraging range between white-tailed tropicbirds breeding on inner and outer Seychelles islands

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ABSTRACT: The foraging ecology and distribution of Phaethontiformes, an order of tropical sea-birds, remains generally poorly understood, despite being essential to inform their conservation. Here, we tracked, for the first time, the foraging movements of breeding white-tailed tropicbirds *Phaethon lepturus*, a common but poorly studied seabird, in the Indian Ocean. We compared the foraging movements and habitat preferences of 2 populations, one from Aride Island in the inner Seychelles and the other from Aldabra Atoll in the outer Seychelles, ca. 1200 km to the southwest. We found considerable differences in foraging trip metrics between populations, with birds from Aride having an average foraging range 2 times greater (231 km on Aride vs. 105 km on Aldabra), and both populations feeding far beyond the protected areas around their respective colony. We also found differences in foraging range between incubation and chick-rearing stages and sexes. Using habitat models, we highlight the birds' preference for deep waters, which may explain the greater foraging range of Aride birds, although human activities may also play a role. Our study provides unprecedented insight into the foraging ecology of white-tailed tropicbirds in the Western Indian Ocean.

KEY WORDS: Foraging movements · Habitat preferences · Population differences · Seabirds · Indian Ocean · *Phaethon lepturus* · Phaethontiformes · GPS tracking · GAMs

1. INTRODUCTION

Marine apex predators, such as seabirds, are especially sensitive to global environmental changes because of their life-history traits (high adult survival, low fecundity, and delayed maturity; Gaston 2004). They are often key indicators of ecosystem health (Cairns 1988) and are the focus of many biodiversity conservation and monitoring programmes (Sergio et al. 2006, Hazen et al. 2019). Key mechanisms driving the declines of marine apex predators, including climate change, overfishing, bycatch, invasive alien species, hunting, or pollution, are generally known (Lewison et al. 2004, Dias et al. 2019).

However, the relative importance of these drivers and their impacts on demographic traits remain poorly understood for many species, which can hinder the implementation of effective local or species-specific conservation measures (Rodríguez et al. 2019, Foskolos et al. 2020).

Seabirds play a major role in marine and island ecosystems as ecological engineers, mainly through nutrient subsidies and physical disturbance of the soil (Croll et al. 2005, Smith et al. 2011, Graham et al. 2018). Their strong philopatry to terrestrial breeding sites makes them easier to study than other marine species. Consequently, seabird monitoring has been successfully used to detect a wide range of environmental trends (Burger & Gochfeld 2004, Rajpar et al. 2018). Understanding how seabirds are affected by environmental change is increasingly important because seabirds are declining globally and are now one of the most threatened groups of birds on Earth (Dias et al. 2019). Although some populations have been studied in depth and causes of their declines are now well understood (e.g. Frederiksen et al. 2004, Pardo et al. 2017), many others, especially tropical species, remain poorly known, which is an obstacle to their conservation (Mott & Clarke 2018, Bernard et al. 2021).

Effective seabird conservation starts with a sound understanding of their ecology. Knowledge of foraging ecology is especially important, because lack of food often results in low breeding success and ultimately population declines (Naef-Daenzer & Keller 1999, Guillemette et al. 2018). Together with diet studies, tracking the foraging movements of breeding seabirds helps to identify important feeding areas around breeding colonies (Cleasby et al. 2020), important environmental factors affecting their distribution (Legrand et al. 2016), and potential threats (Raine et al. 2021). Multi-population approaches can be particularly powerful because one population's foraging patterns cannot always be extrapolated to other populations (Diop et al. 2018), and can be useful to identify drivers of population declines, especially when long-term demographic data are unavailable (Fayet et al. 2021).

To improve foraging efficiency, seabirds often favour specific areas that provide reliable resources (Weimerskirch 2007). This includes frontal zones, shelf edges, seamounts, and currents that create upwelling areas where nutrient-rich waters reach the surface, boosting phytoplankton productivity, with cascading effects on the food chain. However, unlike temperate and polar waters, tropical waters are often characterised by low productivity (Weimerskirch 2007) and patchily distributed resources (Ballance et al. 1997). Understanding how environmental conditions shape tropical seabirds' foraging distributions will provide valuable information to apply conservation management at large scales. For instance, it can help to identify important drivers of population trends, predict how foraging distributions may change in future, and which areas will become important to protect.

The Western Indian Ocean is 1 of 6 marine biodiversity hotspots that are most severely affected by climate change, facing increasing water temperature, slowing current circulation, and decreasing primary productivity (Ramírez et al. 2017). Furthermore, fishing intensity has substantially increased in this area over the past few decades (Ramírez et al. 2017), increasing seabird bycatch and impacting fish stocks. Tuna are especially targeted in this area (Le Corre et al. 2012), impacting seabird communities indirectly through sub-surface predator interactions (Miller et al. 2018). Moreover, seabird tracking studies are relatively limited in this region, especially compared to temperate oceans (Bernard et al. 2021). There is therefore an urgent need to understand accurately the foraging distribution of seabirds in the Western Indian Ocean and how they interact with their environment to investigate potential threats and inform possible conservation measures.

Here we investigated the foraging ecology of a common and widespread seabird species in the Western Indian Ocean, the white-tailed tropicbird *Phaethon lepturus* (hereafter tropicbird). While currently listed as 'Least Concern' on the IUCN Red List of Threatened Species, the global population of this species is decreasing (BirdLife International 2020). Studies of its foraging ecology in the Indian Ocean are limited (e.g. Diamond 1975, Catry et al. 2009b, Sommerfeld & Hennicke 2010). Its foraging distributions in particular are poorly known, which makes it difficult to identify important feeding areas and potential threats at sea and understand whether current protected areas are relevant to the species.

