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At-sea distribution and foraging tactics in a monomorphic tropical seabird

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Abstract

Seabirds are distributed widely over the world's oceans and have adopted a range of foraging tactics to secure food resources necessary for survival and reproduction. To better understand the foraging tactics and at-sea distribution of tropical seabirds, 38 Wedge-Tailed Shearwaters, *Ardenna pacifica* (WTS) from Réunion Island (21.375° S; 55.569° E) were tracked during 81 foraging trips using GPS loggers deployed over three breeding seasons (2016–2019). Clustering algorithms, kernel density estimation and habitat models were applied to this tracking dataset. During incubation, WTS foraged in the open ocean towards the southeast of Madagascar. During chick rearing, however, WTS restricted their distribution and implemented a dual foraging tactic, where they executed several short trips near the colony before performing a single long trip (> 200 km) in a similar south-westerly direction observed for incubating birds. Birds did not seem to show a strong preference for specific environmental conditions or habitat features and arguably cue on marine predators, conspecifics, or fish-aggregating devices to find productive foraging grounds. This study confirmed that WTS foraged in areas that have previously been identified as 'hotspots' for other marine species which are threatened by anthropogenic pressures; further highlighting that these areas are important from a conservation perspective.

Keywords Foraging tactics · Biologging · Wedge-tailed shearwater · Dual foraging · Habitat use · Conservation

Introduction

Biodiversity hotspots that support significant populations of charismatic and economically important marine top predators such as seabirds (Le Corre and Jaquemet 2005; Kappes et al. 2013), cetaceans (Balance and Pitman 1998; Anderson et al. 2006; Albouy et al. 2017) and predatory fishes (Worm et al. 2005; Reygondeau et al. 2012), including sharks (Queiroz et al. 2019), have previously been identified

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for the Indian Ocean. Information on the at-sea distribution of these marine top predators can aid in the identification of these ecologically important areas (Hindell et al. 2020). Once identified, knowledge of such areas can feed into conservation-based marine spatial planning initiatives, thereby potentially reducing threats that these animals are exposed to (Game et al. 2009; Le Corre et al. 2012; Hindell et al. 2020). Over and above the importance of knowledge on their at-sea spatial distribution, understanding an animal's foraging behaviour may also have significant conservation implications (Ludynia et al. 2010; Péron et al. 2013; Evens et al. 2017).

Seabirds are among the worlds' most threatened animal groups (Butchart et al. 2004; Croxall et al. 2012; Dias et al. 2019), and accordingly, insights about their foraging behaviour are important to manage and mitigate threats they face while at sea. The distribution and foraging behavior of seabirds is often governed by the distribution, abundance, mobility, and predictability of their prey (Bell 1991; Baduini and Hyrenbach 2003; McInnes et al. 2019). Consequently, they are often regarded as indicators of lower trophic level

productivity and environmental conditions (Furness and Camphuysen 1997; Einoder 2009; Dias et al. 2019).

During the breeding season, seabirds are central place foragers and must regularly commute between foraging zones and their colonies to incubate their eggs or feed their chicks (Weimerskirch 2007). Seabirds foraging in tropical areas are further constrained as these areas have characteristically low productivity with unpredictable prey resources (Ashmole 1971; Au and Pitman 1988; Jaquemet et al. 2004; Weimerskirch et al. 2007). To combat these constraints and to forage effectively in oceanic environments where food is often patchily distributed over different spatial scales (Weimerskirch 2007), a remarkable diversity of foraging tactics have emerged in different seabird species and populations, often enabled through efficient flight allowing long distance commutes in search of food (Ballance and Pitman 1999; Congdon et al. 2005; Catry et al. 2009; McDuie et al. 2015; Cerveira et al. 2020).

Seabirds may adopt several foraging tactics, including associating with subsurface marine top predators, including tuna, that drive epipelagic prey to the sea surface within reach of the seabirds making prey available to them (i.e., facilitated foraging; Au and Pitman 1988; Jaquemet et al. 2004; Miller et al. 2018a; McInnes and Pistorius 2019). A range of procellariform species, such as Blue Petrels *Halobaena caerulea* (Weimerskirch et al. 1994), Cory's Shearwaters *Calonectris borealis* (Magalhães et al. 2008), Short-tailed Shearwaters *Ardenna tenuirostris* (Weimerskirch and Cherel 1998), Wedge-tailed Shearwaters *Ardenna pacifica* (Congdon et al. 2005; Weimerskirch et al. 2020), Barau's Petrels *Pterodroma baraui* (Pinet et al. 2012), and Wandering Albatrosses *Diomedea exulans* (Weimerskirch et al. 1994) have, furthermore, been shown to implement a dual foraging tactic during chick rearing, where individuals alternate between several short foraging trips, to collect food for chicks, before leaving on a single long foraging trip, for self-maintenance. However, this tactic is likely to be colony specific and dependent on resource availability (Baduini 2002; Congdon et al. 2005; McDuie et al. 2015). Another common feature involves sex-specific foraging, which has been described in many seabird species, where differences are often associated with size-mediated competitive exclusion or habitat specialization (Lewis et al. 2005; Phillips et al. 2006; Gonzalez-Solis et al. 2007; Miller et al. 2018b; Austin et al. 2019; Clay et al. 2020; Orgeret et al. 2021).

We examined the foraging tactics of a tropical monomorphic seabird, the Wedge-Tailed Shearwater (WTS) from Réunion Island, where they breed synchronously during November and December. The WTS is a monomorphic, medium-sized burrowing petrel that have previously been shown to exhibit sex differences in at-sea spatial segregation (Catry et al. 2009) as well as differences in foraging behavior (Peck and Congdon 2005). In the tropics, where

colonies are surrounded by low productivity, breeding WTS have, furthermore, been shown to adopt a dual foraging tactic (Congdon et al. 2005; Pinet et al. 2012; Weimerskirch et al. 2020). However, in the sub-tropics, where areas of relatively high productivity may improve foraging success (e.g. in association with seamounts or mesoscale eddies which increase upwelling associated productivity), WTS tend to implement a unimodal foraging tactic (Baduini 2002; Peck and Congdon 2005; Bakun 2006; McDuie et al. 2018; Miller et al. 2018a). These foraging tactics are, however, flexible, and birds respond to different levels of resource availability (Miller et al. 2018a).

