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Seasonal shifts in foraging distribution due to individual flexibility in a tropical pelagic forager, the Ascension frigatebird

Steffen Oppel[1,*], Sam Weber[2,3], Nicola Weber[2,3], Derren Fox[2], Eliza Leat[2], Jolene Sim[2], Julia Sommerfeld[1,4], Mark Bolton[1], Annette C. Broderick[3], Brendan J. Godley[3]

[1]RSPB Centre for Conservation Science, Royal Society for the Protection of Birds, The David Attenborough Building, Pembroke Street, Cambridge CB2 3QZ, UK

[2]Ascension Island Government Conservation Department, Georgetown, Ascension Island ASCN 1ZZ, South Atlantic

[3]Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Penryn TR10 9FE, UK

[4]Institut für Tierökologie und Spezielle Zoologie, Justus Liebig Universität Gießen, Heinrich-Buff-Ring 38, 35392 Gießen, Germany

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ABSTRACT: Predators exploiting tropical pelagic waters characterised by low fluctuations in seasonal temperature and salinity may require different foraging strategies than predators that can rely on persistently productive marine features. Consistent individual differences in foraging strategies have been found in temperate seabirds, but it is unclear whether such foraging specialisation would be beneficial in unpredictable tropical pelagic waters. We examined whether foraging trip characteristics of a tropical seabird were consistent between seasons and within individuals and explored whether seasonal changes could be explained by environmental variables. Ascension frigatebird *Fregata aquila* trips lasted up to 18 d and covered a total travel distance of up to 7047 km, but adult frigatebirds stayed within a radius of 1150 km of Ascension Island. We found that the 50% utilisation distribution of the population expanded southwestward in the cool season due to individuals performing more and longer trips in a southerly and westerly direction during the cool compared to the hot season. Individual repeatability was low ($R < 0.25$) for all trip characteristics, and we were unable to explain seasonal changes in time spent at sea using oceanographic or atmospheric variables. Instead, frigatebird usage per area was almost exclusively determined by distance from the colony, and although individuals spent more time in distant portions of their foraging trips, the amount of time spent per unit area decreased exponentially with increasing distance from the colony. This study indicates that, in a relatively featureless environment, high individual consistency may not be a beneficial trait for pelagic predators.

KEY WORDS: Seabird · Satellite tracking · Individual consistency · Home range · Central-place foraging

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INTRODUCTION

Marine predators have to locate and exploit prey in an environment where the factors determining prey aggregation are frequently not detectable. In temperate and coastal waters, marine features such as oceanic fronts, upwellings, and seasonal temperature and salinity gradients can lead to conditions that render accessible prey aggregations temporally and spatially predictable (Wakefield et al. 2009). In warm pelagic waters of the tropics, with lower variation in seasonal temperature, there are often few persistent

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*Corresponding author: steffen.oppel@rspb.org.uk

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marine features, and the occurrence of accessible prey aggregations becomes increasingly unpredictable (Weimerskirch 2007).

Terrestrial marine predators, such as seabirds, generally breed in large colonies on islands, from where individuals have to travel to surrounding waters to find prey. These predators are constrained to a central location during the breeding season when they need to return to their nest to feed offspring, which results in strong intraspecific competition that can lead to individually varying foraging strategies (Ashmole 1963, Wakefield et al. 2013, Wakefield et al. 2017). In temperate species, intraspecific competition can be reduced by individuals specialising on a narrow foraging strategy, either in terms of behaviour or in repeatedly exploiting a specific area (Votier et al. 2010, Cleasby et al. 2015, Wakefield et al. 2015). The consistent foraging behaviour by individuals can confer a fitness advantage (Woo et al. 2008, Patrick & Weimerskirch 2014, 2017, Patrick et al. 2014), but it is unclear whether such behaviour would be beneficial in a less predictable environment.

Tropical seabirds frequently exploit all marine areas within a species' flight range, leading to a dispersed distribution around islands (Kappes et al. 2011, Hennicke & Weimerskirch 2014, Oppel et al. 2015). This dispersed distribution could occur by individuals consistently travelling to a certain location, with individuals exhibiting differences in their preferred foraging location, thus leading to a dispersed distribution at the population level. Alternatively, individuals may not benefit from consistently travelling to the same area, and may therefore show considerable within-individual variation in foraging trip directions and distances (Sommerfeld et al. 2013), but so far very little is known about the individual consistency of tropical seabirds. Equally little is known about how tropical seabirds allocate time along foraging trips (Weimerskirch 2007). Because seabirds that nest in large colonies may deplete marine prey resources close to their colony (Ashmole 1963, Gaston et al. 2007, Oppel et al. 2015), lower levels of prey availability near the colony may require birds to allocate more foraging time to distant portions of an individual's foraging trip.

In addition to individual differences, seasonal changes in water temperature, chemistry, stratification, or other properties may lead to changes in prey accessibility in certain areas. Many tropical seabirds breed year-round, and conditions experienced by breeders during one part of the year may differ from conditions at other times of the year, despite similar day length and air temperatures. Although seasonal changes in the distribution of temperate seabirds is well understood and occurs as a consequence of predictable seasonal changes in temperature, day length, and prey availability (Shaffer et al. 2006, Guilford et al. 2009, Block et al. 2011), very little is known about seasonal variation in the distribution of tropical seabirds. Similar to the broad spatial distribution at the population level, seasonal variation in foraging distribution could occur either by specialised individuals breeding at the time of year when prey in their narrow preferred foraging area is most abundant, or by individuals adjusting their search and foraging behaviour in response to changing environmental conditions over time.

Here we investigate the seasonal and individual consistency in the foraging distribution of a tropical pelagic predator, the Ascension frigatebird *Fregata aquila*. Frigatebirds have the lowest wing loading of any bird, and travel very efficiently by using thermals and wind patterns to gain elevation, soar, and glide, but they lack waterproof plumage and therefore cannot land on or dive into the sea to rest or to acquire prey (Weimerskirch et al. 2003, De Monte et al. 2012, Weimerskirch et al. 2016). Frigatebirds prey on flying fish and other marine species acquired at the surface (Stonehouse & Stonehouse 1963), and their prey is likely driven to the surface by subsurface predatory fish or mammals (Ashmole 1971, Diamond 1978, Au & Pitman 1986). The distribution of both prey species and subsurface predators may be influenced by oceanographic patterns, which may ultimately also affect the distribution of frigatebirds (Weimerskirch et al. 2004, 2010, Tew Kai et al. 2009).

We tracked frigatebirds with 2 different tag types to obtain tracking data for short periods with high spatiotemporal resolution and for longer periods with lower spatiotemporal resolution, which allowed us to study both seasonal and individual consistency. We first explored whether adult Ascension frigatebirds remain near their breeding colony year-round, or conduct regular migrations similar to other frigatebirds (Weimerskirch et al. 2017). We then investigated whether there were seasonal changes in foraging distribution and trip characteristics, and explored whether seasonal changes were due to highly consistent individuals foraging in different areas in each season or whether individuals exhibited flexible foraging strategies and adjusted their foraging patterns over time. We then explored whether seasonal shifts in foraging distribution were related to oceanographic conditions that may affect prey availability (Weimerskirch et al. 2004, 2010, Tew Kai et al. 2009), or whether these shifts could be explained by atmospheric conditions that may affect flight costs and thus facilitate efficient travelling (Weimerskirch et al. 2003, 2016, De Monte et al. 2012). Finally, we estimated the proportion of time that frigatebirds spent at various distances from the colony and derived predictions about the foraging effort per unit area that can be useful for assessing spatial distribution and interactions with fisheries.

MATERIALS AND METHODS

Study area and study species

We studied Ascension frigatebirds on Boatswainbird Island (3 ha), a volcanic rock situated 260 m off the southeastern coast of Ascension Island (14° 18′ W, 7° 56′ S). Ascension is a volcanic island situated in deep oligotrophic waters without continental shelf, major seamounts, or current systems that could function as predictable foraging areas with permanently high productivity and prey availability for seabirds (Stonehouse 1962, Oppel et al. 2015). The arid tropical climate is characterised by a hot season (average air temperature 28°C) from January to the end of May, and a slightly cooler season (24°C) from June until December, with steady southeasterly trade winds throughout the year, and we used 1 June as the demarcation point between the hot and cool seasons.

