

# AVIAN BIOLOGY

## Article

### Linking foraging and breeding strategies in tropical seabirds

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#### Journal of Avian Biology

2021: e02670

doi: 10.1111/jav.02670

Subject Editor and

Editor-in-Chief: Jan-Åke Nilsson

Accepted 12 April 2021



The archetypal foraging behaviour of tropical seabirds is generally accepted to differ from that of their temperate and polar breeding counterparts, with the former exhibiting less predictable foraging behaviour associated with the less predictable prey of the tropical marine environment. Similarly, temperate and polar species have predictable, annual breeding seasons, enabling them to profit during periods of the year when prey availability is highest, while tropical seabird species exhibit considerable variability in their breeding strategies. Until now, the reasons for such variation in breeding strategies between tropical seabirds are yet to be investigated. We hypothesise that while some tropical species breed asynchronously in response to unpredictable fluctuations in prey availability, others adopt a seasonal breeding strategy for the same reasons that temperate and polar species do. Consequently, the predictability of seabird foraging behaviour in the tropics may be related to breeding strategy, with populations that breed seasonally exhibiting more predictable foraging behaviour than those that breed aseasonally. To test these predictions, we used GPS tracking to examine the foraging behaviour of two closely related tropical seabird species that colonise the same island yet exhibit markedly different breeding strategies: the asynchronously breeding brown booby *Sula leucogaster* and the seasonal breeding masked booby *Sula dactylatra*. We obtained tracks for 251 birds over five years. We found that brown boobies forage less predictably than masked boobies, indicated by larger core foraging areas, lower levels of foraging area overlap between individuals and exhibit more variability between breeding periods. Our results challenge the view that the foraging behaviour of tropical seabirds is always less predictable than that of seabirds breeding in temperate and polar regions and highlight the considerable variability in the breeding and foraging strategies adopted by tropical seabirds which demand further exploration.

Key words: brown booby, energy flow, masked booby, prey predictability, temperate seabirds



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## Introduction

The oceans' top predators including seabirds, cetaceans and pinnipeds seek out their prey in an environment that is not only vast but often complex. The location and abundance of prey is influenced by localised climatic and physical processes (Santos et al. 2006), and also wide-ranging oceanographic effects such as El Niño (Funes-Rodriguez et al. 2006, Chen et al. 2007, Wang et al. 2016). While many seabirds exhibit high levels of behavioural flexibility to contend with the resultant variability in the location of their food in the oceans (Kowalczyk et al. 2015, Castillo-Guerrero et al. 2016), the degree of flexibility is reported to differ depending on large-scale biogeographical factors (Weimerskirch 2007). In temperate and polar regions, marked seasonal fluctuations in marine productivity cause seabirds to congregate and breed at specific times of the year, ensuring that the energy demands of reproduction coincide with peak food availability, usually driven by warmer summer sea surface temperatures and associated increased ocean productivity (Frederiksen et al. 2004). The typical foraging strategy that seabirds breeding in these regions adopt is to repeatedly visit similar locations at sea throughout a breeding season, usually associated with coastal and oceanic features which drive hotspots of productivity (Hamer et al. 2001, Kappes et al. 2011, Kotzerka et al. 2011, Wakefield et al. 2015). By contrast, in tropical environments which are typically more oligotrophic, marine productivity is both less seasonal and less consistently patchy. As a result, prey are generally thought to be spatially less predictable (Ashmole 1971), thus it may not be profitable for tropical seabirds to consistently frequent the same areas at sea. Tropical seabirds are therefore commonly described to forage less predictably and to exhibit greater flexibility in their foraging behaviour within a breeding period, to account for the spatio-temporal unpredictability in the distribution of their prey (Weimerskirch 2007, Jaquemet et al. 2008).

Differences in the foraging behaviour of tropical and temperate/polar breeding species were formally investigated by Weimerskirch (2007), who reviewed and collated existing literature on seabird foraging site fidelity and foraging movements from 68 datasets. He concluded that seabirds breeding in temperate and polar regions have a good knowledge of the location and concentrations of prey patches, indicated by 'commuting' trips (travelling patterns described by direct pathways to and from the foraging zone (Pettex et al. 2010)) and area restricted search (ARS) behaviour (Kareiva and Odell 1987, Fauchald and Tveraa 2003). These foraging zones were consistently present at repeatable locations within a breeding season. The great majority of work on seabird foraging to date has studied temperate and polar species, and at the time of Weimerskirch's study only six datasets for tropical seabird species were available. For the five tropical populations where degree of foraging site fidelity had been studied, site fidelity was reported to be low. In addition, examination of fine-scale foraging tracks suggested that commuting trips and ARS behaviour by tropical seabirds is uncommon. Weimerskirch (2007) concluded that, in contrast to temperate and polar species, tropical seabirds forage

at many widely located sites during their breeding season, making their foraging behaviour unpredictable (Fig. 1). The results of several subsequent studies of tropical seabird foraging have concurred with Weimerskirch's (2007) conclusions. Oppel et al. (2015), for example, reported that masked boobies *Sula dactylatra* breeding on St Helena and Ascension in the tropical Atlantic departed the colony in all directions on their foraging trips. Similarly, Lerma et al. (2020) found that the foraging areas of masked boobies breeding in the South Pacific were dispersed around the breeding colony with no particular concentration, and individual birds never returned to the same foraging areas from one trip to the next.

Greater variability in tropical seabird foraging behaviour is echoed by their greater variability in breeding behaviour. As a result of tropical oceans exhibiting lower seasonal fluctuations in marine productivity, tropical seabirds are not necessarily constrained to breed during defined, highly productive times of the year. Indeed, tropical seabirds exhibit a diversity of breeding strategies, some of which are relatively similar to those of temperate and polar species and some of which are markedly different. That is, some tropical species mirror temperate and polar species in breeding at a consistent time year after year, while other tropical species are asynchronous breeders, exhibiting breeding periods multiple times annually and at unpredictable times of the year (Reynolds et al. 2014). This diversity can even be observed at a single location (Kappes et al. 2011). For example, in the Galapagos Islands, Harris (1969) reported red-footed boobies *Sula sula* breeding in peaks across the year, blue-footed boobies *Sula nebouxii* breeding throughout the year and masked boobies breeding seasonally. However, the reasons for such variation in breeding strategies between tropical seabirds are yet to be investigated.