To investigate the foraging tactics exhibited by WTS breeding at Réunion Island, we tracked birds over three breeding seasons using miniaturised GPS loggers. We predicted that, during incubation, WTS would be more likely to forage in temporally persistent productive waters (Mannocci et al. 2014; Cerveira et al. 2020), for example along the East coast of Madagascar where seasonal coastal upwelling enhances primary productivity (i.e., positive sea surface height anomalies). We, furthermore, predicted that, like tropical WTS, during both incubation and chick rearing, individuals would implement sex-specific foraging behaviour (i.e., separate spatially and/or differ in foraging trip characteristics). We lastly predicted that during chick-rearing WTS would restrict their foraging range and adopt a dual foraging tactic, where adults make several short trips near the colony to provision for the chicks and a single long trip towards more productive seamounts or areas of mesoscale activity for self-provisioning (Weimerskirch et al. 2020).

Materials and methods

Study area and data collection

This study was conducted over three consecutive breeding seasons of the WTS at Grande Anse, Réunion Island (21° 22′ 30″ S; 55° 34′ 07″ E) from the 2016/17 to 2018/19 breeding seasons. Adult WTS start arriving at Grande Anse in late August and synchronously start breeding in November with the chicks hatching in January and fledging in April and May.

GPS loggers (CatTraQ2™ GPS, Catnip Technologies, USA and Axy-3™ loggers, TechnoSmArt, Italy) were deployed on adult birds during incubation and chick rearing (see Online resource Table S1). Loggers were attached to the WTS's tail feathers using 1–2 g TESA® tape (Beiersdorf AG, Germany). During the incubation period, adults that were confirmed incubating an egg were carefully removed from their burrows and equipped with loggers. These loggers were set to start recording after 2–4 days to avoid wasting battery life, while the birds were still in the burrow. During

chick rearing, adult WTS return at night, feed their chicks, and leave their burrows shortly thereafter. Thus, burrows were monitored between 18:00 and 06:00 to locate and equip chick-rearing birds. Once an adult had finished feeding its chick and started exiting the burrow, it was caught and equipped with a logger that was turned on immediately. On average, loggers (including the total weight of waterproof casing and Tessa® tape) represented $2.7 \pm 0.3\%$ of the body weight of tracked WTS (375 ± 46 g) and is unlikely to have influenced their at-sea foraging behaviour (Phillips et al. 2003). On retrieval, approximately five breast feather samples were plucked for molecular sexing. Average handling time was approximately 8 min.

Molecular sexing

Birds were sexed using molecular techniques using the feather tip extraction method described in (Rishworth et al. 2014); adapted from (Ellegren 1992). In some cases, no feathers were sampled in which case sex could not be established (full methods described in the Online Resource 1).

GPS data preparation

The preparation and analysis of GPS data were performed using R version 3.6.1 (R Core Team 2019). All erroneous GPS locations (speed threshold > 60 km.h^{-1}; Cleeland et al. 2014) were filtered ('speedfilter' in the package trip; McConnell et al. 1992). To deal with different fix rates and positional gaps within the tracks, filtered data were processed using a continuous time-correlated random walk model to estimate movement parameters (crawl package; Johnson et al. 2008). Locations from the foraging tracks were interpolated to 30 min intervals (crawl package; Johnson et al. 2008), except for where there were large gaps in the tracks (> 2 h). As per (Weimerskirch et al. 2020), locations within a 2 km radius around the colony were removed to exclude potential rafting or circling behaviour near the colony. The following trip parameters were calculated using the adehabitatLT package (Calenge 2006): average travel speed (km.h^{-1}), maximum foraging range from the colony (greatest distance reached at sea from the last known point on land; km), trip duration (time difference between the last point on land to the first point on land after a foraging trip (days), and total distance travelled per day (total trip length/duration; km.d^{-1}). Total trip length (sum of distances between all the interpolated points; km) was also estimated but limited to complete trips.

Many tracks started or ended at sea and were incomplete due to the delayed start of the GPS devices or battery failure, respectively (Online Resource 2 Table S2). Trip duration and maximum distance from the colony for incomplete foraging trips were calculated for birds that were clearly returning to the colony. For trip duration, known departure and arrival dates were used. For the maximum distance from the colony, a threshold of 22 km was used as the minimum distance birds needed to have travelled from the colony to estimate the parameter. The threshold was selected as it was the observed minimum travelled distance for a complete foraging trip. Thus, where birds were clearly returning to the colony and if the device stopped recording, the maximum distance and trip duration could still be calculated.

Data analyses

Due to low sample sizes for 2017/18 ($n = 2$) and 2018/19 ($n = 4$), the effect of year on trip metrics were not investigated and foraging trips for the three breeding seasons were pooled for data analysis. During chick rearing, all foraging trips were classified as either short (≤ 4d) or long (> 4d) foraging trips. This classification was based on a Ward Hierarchical clustering approach which was used to identify groups based on foraging trip duration and maximum distance travelled (Online Resource 2 Fig. S3) and the frequency distribution for trip durations (see Results; Congdon et al. 2005; Weimerskirch et al. 2020). Differences in foraging trip parameters between sexes and breeding stages, as well as between long and short trips (Congdon et al. 2005) during early chick rearing, were tested using Linear Mixed Models (LMM) with Gaussian distribution of error terms, using an Identity link function (package lme4; Bates et al. 2015). Since several trips were made per individual, unique individual 'ID' was added as a random effect for all models. The LMM residuals normality and homogeneity were visually assessed, and trip parameters log transformed where needed. Outliers in maximum foraging range and trip duration resulted in a deviation of model assumptions; however, their removal had no influence on the study results.