We provide, for the first time, detailed information about foraging movement of the subspecies *P. lepturus lepturus* in the Indian Ocean. We studied populations in the Seychelles, home to the largest population of white-tailed tropicbirds in the Indian Ocean (56% of *P. l. lepturus*, ~6500 pairs; Le Corre et al. 2012). We compared 2 breeding populations found within 2 longstanding marine protected areas ca. 1200 km apart (Fig. 1). One population is from the northernmost inner granitic islands (Aride Island),
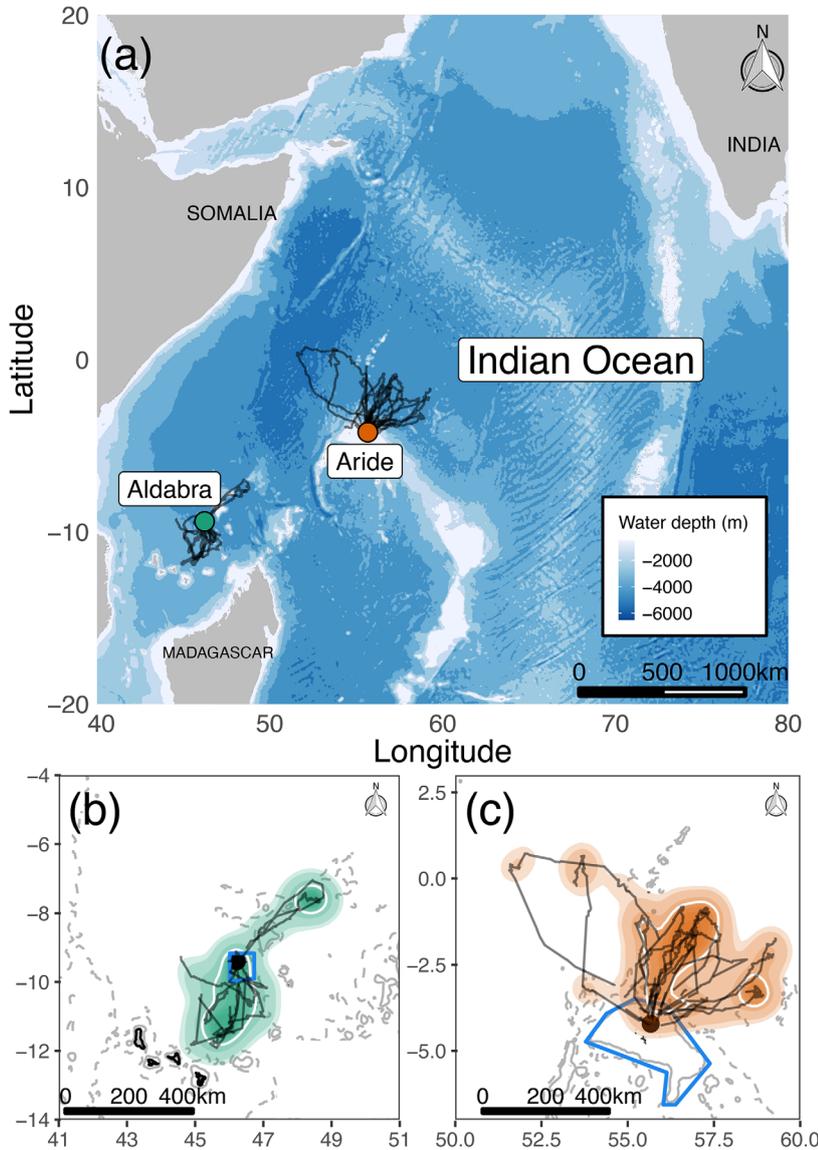
Fig. 1. (a) Western Indian Ocean region showing examples of white-tailed tropicbird foraging trips (black lines) from the northern (Aride, red circle) and southern (Aldabra, green circle) Seychelles. (b,c) Foraging distribution of white-tailed tropicbirds on Aldabra (b) and Aride (c). Densities are shaded from the lightest to the darkest occupancy (from 95 to 10% occupancy) with core foraging area (50% occupancy) marked by a white line. Black lines show foraging trips. Solid grey and dashed grey lines represent the 1000 and 3000 m water depth contours, respectively. Black circles represent colonies. The blue outlines represent the foreign vessel restricted area around the colonies

area. Our objectives were threefold. First, we aimed to fill the gap in knowledge of white-tailed tropicbird foraging ecology in the Seychelles by identifying the foraging distribution and key feeding areas of inner and outer Seychelles populations during breeding. Second, we aimed to investigate potential differences in foraging behaviour between populations, breeding stages (between which foraging ranges can differ), and sexes. Finally, we aimed to explain those differences by investigating the role of environmental parameters in shaping the populations' foraging areas.

2. MATERIALS AND METHODS

2.1. Study site and species

This study was conducted on Aride Island (4° 12′ 48″ S, 55° 40′ 12″ E) and Aldabra Atoll (9° 25′ 00″ S, 46° 20′ 00″ E) during the austral summer monsoon between December 2018 and March 2019. The austral summer monsoon lasts from November to April and is characterised by lighter northwest winds, higher rainfall, and less-productive waters. In contrast, the austral winter monsoon (May to October) is dominated by south-eastern winds, lower rainfall, and a decrease in SST, which leads to increases in chlorophyll (chl) *a* (Jaquemet et al. 2007). White-tailed tropicbirds are wide-ranging pelagic seabirds present in all tropical oceans. They are split into 6 sub-species, and 5 genetically distinct groups have been identified by Humeau et al. (2020), some of which are endangered and/or decreasing (Catry et al. 2009a, Burt et al. 2021). As plunge-divers, they are largely solitary feeders. White-tailed tropicbirds breed year-round on both Aride and Aldabra, but there are 2 breeding peaks on Aride while breeding activity is more constant on Aldabra (Burt et al. 2021). The population on Aride is decreasing (Catry et al. 2009a), while it seems stable on Aldabra, despite declining breeding success (Burt et al. 2021).

whose surrounding waters outside the reserve have high levels of human activity, including fishing and tourism. This island is located inside the fisheries foreign vessel prohibited area covering the Seychelles plateau. The second population is from one of the southern, coralline outer islands (Aldabra Atoll), a remote UNESCO World Heritage Site surrounded by a 2599 km² marine protected

