



Flexible foraging behaviour in a marine predator, the Masked booby (*Sula dactylatra*), according to foraging locations and environmental conditions



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ARTICLE INFO

Article history:

Received 25 July 2014

Received in revised form 8 November 2014

Accepted 11 November 2014

Available online 26 November 2014

Keywords:

Behavioural flexibility

Diving behaviour

Foraging movements

Marine predators

South-west Pacific

ABSTRACT

Flexible foraging behaviour allows marine predators to exploit shifting prey diversity and adjust to spatio-temporal changes in the distribution of prey. In diving marine predators, the number of dives within a dive bout, distances between dives in a bout and distances between bouts have been related to prey patch size, density of prey patches and prey encounter rates, respectively. In addition, the predictability of prey encounters can be examined by studying individuals' foraging site fidelity. Based on this, we examined in chick-rearing Masked boobies (*Sula dactylatra*) from Phillip Island (South-west Pacific), Australia, using GPS and depth–acceleration data logger, how these parameters changed over time (two early breeding phases and one late phase over two years) and according to foraging locations and environmental conditions. Results revealed that birds foraged in two distinct areas: over a nearby shallow shelf (“local area”) and over distant deeper waters (“distant area”). Birds searched for prey in the distant area only during the two latest study periods, indicating less favourable foraging conditions within the local area during this time, although persistent higher chlorophyll-*a* concentrations in the local area were indicative of an upwelling. Our data suggest that birds experienced a trade-off between local and distant trips: although the strong foraging site fidelity within the local area suggests that prey encounters were predictable, smaller dive bouts indicated smaller prey patches, i.e. less prey nearby the colony during the two latest study periods. As a consequence, adults undertook distant trips to forage in larger prey patches, as inferred from larger dive bouts, but distances between these dive bouts were more variable and birds showed no foraging site fidelity, indicating less predictable prey encounters. Local trips presumably allow a high feeding frequency of the chick, while distant trips allow adults to replenish their own body reserves. Observed changes in foraging conditions, although the underlying causes were not determined, appear to be within the eco-physiological limitations of Masked boobies. However, further studies are required to determine the degree of this limitation, especially as changes in the spatio-temporal availability of prey can be expected to increase with global warming and changing oceanic processes.

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1. Introduction

Marine predator foraging behaviour depends largely on the distribution, abundance and reliability of their prey (Staniland et al., 2006), but also on intrinsic factors such as body mass, sex (Hindell et al., 1991; Kato et al., 2008) and breeding stage (Shaffer et al., 2003; Williams and Siegfried, 1980). As marine food resources are scarce and often patchily

distributed (Ashmole, 1971), flexibility in the diet and foraging behaviour is particularly important, as it allows individuals to exploit shifting prey diversity and adjust to changing spatio-temporal distributions of prey (Bowen et al., 2006; Boyd, 1996; Croxall, 1987; Montevecchi et al., 2009). The influences of marine resource patchiness and of spatio-temporal changes therein on predator foraging behaviour are therefore central questions in ecology (Fauchald, 1999; Senft et al., 1987).

Marine predators may increase their foraging efficiency by associating particular meso-scale oceanographic features, such as seamounts, fronts, shelf-edges, eddies or upwelling, with predictable prey encounters and returning repeatedly to such locations (see Hunt et al., 1999 for review; Bradshaw et al., 2004; Weimerskirch, 2007). The knowledge

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of such prey encounters, however, often decreases with distance and/or increasing spatio-temporal variation in resource distribution patterns (Fauchald, 1999). Foraging site fidelity in the Wandering albatross (*Diomedea exulans*) for instance, is related to the distance between the colony and the feeding grounds, with individuals being more faithful to nearby foraging sites and less faithful to more distant sites (Weimerskirch, 2007). The longer it takes for an individual to return to the same foraging ground, the more likely that food resources may have moved (actively or passively) or been depleted (but see foraging site fidelity in Wandering and Black-footed albatrosses (*Phoebastria nigripes*) in Weimerskirch, 2007 and in Fernández et al., 2001).

In diving marine predators, the foraging activity can be separated into distinct sequences of activity, i.e. dive bouts (e.g. New Zealand fur seals *Arctocephalus forsteri* Harcourt et al., 2002; Cape gannets *Morus capensis*, Ropert-Coudert et al., 2004; Peruvian boobies *Sula variegata* and Guanay cormorants *Phalacrocorax bougainvillii*, Weimerskirch et al., 2012). Both dive bout size (i.e. number of dives within a bout) and the distances between feeding events within a dive bout have been related to the size and the density of prey patches, respectively (Boyd, 1996; see Mori, 1998 for a theoretical approach to predict prey patch size from dive bout characteristics; Weimerskirch et al., 2007). Based on this assumption, the higher the number of dives within a dive bout, the larger the size of the prey patch; the smaller the distances between dives within a bout, the higher the density of prey within a patch. Furthermore, distances between bouts, that is, the distance an animal has to travel to find the next available prey patch, can be used as a proxy for prey encounter rates, as the distances marine predators travel between prey patches should increase when prey patches are more dispersed (Boyd, 1996). Consequently, inferences can be drawn about the size, density and distribution of prey patches by investigating dive bout characteristics in diving predators (Boyd, 1996; Harcourt et al., 2002), while the predictability of prey encounters can be examined by studying foraging site fidelity (Weimerskirch, 2007). The investigation of dive bout characteristics as a proxy for prey availability and distribution may be used in regions where information about prey cannot be obtained any other way (e.g. through commercial fisheries), although the degree to which dive bout characteristics reflect the true spatio-temporal distribution of prey remains, to some extent, uncertain without direct observation of adults foraging at sea and in-situ information on the spatio-temporal distribution of prey (Boyd, 1996).