To identify important areas utilized by WTS, the spatial distribution of WTS was estimated by producing core areas and home range kernel utilization distributions (50% UD and 90% UD, respectively; Worton 1989) for each individual, using kernel analysis with a grid of $0.1 \times 0.1°$ cells. An averaged smoothing parameter for each breeding stage was estimated using 'href' method (adehabitatHR package; Calenge 2006). As per Lascelles et al. (2016), to determine whether our sample size was representative of the population breeding on Réunion Island, we used saturation curves based on the 50% UD and 90% UD.

Overlaps of core areas and home ranges utilized by different sexes over different breeding stages were calculated using Bhattacharyya's affinity (BA; Fieberg and Kochanny 2005) using kernel analysis (adehabitatHR package; Calenge 2006). The extent of overlap between sexes during different breeding stages ranged from 0 (no overlap) to 1 (complete

overlap). To test if there was a difference in the spatial distribution utilized by the male and female WTS within different breeding stages, a randomization technique was used, using BA as a measure of spatial overlap. The randomization procedure was used to test the null hypothesis that there were no differences between sexes within different stages (Cleasby et al. 2015; full details in Online Resource 1).

Multiple trips were recorded from several individual birds during chick rearing (Online Resource 2 Table S2) which may exhibit pseudo-replication that could bias results of kernels (Augé et al. 2013). We tested for pseudo-replication using methods following (Lascelles et al. 2016). The significance threshold was set at $\alpha = 0.1$. During incubation, only one bird completed multiple trips and site fidelity was assessed by visually inspecting the trips.

Behaviour classification

Behaviours from GPS tracks were inferred using the expectation–maximization binary clustering ('EMbC' in the package EMbC; Garriga et al. 2016). To avoid incorrect labeling of behavioral states, the built-in post-smoothing function was applied. The algorithm classified four movement types based on travel speed and the turning angle between subsequent locations. This was based on the assumption that foraging can be identified by area restricted search (ARS) behaviours, where birds make wide turning angles between locations, and that travel/commuting movements are associated with fast and straight stints (Garriga et al. 2016). Behaviour labels were accordingly assigned to the movement clusters and included: intensive searching (low velocity/high turning angle), extensive searching (high velocity/high turning angle), travelling/commuting (high velocity/low turning angle), and resting (low velocity/low turning angle; Clay et al. 2019). Online Resource 2 Fig. S1 shows a visualization of the movement behaviours for an individual foraging trip.

A Generalized Linear Model (GLM) using a binomial error distribution was used to calculate differences between the proportion of time WTS spent adopting various behaviours (i.e., commuting, resting, intensive search and extensive search behavior) during incubation and chick rearing. The same was done for long and short trips during the early chick rearing period. Post-hoc pairwise comparisons were made using least square means (emmeans; Lenth and Lenth 2018), following the Bonferroni method (Bretz et al. 2016) to identify differences in behaviours.

Environmental variables and habitat modelling

Bathymetry (m) was extracted at each fix from the NOAA ETOPO1, 1 arc-minute global relief model (in the package marmap; Pante and Simon-Bouhet 2013). The bathymetric gradient (°) was estimated by calculating the slope from the bathymetry variables ('terrain' in the raster package). The remaining environmental variables were downloaded from E.U. Copernicus Marine Service Information (http://marine.copernicus.eu/) and data extracted coincided with the dates of the GPS deployments. Chlorophyll a concentration (CHLA, mg.m^{-3}) was extracted as an indicator of productivity and may indirectly influence seabird distributions (Serratosa et al. 2020) and reproductive success (Monticelli et al. 2007). CHLA concentrations were downloaded in weekly time and 1/2° spatial resolutions from the Global Ocean biochemical analysis and forecast product (BIO 001–014). Sea surface temperature (SST, °C) can influence the composition of the plankton community and structure of the food web (Furness 2016), thus impacting the birds' prey availability (Furness 2016). SST was downloaded at a daily time and 1/12° spatial resolution from the Global Ocean physics and forecast product (PHY 001–024). Mixed layer depth (MLD, m) and the sea surface height (SSH, m) were downloaded at weekly time intervals and 1/4° spatial resolution from the Multi Observation Global Ocean product (MULTIOBS_GLO_PHY_TSUV_3D_MYNRT_015_012). The MLD also influences primary productivity and can affect the timing of phytoplankton blooms (Behrenfeld 2010). Sea surface height anomalies (SSHA) were computed by calculating the difference between the average SSH and the average monthly values for the corresponding period (i.e., 2016–2019). Mesoscale eddies enhance primary productivity and nutrient supply (Bakun 1996; Dufois et al. 2016) in otherwise relatively unproductive tropical ocean basins (Weimerskirch 2007). Anticyclonic mesoscale eddies (denoted by positive SSHA) have a convergent surface water flow in their center; however, the outer edges are often associated with upwelling and divergent zones (Bakun 1996). Cyclonic mesoscale eddies (denoted by negative SSHA) have a divergent surface water flow which brings up deep, nutrient-rich waters to the surface, and can enhance primary productivity (Monticelli et al. 2007). Mesoscale eddies have been shown to be favoured foraging areas for tropical seabirds (Weimerskirch et al. 2004; Jaquemet et al. 2014) and tuna (Weimerskirch et al. 2010b).