The Ascension frigatebird population contains breeding birds at all times of the year, but there is a pronounced peak of egg laying from September to November during the cool season (Ratcliffe et al. 2008). While successful breeders may breed biennally (Nelson 1975, Ratcliffe et al. 2008), about 20–25% of failed breeders re-nest within 2–5 mo after failure (Stonehouse & Stonehouse 1963). The species forages at sea for multiple days and consumes mostly flying fish (Stonehouse & Stonehouse 1963), with a small proportion of the diet derived from kleptoparasitic activities, which may be a more frequent behaviour near the colony. Ascension frigatebirds are considered globally 'Vulnerable' to extinction due to their very limited breeding range, but the current status of the population appears to be stable (Ashmole et al. 1994, Ratcliffe et al. 2008). Following the successful removal of feral cats from Ascension Island in 2004 (Ratcliffe et al. 2010), birds started to re-colonise the main island and this new colony has expanded rapidly as a consequence of immigration from the nearby main colony on Boatswainbird Island (~400 pairs in 2017; Ascension Island Government unpubl. data).

Bird capture and tracking

We captured birds that were either incubating or attending small chicks by hand or with a noose-pole on their nest in February and March 2013 (GPS, n = 19; platform transmitter terminal, PTT, n = 3), September 2013 (GPS, n = 14), March 2014 (PTT, n = 16), and November 2014 (GPS, n = 3, Table S1 in the Supplement at www.int-res.com/articles/suppl/m585p199_supp.pdf). GPS loggers (iGot-U GT-120, Mobile Action Technology, and Ecotone Uria-300, Ecotone) were scheduled to provide a location fix every 300 s and were sealed in heat-shrink tube for waterproofing prior to deployment. PTTs (PTT100, Microwave Telemetry, and Kiwisat® 202 K2G 172A, Sirtrack) were scheduled to provide locations every 90 s for 3 h followed by a 3 h gap to facilitate long-term tracking.

We attached tags to the base of 3 or 4 central tail feathers using Tesa tape. Eggs or chicks were sheltered from the sun (while adults were handled) to avoid offspring loss due to sun exposure. The weight of GPS and PTT loggers with the waterproof sealing was 18–32 g (2.0–2.5% of body mass), below the threshold associated with adverse impacts (Phillips et al. 2003, Sergio et al. 2015), and similar to tags used in other frigatebird studies (Weimerskirch et al. 2006, 2010, Gilmour et al. 2012). All birds were handled for <20 min and returned to their nest on release. GPS loggers were deployed for 5–15 d to ensure that at least 1 foraging trip was recorded. We weighed birds equipped with a GPS tag on first capture (prior to being tagged) and at recapture (after foraging with an attached tag) to assess whether birds maintained or lost body mass. We concluded that GPS loggers did not adversely affect foraging of tracked birds if body mass after logger attachment did not significantly differ from body mass at first capture. Due to the difficulty in accessing Boatswainbird Island and the disturbance caused during every visit, PTT birds were not recaptured and neither their body mass nor their nesting success could be monitored after deployment of the tag. In addition, while the nesting stage at the time of tag deployment was known for birds equipped with PTT devices, a change in breeding status (chick hatched, fledged, failed) could not be objectively and independently determined, and the breeding stage for many foraging trips recorded by PTTs was therefore unknown. Permission to capture and tag birds was granted by the Conservation Department of the Ascension Island Government. The attachment of devices met the ethical guidelines of the Special Methods Panel of the British Trust for Ornithology.

Assessing variation in trip characteristics

We defined foraging trips as a series of >4 locations that extended for at least 3 h in duration and >22.5 km from the colony (Gilmour et al. 2012), and excluded locations in and in the immediate vicinity of the colony from further analyses. The choice of these thresholds was justified by GPS data that did not show short foraging trips, and reduced the influence of the different temporal resolution of PTT and GPS data on further analyses. For each foraging trip, we calculated the minimum total trip distance as the cumulative distance between all locations, assuming straight-line travel between all position fixes, the total duration as the time difference between the departure and return locations in the colony, and the maximum recorded distance from the colony. We refer to these 3 metrics (total distance, duration, and maximum distance from the colony) as trip characteristics. We also calculated the time spent at the colony prior to a trip and following a trip as the time difference between return from a trip and departure on the subsequent trip. To quantify the general direction into which foraging trips were oriented, we calculated the bearing from the colony to the most distant point along each foraging trip, but because frigatebirds frequently travel along looping trips (Weimerskirch 2007, 2010), these directions should only be interpreted at coarse resolution. We used a series of circular ANOVAs (R package 'circular', function 'aov.circular') to test whether mean foraging trip direction varied between sexes, breeding stages, or seasons with different subsets of data: trips for which the breeding stage was unknown were excluded from the analysis of breeding stage effects.

To explore whether variation in trip characteristics could be explained by seasonal differences, we used a subset of data for which the breeding stage was known, because breeding stage affects the foraging range in many seabird species (Sommerfeld & Hennicke 2010, Weimerskirch et al. 2010, Oppel et al. 2015). We used our sample of GPS tracks for which breeding status was known, and the foraging trips that occurred within 2 wk after deployment of a PTT device assuming that breeding status had not changed between deployment and the time of the foraging trip. We fitted 6 competing generalised linear mixed models (GLMMs) hypothesising that trip characteristics would vary by (1) sex, (2) breeding stage (incubation or chick rearing), (3) season, (4 and 5) season and breeding stage (additive and interactive effect), or (6 and 7) sex and breeding stage (additive and interactive effect) (Weimerskirch et al. 2004, 2010, Gilmour et al. 2012, Mott et al. 2017), and we included device type (GPS or PTT) as a controlling factor in each model to account for the coarser temporal resolution of PTT data. We fitted these models in R package 'lmer' using trip characteristics as normally distributed response variables and accounted for non-independence between multiple trips of the same individual by including individual identity as a random effect (Bolker et al. 2009). We compared models using the second-order Akaike's information criterion corrected for small sample size (AIC_c) and inferred which variables best explained variation in trip characteristics based on the models with the greatest AIC_c weight (ωAIC_c, Burnham & Anderson 2002).

Assessing seasonal distribution and individual consistency

To characterise the spatial distribution of the Ascension frigatebird population, we first interpolated all tracking data to regular 5 min intervals to avoid differential weighting of GPS and PTT data due to their different temporal resolution (Börger et al. 2006). We then estimated the core 50% kernel utilisation distribution (UD) of all locations associated with foraging trips for both the hot and the cool seasons using the 'kernelUD' function in R package 'adehabitatHR' (Calenge 2006) with a bandwidth *h* of 12 km determined from first passage time analysis (Pinaud & Weimerskirch 2005, Lascelles et al. 2016). We quantified the overlap between the 2 seasons using Bhattacharyya's affinity index (Fieberg & Kochanny 2005), a statistical measure of affinity that ranges from 0 (no overlap) to 1 (identical distributions), using the 'kerneloverlap' function in R package 'adehabitatHR'.

To explore whether seasonal shifts in distribution were a consequence of tracking different individuals in different seasons, we also calculated the kernel utilisation distribution and overlap for locations from those 14 individuals that were tracked in both the hot and cool seasons, which allowed us to quantify a seasonal distribution shift that was not confounded by individual differences.

For other trip characteristics, we calculated repeatabilities (*R*) to test whether the between-individual variance in foraging trip characteristics was equal to the within-individual variance, which would indicate that individuals use multiple trip strategies over time, rather than the population consisting of a range of specialised individuals (Patrick et al. 2014). We calculated repeatability only for birds tracked with PTT because deployment times for GPS tracked birds were too short to record >1 long foraging trip. We calculated repeatabilities and their associated standard errors using the R package 'rptR' (Nakagawa & Schielzeth 2010), using 'season' as a fixed effect and individual identity as grouping factor. For foraging trip directions, we used a circular ANOVA as described above and calculated the repeatability by using the mean squared error of this ANOVA (Lessells & Boag 1987, Patrick et al. 2014).