Pan-tropical Masked boobies (*Sula dactylatra*) are a suitable species to investigate flexible foraging behaviour in marine predators. Firstly, their foraging movements vary considerably between populations (Sommerfeld et al., 2013; Weimerskirch et al., 2009; Young et al., 2010), most likely due to differences in the availability and distribution of prey near the colonies. This suggests that Masked boobies are capable of adjusting their foraging behaviour according to the prevailing conditions, as was also found in other seabirds (Falk et al., 2002; Peck and Congdon, 2006). Secondly, birds forage mainly by plunge diving (Nelson, 1978), which facilitates the detection and analyses of dives, and thus dive bouts, by means of pressure recording data devices. In the present study, the seasonal and annual flexibility in the foraging behaviour of chick-rearing Masked boobies is examined at Phillip Island (29°02'S, 167°57'E) of the Norfolk Island Group, Australia (South-west Pacific). The duration of foraging trips, foraging ranges and distances travelled are measured and compared within and between two breeding seasons. Based on the assumption that dive bout characteristics reflect prey patch characteristics, we analyse (I) dive bout size and (II) distances between successive dives within a dive bout, as proxies for prey patch size and density, respectively, (III) distances between successive dive bouts as a proxy for prey encounter rates, and (IV) foraging site fidelity between successive foraging trips and seasons to assess the reliability of prey encounters. Satellite images are used to assess whether foraging grounds are static or change within and among seasons with respect to sea surface temperature (SST) and chlorophyll-*a* (CHL) concentration.

2. Material and methods

2.1. Study site and species

Masked boobies were studied on Phillip Island in the South-west Pacific Ocean. Phillip Island (190 ha) is part of the Norfolk Island Group, Australia, located approximately 1670 km north-east of Sydney, Australia and 1070 km north-west of Auckland, New Zealand. This group of islands lies on top of the Norfolk Island Ridge, where water depths range from only several metres to >5000 m (Williams et al., 2006).

Masked boobies are the largest of all boobies and exhibit reversed-sexual dimorphism (RSD, where females are larger than males, Nelson, 1978). Females lay two eggs, but generally only one chick is reared through obligate siblicide (Dorward, 1962). The breeding season of Masked boobies is protracted, with chicks hatching between early September and late March, although the majority of chicks hatch between October and December (Hermes et al., 1986; Priddel et al., 2010).

Birds were studied in three fieldtrips over two successive breeding seasons: (1) between 28–Oct–2009 and 07–Nov–2009, corresponding to the early phase/peak of the breeding season (hereafter *E1*), (2) between 12–Feb–2010 and 03–March–2010, corresponding to the late phase of the same breeding season (hereafter *L1*), and (3) between 27–Oct–2010 and 10–Nov–2010, corresponding to the early phase/peak of the following breeding season (hereafter *E2*). Adults were rearing chicks between 1 and 9 weeks of age during October and November 2009, between 3 and 11 weeks of age during February and March 2010 and between 2 and 7 weeks of age during October and November 2010.

2.2. Data devices and deployment

Three different types of GPS loggers were used to study the foraging movements of Masked boobies: (1) CatTraQ GPS logger (44 × 27 × 13 mm, 22 g, Catnip Technologies, P.O. Box 383, Anderson, SC 29622, USA), (2) Sirtrack Micro GPS logger (64 × 33 × 14 mm, 18 g, Havelock North, New Zealand) and (3) Earth & Ocean GPS data loggers (46 × 32 mm, 20 g, Earth & Ocean Technologies, Kiel, Germany). CatTraQ loggers recorded time, latitude and longitude every 2 min, Sirtrack loggers every 5 min and Earth & Ocean loggers every 4 min. All three devices record highly accurate positions within ± 5 to 10 m. This allowed a comparison of the tracks between the study periods. CatTraQ and Sirtrack loggers were only deployed during *E1* (Table 1). Each CatTraQ unit was put in a heat-shrink tube for waterproofing. GPS loggers were attached on the top of three central tail feathers using waterproof adhesive TESA® tape (Beiersdorf AG, GmbH, Hamburg, Germany) to minimize the damage to the feathers (Wilson et al., 1997).

Cylindrical four channel depth–acceleration loggers (M190-D2GT, 12 bit resolution, 53 × 15 mm, 17 g, Little Leonardo, Tokyo, Japan) were used to study activity patterns of Masked boobies in *L1* and *E2*, simultaneously recording depth (1 Hz), temperature (1 Hz) and acceleration (16 Hz) along two axes. The relative accuracy for the depth sensor was 0.1 m. The loggers contained an acceleration sensor measuring both dynamic (e.g. vibration) and static (e.g. gravity) accelerations. Loggers were attached underneath three central tail feathers (in addition to GPS logger attached on the top) using TESA® tape to measure the surging acceleration along the longitudinal body axis and heaving acceleration dorso-ventrally (for details, see Watanuki et al., 2003; Ropert-Coudert et al., 2004).

Attachment weight, including tape, was 55 g (range 45–60 g, *n* = 49), corresponding to 2.3% of female mean body mass (2436 g, range 2085–2870 g, *n* = 21) and 2.4% of male mean body mass (2108 g, range 1685–2750 g, *n* = 28), which is below the generally accepted 3% (Phillips et al., 2003; Wilson and McMahon, 2006; but see Vandenabeele et al., 2012). Either the female or the male within a pair was chosen randomly and captured with a noose-pole. Adults were

Table 1

Number of Masked boobies equipped with GPS (CatTraQ, Sirtrack or Earth & Ocean) and depth–acceleration logger (DAC) and complete foraging trips recorded during early (*E1*) and late phases (*L1*) of the first breeding season and early phase of the following breeding season (*E2*).