To account for non-linear relationships, Generalized Additive Mixed Models (GAMMs, Wood 2017) were used to assess how movement behaviour (foraging vs traveling, response variables) varied in accordance with environmental variables (covariates) within each breeding stage. To simplify the models, individual GAMMs were built for each breeding stage and were analysed separately. Initially, sex was added as an interaction term; however, sex did not have an effect and was thus excluded from the remaining models. Intensive search behaviours were representative of small scale ARS (Weimerskirch 2007; Weimerskirch et al. 2020) and were considered as active foraging behaviour.

GAMMs were fitted using a binomial error distribution with a logit link function where foraging and traveling (i.e., commuting and exploring behavior, estimated by EMbC, see above) were set as a binary response (1 and 0, respectively; Orgeret et al. 2019). WTS forage mostly during the day and spend less time resting during the day as compared to night (Weimerskirch et al. 2020). Consequently, resting behaviour was associated with behaviours where the birds were actually resting on the sea surface and not foraging and, therefore, excluded from the analysis. Environmental variables were smoothed with cubic regression splines to avoid overfitting the models and bird ID was added as random effect (package mgcv; Wood 2017). To deal with spatial inherent structure in the tracking dataset, longitude and latitude were included as a covariate as smoothed interaction terms (Dormann 2007). Covariates were not significantly correlated (Pearson's $r < |0.7|$, see Online Resource 2 Fig S11; Dormann et al. 2013) and were all thus included in the models. CHLA concentrations were log transformed and the bathymetric gradient was square root transformed. Model selection was implemented using Akaike Information Criteria (Wood 2017) corrected for small samples sizes (AICc; 'dredge' in the package MuMIn) to identify the most parsimonious models (ΔAICc ≤ 2; Burnham and Anderson 2003) and only environmental variables that significantly improved the model were retained. The deviance explained (DE) was used to assess the explanatory power of the best fitting model. Using the same methods discussed above, individual GAMMs were used for both long and short trips during chick rearing to assess how movement behaviour varied in accordance with the environment variables.

All values are reported as mean $\pm$ standard deviation (SD) unless otherwise stated, and significance levels were at $\alpha = 0.05$.

Results

Foraging trip parameters

Foraging trips from 23 incubating (27 trips) and 15 chick-rearing (54 trips) birds were analysed (Fig. 1, Online Resource 2 Table S2.). During incubation, birds dispersed significantly further from the colony (incubation: 469 ± 342 km, $n = 27$; chick rearing: 94 ± 94 km, $n = 54$; $t_{(18)} = 3.474$, $P = 0.003$), covering greater distances (incubation: 1584 ± 1195 km, $n = 14$; chick rearing: 277 ± 409 km, $n = 44$; $t_{(18)} = 3.286$, $P = 0.004$, Fig. 2) and had much longer foraging trips (incubation: 10 ± 7 d, $n = 27$; chick rearing: 2 ± 3 d, $n = 54$; $t_{(18)} = 3.491$, $P = 0.003$) than during chick rearing. Breeding stage did not have a significant effect on the distance travelled per day (incubation: 159 ± 51 km.
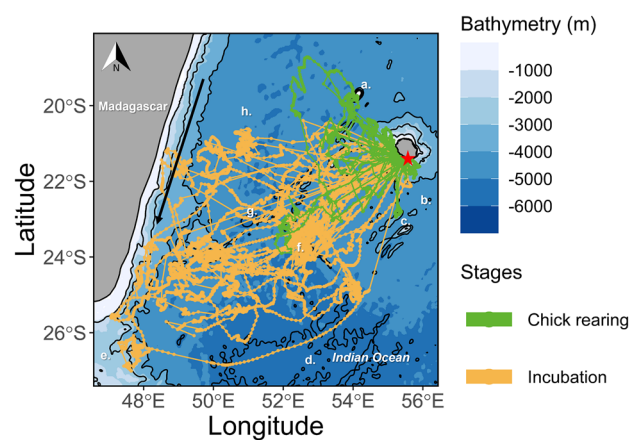

Fig. 1 Map of the at-sea distribution of incubating (yellow tracks, $n = 27$) and chick rearing (green tracks, $n = 52$) Wedge-Tailed Shearwaters *Ardenna pacifica* from Réunion Island (red star) using all complete and incomplete tracks. Principal oceanographic and geomorphological features are indicated by the **a** the Pérouse seamount, **b** Bourdonnais ridge, **c** Mauritius trench, **d** Madagascar basin, **e** Madagascar plateau, **f** Réunion trench, **g** Wilshaw ridge, and the **h** Mascarene basin. The arrow indicates the direction of the east Madagascar current
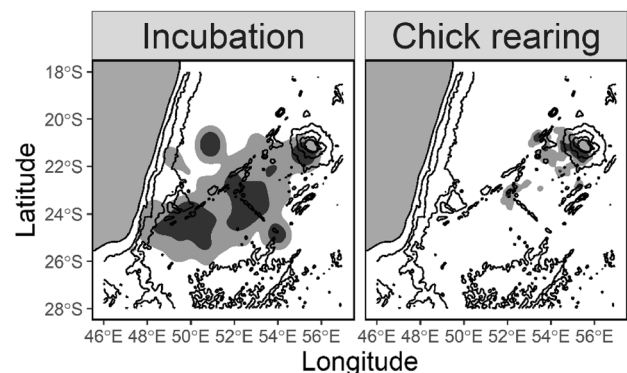

Fig. 2 Core areas (dark grey; 50% utilization distribution contours) and home range (light grey; 90% utilization distribution contours) for incubating (birds $n = 23$, trips $n = 24$) and chick rearing (birds $n = 15$, trips $n = 35$) Wedge-Tailed Shearwaters breeding at Grande Anse, Réunion Island

d^{-1}, $n = 27$; chick rearing: 173 ± 60 km.d^{-1}, $n = 54$; $t_{(32)} = -0.922$, $P = 0.363$) or average travel speed (incubation: 7.6 ± 1.8 km.h^{-1}, $n = 27$; chick rearing: 7.2 ± 2.7 km.h^{-1}, $n = 54$; $t_{(32)} = 0.332$, $P = 0.742$). Sex did not significantly influence any of the trip parameters during incubation or chick rearing ($P > 0.05$, Table 1, Online Resource 2 Table S3).