The adoption of distinct breeding strategies is observed not only between tropical seabird species but also between populations of the same species (Nelson 1978). For example, the breeding strategy of masked boobies breeding on Tromelin Island, Indian Ocean (Kappes et al. 2011) is described as loosely seasonal while the same species is reported to breed year round on Palmyra Atoll in the Pacific (Young et al. 2010). This suggests that tropical seabirds are behaviourally responsive to the environmental cues of their foraging habitats. Thus, populations of tropical species exhibiting breeding behaviour archetypal of temperate and polar seabirds may do so because, similarly to temperate and polar species, fluctuations in prey resources where they forage are relatively predictable. We hypothesise that tropical seabirds which breed predictably should also exhibit predictable foraging behaviour. To investigate this assumption, we examined the inter-individual and inter-annual variability in foraging behaviour during breeding of sympatric populations of two tropical species that are closely related yet exhibit markedly different breeding strategies: the brown booby *Sula leucogaster* and the masked booby. We deployed 319 GPS loggers individually on birds of both species during nine breeding seasons between 2012 and 2016, inclusive. Masked boobies on Dog Island, Anguilla, in the Eastern Caribbean, breed annually and predictably, similarly to temperate and polar seabirds,

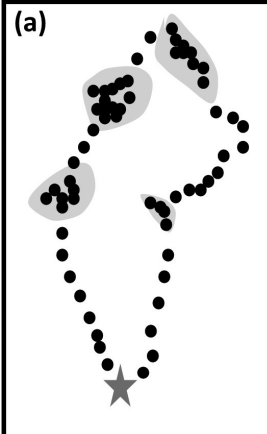
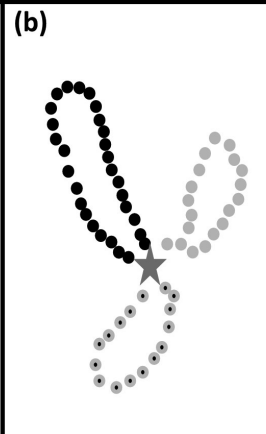
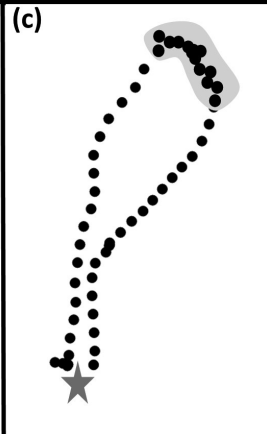
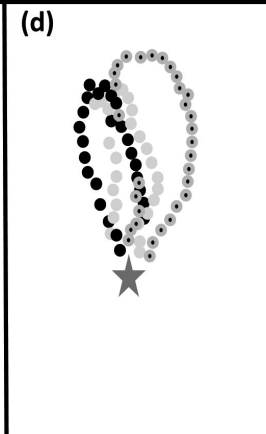
Typical tropical seabird foraging behaviour		Typical temperate seabird foraging behaviour	
(a)	(b)	(c)	(d)
			
<ul style="list-style-type: none"> <li>- Less direct “looping” foraging trips</li> <li>- Core-foraging areas are a high proportion of home-range area</li> </ul>	<ul style="list-style-type: none"> <li>- Low levels of overlap between foraging trips within an individual</li> <li>- Low levels of overlap in foraging areas between individuals</li> </ul>	<ul style="list-style-type: none"> <li>- More direct “commuter” foraging trips</li> <li>- Core-foraging areas are a low proportion of home-range area</li> </ul>	<ul style="list-style-type: none"> <li>- High levels of overlap between foraging trips within an individual</li> <li>- High levels of overlap in foraging areas between individuals</li> </ul>

Figure 1. Categories of typical foraging behaviour associated with temperate (and polar) and tropical breeding seabirds. In panels (a) and (c) one foraging trip is shown indicated by black circles, grey shaded areas represent core foraging areas. Panels (b) and (d) show three separate foraging trips (that could be from the same individual or from three different individuals) represented by different shaded circles. The star represents the breeding colony.

while brown boobies at the same site breed in non-cyclical peaks throughout the year. We posit that even in the tropics where prey resources are generally distributed less predictably in space and time, seabirds can still benefit from a breeding strategy characterised by a consistent annual cycle, linked to a foraging strategy based on repeated exploitation of relatively predictable resources. As such, we hypothesise that the foraging behaviour of masked boobies should conform with the norm for temperate and polar seabirds, i.e. predictable foraging behaviour for more predictable resources, likely in association with static environmental features (such as sea mounts and specific sea depths). In contrast, we hypothesise that the asynchronously breeding brown boobies should conform with the stereotype for tropical seabirds foraging over less predictable environmental resources, thus adopting a more plastic foraging behaviour in order to take advantage of less predictable prey resources which may occur at different times of the year. In addition, they will likely exhibit foraging habitat selection based on dynamic environmental variables such as sea surface temperature, which may result in enhanced localised prey availability (Fig. 1).

## Material and methods

### Study area

Dog Island (18.2783°N, 63.2533°W) is an uninhabited tropical island located in Anguilla, a UK Overseas Territory in the eastern Caribbean. Classified as an Important Bird and

Biodiversity area (IBA) (Sanders 2006), Dog island is home to 10 breeding seabird species. The population of brown boobies (approximately 900 breeding pairs) has been recorded breeding in peaks throughout the year with no fixed seasonality (Bright et al. 2014). In comparison the population of masked boobies (approximately 70 breeding pairs) has a prolonged but regular breeding season spanning from March to August with pairs laying at any time during this period, but rarely outside of it (Lowrie et al. 2012). Both species lay up to three eggs but practice obligate siblicide resulting in only one chick being raised (Anderson 1990). In addition, both species reportedly forage on similar prey species (Castillo-Guerrero et al. 2016, Miller et al. 2018, Lerma et al. 2020a)

### Data collection

Bespoke waterproofed GPS data loggers (IgotU, Mobile Action, Taiwan), set to record a GPS position every 120 s, were attached to opportunistically selected brown boobies during each of the six breeding periods that occurred between April 2012 and March 2016, and to masked boobies during the three breeding seasons that occurred between 2014 and 2016 (with two data sets from 2016 representing early (April) and late (June) breeding activity of the population). Over the study period, in total 211 loggers were deployed on brown boobies and 108 on masked boobies; a total of 251 retrieved loggers, had recorded usable data (Table 1). Birds were captured at their nests using a hand held net and loggers were attached to their tail feathers with waterproof Tesa

tape (Wilson et al. 1997). Loggers were only instrumented to adults raising chicks, to avoid the risk of nest desertion during incubation. They were retrieved 4–7 d after deployment. Adults of both species were sexed by beak colour and vocalisation (Young et al. 2010).