Breeding season	Device type	No. birds equipped	No. complete trips with position and dive data	No. complete trips with position data only
<i>E1</i>	CatTraQ + Sirtrack	21	0	23
<i>L1</i>	Earth & Ocean + DAC	15	23	3
<i>E2</i>	Earth & Ocean + DAC	13	33	5
Total	All devices	49	56	31

sexed using their vocalizations (males have a distinctive higher pitched voice than females) and by measurements (males are smaller than females within a pair) (Nelson, 1978). At first capture, birds were weighed using a spring balance (Pesola®, maximum deviation $\pm 0.3\%$ of load) and colour-marked on the breast with a green or blue sheep crayon for identification of the equipped individual in the field. Non-banded adults were banded with a metal leg band (Darvic®, Australian Birds and Bats Banding Scheme). After attachment of the loggers, adults were released onto their nests. Handling time during deployment and retrieval of loggers was ca. 10–12 min. After handling, birds were released onto their nests. In only three out of 49 birds (6%) did the released bird take off, returning after maximum of 5 min to their nest (nest were observed until birds returned). All data loggers were retrieved after 1–4 days, recording 1–4 successive foraging trips. To minimize disturbance, only one individual in a pair was studied and individuals were never studied twice. No nests were deserted during the entire duration of the study and all loggers were retrieved successfully.

2.3. Foraging areas and coarse-scale foraging site fidelity

Most studies define coarse-scale foraging site fidelity as the proportion of birds that re-visited the same 1–100 km² area from one trip to the next (see Weimerskirch, 2007 for definition of coarse-scale foraging site fidelity). As we have both the foraging tracks and exact dive locations, we defined foraging site fidelity as follows: firstly, all foraging tracks and all dive locations were plotted on a map and overlaid with 0.25° grid cells (each 0.25° grid cell corresponding to approximately 28 km²). Secondly, foraging site fidelity was defined as the proportion of birds that dived within the same site from one foraging trip to the next, the location of at least one of the dives being within the same 0.25° grid as during the previous trip. We decided to use exact diving locations within a 0.25° grid, rather than the wider visited area, as we were interested to which extent birds re-used the same diving area. A grid size of 0.25° was chosen by visually inspecting birds' foraging ranges.

2.4. Dive characteristics

Depth data were analysed using IGOR Pro 6.21 (Wavemetrics software, Portland USA). All dives <0.2 m were excluded from the analyses. Dive bouts were determined using a bout ending criteria following Gentry and Kooyman (1986). Briefly, dives from all individuals were pooled and the dive bout ending criteria defined using the first inflection in a log-survivorship curve of post-dive intervals (Gentry and Kooyman, 1986). This corresponded in Masked boobies to an inflexion point of 780 s, allowing us to define discrete dive bouts. The start of a bout corresponded to the first dive, so that single dives corresponded to bouts of size "1" (taken to indicate the lowest prey patch size).

Dive rates corresponded to the total number of dives divided by the time spent at sea (excluding hours of darkness for overnight trips) within each 0.25° grid during each foraging trip.

Distances between dives in a bout were calculated as the linear distance between two dive locations and used as a proxy for prey density

within a patch. Distances between bouts were calculated as the linear distance between the mean locations of two bouts and used as a proxy for prey encounter rates.

2.5. Environmental data and foraging habitat characteristics

Three different environmental variables downloaded from <http://coastwatch.pfeg.noaa.gov/erddap> were selected to characterize birds' foraging habitat: (1) bathymetry, (2) SST and (3) CHL concentration (SST and CHL as proxies for the regions productivity). Monthly composites of daytime SST and surface CHL concentration were obtained from Aqua MODIS satellite images, provided at 0.05° spatial resolution. Bathymetry (Global topography, ETOPO1) was obtained at a 0.01° spatial resolution. For comparison of environmental characteristics between foraging areas (see Results section), bathymetry, monthly SST and CHL values were averaged for each 0.25° grid located within each foraging area.

2.6. Statistical analysis

All statistical analyses were performed using R 2.15.1 (R Development Core Team, 2012). Generalized linear mixed models (GLMMs, Faraway, 2006), generalized linear models (GLMs) and linear mixed models (LMMs, Pinheiro and Bates, 2004) were applied using the functions *glmer* and *glm* in R package *lme4* (Bates et al., 2011) and *lme* in R package *nlme* (Pinheiro and Bates, 2004), respectively. To test for differences in the duration of foraging trips between seasons, a LMM with \log_{10} transformed trip duration as a response variable, season as a fixed effect and bird ID as a random factor to account for pseudo-replication, was applied. Dive bout size, total number of dives and the number of dive bouts per trip were included in the GLMM as response variables with a Poisson error distribution. Dive rates, distances between dives within a bout and distances between dive bouts were \log_{10} transformed and analysed in a GLMM with a normal error distribution. Foraging areas (see Results section) and season were included as explanatory variables, with bird ID nested within each unique 0.25° grid as a random factor. To compare the variances in dive bout size, dive rate and distances between bouts, an *F* test was performed. We tested for significant differences in water depths between foraging areas (see Results section) using a LMM with bathymetry as a response variable, foraging area as a fixed effect and grid cell ID as a random effect. To test for differences in SST and CHL (response variables) between foraging areas (see Results section) and among seasons, we included an interaction between the foraging areas and seasons in the model and used grid ID as a random effect. Model assumptions were checked following Crawley (2007). All tests were two-tailed, with a significance level of $p < 0.05$. Mean (\pm SD) results are reported.