Relating seasonal changes to environmental variables

To explore whether Ascension frigatebirds shifted their spatial distribution seasonally in response to environmental variation, we considered 2 distinct mechanisms, namely energy expenditure required for travel and energy acquisition resulting from foraging. We considered that changes in thermal updraft, wind, air temperature, cloud cover, and air pressure may have affected the energy landscape and therefore altered the relative suitability of certain areas (Shepard et al. 2011, 2013, Wilson et al. 2012, Dodge et al. 2014). Alternatively, the distribution of both prey species and other predators that facilitate prey availability for surface-feeding frigatebirds may be influenced by oceanographic patterns, such as water temperature, salinity, currents, or ocean stratification (Weimerskirch et al. 2004, 2010, Tew Kai et al. 2009).

To relate frigatebird usage of a certain area to both atmospheric and oceanographic variables, we first calculated the proportion of time that tracked frigatebirds spent in 1° × 1° grid cells encompassing the entire adult foraging range of the species in each of 9 monthly tracking periods (Table S1 & Fig. S1 in the Supplement). We calculated the time-in-area using the function 'tripGrid' in R package 'trip' (Sumner 2015), which adequately represents the foraging intensity in a given area for pelagic seabirds (Warwick-Evans et al. 2015). We then downloaded environmental variables corresponding both spatially and temporally to the tracking data from the Env-DATA system in Movebank (Dodge et al. 2013) and from the Copernicus Marine Environmental Monitoring Service (http://marine.copernicus.eu/services-portfolio/access-to-products/) (Table S2 in the Supplement). For oceanographic data, we used values at the sea surface because the mixed layer depth was >30 m in our data and processes at greater depth are unlikely to be discernible for surface-feeding seabirds. For atmospheric data, we used vertically integrated measurements because frigatebirds can soar to over 4000 m above sea level and regularly reach altitudes of 2000 m above sea level (De Monte et al. 2012, Weimerskirch et al. 2016).

We related the proportion of time used by frigatebirds in a grid cell to 21 environmental variables (Table S2) using a powerful random forest algorithm that can accurately identify the relative importance of variables under these conditions (Cutler et al. 2007, Hochachka et al. 2007, Strobl et al. 2008). A random forest is a machine learning algorithm based on ensembles of regression trees that can accommodate a large number of predictor variables while maintaining sufficient generality to yield highly accurate predictions (Breiman 2001, Cutler et al. 2007, Hochachka et al. 2007). Because a random forest does not assume that data are independent or follow a specified statistical distribution, the approach was useful to analyse repeated observations from the same grid cells, where pseudo-replication is avoided by specifying the re-sampling structure for internal cross-validation (Karpievitch et al. 2009, Buston & Elith 2011). We used a random forest model based on a conditional inference framework to account for correlated predictors and for missing data (Hothorn et al. 2006b, Strobl et al. 2008, Hapfelmeier et al. 2012). We fitted this model in a regression framework with the R package 'party' (Hothorn et al. 2006a) and manually specified the internal cross-validation structure to ensure that observations from the same time period were not simultaneously used to fit and evaluate trees in the forest, which is equivalent to incorporating a temporal random effect in a linear modelling framework (Buston & Elith 2011). To evaluate the explanatory ability of the model, we performed a correlation test between the observed and predicted proportion of time in an area, with predictions being based on the internal cross-validation data that were not used for model fitting (Phillips & Elith 2010). To assess which variables had the greatest influence on our response variable, we used a permutation procedure that assesses the loss in predictive accuracy of the random forest model after randomly permuting a given variable (Strobl et al. 2007, Janitza et al. 2013, Hapfelmeier et al. 2014). We implemented this assessment using the R function 'varimp' with 100 permutations per variable and present results as relative variable importance, with the most important variable assigned a value of 100%.

Because a random forest is a non-parametric algorithm, the direction and size of effects by given variables cannot be expressed with numeric parameter estimates. For the most important variables, we therefore produced partial dependence plots that show the direction and magnitude of the effect of an environmental variable on the spatiotemporal distribution of frigatebirds after accounting for the effects of all other variables in the model (Cutler et al. 2007, Strobl et al. 2008).

Spatial distribution of foraging effort

Tropical seabirds that nest on oceanic islands may deplete marine prey resources close to their colony, which may result in greater allocation of foraging time to distant portions of an individual's foraging trip. To relate the relative foraging effort to distance from the colony, we used our high-resolution GPS data to first calculate the amount of time that individual frigatebirds spent within distance bands of 10 km width from the colony during each of their tracked foraging trips. We also calculated the total duration of the foraging trip to effectively convert the absolute amount of time spent in any distance band to the proportion of time for a given foraging trip. We then explored whether distance could adequately describe the time in each distance band by fitting 6 competing GLMMs hypothesising that temporal effort allocation (1) was constant, (2) varied by sex or (3) breeding stage, (4) was linearly related to distance from colony, (5) followed a quadratic function with distance from colony, or (6) was linearly related to distance from colony with differing gradients between breeding stages to reflect the fact that birds with small chicks generally have smaller foraging ranges (Weimerskirch et al. 2010, Mott et al. 2017). We fitted these models using time as a response variable and total trip time as an offset, and included individual identity as a random effect. We compared models using $\mathrm{AIC_c}$ and present parameter estimates (β) of the most parsimonious model.

Because the area encompassed by concentric distance bands around the colony increases, we divided the predicted temporal effort distribution by the area encompassed in each distance band. We calculated the area of sea available in each 10 km distance band, and related the predicted proportion of time that frigatebirds spent during their foraging trips in each distance band by the available area in that distance band. This metric effectively reflects the temporal effort distribution of frigatebirds per unit area across the distance bands around the colony, and can indicate whether birds search areas that are farther away from the colony more intensively.

RESULTS

We recorded 804 foraging trips from 51 different individuals (11 incubating males, 8 chick-rearing males, 16 incubating females, 16 chick-rearing females), with 241 trips from 28 individuals recorded in the cool season between June and December, and 563 trips from 37 individuals recorded in the hot season between January and the end of May (Table 1). The PTT devices allowed us to track 14 individuals for up to 5 mo covering both the hot and cool seasons.

Ascension frigatebirds foraged in all directions from the island, with trips lasting between 1 and 18 d and covering a total travel distance ranging from a minimum of 50 km to a maximum of >7000 km

Table 1. Mean, SD, minimum (min), and maximum (max) trip characteristics of 51 Ascension frigatebirds *Fregata aquila* tracked with GPS and PTT devices in 2013 and 2014 during the hot and cool seasons and divided by sex. n is the number of distinct foraging trips. Note that the breeding stage was not known for 70% of foraging trips

Trip characteristic	Season	Sex	n	Mean	SD	Min	Max
Trip duration (h)	Cool	Female	191	58.1	69.1	4.0	434.8
		Male	50	78.1	71.3	4.7	408.7
	Hot	Female	383	44.3	56.4	3.0	429.3
		Male	180	47.2	63.3	3.3	412.0
Maximum distance from colony (km)	Cool	Female	191	245.8	173.8	37.3	988.7
		Male	50	329.4	180.1	37.9	685.4
	Hot	Female	383	187.0	137.0	24.8	896.3
		Male	180	233.4	210.7	27.6	1153.3
Total trip distance (km)	Cool	Female	191	736.1	674.3	77.0	3613.7
		Male	50	1028.2	821.3	75.8	4122.9
	Hot	Female	383	560.5	552.7	50.0	3574.6
		Male	180	686.9	880.4	58.3	7047.3