## Comparison of foraging behaviour between species and breeding periods

### Foraging trip characteristics

Commonly used foraging trip metrics to describe the foraging behaviour of breeding seabirds include total trip distance, maximum distance travelled from the colony and trip duration (Soanes et al. 2014). However, these metrics are also influenced by population size, with individuals from larger populations more likely to make longer foraging trips that are further away from the colony due to competition effects (Wakefield et al. 2013, Oppel et al. 2015). As our two study populations have markedly different population sizes, we selected foraging trip metrics that are not likely to be as influenced by population size, these were: 1) the size of individual core foraging areas, defined as the 25% utilisation distribution (UD) of each foraging trip calculated in R package ‘AdehabitatHR’ (Calenge 2007), 2) the sinuosity of each foraging trip which was measured as an index of path directness, defined as the ratio of the total distance travelled to the shortest distance to and from the furthest location away from the colony (Benhamou 2004, Zavalaga et al. 2011, Mott et al. 2017) and 3) the ratio of core foraging area (defined as the 25% utilisation distribution) as a proportion of the home range area (95% utilisation distribution) of each foraging trip (referred to from hereon as ‘CFA:HRA ratio’), used as a measure of directed versus area-restricted movement (Weimerskirch et al. 2005). The metrics described above were used to determine if the foraging trips of each species conformed to the typical foraging behaviour associated with tropical or temperate/polar seabirds (Weimerskirch et al. 2005, Oppel et al. 2017, Wiley et al. 2019, Lerma et al.

Table 1. Population size and number of birds tracked along with number of foraging trips recorded during each breeding period for brown and masked boobies.

	Population size	No of loggers deployed	No. of birds tracked	No. foraging trips
Brown booby				
March 2012	1231	20	19	55
November 2013	1518	49	42	223
February 2014	100	28	20	74
October 2014	1482	45	32	185
August 2015	1060	35	30	110
March 2016	922	34	29	123
Masked booby				
August 2014	50	33	17	120
July 2015	41	30	24	207
April 2016 (early breeders)	59	21	19	199
June 2016 (late breeders)	55	24	19	70

2020) (Fig. 1), and to examine if any differences in foraging strategy were apparent between the species.

Generalised estimation equations (GEE) (Liang and Zeger 1986) tested the effect of the following factors 1) species, 2) breeding period and 3) sex on the three foraging trip variables. The effect of sex was included as a factor in this analysis as it has previously been shown to influence the foraging behaviour of boobies (Lewis et al. 2005, Weimerskirch et al. 2009). Our aim was to determine which, if any, of the factors listed above might account for the variation in foraging behaviour that was observed between individuals. All foraging trip variables were transformed with Naperian logs to account for their non-normal distribution. GEEs were used in the analysis since it allows for compound correlation structures to be specified for each individual, in order to account for within-individual correlation. They also are more suitable than the more commonly used general linear models for understanding population effects rather than individual-specific effects (Liang and Zeger 1986). The GEE models were implemented in the R package ‘geepack’ ver. 1.1-6 (Højsgaard et al. 2012).

### Individual and population core foraging area overlap

The foraging areas of an individual or a population may range from widely dispersed to highly concentrated in a relatively restricted area (Young et al. 2015, Oppel et al. 2018). Thus, we assessed the level of spatial aggregation in core foraging areas 1) between trips within an individual and 2) between individuals within a breeding period. The overlap in core areas was quantified using Bhattacharyya’s affinity index (BA) (Fieberg and Kochanny 2005), a non-directional measure of home-range overlap that ranges between 0 (complete separation) and 1 (completely matching probability distributions), and is considered the most appropriate index for quantifying the similarity between utilisation distributions (Oppel et al. 2018). The BA statistic was calculated using rasters representing the 50% utilisation distribution. This allowed a reasonable size of area over which to calculate the similarity index (because the area of overlap reduces markedly with higher UD), while excluding areas of very low usage which are of less interest and may otherwise complicate the interpretation of the calculation (Sansom et al. 2018). Because the BA index is calculated between pairs of foraging trips made by one individual or between pairs of foraging trips made by different individuals within the population, the BA index across all pairwise comparisons were averaged for a given dataset. Kruskal–Wallis tests were used to statistically compare the levels of BA overlap within an individual and between individuals within a population.

### Direction of foraging trips

The direction of each foraging trip (defined as the bearing of the furthest point away from the colony) was determined in ArcMap 10.5.1. In an attempt to ensure that those individuals that made a greater number of foraging trips were



not over-represented in this analysis, we included only the first three foraging trips made by each individual. The uniformity of directions during and between breeding periods and between species was analysed using the directional statistics package Oriana ver. 4.02 (Kovack Computing Services) using Rao's spacing test to determine if direction of foraging trips was uniformly distributed during each breeding period. The Mardia–Watson Wheeler multi-sample test determined if the direction of foraging trips was statistically significantly different between breeding periods (Batschelet 1981) for each species. Mean direction, circular variance and mean vector length ( $r$ ) were used to represent how closely clustered all trip directions were to the mean direction.