3. Results

3.1. Foraging areas and site fidelity

Of the 49 equipped birds, eight made overnight trips: one male in *E1*, one female in *L1*, and four males (with one male spending two nights at

sea) and two females in *E2*. Four of these overnight foraging trips were excluded from the dive data analysis, three due to battery exhaustion in the depth–acceleration loggers before birds returned to the colony, and a further one as the male in *E1* had only a GPS attached with no depth recorder. The total number of equipped birds and foraging trips recorded with GPS and depth–acceleration loggers is summarized in Table 1. Due to low sample size, the effect of sex on foraging parameters could not be tested. Data of both sexes were therefore pooled.

A classification analysis of the foraging trips revealed two groups of foraging areas relative to trip duration and water depth (ANOVA $F_{1,253} = 77.64$, $p < 0.001$): one area over the nearby shallow shelf in trips < 5 h and mean bathymetry of 579.3 ± 489.2 m (range 1466 to 38.1 m, $n = 44$ trips; hereafter referred to as the “local foraging area” and “local foraging trips”; Fig. 1) and the other area located over distant, deeper waters in trips > 5 h and mean bathymetry of 2732.7 ± 765.6 m (range 4033.9 to 676.2 m, $n = 43$ trips; hereafter referred to as “the distant foraging area” and “distant foraging trips”; Fig. 1). This resulted in a local foraging area of approximately 250 km^2 ($9 \times 0.25^\circ$ adjacent grids) located, except for one grid, to the south of Norfolk Island (Fig. 2). The distant foraging area measured approximately 1150 km^2 in size ($41 \times 0.25^\circ$ grids) (Fig. 2).

In *E1*, Masked boobies concentrated their foraging activity almost exclusively within the local foraging area to the south of Norfolk Island, whereas in *L1* and predominantly in *E2*, numerous long displacements were observed to the north, with few trips to the south (Fig. 2). Irrespective of these very distinctive foraging movements, both types of trip (local and distant, see Table 2) were of similar durations across the three study periods (ANOVA $F_{2,25} = 2.35$, $p = 0.116$, $F_{2,25} = 1.17$, $p = 0.325$, respectively). Foraging ranges of trips were similar between study periods within groups (local and distant: ANOVA $F_{2,25} = 0.31$, $p = 0.736$ and $F_{2,25} = 1.61$, $p = 0.220$, respectively), although the maximum foraging range in distant trips was almost four times greater in *E2* than in *E1* (Table 2). The total distance that the birds travelled did not differ significantly between study periods (ANOVA $F_{2,25} = 0.65$, $p = 0.531$ and $F_{2,25} = 2.02$, $p = 0.154$, respectively) (Table 2).

In 14 out of 24 individuals (58%) more than one foraging trip was recorded within the local foraging area ($n = 43$ foraging trips). Out of the 14 individuals, 10 (71%) dived within 28 km (i.e. within the same 0.25° grid) of their previous dive location, indicating high foraging site fidelity, while the remaining four individuals dived within 56 km of their previous location. Conversely, in only four out of 12 individuals (33%) successive foraging trips were recorded outside the local foraging area. Of these four individuals, one adult had at least one dive within 28 km, one adult dived within 56 km and two adults dived within 112 km of their previous dive locations.

3.2. Foraging habitat characteristics

Sea-surface temperatures were similar between both foraging areas in *E1* and *L1*, but highest overall in *L1* (Fig. 2). Whereas in *E2*, SST was significantly lower within the local foraging area than it was in the distant area, as indicated by the significant interaction between foraging areas and the three study periods (LMM $\chi^2 = 103.318$, $df = 3$, $p < 0.001$) (Fig. 2, Table 3). Chlorophyll-*a* concentration, although generally low, was higher overall within the local foraging area, with similar CHL levels in *E1* and *L1* and the highest level observed in *E2* (Fig. 2, Table 3). In the distant foraging area, CHL was lower overall than in the local area, but again it was the highest in *E2* and relatively low in *E1* and *L1* (LMM $\chi^2 = 890.75$, $df = 3$, $p < 0.001$) (Fig. 2, Table 3). During all three study periods, birds foraged within the local area of higher CHL values, but they did not travel to the higher CHL zones and cooler waters available within their southern foraging range in *E2*.

3.3. Dive characteristics

A total of 121 dives (16.3%) were recorded within the local foraging area and 623 dives (83.7%) within the distant area in *L1* and *E2*. In four foraging trips within the local foraging area (three males and one female), birds performed no dives; these trips lasted between 0.34 and 3.46 h, with total distance travelled ranging from 7.72 to 188.84 km. Adults performed on average 4.84 ± 4.48 dives per trip (range 0–18, $n = 25$) within the local area and 20.10 ± 18.81 dives per trip (range 1–73, $n = 31$) in the distant area, which was significantly more (GLMM $\chi^2 = 45.95$, $df = 1$, $p < 0.001$). Season had no effect on the number of dives (GLMM $\chi^2 = 2.17$, $df = 1$, $p = 0.141$).

Overall, dives were shallow (Table 4), with individuals diving to similar depths within and outside the local foraging area (GLMM $\chi^2 = 1.49$, $df = 1$, $p = 0.222$) and between seasons ($\chi^2 = -0.35$, $df = 1$, $p = 1.0$). Dive rates were significantly higher (GLMM $\chi^2 = 11.65$, $df = 1$, $p < 0.001$) and more variable (F-test $F_{67,62} = 0.50$, $p = 0.006$) outside the local foraging area, but did not change between the two seasons (GLMM $\chi^2 = 2.22$, $df = 1$, $p = 0.136$) (Table 4).