During chick rearing, the frequency distribution of the foraging trip duration (Fig. 3) was typical of a dual foraging tactic where both sexes made several short trips (1 ± 1 d, $n = 49$) within 19–198 km (68 ± 40 km) of the colony before/after executing a single long trip (9 ± 3 d, $n = 5$) up

Table 1 Foraging trip parameters of male (M) and female (F) Wedge-Tailed Shearwaters (mean $\pm$ SD) breeding on Réunion Island

Sex	Bird (Trips)	Maximum distance (km)	Trip length (km)	Trip duration (d)	Distance travelled (km.d^{-1})	Travel speed (km.h^{-1})
Incubation						
M	5 (5)	488.10 ± 410.70	1517.00 ± 1310.00	8.69 ± 7.54	171.03 ± 32.23	7.24 ± 1.33
F	10 (14)	445.70 ± 392.30	1408.00 ± 1293.00	8.34 ± 7.30	160.12 ± 46.89	7.24 ± 1.94
Chick rearing						
M	6 (24)	112.30 ± 112.40	345.10 ± 520.00	1.97 ± 3.38	197.53 ± 62.00	8.42 ± 2.84
F	4 (24)	88.45 ± 81.00	253.30 ± 316.90	1.54 ± 1.82	163.38 ± 52.95	6.95 ± 2.27
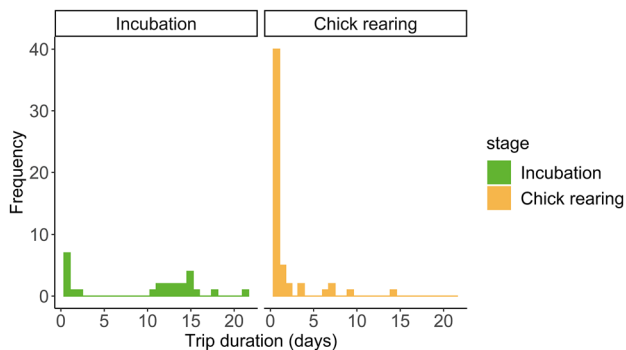
Fig. 3 Frequency distribution of the trip duration (days) for all the foraging trips of Wedge-Tailed Shearwaters during incubation (2016/17–2018/19 breeding seasons) and chick rearing (2016/17 breeding season)
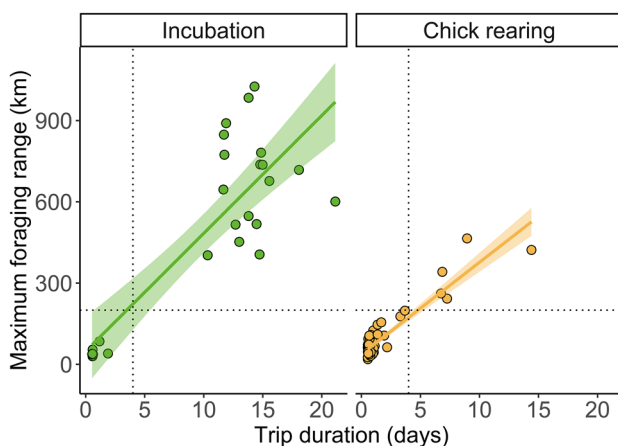
Fig. 4 Relationship between the duration (days) of foraging trips and maximum foraging range during incubating (green; $y = 43.537x + 48.258$, $R^2 = 0.73$, $n = 27$) and chick rearing (yellow; $y = 33.925x + 37.41$, $R^2 = 0.85$, $n = 54$) Wedge-Tailed Shearwaters from Réunion Island. The dashed line separates short (≤ 4 d) and long (> 4 d) foraging trips

to 465 km (347 ± 97 km) from the colony (Figs. 3 and 4, Online Resource 2 Fig. S1). This behaviour was identified in five birds, and six birds only performed multiple (3–9) short trips. There were no consecutive long trips recorded and all long trips extended past the 4000 m isobath. Trip duration was strongly correlated with the maximum foraging distance (Fig. 4).

At-sea distribution and behaviour

The representative analysis indicated that the main foraging areas of the entire WTS population were captured. Core foraging areas during incubation (UD 50% = 72.4%) and chick rearing (UD 50% = 78.8%) had a relatively high representative index (Online Resource 2 Fig. S11). Home ranges during both breeding stages (UD 90% = 85.5% and 93.3% for incubation and chick rearing, respectively) were highly representative of the whole population (Online Resource 2 Fig. S11).

During the incubation period, the foraging areas (Figs. 1 and 2) were in a southwest to westerly direction of the colony and WTS mainly foraged in deep waters (> 1745 m deep) and dispersed as far as the edge of the continental shelf of Madagascar in the South–East Madagascar Current (SEMC) and near the Madagascar plateau (Fig. 1). Core areas were identified near the island as well as areas dispersed in the open ocean near the Réunion and Mauritius trench and along the Wilshaw ridge (Fig. 2), over deep, pelagic waters. During the chick rearing period, home ranges were restricted to areas south–southeast to northwest of the colony and extended eastwards into the Mascarene Basin towards the Wishaw Ridge and south near the Bourdonnais Ridge (Fig. 2). Core areas were predominantly found in nearby waters surrounding Réunion near the colony in relatively shallower water (> 720 m depth, Fig. 2). The overlap of core areas and home ranges between different sexes (Online Resource 2 Fig. S7) was not significantly lower than the null expectation during incubation and chick rearing ($P > 0.1$).