## Habitat preferences

### Habitat data

Data representing four environmental variables were downloaded from <<http://marine.copernicus.eu/>>. These were (a) the global ocean OSTIA sea surface temperature (SST) and sea ice analysis dataset (SST\_610\_SST\_L3\_NRT\_OBSERVATIONS\_010\_010) at  $0.005^\circ \times 0.005^\circ$  horizontal resolution), which was used to extract 1) sea surface temperature data for the study area, and (b) the global ocean biogeochemistry analysis and weekly forecast (BIO-001-014) dataset at 0.5 degree resolution which was used to extract 2) net primary productivity of carbon per unit volume ( $\text{g m}^{-3} \text{ day}^{-1}$ ), 3) chlorophyll concentration (chl-a): mass concentration of chlorophyll in sea water ( $\text{mg m}^{-3}$ ) and 4) phytoplankton concentration: mole concentration of phytoplankton expressed as carbon in sea water ( $\text{mmol m}^{-3}$ ). All datasets were downloaded as monthly averages. All of these variables have been reported previously to influence the breeding behaviour of seabirds (Cubaynes et al. 2011, Catry et al. 2013, Hernandez-Vazquez et al. 2017, Poli et al. 2017). A fifth environmental variable of sea floor depth around the breeding colony were also downloaded from the Gebco\_2014 dataset at 30 arc-second intervals from <[www.gebco.net](http://www.gebco.net)>.

### Habitat preference analysis

The four environmental variables described above, along with distance to the breeding colony, were used to evaluate habitat selection to describe foraging locations. A use-versus-availability framework (Kappes et al. 2015, Roeleke et al. 2016, Karelus et al. 2018) compared the foraging areas used by boobies with the foraging areas available to them within their mean maximum foraging range. The mean maximum radius was calculated as the mean of each maximum foraging trip distance recorded in each breeding period and has previously been demonstrated to best reflect seabird colony foraging areas (Soanes et al. 2016), thus reducing the probability that habitat availability data does not adequately reflect usage data (Aarts et al. 2008). The potential availability of resources was derived using the R function *ruinf* to select 10 000 random GPS points (Northrup et al. 2013) from within the mean maximum foraging range of each species. To determine habitat used, a single GPS location

was extracted from the centre of each foraging trip's core foraging area (25% UD polygon) to represent habitat use. Based on the spatial resolution of the environmental data a single GPS point from each core foraging area polygon would adequately represent the entire polygon's environmental characteristics while overcoming the problem of spatial autocorrelation of GPS points from a single individual (Aarts et al. 2008). Using the ArcMap 10.5.1 spatial analysis tool 'extract multi-values to points' the explanatory environmental variables were extracted for both the used and available data sets. Additionally, distance to the colony was calculated for each data point in all data sets using the 'near' tool. Pearson's moment correlation was applied to the data to ensure that potential explanatory variables were not correlated (Pearson's  $[r] < 0.25$ ). Strong correlations were found between sea surface temperature and primary productivity, and sea surface temperature and phytoplankton abundance. Thus, for further analysis only sea surface temperature, chlorophyll-a abundance, sea-floor depth and distance to the breeding colony were used as explanatory variables. All variables were centered and scaled for the analyses. Foraging data were analysed using a mixed-effects hurdle model. Hurdle models are a class of model that specifies one process for zero counts and another process for positive counts (Mullahy 1986). Essentially, hurdle models consist of a binomial 'hurdle' part which estimates the probability of a non-zero count occurring; here this may be thought of as the probability of a habitat patch/foraging area being utilised or not, while the 'count' or Poisson part of the model estimates the distribution of non-zero counts, i.e. the number of uses of a patch possessing given environmental properties or, alternatively, if a patch is used, how many times. This approach is suitable because the data exhibit a naturally high degree of zero-inflation and the models allow for patch choice to be analysed independently of patch use. Individual identity was chosen as a random effect operating on both parts of the model, the intention of which was to remove individual foraging preferences as we were interested in population-level responses. The model was implemented using the MCMCglmm v.2.29 package (Hadfield 2010) in the R statistical environment v.3.6.1 (<[www.r-project.org](http://www.r-project.org)>). A Bayesian framework was chosen as the sampling process is robust when data exhibit high levels of over-dispersion, as they do here, and also provide robust 95% confidence intervals during the posterior sampling process. The specified prior was parameter expanded and allowed for random slopes and unequal variances for each individual; this allowed for estimation of individual-level correlation in both parts of the model. The model sampled every 60th iteration for  $3.0 \times 10^6$  iterations after a  $5.0 \times 10^5$  burn-in. Convergence was assessed through inspection of trace plots.

## Results

Loggers were retrieved from 172 brown boobies and 79 masked boobies recording 770 and 596 foraging trips,

respectively. Loggers that were not retrieved had fallen off the birds before recapture was possible (Table 1), none of the nests of tracked birds were abandoned during the tracking period.

### Differences in foraging behaviour between species

There were significant differences between masked and brown boobies in the size of core foraging areas and the CFA:HRA ratios. Individual brown boobies had core foraging areas on average 2–3× larger ( $F_1=158.2$ ,  $p < 0.01$ ) (Fig. 2a), than those of masked boobies suggesting that their foraging was less concentrated. However, the size of their core foraging area was a slightly lower proportion of their home range area (CFA:HRA ratio) than was the case for masked boobies ( $F_1=18.5$ ,  $p \leq 0.01$ ) (Fig. 2d). The level of foraging trip sinuosity did not differ between species ( $F_1=2.1$ ,  $p=0.2$ ).

The level of core foraging area overlap within individuals was not significantly different when comparing masked and brown boobies ( $\chi^2_1=1.7$ ,  $p\text{-value}=0.2$ , Fig. 2b). However, the level of core foraging area overlap between individuals from the same population in the same breeding period was higher for masked boobies ( $\chi^2_1=6545.1$ ,  $p\text{-value}=0.01$ ) (Fig. 2c), suggesting that the population of masked boobies used a more similar area to forage than the population of brown boobies.

Directions travelled during each breeding period were not uniformly distributed around the breeding colony within any breeding period for brown boobies or masked boobies ( $p < 0.01$  in all cases; Supporting information, Fig. 3).