2.2. GPS data collection

On both islands, incubating and chick-rearing birds were caught at the nest by hand and equipped with miniature GPS loggers all set to record positions every 5 or 10 min during daytime (05:00 to 20:00 h) and every 80 or 90 min during night-time (20:00 to 05:00 h). Three models of loggers were used: PathTrack Nanofix, 3–4 g; TechnoSmart AxyTrek, 6 g; or CatLog Gen 2, 10 g. Loggers were on average ~2% of body mass (average bird mass: 333 ± 5 g on Aride, 325 ± 5 g on Aldabra) and did not exceed 3% as recommended (Phillips et al. 2003). They were attached with thin strips of marine tape (Tesa® 4651) to the central 3 to 5 rectrices, below the preening gland, as in Campos et al. (2018). Devices were removed manually after 1–14 d or they fell off naturally after ca. 2 wk if the bird was not recaptured (estimate based on the solidity of the attachments on birds recaptured after different durations of tag deployment). Five small breast feathers were sampled for DNA sexing. In total, we obtained tracks for 12 birds on Aldabra (4 females, 7 males, and 1 of unknown sex) and 21 birds on Aride (12 females, 9 males). The smaller sample size on Aldabra was due to nests being less accessible (on islets in the lagoon) and to a high nest failure rate making it difficult to recover loggers.

Data processing and analyses were conducted in R version 4.0.5 (R Core Team 2021). We applied a 10 min piecewise cubic Hermite polynomial interpolation on each track to standardise the dataset with the packages 'adehabitatLT' and 'pracma'. Gaps longer than 60 min (i.e. ≥6 missing points) were not interpolated and were excluded from further analysis to avoid interpolating unrealistic behaviours. Night-time locations at sea were removed, as tropicbirds are inactive at night (Campos et al. 2018), which was confirmed in our dataset.

Data points within 2 km from the colony were removed to exclude colony-based behaviours (e.g. nest attendance and rafting near the colony). Foraging trips were identified as the positions between the first and last position outside a 2 km radius around the colony. In total, we recorded 73 trips (37 from Aldabra and 36 from Aride), including 15 incomplete tracks. Nine trips shorter than 20 min were excluded as they were deemed unlikely to represent true foraging trips. In addition, 1 trip was removed because the bird went to rest on the ground (a common behaviour on Aldabra). One bird could not be sexed, and its 3 trips were also removed from further analyses. Our final dataset therefore contained 60 trips: 26 from Aldabra (including 4 incomplete) and 34 from Aride (including 11 incomplete).

For each trip, maximum distance to the colony, total distance travelled, and total trip duration were calculated. Incomplete trips where the bird was clearly on the way back to the colony were included, and the distance between the last point and the nest was added to the total distance travelled. Incomplete trips where it was not clear that the bird was returning were excluded from the total distance travelled and total trip duration calculations.

We identified foraging behaviour in the tracking data using hidden Markov models (HMMs) with the package 'moveHMM' (Michelot et al. 2016), due to their good performance for this task (Dean et al. 2013, Bennison et al. 2018). We used a 3-state model which allocated each location to 1 of 3 states corresponding to 3 modes of movement/behaviours, which we identified as commuting, foraging, and resting (for details, see Text S1 and Figs. S1–S3 in the Supplement at www.int-res.com/articles/suppl/m724p141_supp.pdf). The proportion of activity was assessed per colony and per time of the day with a step of 30 min.

Density kernels were calculated with the package 'adehabitatHR' (Calenge 2006) with a grid factor set at 150 and a bandwidth estimated at $h = 0.367$ for Aldabra and $h = 0.335$ for Aride (see Text S2 for details). We used 50 and 95% occupancy contours to define core and total foraging areas, respectively.

To test for differences in trip metrics between colonies, sex, and breeding stages (incubation or chick-rearing), we ran linear models (LMs) and linear mixed models (LMMs; 'lme4' package, Bates et al. 2014). We assessed differences in (1) total distance travelled per trip; (2) total trip duration; and (3) maximum distance from the nest. Trips during which the chick hatched before the bird returned were considered as incubating trips. All 3 variables (colony, sex, and breeding stage) were included as covariates. Bird ID was used as a random effect in LMMs, as our dataset included multiple trips per bird. In models of trip duration and total distance travelled, the variance of the random effect Bird ID was null for the full model; therefore, linear models were used instead. Total trip duration was log-transformed to meet assumptions of normally distributed residuals.

2.3. Environmental data

High-productivity waters are often characterised by different physical parameters such as high chl *a* concentration and low sea surface temperature (SST), commonly used as proxies for primary productivity

(Mannocci et al. 2014). They can also have specific water depth, bottom sea slope, and distance to nearest seamount signatures (Jaquemet et al. 2004). Here we used 7 variables to investigate tropicbirds' foraging habitat preferences: chl *a* concentration, SST, water depth, fishing effort, wind speed, distance to nearest seamount, and sea floor slope. All variables except water depth were extracted with 0.1° resolution. We calculated the average value of the 7 parameters for each GPS point classified as 'foraging activity'. Daily values of chl *a* and SST were extracted from the Environmental Research Division Data Access Program (ERDDAP; https://coastwatch.pfeg.noaa.gov/erddap/griddap/, from the 'erdMH1chla1day' and 'jplMURSST41' datasets, respectively) and used to calculate means over the month leading to each GPS location. Water depth data were extracted from the General Bathymetric Chart of the Oceans (GEBCO) Gridded Bathymetry Data website (https://download.gebco.net/) with a spatial resolution of 15 arc seconds (~0.004°). Sea floor slope was calculated with the Horn algorithm of the 'raster' package. Distance to the nearest seamount was calculated by extracting seamounts from the Global Seamount Database (Kim & Wessel 2011) (https://www.soest.hawaii.edu/pwessel/smts/). Wind speed data were extracted with the package 'rWind', which uses the Global Forecasting System. Fishing effort data (mostly vessels >24 m long and very few vessels <15 m) were extracted from Global Fishing Watch (https://global-fishingwatch.org/dataset-and-code-fishing-effort/) and summed over the study period to obtain the total fishing effort during that period in every grid cell.