Within foraging trips, WTS implemented typical area restricted search (ARS) behaviours where birds rapidly
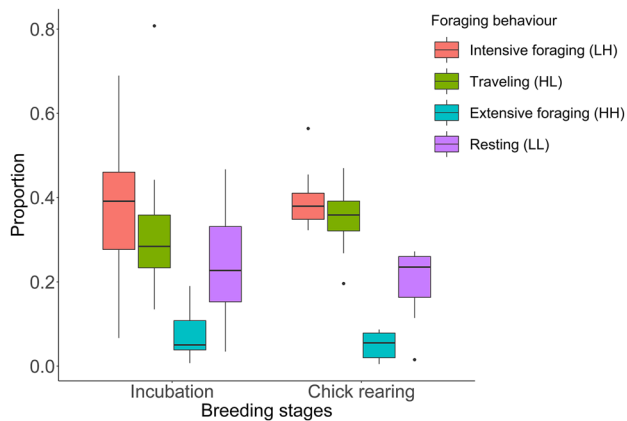
Fig. 5 Proportion of at-sea behaviours that were identified and classified for each individual Wedge-Tailed Shearwater tracked from Réunion Island during the incubation and chick rearing period

changed their direction and slowed their movement speed, throughout commuting sections (Online Resource 2 Fig. S5). During incubation, WTS spent significantly more time engaging in intensive (incubation: $40 \pm 14\%$, chick rearing: $40 \pm 7\%$) and extensive searching behaviour (incubation: $8 \pm 5\%$, chick rearing: $6 \pm 3\%$) than during chick rearing (Fig. 5).

In terms of habitat use, selected models did not include the bathymetric gradient for both breeding stages and SST for chick rearing (Online Resource 2 Table S4 and S5). Overall, models had a low explanatory power, both for incubation (DE = 6.03%, Fig. 6) and chick rearing (DE = 7.41%, Fig. 6). Nevertheless, during incubation, WTS were more likely to forage in deep waters (> 1000 m), and foraging probability decreased with increasing CHLA concentrations and SST. During chick rearing, WTS foraging probability was higher in both relatively deep and shallow waters, areas associated with positive SSHA, MLD, and a overall increase in foraging probability with an increase in CHLA concentrations.

For the dual foraging trips during chick rearing, models for long trips did not feature SST and the bathymetric gradient, and for short trips SSHA were not included (Online Resource 2 Fig. S12, Table S4 and S5). The environmental variables also showed a low explanatory power when predicting the foraging probability between foraging areas selected for long (DE = 13.4%) and short trips (DE = 11.4%). During chick rearing, long foraging trips were associated with relatively deeper waters than short trips and birds foraged over areas with a positive SSHA. Foraging probability for both long and short trips fluctuated with increasing CHLA concentrations and was highest at relatively deep MLD. During short trips, the foraging probability decreased in areas with both relatively low and high SST, and steep slopes.

Discussion

This study is the first to look at the fine scale foraging distribution of WTS breeding on Réunion Island. We aimed to identify different foraging tactics adopted by WTS and identify important foraging areas during the breeding period. We found that there were no differences between the spatial distribution, or foraging trip parameters between sexes. Furthermore, during chick rearing, both sexes implemented a dual foraging tactic with 3–9 short foraging trips (≤ 4 d) followed by one longer foraging trip (> 4 d). To understand mechanisms driving the selection of important foraging areas, we, furthermore, assessed environmental variables associated with their foraging behaviour. Despite foraging behaviours only being weakly influenced by environmental variables, during incubation, within all three breeding seasons, WTS consistently foraged southwest of the breeding colony towards the southeast of Madagascar and during chick rearing individuals implemented multiple foraging trips near the colony.

Seasonal fluctuations in local oceanography strongly influence food availability in temperate and polar regions (Thorne and Read 2013; Weimerskirch 2007), thus these regions are thought to be more persistent and foraging behaviour is often closely associated with specific environmental conditions (Dehnhard et al. 2020; Robertson et al. 2014). However, in the tropics, where there is limited seasonal variation and generally a lower predictability of prey resources, relatively low productivity and homogenous environments compared to higher latitudes, there seems to be less selection for particular environmental features by seabirds (Ashmole 1971; Au and Pitman 1986, 1988; Weimerskirch 2007; Mannocci et al. 2014). In the tropics, foraging locations are often more closely associated with the distance from the colony and more persistent oceanographic features that are reoccurring (Mannocci et al. 2014; Cerveira et al. 2020).

During incubation, WTS spent significantly more time at sea and foraged further from the colony than during chick rearing. Birds foraged up to the SEMC during incubation which is also an important foraging area for several other seabird species (Pinet et al. 2012; Mannocci et al. 2014). Their at-sea distribution was consistent with previous studies in the tropics where WTS have been shown to typically forage over deep waters (Catry et al. 2009; Miller et al. 2018a; Weimerskirch et al. 2020), in the open ocean and/or on the south–southwest of Réunion Island nearing 28°S, and near Madagascar (Bailey 1968; Jaquemet et al. 2004; Le Corre et al. 2012). Moreover, during incubation, WTS foraged where the annual summer phytoplankton blooms occurs along the southeast of Madagascar (Longhurst 2001; Raj et al. 2010) and within the SEMC which has a high