### Differences in foraging behaviour between breeding periods

Statistically significant differences were observed between breeding periods in the size of core foraging areas (Supporting information) for both brown (Fig. 4a) and masked boobies (Fig. 4b) with greater variability in brown boobies than in masked boobies. No statistically significant differences were reported between breeding periods in the CFA:HRA ratios for either brown boobies ( $\chi^2_5=5.8$ ,  $p\text{-value}=0.3$ ) or masked boobies ( $\chi^2_3=0.7$ ,  $p\text{-value}=0.9$ ).

The level of core foraging area overlap within individuals did not vary between years for either brown boobies ( $\chi^2_5=4.6$ ,  $p\text{-value}=0.5$ ) or masked boobies ( $\chi^2_3=1.1$ ,  $p\text{-value}=0.8$ ). Significant differences were found between years in the level of population core foraging area overlap for both brown boobies ( $\chi^2_5=2791.8$ ,  $p\text{-value} < 0.01$ , Fig. 4c) and masked booby ( $\chi^2_3=2146.8$ ,  $p\text{-value} < 0.01$ , Fig. 4d). However, the Mardia–Watson–Wheeler test did reveal statistically significant differences in the directions travelled between breeding periods for both brown boobies ( $W=125.1$ ,  $p < 0.001$ ) and masked boobies ( $W=131.9$ ,  $p < 0.01$ ). Although, mean foraging trip directions were more clustered for masked boobies than brown boobies (Supporting information).

### Differences in foraging behaviour between sexes

The sex of the bird only significantly affected the trip sinuosity of brown boobies, with males exhibiting more sinuous flight

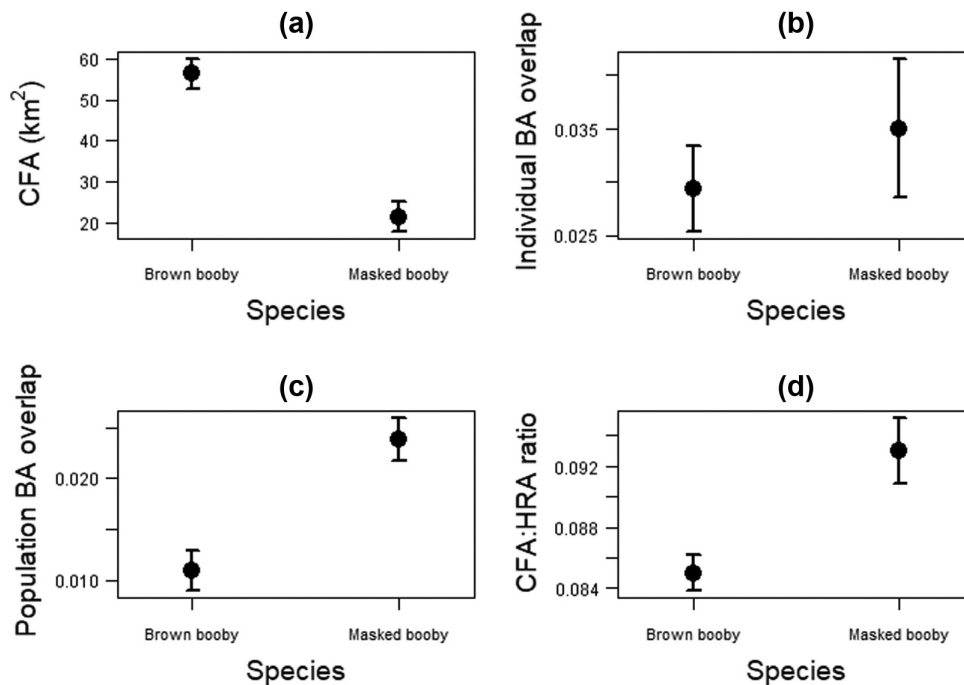


Figure 2. Brown boobies foraged more unpredictably than masked boobies indicated by (a) larger core foraging areas and lower levels of core foraging area overlap (b) within and (c) between individuals within a breeding period. However, core foraging area as a proportion of home-range area was lower for brown boobies indicating a more direct (commuter-style) foraging trip (d). Means and standard errors derived from GEE models are represented.