(Table 1, Fig. S1). We did not detect any migratory movements, and adult frigatebirds stayed within a radius of 1150 km of Ascension Island for at least 5 mo after PTT deployment when several of the tracked birds likely had completed their breeding season. Based on 138 trips for which breeding status was known, there was strong support for total travel distance ($\omega AIC_c = 0.98$) and maximum distance from the colony ($\omega AIC_c = 1.0$) to vary by season and breeding stage, while trip durations varied mostly by breeding stage and to a lesser extent by season (Table 2). Incubation trips extended on average up to 545 km (±203 km SD; n = 12) from the colony during the cool season, but only up to 301 km (±199 km; n = 35) during the hot season, while chick-rearing trips were similar between both seasons (cool: 199 ± 80 km, n = 14; hot: 218 ± 127 km, n = 77). Similarly, the total trip distance and duration during chick rearing was consistent between the 2 seasons (cool: 627 ± 321 km, 38 ± 23 h; hot: 589 ± 391 km, 41 ± 32 h), but on average 80 % farther and 50 % longer during incubation in the cool season (1894 ± 765 km, 120 ± 58 h) than in the hot season (1032 ± 820 km, 78 ± 70 h). Sex consistently explained the least amount of variation in all foraging trip characteristics (Tables 1 & 2). Further support for equal time allocation to foraging trips between members of a pair can be inferred from the positive correlation between trip duration and both the preceding (Pearson correlation r = 0.27; 95 % CI 0.21–0.34) and subsequent (r = 0.40; 0.34–0.46) intervals that a bird spent at the colony.

There were no differences in the mean foraging direction between breeding stages ($F_{1,136} = 0.128$, p = 0.72) or between sexes ($F_{1,802} = 0.830$, p = 0.36), but foraging trips during the cool season were on average in a more westerly direction (mean 294°) than during the hot season (149°; $F_{1,802} = 90.68$, $p < 0.001$). However, trips in all directions occurred in both the hot and the cool season.

Seasonal shift in distribution and individual repeatability

The kernel UD of all foraging trip locations during the hot season from February to May indicated that the 95 % UD was 529 622 km^2 and centred slightly to the northeast of the island (Fig. 1), while the 95 % UD during the cool season between June and December was 798851 km^2 and centred on Ascension Island. The overall foraging range of Ascension frigatebirds was therefore 1.20 (hot season) to 1.81 (cool season) times larger than the exclusive economic zone (EEZ) of Ascension (441 658 km^2). The core foraging areas characterised by the 50 % UD comprised only 19.9 % (hot season; 88 052 km^2) and 35.5 % (cool season; 156 933 km^2) of Ascension's EEZ, respectively (Fig. 1). Despite the slight seasonal shift in distribution, the Bhattacharyya's affinity index indicated large overlap of the 2 seasonal distributions (BA = 0.771, Fig. 1).

The slight expansion in the core 50 % UD between the hot and cool seasons persisted if we used only data from 14 birds tracked over 5 mo during both the hot season and subsequent cool season (BA = 0.775). These changes were therefore a consequence of individual changes in foraging trip characteristics, rather than a consequence of tracking different individuals. We found low repeatability for trip duration (*R* = 0.235, 95 % CI: 0.10–0.37; n = 631 trips), maximum distance from

Table 2. Model selection table evaluating the effect of sex, stage, and season on foraging trip characteristics of adult Ascension frigatebirds *Fregata aquila* tracked with PTT and GPS in 2013 and 2014 at a time when their breeding stage was known (n trips = 138). *k*: number of estimable parameters; AIC_c: second-order Akaike's information criterion; ΔAIC_c: difference in AIC_c units to the most parsimonious model; ωAIC_c: relative weight of evidence for each model

Trip characteristic	Model	*k*	AIC_c	ΔAIC_c	ωAIC_c
Trip duration	Season + Stage	6	1436.60	0.00	0.37
	Season × Stage	7	1437.01	0.41	0.30
	Stage	5	1437.09	0.49	0.29
	Stage × Sex	7	1440.81	4.21	0.04
	Season	5	1456.02	19.42	0.00
	Null	4	1457.61	21.01	0.00
	Sex	5	1458.94	22.34	0.00
Maximum distance from colony	Season × Stage	7	1773.71	0.00	0.97
	Season + Stage	6	1780.90	7.18	0.03
	Stage	5	1789.17	15.46	0.00
	Stage × Sex	7	1792.04	18.33	0.00
	Season	5	1798.92	25.21	0.00
	Null	4	1808.06	34.35	0.00
	Sex	5	1808.61	34.90	0.00
Total trip distance	Season × Stage	7	2127.61	0.00	0.77
	Season + Stage	6	2130.22	2.61	0.21
	Stage	5	2135.48	7.87	0.02
	Stage × Sex	7	2139.44	11.83	0.00
	Season	5	2151.66	24.05	0.00
	Null	4	2157.61	29.99	0.00
	Sex	5	2159.06	31.45	0.00

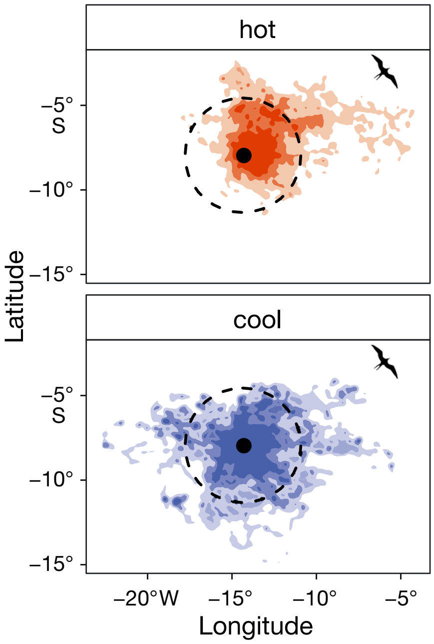

Fig. 1. Foraging distribution of 51 adult Ascension frigatebirds *Fregata aquila* tracked with GPS and PTT from Ascension Island in 2013 and 2014. Polygons represent the 95, 75, and 50% kernel utilisation distributions, respectively, of all locations from the hot season (February–May, red, top panel) and the cool season (June–December, blue, bottom panel); the black point indicates the location of Ascension Island, and the dashed circle indicates the exclusive economic zone of Ascension Island

colony (R = 0.192, 0.07–0.32), total trip length (R = 0.183, 0.07–0.30), and trip direction (R = 0.22, 0.08–0.35), and individual birds added more and much longer trips in a westerly direction during the cool season (Fig. 2).

Environmental correlates of seasonal shift in distribution

Despite a noticeable expansion in the general distribution and changes in the length and average direction of foraging trips between hot and cool seasons, the amount of time that tracked frigatebirds spent in a given grid cell could not be explained by any oceanographic or atmospheric variable in our random forest model. The model was able to predict the amount of time spent by frigatebirds reasonably well in cross-validation (Spearman correlation coefficient $r_s = 0.547$). However, distance to the island explained virtually all variation in frigatebird foraging intensity that was captured by the model (Table 3) and suggested that the amount of time spent per grid cell declined very sharply within the first 150 km (Fig. 3). This result did not change when we repeated the analysis at a higher (0.5° grid cell size) or lower (2° grid cell size) spatial resolution.

Spatial distribution of individual time allocation

To explore whether distance to the colony was also an important predictor in the relative proportion of time that individuals allocated to portions of their foraging trips, we used 61 GPS tracks with known breeding status from 29 individuals. Most trips were of a looping nature, and frigatebirds spent more time in the more distant parts of their trips. The most supported model indicated that the time spent in a given 10 km distance band from the island increased linearly with distance (Table 4), but that the increase was much steeper during incubation trips ($\beta = 0.057 \pm 0.009$ SE) than during chick-rearing trips ($\beta = 0.015 \pm 0.006$, Fig. 4).