Fig. 6 Response curves for generalized additive mixed models (GAMM) of the probability of incubating (deviance explained = 6.03%) and chick rearing (deviance explained = 7.41%) Wedge-Tailed Shearwaters foraging according to environmental variables. Chlorophyll *a* concentrations (CHLA) were log transformed. The red line indicates when foraging and non-foraging events are equally likely to occur
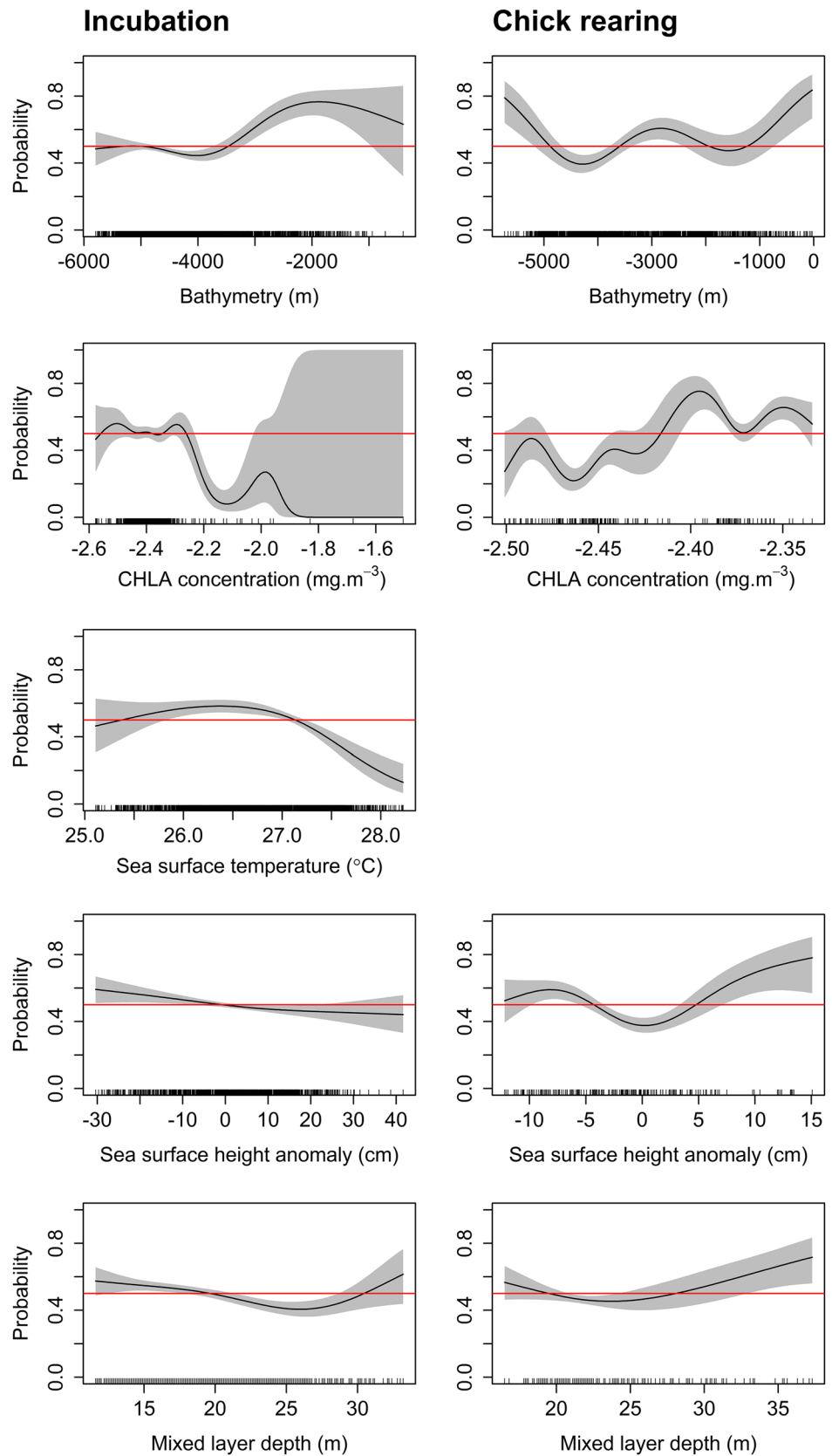
surface CHLA based enrichment index (Demarcq et al. 2020). Changes in the timing and intensity of phytoplankton blooms have been shown to impact tropical seabirds' phenology and reproductive productivity, indicating that they may be indirectly impacted by seasonal variability in primary productivity (Monticelli et al. 2007). It is possible that the WTS synchronise their breeding period when annual primary productivity is relatively high, more persistent, and localized (Mannocci et al. 2014), allowing them to meet the high energetic requirements of breeding. This pattern has been described for other seabird species in the tropical western Indian Ocean (Jaquemet et al. 2007; Pinet et al. 2012; Soanes et al. 2021). Thus, this distant site should provide some advantage (e.g. potential energy gain) to overcome the increased energy expenditure (Weimerskirch and Cherel 1998). Subsequently, these sites are potentially areas of high and/or reliable prey availability for birds to maintain long-term reproductive success (McDuie et al. 2015). However, similar to other tropical WTS populations in the Indian Ocean (Catry et al. 2009), Pacific Ocean (McDuie et al. 2015; Weimerskirch et al. 2020), and Coral Sea (Miller et al. 2018a) birds foraged in oligotrophic (Catry et al. 2009; McDuie et al. 2015; Weimerskirch et al. 2020) waters and CHLA concentration showed very little variation over the WTS foraging range (0.08–0.14 mg.m^{-3}) and it did not have a strong influence on localised foraging probability (Online Resource 2 Fig. S12). The lack of any clear relationship between foraging areas of WTS and CHLA concentrations may be a result of a mismatch between primary production and prey (Grémillet et al. 2008) or where changes in higher trophic level biomass responses to changes in primary productivity may lag over weeks–months (Hayward and Venrick 1998). It may thus be more effective to use longer time-series data on CHLA concentrations (as opposed or fine-temporal scale measurements used in this study) to estimate the distribution of productive areas and how they are utilised by foraging seabirds (Suryan et al. 2012).