2.4. Habitat modelling

Generalised additive models (GAMs) (Wood 2017, 'mgcv' package) were used to explore tropicbirds' foraging habitat preferences. We used foraging activity as a binary response variable (see below) and the 7 environmental parameters listed above as explanatory variables. GAMs are well suited for this task since animals do not react linearly to their environment (Aarts et al. 2008). The models do not need any assumption about the nature of the relationship between response and explanatory variable, and can include different non-linear relationships that can reflect the pattern within the data (Forney 2000). To build the response variable, foraging points from the real tracks (see Text S7, Fig. S5) were used as 'presence of foraging activity' and a null distribution of pseudo-foraging points was randomly generated within each bird's foraging range to represent 'absence of foraging activity' (see Text S3 for details).

Separate models were run for each population and breeding stage, as there could be differences in environmental preferences among these (Weimerskirch et al. 1993). There were not enough chick-rearing data on Aldabra to run a valid model separately, so we only ran models for incubation on Aldabra, and both incubation and chick-rearing models on Aride. We followed the stepwise forward approach used by Carneiro et al. (2016) and Dehnhard et al. (2020). Details of the method are available in Text S3. Briefly, penalised cubic regression splines were used to produce GAM smoothing terms with shrinkage to reduce the risk of over-parametrisation (Cleasby et al. 2015, Wood 2017). The number of knots representing the maximum degrees of freedom of each smoother were set at $k = 4$ to avoid overfitting and to make biological interpretation possible (Forney 2000, Carneiro et al. 2016). We then adjusted k within the best model with the function 'compareML' ('itsadug' package) and the function 'gam.check' ('mgcv' package).

For each dataset, all environmental variables were first tested individually, then covariates were gradually added to the best model (see below for model selection) with a maximum of 3 covariates per model to avoid overfitting. We then checked if adding variables significantly increased model quality with paired *t*-tests (details in Text S3). Correlated variables (Spearman's rank > 0.5) were not used in the same model, and the variable with the best explanatory power (highest χ^2) was kept. Distance from the nest was included in all models as an additional smoothing parameter to take into consideration the energetic cost of travel. We used a *k*-fold cross validation with birds as data-folds to compare models. We used the area under the curve (AUC; 'pROC' package) to assess model performance, with AUC <0.7 considered poor, 0.7–0.9 reasonable, and >0.9 very good (Pearce & Ferrier 2000). For each dataset, the best most parsimonious model was then selected.

3. RESULTS

Birds from different colonies foraged in different directions, but the main direction was highly consistent within populations (Fig. 1a). On Aride, all trips headed in a northerly direction (Fig. 1c), whereas on Aldabra, all birds except 2 went south (Fig. 1b).

3.1. Population differences in trip metrics

We found clear differences in trip characteristics between breeding islands and breeding stages, and a slight difference between sexes (Table 1; all statistics in Table 2). Birds on Aride had a substantially greater foraging range than birds on Aldabra, both during incubation and chick-rearing (Table 1). Males travelled on average 40 km further from the colony and their trips lasted more than 30 h longer than females; total distance travelled was also higher for males, but the difference was not statistically significant (Table 2).

We found no difference in the temporal distribution of different behaviours between colonies. Tropicbirds from both colonies tended to commute all day with an increase at dawn and dusk and a drop around midday; resting took place across the day, with more around midday and less around dawn and dusk (Fig. 2). The total proportion of time spent foraging (mean ± SD) was slightly higher in tropicbirds from Aldabra (0.48 ± 0.31; Text S4, Table S1) than Aride (0.42 ± 0.20), while we observed the opposite for commuting behaviour. The proportion of time spent foraging appeared similar between nesting stages (Table S1). However, the proportion of time spent resting
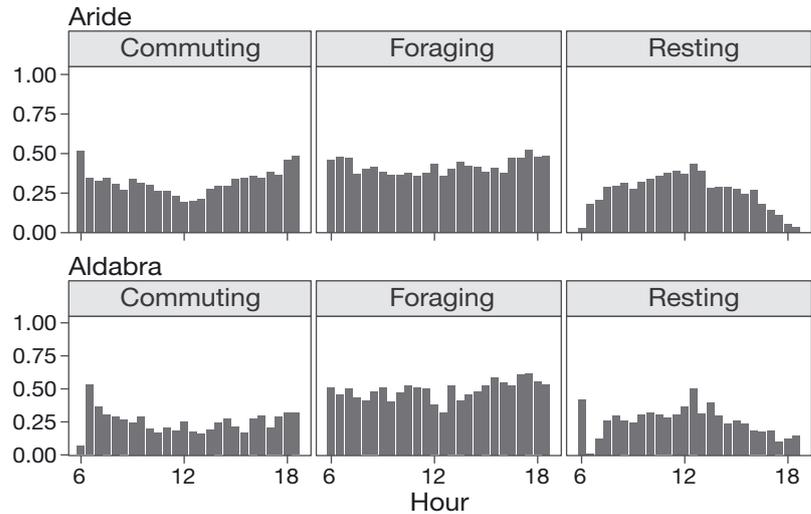
Fig. 2. Activity patterns during daylight hours for white-tailed tropicbirds from (a) Aride and (b) Aldabra. The day was divided in 30 min windows, and the proportion of commuting, foraging, and resting was calculated for each window

Table 1. Mean (SD) maximum distance from the nest, distance travelled, trip duration, and maximum range of foraging trips of white-tailed tropicbirds on Aride and Aldabra during incubation and chick-rearing, with the number of trips and birds per colony and breeding stage