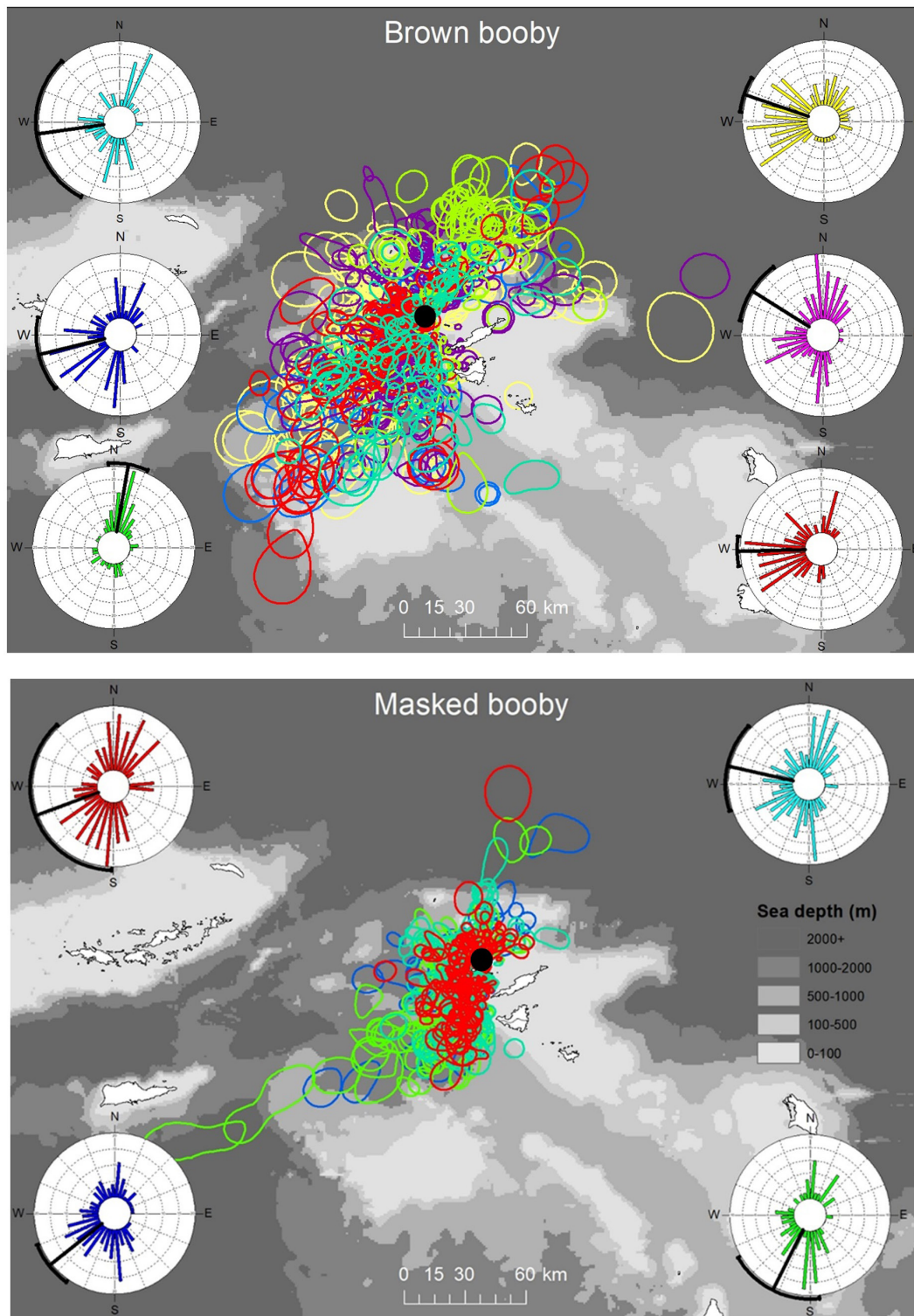


Figure 3. Foraging movement of tropical boobies from Dog Island, eastern Caribbean ( $18.2783^{\circ}\text{N}$ ,  $63.2533^{\circ}\text{W}$ ). Brown boobies exhibit greater variability in their foraging behaviour and foraging areas within breeding seasons than masked boobies. The main illustration in each panel presents the individual core foraging areas (25% utilisation distribution) of the sampled boobies during all breeding periods. Each colour represents a different breeding period. The colours for each breeding period are coded to the peripheral, circular histograms. These histograms show the direction of foraging trips recorded from each tracking period. The black anchor in each histogram indicates mean direction travelled, and the arcs extending either side of this mean represent the 95% confidence limits. Black circle represents location of breeding colony. Maps are overlaid on bathymetric maps of the area downloaded from [www.gebco.net](http://www.gebco.net).

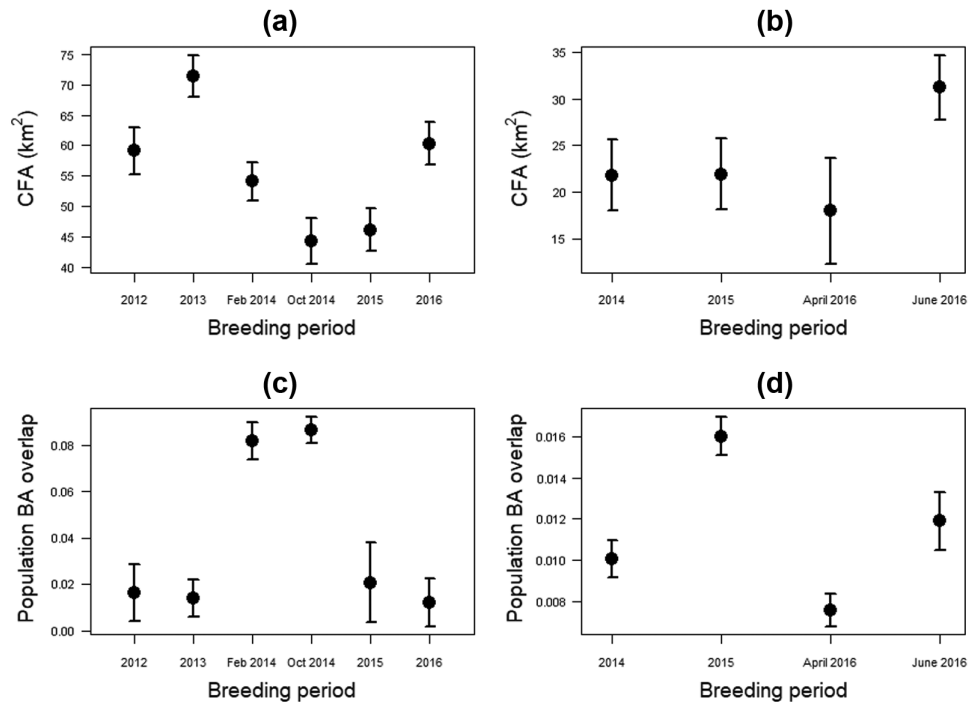


Figure 4. The size of core foraging areas (a–b) and core foraging area overlap (c–d) differed significantly between each breeding period for both brown (a and c) and masked boobies (b and d). Means and standard errors derived from GEE models are presented.

paths than females ( $F=10.1$ ,  $df=1$ ,  $p < 0.01$  (Supporting information)). All other factors were not influenced by sex for either species.

### Habitat use

The results of the hurdle model can be thought of as representing two processes with regards to foraging; the first (binomial) part relating to patch choice and the second (Poisson) part relating to patch use. All results are summarised in Table 2, Fig. 5. Here we found that the model converged well and significant effects were identified (Intercept:  $1.44 \pm 0.22$ ;  $p_{\text{MCMC}} < 0.001$ ). Concerning patch choice, the only significant effect found was a negative response to SST for brown boobies ( $p_{\text{MCMC}}=0.015$ ). All other responses were found to be not statistically different from zero. For all environmental variables there were significantly different effects on patch use for both species; for brown boobies there were negative effects found for SST, sea depth and distance from the colony (all  $p_{\text{MCMC}} < 0.001$ ) and a significant positive effect of chlorophyll ( $p_{\text{MCMC}} < 0.001$ ), whilst for masked boobies the opposite was found, with positive effects of SST ( $p_{\text{MCMC}} < 0.001$ ), sea depth ( $p_{\text{MCMC}}=0.012$ ) and distance from the colony ( $p_{\text{MCMC}} < 0.001$ ), and a negative effect of chlorophyll ( $p_{\text{MCMC}} < 0.001$ ).