Because the area of the 10 km distance bands increased by 628 km^2 for each successive band, the increasing proportion of time spent by an individual in more distant marine areas was more than offset by

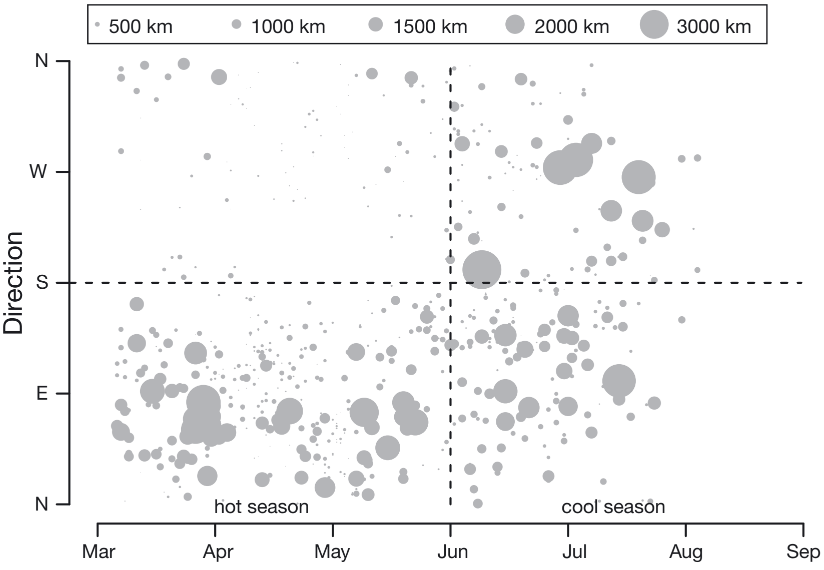

Fig. 2. Seasonal changes in foraging trip distance and direction of 14 Ascension frigatebirds *Fregata aquila* tracked with PTT for 5 mo from early March until August 2014 from Ascension Island. Each point represents one foraging trip, with increasing point size representing longer total foraging trip distances. Mean foraging direction (bearing from colony to farthest point from colony) is shown on the y axis; dashed lines indicate separation between hot and cool seasons (1 June) and between eastern and western areas

Table 3. Relative importance (in %) of 21 environmental variables used to explain variation in the amount of time Ascension frigatebirds *Fregata aquila* spent in 1° × 1° grid cells around Ascension during 9 tracking periods in 2013 and 2014. Variable importance is assessed by the decrease in predictive accuracy of a conditional random forest model after random permutation of a variable—negative importance indicates that predictive performance increased when a variable was randomly permuted

Environmental variable	Type	Relative importance
Distance to colony	Physical	100
Wind speed (E–W)	Atmospheric	0.59
Chlorophyll *a* concentration	Oceanographic	0.51
Current velocity (E–W) at surface	Oceanographic	0.03
Ocean depth	Physical	0
SD of depth (ruggedness)	Physical	0
Sea surface height	Oceanographic	−0.23
Current velocity (N–S) at surface	Atmospheric	−0.34
Net primary productivity	Oceanographic	−0.37
Salinity	Oceanographic	−0.4
Mixed-layer depth	Oceanographic	−0.44
Finite size Lyapunov exponent	Oceanographic	−0.44
Thermal uplift velocity	Atmospheric	−0.49
Eddy kinetic energy	Oceanographic	−0.52
Wind speed (N–S)	Atmospheric	−0.52
Air temperature	Atmospheric	−2.52
Air pressure	Atmospheric	−3.05
Water temperature at surface	Oceanographic	−3.45
Total cloud cover	Atmospheric	−4.31
Frequency of Lagrangian coherent structures	Oceanographic	−5.15
Sunshine duration	Atmospheric	−7.91

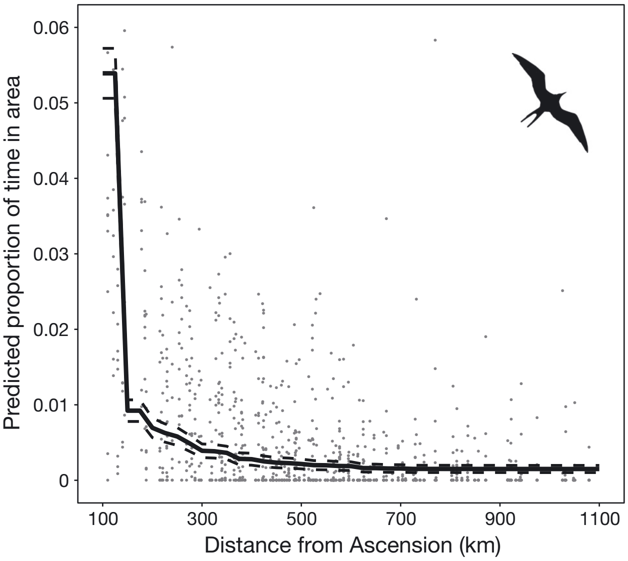

Fig. 3. Partial dependence plot of the predicted time that Ascension frigatebirds *Fregata aquila* tracked with GPS and PTT from Ascension Island in 2013 and 2014 spent in 1° × 1° grid cells with increasing distance from the island derived from a conditional random forest model. Dashed lines indicate 1 SD. Grey points indicate raw data

the increasing area. Therefore, the amount of time spent by an individual frigatebird per unit area (E_a) declined exponentially with increasing distance from the island (Fig. 4), following a similar shape as the decline in overall time spent by the population predicted from the random forest model including oceanographic and atmospheric covariates (Fig. 3). The shape of this function was best described by the following 2 equations:

$$E_a = e^{(-3.62 - 0.13 \times \text{distance})} \qquad (1)$$

during chick rearing, and

$$E_a = e^{(-3.50 - 0.15 \times \text{distance})} \qquad (2)$$

during incubation.

DISCUSSION

Ascension frigatebirds exhibit low individual consistency and roam widely in search of prey, and their distribution around the colony appears to be a random diffusion process that is poorly explained by easily measurable atmospheric or oceanographic variables. We found large variability in trip durations and directions both within and among individuals, with a pronounced distribution expansion from primarily northeast of the island during the hot season to more west and south of the island during the cool season (Fig. 1). This expansion was a consequence of individual birds undertaking more and longer trips in a southerly and westerly direction (Fig. 2), but we found no environmental correlates that could adequately explain this temporal shift in the frequency of use. Instead, distance to colony explained most of the variation in relative frigatebird use of an area, with much more time spent per unit area near the colony than in areas farther out at sea (Figs. 3 & 4).

We found a typical foraging strategy in Ascension frigatebirds as for many other seabirds, with foraging trips during incubation being often more than twice as long as during chick rearing when high energy demands of the growing chick require more frequent food deliveries by adults (Stonehouse & Stonehouse 1963, Sommerfeld & Hennicke 2010, Weimerskirch et al. 2010). As a consequence of this time limitation, Ascension frigatebirds were less able to devote substantial amounts of time to offshore foraging efforts

Table 4. Model selection table evaluating the effect of sex, breeding stage, and distance to colony on the proportion of time that adult Ascension frigatebirds *Fregata aquila* tracked with GPS in 2013 and 2014 spent in 10 km distance bands around the colony (n trips = 61). *k*: number of estimable parameters; AIC_c: second-order Akaike's information criterion; $\Delta\text{AIC}_\text{c}$: difference in AIC_c units to the most parsimonious model; $\omega\text{AIC}_\text{c}$: relative weight of evidence for each model

Model	*k*	AIC_c	$\Delta\text{AIC}_\text{c}$	$\omega\text{AIC}_\text{c}$
Distance × Stage	6	6660.43	0.00	0.96
Distance^2	4	6666.68	6.25	0.04
Distance	4	6678.93	18.50	0.00
Sex	4	6739.26	78.84	0.00
Constant	3	6739.28	78.85	0.00
Stage	4	6740.80	80.37	0.00