Colony	Breeding stage	No. of trips (birds)	Max. distance from nest (km) [range]	Total distance travelled (km)	Trip duration (h)
Aride	Incubation	13 (13)	401 ± 140 [158–683]	856 ± 437	123 ± 61 (5.1 d)
Aldabra	Incubation	17 (9)	132 ± 134 [3–367]	357 ± 372	71 ± 77 (3.0 d)
Aride	Chick-rearing	21 (8)	126 ± 112 [21–414]	295 ± 327	35 ± 64 (1.5 d)
Aldabra	Chick-rearing	9 (2)	53 ± 84 [3–252]	141 ± 237	23 ± 47 (1.0 d)

Table 2. Outputs from linear models (LMs) and linear mixed models (LMMs, with Bird ID as random effect) comparing trip metrics as a response variable (maximum distance from the nest, total distance travelled, and total trip duration) between colonies, sexes, and breeding stages (all included as covariates). The mean ± SE of each response variable for each category is shown, as well as the model statistic (χ^2 or F) and the p-value. Significant p-values (<0.05) are in **bold**. F: Female; M: Male; INC: incubation; CR: chick-rearing

	No. of trips	Max. distance from nest (km), LMM			Total distance travelled (km), LM			Total trip duration (h), LM		
		Mean ± SE	χ^2	p	Mean ± SE	F	p	Mean ± SE	F	p
Colony	Aldabra (n = 26)	105 ± 124	27.4	**<0.001**	283 ± 343	9.1	**0.004**	55 ± 71	9.1	**0.004**
	Aride (n = 34)	231 ± 182			510 ± 459			69 ± 76		
Sex	F (n = 29)	157 ± 166	12.1	**<0.001**	335 ± 383	3.0	0.08	46 ± 62	5.6	**0.02**
	M (n = 31)	195 ± 175			482 ± 456			78 ± 80		
Stage	INC (n = 30)	249 ± 191	33.4	**<0.001**	653 ± 492	32.0	**<0.001**	94 ± 74	26.8	**<0.001**
	CR (n = 30)	104 ± 108			266 ± 327			31 ± 59		

seemed higher during incubation, whereas the proportion of time spent commuting was higher during chick rearing (Table S1). There were no obvious sex differences in the proportion of time engaged in different behaviours.

3.2. Habitat differences and preferences

The average environmental conditions experienced at sea by the birds from each population are presented in Table 3. On Aride, SST was negatively correlated with chl *a* concentration, and distance from the nest was positively correlated with water depth, during both incubation ($|\rho| = 0.53$, $|\rho| = 0.59$) and chick rearing ($|\rho| = 0.66$, $|\rho| = 0.68$). Those combinations of variables were therefore not used in the same models to avoid collinearity. Water depth was more influential than distance from the nest for both

breeding stages and was therefore kept for further analyses.

For Aride, the best single-predictor GAM (based on AUC) and also the most parsimonious model of tropicbird foraging activity was that with water depth as a covariate (besides distance from the colony, which was included in all models), during both incubation and chick-rearing (Table 4). In contrast, the best single predictor of foraging activity for incubating birds from Aldabra was chl *a* (Table 4), but this was not significantly different from the simplest model with only distance from the nest (paired *t*-test, $t = 0.184$, p = 0.859). The latter was therefore preferred, as it was the most parsimonious, but it was considered a relatively poor predictor (AUC = 0.69; note that AUC < 0.7 is considered poor).

For all 3 datasets, the addition of a second environmental covariate to the best single-predictor model did not significantly improve the average model fit, although models with 2 environmental covariates had reasonable performances. On Aldabra, during incubation, the best 2-predictor model was chl *a*–water depth, with an average AUC of 0.78 (comparison with distance from the nest-only model: paired *t*-test $|t|$ = 1.44, p = 0.187). On Aride, during incubation, the model with water depth and SST had a mean AUC of 0.80 ± 0.11 (comparison with water depth-only model: paired *t*-test $|t|$ = 1.75, p = 0.106), while during chick-rearing, the model with water depth and sea floor slope had a mean AUC of

Table 3. Average values (mean ± SD) of environmental parameters and fishing effort in the white-tailed tropicbird foraging areas around Aride and Aldabra

	Aride	Aldabra
Number of foraging locations	2868	1200
Chlorophyll *a* concentration (mg m^{-3})	0.15 ± 0.04	0.09 ± 0.02
Sea surface temperature (°C)	29.01 ± 0.41	29.28 ± 0.20
Sea floor slope (degrees)	1.08 ± 2.17	2.25 ± 4.90
Water depth (m)	4109 ± 964	3635 ± 1060
Fishing effort (hours per 123 km^2)[a]	3.43 ± 5.25	2.80 ± 4.51
Wind intensity (m s^{-1})	3.84 ± 1.61	5.65 ± 1.82
Distance to nearest seamount (km)	80.18 ± 36.89	74.49 ± 53.65

[a]123 km^2 = 0.1° × 0.1° = grid resolution

Table 4. Area under the curve (AUC; mean ± SD and range) as an indicator of model fit for generalised additive models (GAMs) testing environmental variables on white-tailed tropicbird foraging probabilities. Only models with distance from the colony and another predictor are shown, as adding more predictors did not significantly improve model fit. **Bold** numbers indicate the model with the best fit for each dataset. Mean AUC calculated from *k*-fold cross validation on N = 9 birds for Aldabra incubation, N = 8 for Aride during chick-rearing, and N = 13 for Aride during incubation (we did not have data from enough birds on Aldabra to build a chick-rearing model). Dist-nest: distance from the nest; slope: sea floor slope; *y*: response variable (presence/absence, i.e. real or pseudo-foraging points)