The average number of bouts per trip was 2.08 ± 1.61 (range 0–6, $n = 25$) within the local area, which was significantly lower (GLMM $\chi^2 = 36.37$, $df = 1$, $p < 0.001$) than the 6.84 ± 5.52 bouts per trip (range 1–27) recorded outside the local foraging area. However, the average number of bouts was similar between the two seasons (GLMM $\chi^2 = 1.16$, $df = 1$, $p = 0.281$). Dive bout size was significantly greater (GLMM $\chi^2 = 11.57$, $df = 1$, $p = 0.001$) and significantly more variable (F-test $F_{113,143} = 0.24$, $p < 0.001$) in the distant foraging area, suggesting

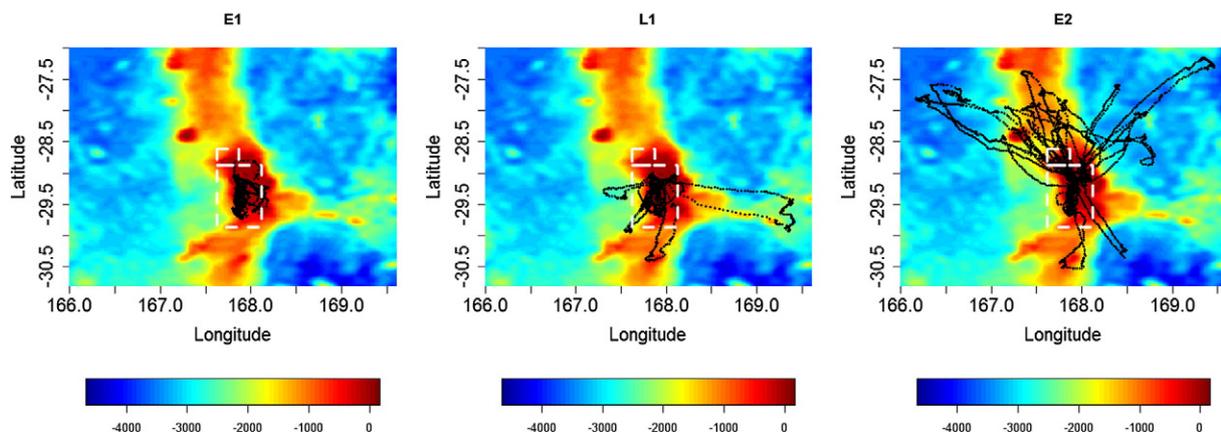


Fig. 1. Foraging tracks of chick-rearing Masked boobies relative to bathymetry during early (*E1*) and late (*L1*) phases of the first breeding season and following early season (*E2*). The local foraging area is represented by the dashed line. Note that one 0.25° grid within the local foraging area is located north of Norfolk Island.

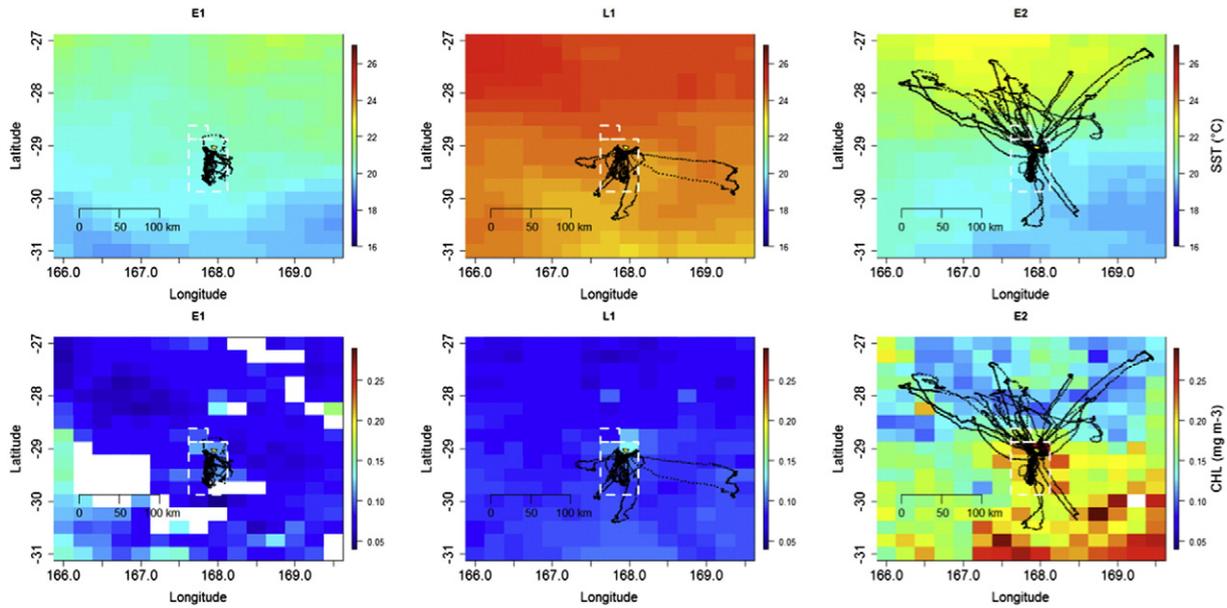


Fig. 2. Foraging movements of chick-rearing Masked boobies during early (*E1*) and late (*L1*) phases of the first breeding season and following early season (*E2*). Sea surface temperature (SST, top row) and chlorophyll-*a* concentration (CHL, bottom row) are mean monthly values per 0.25° grid. White grids correspond to missing CHL values. The local foraging area is represented by the dashed line. Note that one 0.25° grid within the local foraging area is located north of Norfolk Island.

that Masked boobies may have encountered prey patches that were on average of larger size, although more variable, in deeper waters farther from the colony (Fig. 3, Table 4). Again, this did not change between *L1* and *E2* (GLMM $\chi^2 = 0.40$, $df = 1$, $p = 0.528$). Within the local foraging area, bout size did not differ between seasons (GLMM $\chi^2 = 1.53$, $df = 1$, $p = 0.216$).