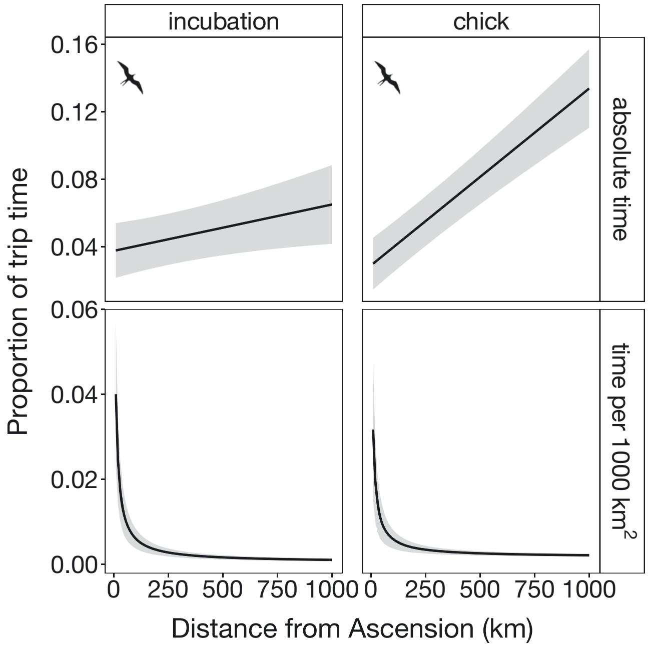

Fig. 4. Adult Ascension frigatebirds *Fregata aquila* tracked with GPS in 2013 and 2014 spent more time in more distant portions of their foraging trips (upper panels), but the amount of time spent per unit area decreased sharply due to the increasing amount of area available at larger distances (lower panels). Predicted proportion of time of an individual foraging trip (upper panels) and time allocated to a unit area of 1000 km^2 (lower panels) in 10 km distance bands from Ascension Island during either the incubation (left panels) or the chick-rearing stage (right panels) derived from a generalised linear mixed model with individual as a random effect; grey bands indicate 95 % confidence intervals

during chick rearing. But even during long incubation trips, lasting up to 2 wk and covering several thousand kilometres, frigatebirds did not allocate similar amounts of time per unit area of sea to regions farther away from the colony (Fig. 4). Intense competition in waters close to the colony may lead to prey depletion and render foraging in near-colony waters less efficient (Ashmole 1963, Gaston et al. 2007, Oppel et al. 2015). We would therefore predict that birds allocate proportionately more time to those areas farther away from the colony with less-intense competition and prey depletion. Although we found such a pattern at the individual trip level, the level of intraspecific competition and prey depletion may decrease rapidly with increasing distance from the colony, such that even a smaller relative time per unit area could be energetically efficient. This pattern of exponentially declining bird use per area with distance from the colony is important for marine spatial planning, as the encounter probability of globally threatened seabirds such as the Ascension frigatebird with anthropogenic threats such as fishing vessels or industrial infrastructure would be predicted to decrease at a similar rate in farther offshore areas. Ascension frigatebirds offer a useful null distribution of pelagic seabird foraging effort that appears to be almost independent of easily measurable oceanographic or atmospheric patterns (Ashmole 1971, Weimerskirch 2007).

Although we found distinct seasonal differences in the distribution of Ascension frigatebirds, the time spent per area was not explained by either atmospheric soaring conditions or oceanographic conditions that are frequently used to predict productive foraging environments. Other frigatebird studies have shown that some populations forage preferentially in areas of high productivity (Weimerskirch et al. 2004, 2010, Mott et al. 2017) or frontal systems (Tew Kai et al. 2009, De Monte et al. 2012), but the studied colonies either exhibited clear environmental differences in the marine areas surrounding the colonies (Weimerskirch et al. 2004, 2010), or consisted of sympatric frigatebird assemblages that may have resulted in niche partitioning between species (Mott et al. 2017). In contrast, Ascension frigatebirds forage from a mid-Atlantic island that is surrounded by relatively featureless tropical ocean without continental shelf or upwelling areas and only very minor environmental gradients within the accessible foraging range. There are no other frigatebirds in the central Atlantic Ocean, and Ascension frigatebirds may only compete with other seabirds eating flying fish, such as masked boobies *Sula dactylatra* or brown boobies *S. leucogaster* or tropicbirds *Phaethon* sp. which breed on Ascension (Dorward 1962, Stonehouse & Stonehouse 1963). However, the flying capabilities allow Ascension frigatebirds to explore more distant areas at sea than boobies, which range a maximum of 350 km from Ascension (Oppel et al. 2015). In the absence of distinct environmental gradients and substantial interspecific competition, it is plausible that frigatebirds forage very broadly, rendering their distribution very difficult to predict based on readily available environmental variables (Lavers et al. 2014). Alternatively, our tracking efforts, which mostly followed individuals outside the peak breeding phase, may not have occurred at the appropriate time to detect environmental relationships. Population-level demand for prey will be substantially higher during the peak breeding season (Ashmole 1963, Birt-Friesen et al. 1989), and it is possible that bird–habitat relationships may have been stronger during the peak breeding season. However, the breeding peak may only occur due to generally higher prey availability (Le Corre 2001, Wingfield 2008), which may actually reduce intraspecific competition and the strength of bird–habitat relationships, while the off-peak nesting may only occur due to nest site space constraints and may force individuals to raise chicks at times when prey availability is low (Ratcliffe et al. 2008). We therefore do not believe that the temporal distribution of our tracking efforts substantially affected our ability to detect bird–habitat relationships.

Further support for the fairly broad foraging strategy of Ascension frigatebirds comes from the low consistency of individuals. We found that the spatial distribution shift between hot and cool seasons was not a consequence of tracking different individuals in different seasons, but that individuals tracked across both seasons conducted more and longer foraging trips into a westerly and southerly direction during the cool season. As a consequence, we found low repeatabilities in all foraging trip characteristics, which were marginally higher than expected under a complete random distribution, but lower than for some temperate seabirds that specialise on discrete foraging areas (Patrick et al. 2014, 2015, Wakefield et al. 2015). This low individual consistency suggests that individuals explore vast areas in different foraging trips, potentially due to the low consistency of highly productive marine areas that are unlikely to persist at a location for long enough to warrant repeat visits during subsequent foraging trips (Weimerskirch 2007, Hennicke & Weimerskirch 2014).

Because we marked birds during the breeding period but were not able to follow their nests after tag deployment, it is possible that some of the within-individual changes in foraging trip characteristics and directions were caused by changes in breeding status. Specifically, birds that were marked during incubation but successfully hatched a chick may have shortened their foraging trips, while birds that lost their egg or chick may have expanded their foraging trips after being relieved from parental duties. However, we found substantial variability in individual trip durations that did not allow an objective distinction between breeding stages from trip characteristics. In addition, it is highly unlikely that all birds tracked with PTT successfully fledged offspring given that Ascension frigatebirds have generally low breeding success of 19–34 % (Stonehouse & Stonehouse 1963, Ratcliffe et al. 2008); thus, some of our tracked birds were almost certainly no longer breeding or raising fledglings during the cool season when more and longer trips occurred in westerly directions. One potential explanation for changing foraging directions and distances after breeding could be the freedom to perform exploratory movements or exploit areas with lower competition. During time of high-energy demand, birds are expected to forage in familiar areas with a reliable energy supply (Irons 1998, Piper 2011, Wakefield et al. 2015). Once relieved from energy-demanding parental duties, birds may have the liberty to explore different areas to build knowledge that can be beneficial in the future. Such exploratory movements have been proposed in other bird species (Bennetts & Kitchens 2000, Oppel et al. 2009, Guilford et al. 2011), and may be the underlying motivation for long pre-breeding and intermittent non-breeding journeys of long-lived pelagic predators (Wakefield et al. 2015, Weimerskirch et al. 2015, 2017). Multi-annual tracking studies in combination with demographic studies that assess the consequences of persistent individual strategies are required to further investigate the causes and consequences of seasonal changes in the foraging patterns of Ascension frigatebirds.

Unlike other frigatebird species, Ascension frigatebirds are year-round central-place foragers that do not appear to embark on post-breeding migrations or roost on islands different from their breeding colony (Weimerskirch et al. 2006, 2017). Although juvenile birds may roam widely across the Atlantic (Williams et al. 2017), the adult birds that we tracked for up to 5 mo exhibited similar foraging trips during the breeding season and afterwards. The reason for this 'residential' behaviour is unknown; however, we speculate that due to the requirements of moult (Stonehouse & Stonehouse 1963, De Korte & De Vries 1978) and sleep (Rattenborg et al. 2016), frigatebirds may need to periodically return to land to rest (Weimerskirch et al. 2017). Because there is no nearby land mass, Ascension frigatebirds may not be able to migrate to other roosting areas as has been speculated for frigatebirds in the equally isolated Galapagos archipelago (Weimerskirch et al. 2017), although the nearest island of Saint Helena is only marginally farther (1250 km) than the maximum distance from the colony recorded in our study. The somewhat limited dispersal outside the breeding season, which does not appear to overlap with the foraging area of any other frigatebird species, may have led to genetic isolation and contributed to the speciation of Ascension frigatebirds (Dearborn et al. 2003).