### Discussion

Tropical breeding seabirds exhibit markedly different breeding strategies between species and sometimes also populations. We hypothesised that these differing breeding

strategies associate with differing foraging strategies, in that tropical seabirds that breed on an annual cycle also forage predictably, while seabirds that breed asynchronously forage unpredictably. Thus, for the seasonal breeding masked boobies in Anguilla, we hypothesised that foraging behaviour resembles the more predictable foraging behaviour associated with temperate and polar seabirds, and for the asynchronous breeding brown booby in the same location we hypothesised that foraging behaviour resembles the more unpredictable foraging behaviour typically associated with tropical seabirds. The multiple strands of evidence arising from our analyses of 9 breeding seasons consistently support these hypotheses. Our study highlights that the foraging behaviour of tropical seabirds is more complex than the general assumption that tropical seabirds forage unpredictably and suggests that there may be close links between foraging and breeding strategies in this guild.

The brown booby population that we studied, which has a non-seasonal ('tropical') breeding strategy, exhibited foraging trips that vary not only within and between individuals, but also between breeding periods. As a result, brown boobies exhibited less population-level overlap in core foraging areas than did masked boobies. The core foraging areas of brown boobies were larger than those used by masked boobies, but the proportion of their home range area used for foraging on each trip was lower (represented by the CFA:HRA ratio). Brown boobies selected foraging areas (patch choice) with lower temperatures than were available within the mean foraging distance from the breeding colony. Of the foraging areas used by brown boobies (patch use) those patches with



Table 2. Hurdle-modelled effects of environmental variables on patch choice and patch use in foraging for brown and masked boobies. Significance values are Bayesian p-values ( $p_{\text{MCMC}}$ ).

Model	Species	Variable	Estimate	L-95% CI	U-95% CI	$P_{\text{MCMC}}$
Patch choice	Brown booby	Intercept	1.443	1.212	1.666	< 0.001***
		SST	-0.431	-0.777	-0.076	0.015*
		Chlorophyll	0.241	-0.218	0.691	0.449
		Depth	-0.207	-0.434	0.034	0.303
		Distance	0.039	-0.065	0.148	0.284
	Masked booby	SST	-0.012	-0.044	0.019	0.086
		Chlorophyll	-0.034	-0.096	0.030	0.165
		Depth	0.159	-0.077	0.382	0.487
		Distance	0.072	-0.098	0.245	0.380
		Patch use	Brown booby	SST	-2.910	-3.608
Chlorophyll	3.821			3.130	4.517	< 0.001***
Depth	-1.344			-1.673	-1.016	< 0.001***
Distance	-2.951			-3.283	-2.638	< 0.001***
Masked booby	SST			4.523	3.493	5.701
	Chlorophyll		-2.016	-2.600	-1.477	< 0.001***
	Depth		0.859	0.217	1.511	0.012*
	Distance		4.685	3.798	5.605	< 0.001***

higher chlorophyll a concentration, and that were shallower and closer to the colony were utilised to a greater extent. Masked boobies, in contrast, foraged less broadly across the seascape, did not associate with dynamic environmental variables at the wider foraging area scale and exhibited higher levels of individual and population overlap within and between years. They also had more defined and smaller core foraging areas. However, the proportion of each trip's home range area

used for foraging was higher for masked boobies. This may be driven by foraging areas of brown boobies being further from the colony, but the confound between population size and distance to foraging areas would make this hard to analyse and interpret.

Differences in the foraging strategies adopted by closely related tropical breeding seabird species at the same colony and the same species breeding at different colonies have

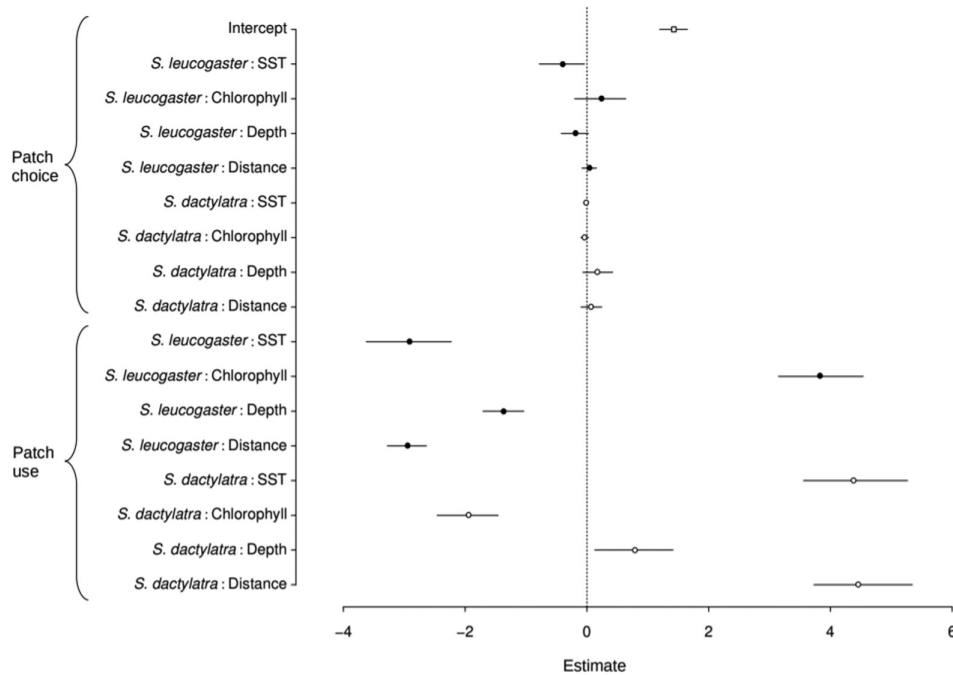


Figure 5. Brown boobies selected foraging areas (patch choice) with lower sea surface temperatures than those available to them, while masked boobies did not exhibit a preference for any of the environmental variables tested. However, for all environmental variables there were significant effects on patch use for both species. With brown boobies utilising to a greater extent patches that were shallower, closer to the colony with higher chlorophyll-a abundance, while the opposite was found for masked boobies. Points are estimated mean response and whiskers are Bayesian 95% credible interval.