The distances birds travelled between successive dives within a bout were similar in both foraging areas (GLMM $\chi^2 = 0.08$, $df = 1$, $p = 0.770$) and between the two seasons *L1* and *E2* ($\chi^2 = -1.92$, $df = 1$, $p = 1.000$) (Table 4), suggesting similar densities of prey within patches. Distances between dive bouts were also similar in both foraging areas (LMM $\chi^2 = 1.09$, $df = 1$, $p = 0.297$), but significantly more variable (F-test $F_{200,200} = 7.03$, $p < 0.001$) in the distant foraging area. The greatest distance between bouts recorded in the distant foraging area was, with 133.72 km, almost twice the maximum distance recorded inside the local foraging area (76.78 km; Table 4). Season had no effect on the distances between dive bouts (GLMM $\chi^2 = 0.12$, $df = 1$, $p = 0.729$).

4. Discussion

Our results demonstrate that Masked boobies nesting at Phillip Island exhibited a flexible foraging behaviour by changing markedly their foraging movements within and between seasons, and their diving

behaviour according to the foraging areas visited by the birds. Such flexible foraging behaviour has not been previously reported in this species. Dive bout size was on average larger, yet more variable, in more distant, deeper waters than over the shallower shelf close to the colony. Although the true spatio-temporal distribution of prey remains unknown, we believe that the differing dive bout size reflects, at least to some extent, prey patches of differing sizes in the two foraging areas. However, despite the potentially smaller prey patches within the local area, individuals showed strong foraging site fidelity to this area from one trip to the next and also between study periods, suggesting predictable prey encounters nearby the colony.

The spatio-temporal predictability of prey modulates foraging site fidelity in marine predators (Weimerskirch, 2007). Individuals learn where and when to find prey within their potential foraging range and return to the same feeding areas between trips or breeding seasons so as to maximize foraging efficiency (Cape gannets, Grémillet et al., 1999; Northern gannets *Morus bassanus*, Hamer et al., 2001). Physical factors, such as upwelling, may locally increase primary production (Haury et al., 1978), thereby influencing the availability and predictability of prey for seabirds and other marine predators (Jaquemet et al., 2005). Persistent higher CHL concentrations in combination with low SST within the local foraging area over the shallower shelf located at the western edge of the plateau, where prevailing currents meet shallow water, are indicative of an upwelling (Williams et al., 2006). The

Table 2

Foraging trip duration, range and total distance travelled of Masked boobies during early (*E1*) and late phase (*L1*) of the first breeding season and early phase of the following season (*E2*). Values are given as mean ± SD. Ranges in parentheses. Sample size (n).

Foraging parameters	Breeding season					
	<i>E1</i>		<i>L1</i>		<i>E2</i>	
	Local trips (n = 17)	Distant trips (n = 6)	Local trips (n = 16)	Distant trips (n = 10)	Local trips (n = 11)	Distant trips (n = 27)
Trip duration (h)	2.7 ± 1.0 (0.2–4.3)	14.7 ± 5.3 (8.4–23.4)	3.3 ± 1.2 (0.6–4.9)	18.4 ± 13.5 (5.0–37.0)	3.8 ± 0.9 (0.3–4.8)	23.3 ± 15.2 (5.4–52.2)
Foraging range (km)	23.1 ± 18.3 (2.6–63.9)	64.5 ± 2.9 (61.5–69.3)	24.3 ± 18.7 (4.5–59.8)	74.7 ± 47.8 (16.5–163.4)	29.5 ± 17.5 (3.9–54.8)	115.8 ± 67.5 (15.7–258.)
Distance travelled (km)	53.3 ± 43.1 (4.6–151.7)	251.5 ± 43.2 (207.8–323.8)	58.4 ± 39.9 (10.4–139.2)	195.5 ± 116.1 (49.7–426.9)	72.7 ± 40.5 (7.7–132.8)	303.5 ± 167.2 (76.2–602.4)

Table 3
Foraging habitat characteristics within the local and distant foraging areas during early (*E1*) and late phase (*L1*) of the first breeding season and early phase of the following season (*E2*). Sea surface temperature (SST), chlorophyll-*a* concentration (CHL). Values are given as mean \pm SD. Ranges in parentheses.