In summary, Ascension frigatebirds exploit large marine areas surrounding their only breeding colony on Ascension, with greater effort per unit area spent in marine areas closer to the colony. Although there appear to be discernible shifts in foraging behaviour between the hot and the cool seasons, large within- and between-individual variability in foraging trip directions and distances obscure any relationships that may exist with temporary oceanographic features. Marine spatial planning for the conservation of Ascension frigatebirds should therefore operate under the assumption that all areas within 1200 km of the island will be explored by the population, with exponentially decreasing density of birds at greater distances from the colony.

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LITERATURE CITED

Ashmole NP (1963) The regulation of numbers of tropical oceanic birds. Ibis 103b:458–473

Ashmole NP (1971) Seabird ecology and the marine environment. In: Farner DS, King JR (eds) Avian biology, Vol 1. Academic Press, New York, NY, p 223–286

Ashmole NP, Ashmole MJ, Simmons KEL (1994) Seabird conservation and feral cats on Ascension Island, South Atlantic. In: Nettleship DN, Burger J, Gochfeld M (eds) Seabirds on islands: threats, case studies and action plans. BirdLife International, Cambridge, p 94–121

Au DWK, Pitman RL (1986) Seabird interactions with dolphins and tuna in the eastern tropical Pacific. Condor 88: 304–317

Bennetts RE, Kitchens WM (2000) Factors influencing movement probabilities of a nomadic food specialist: proximate foraging benefits or ultimate gains from exploration? Oikos 91:459–467

Birt-Friesen VL, Montevecchi WA, Cairns D, Macko SA (1989) Activity-specific metabolic rates of free-living Northern Gannets and other seabirds. Ecology 70: 357–367

Block BA, Jonsen ID, Jorgensen SJ, Winship AJ and others (2011) Tracking apex marine predator movements in a dynamic ocean. Nature 475:86–90

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127–135

Börger L, Franconi N, de Michele G, Gantz A and others (2006) Effects of sampling regime on the mean and variance of home range size estimates. J Anim Ecol 75: 1393–1405

Breiman L (2001) Random forests. Mach Learn 45:5–32

Burnham KP, Anderson DR (2002) Model selection and multimodel inference. A practical information-theoretic approach, 2nd edn. Springer, New York, NY

Buston PM, Elith J (2011) Determinants of reproductive success in dominant pairs of clownfish: a boosted regression tree analysis. J Anim Ecol 80:528–538

Calenge C (2006) The package 'adehabitat' for the R software: a tool for the analysis of space and habitat use by animals. Ecol Modell 197:516–519

Cleasby IR, Wakefield ED, Bodey TW, Davies RD and others (2015) Sexual segregation in a wide-ranging marine predator is a consequence of habitat selection. Mar Ecol Prog Ser 518:1–12

Cutler DR, Edwards TC, Beard KH, Cutler A, Hess KT, Gibson J, Lawler JJ (2007) Random forests for classification in ecology. Ecology 88:2783–2792

De Korte J, De Vries T (1978) Moult of primaries and rectrices in the greater frigatebird *Fregata minor* on Genovesa, Galapagos. Bijd tot de Dierk 48:81–88

De Monte S, Cotté C, d'Ovidio F, Lévy M, Le Corre M, Weimerskirch H (2012) Frigatebird behaviour at the ocean–atmosphere interface: integrating animal behaviour with multi-satellite data. J R Soc Interface 9: 3351–3358

Dearborn DC, Anders AD, Schreiber EA, Adams RMM, Mueller UG (2003) Inter-island movements and population differentiation in a pelagic seabird. Mol Ecol 12: 2835–2843

Diamond AW (1978) Feeding strategies and population size in tropical seabirds. Am Nat 112:215–223

Dodge S, Bohrer G, Weinzierl R, Davidson S and others (2013) The environmental-data automated track annotation (Env-DATA) system: linking animal tracks with environmental data. Mov Ecol 1:3

Dodge S, Bohrer G, Bildstein K, Davidson SC and others (2014) Environmental drivers of variability in the movement ecology of turkey vultures (*Cathartes aura*) in North and South America. Philos Trans R Soc Lond B Biol Sci 369:20130195

Dorward D (1962) Comparative biology of the white booby and the brown booby *Sula* spp. at Ascension. Ibis 103: 174–220

Fieberg J, Kochanny CO (2005) Quantifying home-range overlap: the importance of the utilization distribution. J Wildl Manag 69:1346–1359

Gaston AJ, Ydenberg RC, Smith GJ (2007) Ashmole's halo and population regulation in seabirds. Mar Ornithol 35: 119–126

Gilmour ME, Schreiber E, Dearborn DC (2012) Satellite telemetry of Great frigatebirds *Fregata minor* rearing chicks in Tern Island, North Central Pacific Ocean. Mar Ornithol 40:17–23

Guilford T, Meade J, Willis J, Phillips RA and others (2009) Migration and stopover in a small pelagic seabird, the Manx shearwater *Puffinus puffinus*: insights from machine learning. Proc R Soc B 276:1215–1223

Guilford T, Freeman R, Boyle D, Dean B, Kirk H, Phillips R, Perrins C (2011) A dispersive migration in the Atlantic puffin and its implications for migratory navigation. PLOS ONE 6:e21336

Hapfelmeier A, Hothorn T, Ulm K (2012) Recursive partitioning on incomplete data using surrogate decisions and multiple imputation. Comput Stat Data Anal 56: 1552–1565

Hapfelmeier A, Hothorn T, Ulm K, Strobl C (2014) A new variable importance measure for random forests with missing data. Stat Comput 24:21–34

Hennicke JC, Weimerskirch H (2014) Coping with variable and oligotrophic tropical waters: foraging behaviour and flexibility of the Abbott's booby *Papasula abbotti*. Mar Ecol Prog Ser 499:259–273

Hochachka WM, Caruana R, Fink D, Munson ART, Riedewald M, Sorokina D, Kelling S (2007) Data-mining discovery of pattern and process in ecological systems. J Wildl Manag 71:2427–2437

Hothorn T, Hornik K, Zeileis A (2006a) party: a laboratory for recursive partytioning. R package version 1.2-3; https://cran.r-project.org/web/packages/party/index.html

Hothorn T, Hornik K, Zeileis A (2006b) Unbiased recursive partitioning: a conditional inference framework. J Comput Graph Stat 15:651–674

Irons DB (1998) Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. Ecology 79: 647–655

Janitza S, Strobl C, Boulesteix AL (2013) An AUC-based permutation variable importance measure for random forests. BMC Bioinformatics 14:119

Kappes MA, Weimerskirch H, Pinaud D, Le Corre M (2011) Variability of resource partitioning in sympatric tropical boobies. Mar Ecol Prog Ser 441:281–294

Karpievitch YV, Hill EG, Leclerc AP, Dabney AR, Almeida JS (2009) An introspective comparison of random forest-based classifiers for the analysis of cluster-correlated data by way of RF++. PLOS ONE 4:e7087

Lascelles BG, Taylor PR, Miller MGR, Dias MP and others (2016) Applying global criteria to tracking data to define important areas for marine conservation. Divers Distrib 22:422–431

Lavers JL, Miller MGR, Carter MJ, Swann G, Clarke RH (2014) Predicting the spatial distribution of a seabird community to identify priority conservation areas in the Timor Sea. Conserv Biol 28:1699–1709

Le Corre M (2001) Breeding seasons of seabirds at Europa Island (southern Mozambique Channel) in relation to seasonal changes in the marine environment. J Zool (Lond) 254:239–249