	Aldabra incubation		Aride chick-rearing		Aride incubation	
	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
y ~ dist-nest	0.69 ± 0.15	0.46–0.86	0.63 ± 0.12	0.43–0.83	0.63 ± 0.16	0.44–1
y ~ water depth + dist-nest[a]	0.67 ± 0.14	0.49–0.86	**0.76 ± 0.21**	0.32–0.95	**0.74 ± 0.11**	0.58–0.94
y ~ chlorophyll *a* + dist-nest	**0.70 ± 0.13**	0.53–0.96	0.67 ± 0.10	0.55–0.79	0.64 ± 0.07	0.53–0.77
y ~ dist. to nearest seamount + dist-nest	0.64 ± 0.11	0.53–0.88	0.71 ± 0.14	0.53–0.88	0.62 ± 0.07	0.50–0.74
y ~ fishing effort + dist-nest	0.67 ± 0.15	0.48–0.87	0.64 ± 0.11	0.52–0.82	0.69 ± 0.12	0.48–0.97
y ~ SST + dist-nest	0.67 ± 0.15	0.47–0.94	0.74 ± 0.07	0.60–0.84	0.72 ± 0.15	0.49–1
y ~ slope + dist-nest	0.64 ± 0.14	0.44–0.80	0.71 ± 0.09	0.57–0.86	0.64 ± 0.13	0.45–0.89
y ~ wind speed + dist-nest	0.65 ± 0.13	0.50–0.85	0.61 ± 0.11	0.50–0.80	0.64 ± 0.13	0.49–1

[a]For Aride chick-rearing and incubation, we only used water depth because of collinearity between the 2 variables

0.82 ± 0.09 (comparison with water depth-only model: paired *t*-test |*t*| = 1.08, p = 0.316).

On Aride, the influence of water depth on foraging probability was similar between breeding stages (Fig. 3a). The foraging probability increased in waters deeper than 3200 m, with the slope of the response increasing during chick-rearing compared to incubation. However, the threshold above which the foraging probability started to increase was slightly higher (i.e. deeper waters) than during incubation. On Aldabra during incubation, the foraging probability was low and stable until 200 km from the colony, then increased continually above this threshold (Fig. 3b).

Although they were not the most parsimonious models, those with 2 covariates performed reasonably well, providing insight into how other environmental covariates can shape white-tailed tropicbirds' foraging distributions. On Aldabra, chl *a* concentration was a reasonable predictor of foraging activity during incubation (AUC = 0.7), although it did not improve model fit when added to distance from the nest. Foraging probability increased with chl *a* concentration until 0.2 mg m^{-3}, and then stayed relatively stable (Fig. S4). SST was a better predictor on Aride than on Aldabra, although the average value was broadly similar between the 2 areas (Table 3). On Aride, SST was also a reasonable predictor during both breeding stages (AUC$_{chick-rearing}$ = 0.74, AUC$_{incubation}$ = 0.72; Fig. S4). During chick-rearing, the foraging probability peaked between 28.5 and 29°C and was low at temperatures above and below these values. In contrast, during incubation, foraging probability decreased constantly with increasing SST but remained stable between 29 and 30°C.

4. DISCUSSION

Our results provide unprecedented insight into the foraging ecology of breeding white-tailed tropicbirds. They reveal their foraging movements and feeding habitat selection in the Indian Ocean, helping to fill the knowledge gap on the species' foraging ecology during breeding.
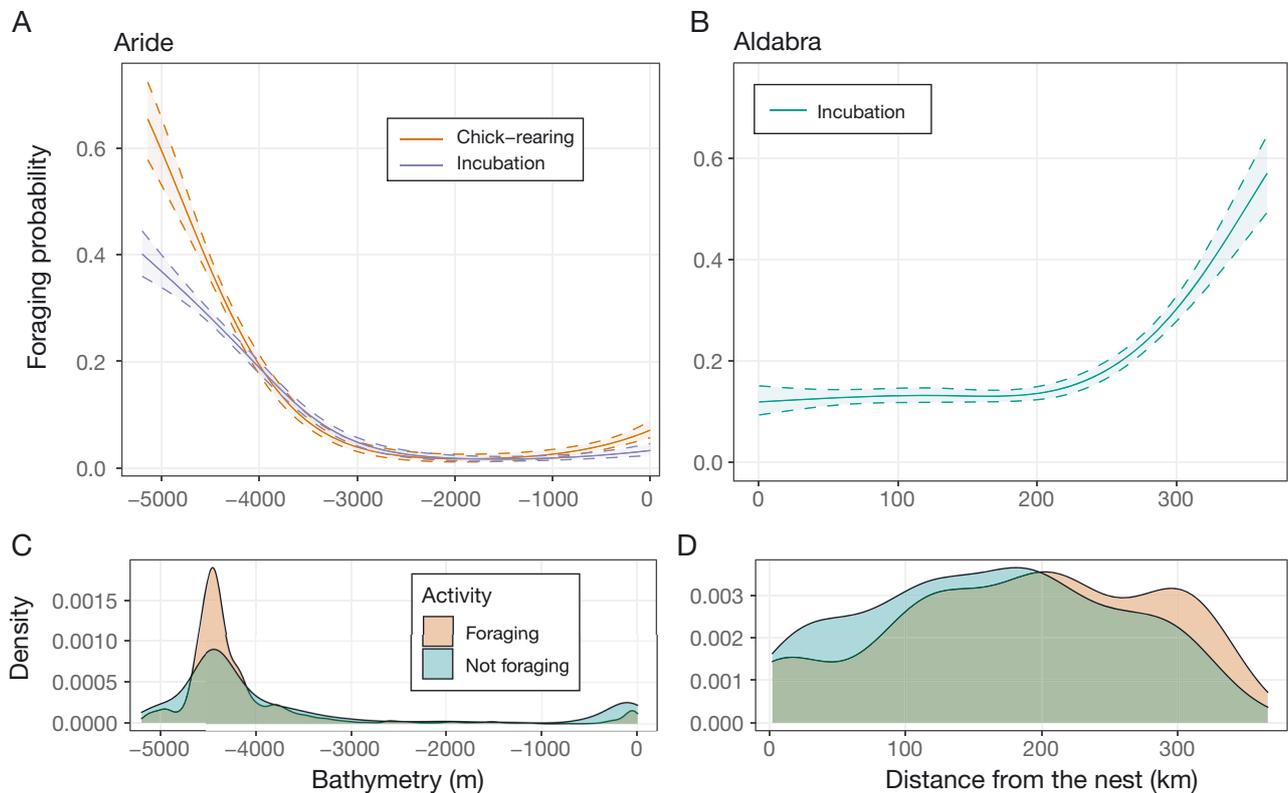
Fig. 3. Generalised additive model (GAM) smoother response curves for the best GAMs for (a) Aride and (b) Aldabra. Dashed lines and shaded areas represent the 95% confidence interval. Higher *y*-axis values mean there is a greater probability of the birds foraging for the given *x*-axis value of the covariate. (c,d) Density curves of foraging and non-foraging points for Aride (c) and Aldabra (d)