Breeding season	Local foraging area			Distant foraging area		
	<i>E1</i>	<i>L1</i>	<i>E2</i>	<i>E1</i>	<i>L1</i>	<i>E2</i>
SST ($^{\circ}$ C)	20.3 \pm 0.8 (19.2–21.8)	24.0 \pm 0.3 (23.3–24.8)	20.2 \pm 0.5 (19.2–21.7)	20.4 \pm 0.9 (17.7–22.9)	24.2 \pm 0.6 (22.5–25.7)	20.8 \pm 1.2 (18.4–25.5)
CHL (mg m^{-3})	0.10 \pm 0.02 (0.08–0.12)	0.10 \pm 0.01 (0.08–0.13)	0.21 \pm 0.03 (0.17–0.27)	0.08 \pm 0.02 (0.04–0.16)	0.08 \pm 0.01 (0.06–0.11)	0.16 \pm 0.04 (0.08–0.29)

repeated use of this area throughout the study period suggests that Masked boobies associate the shallow shelf-edge with predictable prey encounters. Foraging site fidelity in tropical species is rare, although studies investigating this remain scarce (Weimerskirch, 2007). For instance, Masked boobies breeding at Clipperton Island in the eastern central pacific ($10^{\circ}18'N$, $109^{\circ}13'W$) showed no foraging site fidelity between trips (Weimerskirch et al., 2008). As such, the shallow shelf-edge nearby Phillip Island appears to be a determinant factor in shaping the foraging decisions of Masked boobies.

Interestingly, birds did not forage within the zones of lower SST and higher CHL located south of the colony during their distant trips (*E2*). Both SST and CHL parameters have been extensively used to predict the location of possible foraging grounds and to describe the distribution and foraging movements of top marine predators (e.g. Bailleul et al., 2005; Paiva et al., 2010; Polovina et al., 2004; Zainuddin et al., 2006). However, the correlation between seabird distribution and indices of primary productivity measured by means of SST and CHL can be misleading, as seabirds are top predators that usually feed two to three trophic levels higher in the food chain (Grémillet and Boulinier, 2009; Grémillet et al., 2008). Such a mismatch could explain why Masked boobies were not observed feeding in the areas with lower SST and higher CHL values south of the colony. Whereas the persistent upwelling, and thus higher CHL and lower SST within the local foraging, may provide a constant food source for Masked boobies and other species. Yet, the quality of this food source, i.e. prey availability and distribution, appears to vary over time, forcing individuals to search for prey in more distant feeding grounds.

In the conceptual framework of classical central-place foraging theory, travelling to more distant feeding grounds will incur increased costs in both time and energy (Orians and Pearson, 1979; Stephens and Krebs, 1986). These costs must therefore be compensated by increased net energy gain in the prey patches encountered (Orians and Pearson, 1979; Stephens and Krebs, 1986). Although we acknowledge that we have no information on the changes in adult body mass after local and distant foraging trips, it is reasonable to assume that the increased costs associated with travelling to distant foraging grounds may be paid-off by foraging in larger prey patches and by a higher dive rate, i.e. by a higher prey intake rate. While foraging in smaller

prey patches within the local foraging area may ensure that chicks are fed more frequently, the yield of these local trips must be insufficient for adults to maintain their own body reserves in *L1* and *E2*. As a consequence, adults presumably undertake distant foraging trips to restore body reserves (but see Weimerskirch et al., 2009 for differential parental roles in Masked boobies). The alternation between shorter, nearby foraging trips with longer, distant foraging trips has been reported in a range of species (Granadeiro et al., 1998; Paiva et al., 2010; Peck and Congdon, 2006; Saraux et al., 2011; Weimerskirch et al., 1994). However, on Phillip Island, Masked boobies not only accept the increased costs associated with distant foraging trips, birds also accept the risk of foraging in an environment where prey encounters are less predictable, as inferred from the variable dive bout sizes and distances between dive bouts. In Wandering albatrosses, for instance, distances between dive bouts were shorter over the nearby shelf and slopes than over deep oceanic waters, indicating that their prey, mainly squid, were more dispersed in deeper waters and thus less predictable (Weimerskirch et al., 2007). Although we assumed a direct relationship between dive bout characteristics and the size and distribution of prey patches, we cannot exclude that observed differences in dive bout size over the shallow shelf-edge and deeper waters (*L1*, *E2*) could reflect the spatial distribution of two (or more) different prey species. White-chinned petrels (*Procellaria aequinoctialis*), for example, fed mainly on fish when foraging over a nearby shallow shelf and on a mixed diet of pelagic fish and Antarctic krill (*Euphausia superba*), when foraging over distant, deeper oceanic waters (Catard et al., 2000). As we lack information on prey species composition and the real in-situ spatio-temporal availability and distribution within the region, further investigations are necessary to help with the interpretation of our results.

Chick-rearing adults foraged exclusively within the local foraging area in *E1*, but alternated between both foraging areas in *L1* and *E2*. Three explanations, which may be non-mutually exclusive, could explain the observed changes in foraging movements between the three study periods. (1) Intra- and inter-specific competition for prey may have been higher in *L1*, and particularly in *E2*, compared to *E1*. Masked boobies may have undertaken long foraging trips to reach more distant foraging grounds to avoid foraging in 'Ashmole's halo' (i.e. a zone near dense seabird colonies in which prey is less abundant due to high

Table 4
Foraging parameters recorded in Masked boobies with respect to foraging area (local and distant) and statistics. Values are given as mean \pm SD. Ranges in parentheses. Sample size (n). Generalized linear mixed models (GLMM). Significant results in bold.