Moreover, the continuous use of foraging areas south–southwest of the breeding colony during incubation may be to avoid intraspecific competition with breeding WTS from Round Island, Mauritius, which is home to the largest population (33.9%) of WTS in the Western Indian Ocean (MWF & NPCSM 2008 in Kappes et al. 2013). Round Island is approximately 280 km away from Réunion, within a range that would allow overlap between foraging birds from the two colonies. Some WTS also foraged very close to the island and performed short trips (< 2 d). However, it should be noted that of the five individuals that performed short trips, four implemented a single short trip near the end of the incubation period, a few days before/on the day the chick hatched. Short trips during this period may have thus been initiated to ensure that the newly hatched chick was fed and is potentially not indicative of a typical dual foraging tactic.

During the chick rearing period, WTS reduced their foraging range and spent more time commuting than during the incubation period. This was likely to regularly provision the chicks to meet their high energetic demands (Ricklefs 1983) and is consistent with results from other central place foragers (Fernández et al. 2001; Phillips et al. 2006; Pinet et al. 2012). Furthermore, foraging locations during chick rearing near the colony were associated with shallow shelf regions (< 200 m) which are low in productivity (Online Resource 2 Fig. 6) and WTS' core areas were concentrated near the breeding colony which is also important to other seabirds breeding on Réunion Island (Jaquemet et al. 2004; Pinet et al. 2012). This has been identified as a biodiversity hotspot for marine species (Bourmaud et al. 2005), making it an important area for marine life from Réunion for conservation-based management. The ecological importance of the southwestern coastal waters has been recognized, and in 2007 a Nation Marine Reserve was established. However, these coastal areas are under threat from anthropogenic pressures (Magnan and Duvat 2018; Bigot et al. 2019) including unstainable fisheries activities, reef resource overexploitation and increased pollution levels (Bigot et al. 2019).

During chick rearing, some WTS exhibited a dual foraging tactic with a clear separation between short-trips (≤ 4 d) which were near the colony (< 200 km), and long-trips (> 4 d) that were in distant offshore waters (> 200 km). These distances and durations are comparable with other WTS populations (Congdon et al. 2005; McDuie et al. 2015; Weimerskirch et al. 2020). Generally, short trips are thought to allow birds to increase the frequency at which the adults can feed the chicks, at the cost of their own body condition, whereas long trips would be more associated with building up of body reserves (Weimerskirch et al. 1994). WTS foraging probability during short trips were associated with relatively shallow nearshore waters and deep MLD (~ 17 M). Unlike WTS in the Pacific Ocean (Weimerskirch et al. 2020), it is unlikely that the dual foraging tactic is implemented as a result of intra-specific competition due to low population sizes of WTS breeding on Réunion Island (900 pairs; Faulquier et al. 2017). Within long trips, WTS travelled to distant areas and foraged either westwards into the Mascarene Basin, or southwest towards the deep-ocean Wilshaw Ridge. During these foraging trips, WTS foraged in deeper waters, over areas with steeper slopes and were associated with mesoscale anticyclonic eddies which possibly make prey available to WTS and other subsurface predators (Weimerskirch et al. 2010b). Enhancement of prey availability may enable WTS to potentially forage more successfully and build their body reserves (Pereira et al. 2020) during long trips. Furthermore, WTS from Réunion are known to associate with sub-surface predators, especially tuna (Jaquemet

et al. 2004) which associate with mesoscale eddies (Kai and Marsac 2010). WTS may opportunistically forage in areas known to have higher tuna abundance (Miller et al. 2018a, b); such as the mesoscale eddies or near fish aggregating devices (FADs) close to the colony (Jaquemet et al. 2004). During the breeding period, WTS were observed arriving and leaving the colony in large groups and after feeding the chick adults would often sit near other birds before leaving the colony. Here the colony may act as an information-center where information about prey availability may be shared at the colony (Ward and Zahavi 1973; Weimerskirch et al. 2010a). Though further investigation would be necessary to identify social foraging in WTS, they are often observed as the dominant species in multispecies flocks (Jaquemet et al. 2004) suggesting that they may positively associate with conspecifics to locate foraging areas.

In contrast to previous studies on WTS in temperate regions (Peck and Congdon 2006) or elsewhere in the tropical western Indian Ocean (Catry et al. 2009), WTS from Réunion did not show any substantial spatial segregation or differences in foraging behaviour between sexes during the breeding period. It is possible that sex specific foraging in WTS may vary temporally (Deakin et al. 2019), depend on the environmental conditions (Paiva et al. 2017), or it may also depend on the size of the breeding population which largely influences the amount of competition during the breeding period (Lewis et al. 2001). However, to improve the ability to detect sexual segregation, the sample size for males and females should be increased and further monitoring will be required to make robust conclusions for the WTS population on Réunion.

Conclusions

This study demonstrated the importance of the area to the southwest of Réunion Island, as well as parts of the South West Indian Ocean near the EMC, as important foraging grounds for breeding WTS. The WTS consistently foraged southeast to northwest of the breeding colony, but foraging locations were only weakly associated with environmental variables, potentially a function of the limited environmental variability within these tropical waters. Consequently, WTS may rely more on other marine top predators and possibly other environmental or "human-related" factors such as FADs not tested in this study to locate foraging areas. WTS implemented a dual foraging tactic and long trips were associated with anti-cyclonic eddies, which may enhance prey availability. In addition, distant foraging locations coincided with hotspots for other tropical seabirds in the western Indian Ocean which have previously been identified as areas that are threatened by anthropogenic pressures such as industrial longline fisheries and maritime pollution (Le Corre et al. 2012); further highlighting these areas as being important for conservation-based management.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Handling, banding and equipping birds with telemetry devices was done under the authorization provided by the Bird Population Biology Research Center (CRBPO, PP 609 leaded by Matthieu Le Corre). The authorization to work at Grande Anse protected area was given by Conservatoire du Littoral Antenne Océan Indien and all procedures performed were in accordance with the ethical standards of Nelson Mandela Metropolitan University (permit number: A16-SCI-ZOO-013) and with the Ethic Committee of Réunion Island.

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