A key finding of our study was that breeding trop-icbirds foraged far from their colony. This was espe-cially the case during incubation, with foraging trips reaching, on average, 130 and 400 km, and up to 370 and 680 km, from Aldabra and Aride, respectively. These considerable foraging ranges are shorter than those of the larger red-billed tropicbird *Phaethon aethereus* in the eastern and mid-Atlantic Ocean (>680 km during incubation, ~400 km during chick-rearing; Diop et al. 2018), but comparable to red-billed tropicbirds in the Caribbean during chick-rear-ing (~117 km; Madden et al. 2023). Previous GPS tracking studies of breeding white-tailed tropicbirds tracked only chick-rearing birds, and reported an av-erage range of 25 km near the coast of Brazil on short (<24 h) trips (Campos et al. 2018), compared to 13 and 79 km on Aldabra and Aride (if using the same 24 h criterion), respectively. Although there may be addi-tional foraging areas that our sample size did not allow us to detect, the considerable foraging ranges in our study have implications for the species' conserva-tion in the Indian Ocean. Indeed, the birds foraged well beyond the no-fishing zones around their colonies (1 km around Aride, 25 km around Aldabra) and also far beyond the larger areas prohibited to for-eign fishing vessels (63 890.52 km^2 on the Seychelles plateau, 6970 km^2 around Aldabra). The foraging birds are therefore potentially exposed to industrial fisheries activity (see below). Some birds from both colonies even foraged beyond the Seychelles' Exclu-sive Economic Zone and therefore beyond Seychelles' jurisdiction. This is also the case for other seabirds breeding in the Seychelles, such as wedge-tailed shearwaters *Puffinus pacificus* (Catry et al. 2009c, Calabrese 2015), sooty terns *Onychoprion fuscatus* (Neumann et al. 2018), and great frigatebirds *Fregata minor* (Weimerskirch et al. 2010), and likely other species whose foraging movements have not yet been tracked. This highlights the need for international co-operation to protect important marine areas in inter-national waters such as the Marine Important Bird Areas initiative from BirdLife International (e.g. Las-celles et al. 2016).

Our results revealed substantial differences in for-aging behaviour between colonies. Foraging range was much greater on Aride than on Aldabra during both breeding stages. However, chick-rearing nests on Aldabra were skewed towards young chicks, due to high predation (Fayet et al. 2023). Chick-provisioning frequency in white-tailed tropicbirds remains largely constant for the first 60 d (Ramos & Pacheco 2003), so this age bias is unlikely to have caused the large differences in foraging range;

nevertheless it may partly explain the shorter trips on Aldabra during chick-rearing. While the birds' activity patterns throughout the day were similar between the 2 colonies, they were likely impacted by the different travelling distances. Indeed, birds from Aride spent less time foraging and more time commuting than those from Aldabra, although dif-ferences were small. This, and the greater foraging range of Aride birds, could lead to higher energy expenditure for birds foraging from Aride, and could negatively impact breeding productivity. This has been reported in other seabirds, either directly, via reduced provisioning frequency to chicks (e.g. Fayet et al. 2021) or indirectly, whereby longer foraging trips by one parent can lead to more short foraging trips by the other parent responsible for guarding the nest, increasing the likelihood of nest predation in the absence of the adults (Campos et al. 2018, Saunier et al. 2022, Fayet et al. 2023).

White-tailed tropicbird breeding success is sub-stantially lower on Aldabra than on Aride due to high nest predation (Burt et al. 2021), so we could not directly measure the effect of trip distance on repro-ductive success. Despite this higher breeding suc-cess, the population on Aride is decreasing, while it is stable on Aldabra (Burt et al. 2021). Assessing the survival of white-tailed tropicbirds across Seychelles' populations, and potential costs of greater foraging distance during breeding on adult survival and reproductive success, would help to understand the mechanisms behind the different demographic trends in the 2 regions. Additionally, white-tailed tropic-birds breed year-round, and our study covered only part of the year. Future research should therefore also focus on foraging distributions during the austral winter monsoon.

Our results also showed a clear difference in forag-ing distance between breeding stages, with shorter trips during chick-rearing than during incubation. This is common in many seabird species (Schreiber & Burger 2002), and confirms previous nest-based observations of trip durations of white-tailed trop-icbirds on Aldabra (Diamond 1975). It is worth noting that the incubation trip durations measured from our tracking data are likely an underestimate, due to some batteries failing en route, especially on the longer trips. Interestingly, nest observations during the study suggest that at both colonies, the average incubation trip duration has increased (8.6 ± 1.8 d on Aride vs. 6.6 d on neighbouring Cousin Island in 1985, Phillips 1987; and 6.3 ± 1.1 d on Aldabra vs. 3–6 d in the late 1960s; Diamond 1975) (see Text S5 for details on trip duration calculations).

We also found statistically significant sex differences in foraging range: males from both colonies went further from the colony and their trips lasted longer. While sex differences in foraging range are more common among sexually dimorphic seabirds (Cleasby et al. 2015, Austin et al. 2019), they do occur among monomorphic species (e.g. Elliott et al. 2010), potentially due to inter-sexual competition (one sex outcompeting the other) or differences in incubating or chick-provisioning behaviour (Peck & Congdon 2006). In white-tailed tropicbirds, this is the first time that sex differences have been observed with reliable sex determination, and they are worth further investigation. It would also be useful for future research to assess sex differences in diet and energetic constraints in white-tailed tropicbirds.