Foraging parameters	Local foraging area	n	Distant foraging area	n	Statistics	p value
Dive depth (m)	2.35 \pm 1.51 (0.24–6.35)	246	2.77 \pm 1.31 (0.24–6.20)	498	GLMM	0.222
Dive rate	2.6 \pm 2.5 (0.22–12.08)	68	4.47 \pm 3.53 (0.16–18.09)	63	GLMM	<0.001
Variance of dive rate	6.27	68	12.50	63	F test	0.006
Dive bout size	2.11 \pm 1.75 (1–9)	114	3.49 \pm 3.39 (1–23)	144	GLMM	0.001
Variance of dive bout size	3.06	114	12.89	144	F test	<0.001
Distance between successive dives within a dive bout (km)	0.86 \pm 1.32 (0.01–7.34)	132	1.37 \pm 2.32 (0.01–22.42)	355	GLMM	0.770
Distance between dive bouts (km)	16.77 \pm 17.96 (0.26–76.78)	72	12.58 \pm 19.15 (0.18–133.72)	129	GLMM	0.250
Variance of the distance between dive bouts	322.5	72	366.8	129	F test	<0.001

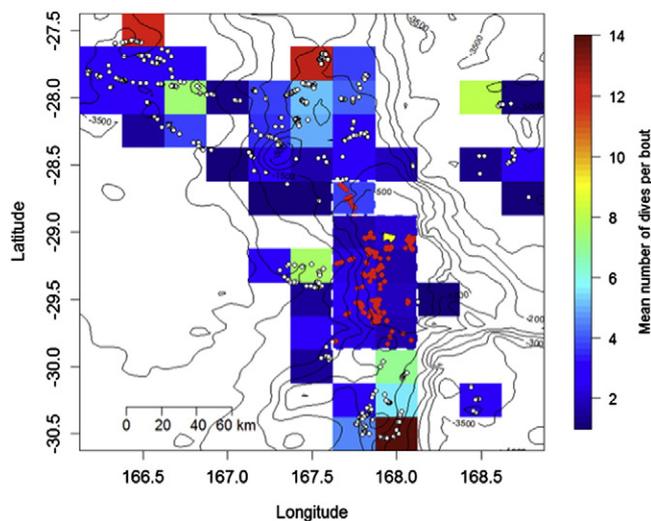


Fig. 3. Mean number of dives per bout within each 0.25° grid. Red dots are dives within the local foraging area (dashed line). White dots are dives outside the local foraging area. Note the smaller mean dive bout size within the local foraging area and the increased, but more variable, dive bout size in the distant foraging area. Bathymetry contours are represented by black solid lines (each line represents 500 m increase). The small filled area within the local area represents Norfolk Island.

intra- and inter-specific competition, Ashmole and Ashmole, 1967; Birt et al., 1987), in *L1* and *E2*, but not in *E1*. However, a change in the availability and abundance of prey nearby the colony due to prey depletion seems unlikely. Distances between dive bouts (i.e. prey encounter rates) and dive bout size (i.e. prey patch size) within the local foraging area were similar between *L1* and *E2*, i.e. between the late breeding season when considerably less birds are breeding (less competition) and the early peak of the breeding season when bird numbers were highest (more competition). (II) Larger prey patches (of the same prey species composition) were available nearby the colony in *E1*, but not in *L1* and *E2*, enabling adults to feed the chick at regular intervals and maintain their own body mass, making it unnecessary to search for prey elsewhere. (III) Lastly, the spatial distribution of Masked boobies' preferred prey, presumably flying fish (Exocoetidae) and squid (Ommastrephidae), may have shifted northwards in *E2*. Such inter-annual changes in prey fields were found to trigger different foraging tactics in chick-rearing Northern gannets and correlated with temperature anomalies (Garthe et al., 2011). Both the occurrence of smaller prey patches within the local area, as well as a reduced availability of their preferred prey nearby the colony, seem plausible in explaining observed foraging patterns.

5. Conclusions

Although we only recorded data over two breeding seasons, and despite some logistical limitations, we demonstrated that chick-rearing Masked boobies adjust their foraging behaviour within and between breeding seasons according to foraging locations and to changing foraging conditions nearby the colony. Such foraging plasticity has previously not been reported in this species, and also highlights the need to investigate a population over several consecutive breeding periods.

Seabirds are capable of adjusting their foraging behaviour to buffer a shift in the distribution of prey species or reduced availability of their preferred prey (Arcos and Oro, 1996; Litzow et al., 2002). However, there are clear eco-physiological limits to such foraging plasticity, and below a certain threshold of prey availability, foraging is unprofitable (Enstipp et al., 2007), negatively affecting reproduction (Harding et al., 2007) and threatening adult survival (Grémillet and Boulinier, 2009). Observed changes in the foraging conditions surrounding Phillip Island,

although the ultimate causes were not determined, appear to be within the eco-physiological limitations of Masked boobies. However, considering that changes in the spatio-temporal availability of prey is expected to increase over the next decades due to global warming and changing oceanic processes (Barbraud et al., 2011; Grémillet and Boulinier, 2009), we urge to monitor closely this Masked booby population, as well as other species inhabiting this area, to determine the extent of such eco-physiological limitation.

Acknowledgments

This research was funded by the Australian Holsworth Wildlife Research Endowment (H0018361), the Australian Geographic Society (H18530) and Birds Australia (H18690). J. Sommerfeld was supported by an International Postgraduate Research Scholarship (111147). The funding sources had no involvement in the study design or preparation of this manuscript. Many thanks for the logistical support provided by Norfolk Islands National Park. We gratefully thank D. and J. Bigg from Norfolk Islands Charter Marine for safe boat trips to and from Phillip Island and accommodation. Special thanks to P. Buffet J. C. Bailey for providing volunteer accommodation. We deeply thank H. McCoy and B. and O. Evans for their support and invaluable knowledge. Many thanks to M. Holdsworth, K. Kreger, R. Hohnen and F. McDuie, for assistance in the field. We thank F. Korner-Nievergelt from Oikostat, Switzerland, for statistical guidance. This study was carried out under permission of Norfolk Islands National Park (permit No. 2009/0003/01) and in accordance with the principles and guidelines of the Animal ethics committee of the University of Tasmania (permit No. A10756). [SS]

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