been previously related to niche partitioning (Young et al. 2010, Ponton-Cevallos et al. 2017) and a variable reliance on sub-surface predators (Miller et al. 2018). For example Mendez et al. (2017) reported on the variable foraging behaviour of red footed boobies across six study colonies and suggested that these differences were related to intra- and inter specific competition. While Miller et al. (2018) suggested that short-tailed shearwaters *Puffinus tenuirostris* breeding at a tropical colony exhibited more dependence on a facilitative foraging strategy with tunas, while the foraging behaviour of individuals breeding at a sub-tropical colony was more associated with enhanced productivity. In short, species that are in competition for shared ephemeral resources have evolved different strategies to operate simultaneously in the same environment. Our data suggest that at Dog Island, both the foraging and breeding strategies of brown and masked boobies have diverged. As a result, we propose that the observed differences in foraging strategy are likely to be causally associated with the differences in their breeding behaviour.

The seasonal breeding masked booby appears to be making use of more predictable prey resources that occur at the same time each year, or related to warmer sea surface temperatures and/or the seasonal abundance of prey fish. Thus, masked boobies adopted a more predictable style of foraging behaviour, indicative of a more predictable prey resource with greater overlap in individual and population core foraging areas, and smaller core foraging areas. Indeed, the greater degree of overlap between individuals of these smaller foraging areas, despite the much smaller population size, strongly suggests a greater clustering of foraging activity within the masked booby population. It appears that masked boobies have a foraging strategy more based on memory, visiting the same localised, seasonally predictable foraging areas and searching for prey frequently within a small area until they encounter a profitable prey patch (Grunbaum and Veit 2003, Yoda et al. 2011, Boyd et al. 2016). In contrast, brown boobies, which breed at any time of the year, exhibit more behavioural flexibility presumably as they respond to the less predictable prey resources which vary in space between breeding periods, but may be associated with localised patches of lower sea surface temperature which indicate ephemeral prey patches, likely facilitated in part by a conspecific or heterospecific local enhancement (Grunbaum and Veit 2003). Indeed, recent evidence from video data loggers suggests that brown boobies frequently forage as part of mixed species aggregations (Austin R. E. et al. unpubl.). This divergence in coupled breeding and foraging strategy allows for coexistence between the species, though arguably the strategy adopted by the brown booby is more successful, as evidenced by the larger population size. This may explain why brown boobies tend not to copy the use of predictable foraging locations used by masked boobies, the opportunity for which is further reduced by relatively low temporal overlap in breeding seasons.

Accepted wisdom states that tropical seabirds forage unpredictably and without focussing on particular areas of the sea (Weimerskirch 2007, Oppel et al. 2015, Nunes et al. 2018). However, our study reveals that during each breeding

season, both brown and masked boobies exhibit a non-uniform distribution of movement around Dog Island, suggesting a non-random, perhaps partly predictable distribution of prey. Prey predictability, however, is a matter of scale (Weimerskirch 2007, Deppe et al. 2014, Sommerfeld et al. 2015), and masked boobies show subtly greater differences in their foraging predictability within and between breeding seasons than do brown boobies. Our study highlights some of the considerable variability in breeding and foraging strategies adopted by tropical seabirds, which are only just starting to be recognised and explored (Monteiro and Furness 1998, Mendez et al. 2017, Fagundes et al. 2016, Miller et al. 2018), and which probably associate with attempts to optimise energy flow from the environment to the reproductive output (Suryan et al. 2006, Kappes et al. 2011, Ruzicka et al. 2012). However, as noted above, different breeding and/or foraging strategies adopted by a population may not be equal in terms of inferred benefits to survival and breeding success. Both species in this study nest on the same predator-free island, which appears to have considerable space for additional nests at all times of year, and both species are ground-nesting seabirds that often nest in mixed colonies, both also appear to have the ability to adopt flexible foraging strategies, as can be observed from their behaviour as both nearshore and pelagic foragers across their range (Sommerfeld et al. 2015, Soanes et al. 2016, Poli et al. 2017). Despite this, the masked booby breeding population is considerably smaller than the brown booby breeding population. Further investigation is required to examine the determinants and benefits of the different foraging and breeding strategies adopted by these two phylogenetically close yet behaviourally disparate species.

It is now clear that tropical seabirds do not exhibit a ‘one size fits all’ foraging strategy. Despite the increasing number of published datasets of tropical seabird tracks, our understanding of the variability in tropical seabird foraging behaviour is limited. Here, we have suggested links between foraging behaviour and environmental features, but this is only a start. A review of the current literature to investigate the differences in foraging behaviour of seabirds breeding at different latitudes should provide generalizable insights into how specific seabird foraging strategies relate to the details of their local environment and what impacts this may have for global seabird conservation.

*Acknowledgements* – We would like to thank the Anguilla National Trust staff and volunteers for assisting with fieldwork.

*Funding* – This work was undertaken with permission from the Government of Anguilla and funded by the UK’s Darwin plus initiative (DPLUS0007) and a Leverhulme Early Career research grant (‘The curious case of asynchronous breeding in tropical seabirds’).

## Author contributions

**Louise Soanes:** Conceptualization (lead); Data curation (lead); Formal analysis (equal); Funding acquisition (equal);

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### Transparent Peer Review

The peer review history for this article is available at <<https://publons.com/publon/10.1111/jav.02670>>.

### Data availability statement

Data are available from <[https://www.movebank.org/cms/webapp?gwt\\_fragment=page=studies,path=study15706394](https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study15706394)>, <[https://www.movebank.org/cms/webapp?gwt\\_fragment=page=studies,path=study70671296](https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study70671296)>

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