We initially aimed to investigate diet at both colonies via visual identification of regurgitates and DNA metabarcoding of faecal samples, but most samples did not yield sufficient DNA to represent the full range of prey diversity. Nevertheless, our findings (Text S6, Table S2) provide valuable insights, confirming that for both populations, flying fish (Exocoetidae; found in 6 of 15 samples) are a key prey item (Diamond 1975, Catry et al. 2009a) and revealing new prey species for white-tailed tropicbirds (e.g. undulated moray *Gymnothorax undulatus* on Aldabra, mackerel scad *Decapterus macarellus* on Aride).

Altogether, our results show clear differences in white-tailed tropicbird foraging behaviour between the inner and outer Seychelles. Our foraging habitat models suggest that this is due to differences in foraging conditions, mainly driven by water depth. On Aride, water depth was the main predictor of foraging probability, which greatly increased in waters deeper than 3200 m during both breeding stages. Aldabra's tropicbirds also foraged in similarly deep waters, but water depth was not a good predictor of foraging probability. This is likely because, being atop a seamount, shallow waters are restricted to the immediate vicinity of the atoll. This may have led our null distribution (of pseudo-foraging points randomly generated within each bird's range) to mostly contain points over deep water, making it more difficult for the model to detect a link between foraging and water depth. This preference for deep water could also partly explain the difference in foraging range between populations, as birds from Aride must travel beyond the edge of the Seychelles plateau to reach deep waters, a behaviour also seen in wedge-tailed shearwaters from Aride (Cecere et al. 2013) and sooty terns from Bird Island, Seychelles (Neumann et al. 2018).

Habitat preferences of tropicbirds are likely associated with the presence of their main prey types. For instance, tropical seabirds feeding on squid — an important prey for tropicbirds — also show preferences for waters with deep thermoclines (Vilchis et al. 2006), and some of the foraging areas used by tropicbirds from Aride overlap with areas known to be rich in cephalopods (through predator sampling; Potier et al. 2007). While our models suggest that water depth is an important environmental predictor of white-tailed tropicbird foraging distribution, the other associations we found with SST and chl *a* may also be related to prey availability. Tropicbird foraging probability peaked around SSTs of 29°C during chick-rearing on Aride, while during incubation on Aldabra, it increased with chl *a* concentrations only until 0.2 mg m^{-3} and then plateaued. One explanation for this could be the distribution of flying fish, which favour warm SST and high chl *a* concentration (Lewallen et al. 2018). An equilibrium between those 2 parameters may therefore generate the observed patterns of tropicbird foraging probabilities. Increased foraging probability with SST (but not chl *a*) was also found in white-tailed tropicbirds breeding in Brazil (Santos et al. 2019), suggesting that the warmer waters favoured by the birds are likely the best habitat for flying fish. Sea temperatures in the Western Indian Ocean are predicted to increase, while marine phytoplankton will likely continue to decrease (Roxy et al. 2020). Based on the narrow peak of preferred temperatures for tropicbirds on Aride, and the positive relationship between foraging probability and chl *a* on Aldabra, such changes would prove detrimental for the foraging habits of both populations. Drawing further links between tropicbird habitat selection and prey distribution will require a better understanding of the environmental preferences of their prey, which is currently patchy.

Human activity is another potential driver of the observed differences in foraging range between colonies, despite fishing effort not being an important predictor of foraging activity in our analysis. Tropical seabirds often associate with sub-surface predators, which bring schools of smaller fish closer to the surface (Ashmole & Ashmole 1967). White-tailed tropicbirds are known to do so (Spear & Ainley 2005), although less than other species (Jaquemet et al. 2004). In Seychelles waters, tuna also often feed on squid (Potier et al. 2007), thereby sharing a main prey type with tropicbirds. By reducing the number of sub-surface predators with which tropical seabirds may associate, fisheries can reduce foraging opportunities for seabirds (Le Corre & Jaquemet 2005,

Danckwerts et al. 2014). This is likely the case in the Indian Ocean (Feare et al. 2007, Weimerskirch et al. 2010), where tuna has been consistently overfished (Heidrich et al. 2023), and stocks have sharply declined (Nisar et al. 2021). In this study, the low predictive power of fishing effort might be due to our fishing effort data not representing tuna distribution accurately (e.g. see a similar result in frigatebirds in Weimerskirch et al. 2010); alternatively, the association between tropicbirds and tuna may not be strong enough to influence their distribution. Nevertheless, there are higher levels of industrial fishing effort in the foraging area of tropicbirds from Aride, which also hosts local fishing and tourist boats (activities not accounted for in the Global Fishing Watch dataset), while there is substantially less human activity around Aldabra. Except for birds taking short foraging trips on Aldabra, birds from both colonies also foraged well beyond the areas prohibited to industrial fishing vessels around the islands, and so may be impacted by such activities. Reducing tuna fishing quotas in Seychelles waters and in the wider region would not only help to avoid the collapse of the tuna stock, but also simultaneously benefit many seabird species.

5. CONCLUSION

Our study reveals the foraging distribution and habitat preference of white-tailed tropicbirds breeding in the 2 main groups of islands in the Seychelles, which host the largest population of the species in the Indian Ocean, providing novel insight into important marine areas for breeding seabirds in this region. The extensive foraging range of both populations highlights the limitations of current marine protected areas in protecting important feeding areas for seabirds. This is especially the case in the inner Seychelles, where the Aride white-tailed tropicbird population is in decline, and these birds are exposed to greater levels of industrial fishing in their foraging grounds, which could have indirect impacts on their ability to access prey. With tuna overfishing in the Western Indian Ocean over the last decades, better understanding the extent to which seabirds rely on sub-surface predators in this region would provide critical information on the impact of declining tuna stock on local seabirds and underpin recommendations towards industrial fishing quotas. Additionally, further tracking of tropicbirds and other sympatric species during other times of year (e.g. during the austral winter monsoon and non-breeding season) and in other life-stages (e.g. juveniles), and assessing

survival, will refine our understanding of how seabirds use different areas of the Western Indian Ocean and the threats they face at sea, which is much needed in the current context of global seabird declines.

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