Lessells C, Boag PT (1987) Unrepeatable repeatabilities: a common mistake. Auk 104:116–121

Mott R, Herrod A, Clarke RH (2017) Resource partitioning between species and sexes in great frigatebirds and lesser frigatebirds. Auk 134:153–167

Nakagawa S, Schielzeth H (2010) Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. Biol Rev Camb Philos Soc 85:935–956

Nelson JB (1975) The breeding biology of frigatebirds: a comparative review. Living Bird 14:113–155

Oppel S, Powell AN, Dickson DL (2009) Using an algorithmic model to reveal individually variable movement decisions in a wintering sea duck. J Anim Ecol 78: 524–531

Oppel S, Beard A, Fox D, Mackley E and others (2015) Foraging distribution of a tropical seabird supports Ashmole's hypothesis of population regulation. Behav Ecol Sociobiol 69:915–926

Patrick SC, Weimerskirch H (2014) Consistency pays: sex differences and fitness consequences of behavioural specialization in a wide-ranging seabird. Biol Lett 10: 20140630

Patrick SC, Weimerskirch H (2017) Reproductive success is driven by local site fidelity despite stronger specialisation by individuals for large-scale habitat preference. J Anim Ecol 86:674–682

Patrick SC, Bearhop S, Grémillet D, Lescroël A and others (2014) Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator. Oikos 123:33–40

Patrick SC, Bearhop S, Bodey TW, Grecian WJ, Hamer KC, Lee J, Votier SC (2015) Individual seabirds show consistent foraging strategies in response to predictable fisheries discards. J Avian Biol 46:431–440

Phillips SJ, Elith J (2010) POC plots: calibrating species distribution models with presence-only data. Ecology 91: 2476–2484

Phillips RA, Xavier JC, Croxall JP (2003) Effects of satellite transmitters on albatrosses and petrels. Auk 120: 1082–1090

Pinaud D, Weimerskirch H (2005) Scale-dependent habitat use in a long-ranging central place predator. J Anim Ecol 74:852–863

Piper WH (2011) Making habitat selection more 'familiar': a review. Behav Ecol Sociobiol 65:1329–1351

Ratcliffe N, Pelembe T, White R (2008) Resolving the population status of Ascension frigatebird *Fregata aquila* using a 'virtual ecologist' model. Ibis 150:300–306

Ratcliffe N, Bell MB, Pelembe T, Boyle D and others (2010) The eradication of feral cats from Ascension Island and its subsequent recolonization by seabirds. Oryx 44:20–29

Rattenborg NC, Voirin B, Cruz SM, Tisdale R and others (2016) Evidence that birds sleep in mid-flight. Nat Commun 7:12468

Sergio F, Tavecchia G, Tanferna A, López Jiménez L and others (2015) No effect of satellite tagging on survival, recruitment, longevity, productivity and social dominance of a raptor, and the provisioning and condition of its offspring. J Appl Ecol 52:1665–1675

Shaffer SA, Tremblay Y, Weimerskirch H, Scott D and others (2006) Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. Proc Natl Acad Sci USA 103:12799–12802

Shepard EL, Lambertucci SA, Vallmitjana D, Wilson RP (2011) Energy beyond food: foraging theory informs time spent in thermals by a large soaring bird. PLOS ONE 6: e27375

Shepard EL, Wilson RP, Rees WG, Grundy E, Lambertucci SA, Vosper SB (2013) Energy landscapes shape animal movement ecology. Am Nat 182:298–312

Sommerfeld J, Hennicke JC (2010) Comparison of trip duration, activity pattern and diving behaviour by red-tailed tropicbirds (*Phaethon rubricauda*) during incubation and chick-rearing. Emu 110:78–86

Sommerfeld J, Kato A, Ropert-Coudert Y, Garthe S, Hindell MA (2013) The individual counts: within sex differences in foraging strategies are as important as sex-specific differences in masked boobies *Sula dactylatra*. J Avian Biol 44:531–540

Stonehouse B (1962) Ascension Island and the British Ornithologists' Union Centenary Expedition 1957–59. Ibis 103b:107–123

Stonehouse B, Stonehouse S (1963) The frigate bird *Fregata aquila* of Ascension Island. Ibis 103b:409–422

Strobl C, Boulesteix AL, Zeileis A, Hothorn T (2007) Bias in random forest variable importance measures: illustrations, sources and a solution. BMC Bioinformatics 8: 25–45

Strobl C, Boulesteix AL, Kneib T, Augustin T, Zeileis A (2008) Conditional variable importance for random forests. BMC Bioinformatics 9:307

Sumner MD (2015) trip: tools for the analysis of animal track data. R package version 1.1-21; https://CRAN.R-project.org/package=trip

Tew Kai E, Rossi V, Sudre J, Weimerskirch H and others (2009) Top marine predators track Lagrangian coherent structures. Proc Natl Acad Sci USA 106:8245–8250

Votier SC, Bearhop S, Witt MJ, Inger R, Thompson D, Newton J (2010) Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. J Appl Ecol 47: 487–497

Wakefield ED, Phillips RA, Matthiopoulos J (2009) Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review. Mar Ecol Prog Ser 391:165–182

Wakefield ED, Bodey TW, Bearhop S, Blackburn J and others (2013) Space partitioning without territoriality in gannets. Science 341:68–70

Wakefield ED, Cleasby IR, Bearhop S, Bodey TW and others (2015) Long-term individual foraging site fidelity—why some gannets don't change their spots. Ecology 96: 3058–3074

Wakefield ED, Owen E, Baer J, Carroll MJ and others (2017) Breeding density, fine-scale tracking and large-scale modeling reveal the regional distribution of four seabird species. Ecol Appl 27:2074–2091

Warwick-Evans V, Atkinson PW, Gauvain RD, Robinson LA, Arnould JPY, Green JA (2015) Time-in-area represents foraging activity in a wide-ranging pelagic forager. Mar Ecol Prog Ser 527:233–246

Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? Deep Sea Res II 54:211–223

Weimerskirch H, Chastel O, Barbraud C, Tostain O (2003) Frigatebirds ride high on thermals. Nature 421:333–334

Weimerskirch H, Le Corre M, Jaquemet S, Potier M, Marsac F (2004) Foraging strategy of a top predator in tropical waters: great frigatebirds in the Mozambique Channel. Mar Ecol Prog Ser 275:297–308

Weimerskirch H, Le Corre M, Marsac F, Barbraud C, Tostain O, Chastel O (2006) Postbreeding movements of frigatebirds tracked with satellite telemetry. Condor 108:220–225

Weimerskirch H, Le Corre M, Tew Kai E, Marsac F (2010) Foraging movements of great frigatebirds from Aldabra Island: relationship with environmental variables and interactions with fisheries. Prog Oceanogr 86:204–213

Weimerskirch H, Delord K, Guitteaud A, Phillips RA, Pinet P (2015) Extreme variation in migration strategies between and within wandering albatross populations during their sabbatical year, and their fitness consequences. Sci Rep 5:8853

Weimerskirch H, Bishop C, Jeanniard-du-Dot T, Prudor A, Sachs G (2016) Frigate birds track atmospheric conditions over months-long transoceanic flights. Science 353: 74–78

Weimerskirch H, Borsa P, Cruz S, de Grissac S and others (2017) Diversity of migration strategies among great frigatebirds populations. J Avian Biol 48:103–113

Williams SM, Weber SB, Oppel S, Leat EHK and others (2017) Satellite telemetry reveals the first record of the Ascension frigatebird (*Fregata aquila*) for the Americas. Wilson J Ornithol 129:600–604

Wilson RP, Quintana F, Hobson VJ (2012) Construction of energy landscapes can clarify the movement and distribution of foraging animals. Proc R Soc B 279:975–980

Wingfield JC (2008) Organization of vertebrate annual cycles: implications for control mechanisms. Philos Trans R Soc Lond B Biol Sci 363:425–441

Woo KJ, Elliott KH, Davidson M, Gaston AJ, Davoren GK (2008) Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. J Anim Ecol 77:1082–1091

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Swansea, UK

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