

Coping with variable and oligotrophic tropical waters: foraging behaviour and flexibility of the Abbott's booby *Papasula abbotti*

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ABSTRACT: Seabirds of tropical oceanic waters have to cope with an extremely oligotrophic habitat, but little is known about their foraging behaviour and flexibility which enables them to catch sufficient prey for themselves and their chicks. In a 7 yr study encompassing contrasting oceanographic conditions, the foraging behaviour of chick-rearing Abbott's boobies *Papasula abbotti*, seabirds endemic to Christmas Island, Indian Ocean, was investigated using GPS- and dive-loggers to examine (1) if the species exhibits foraging strategies that indicate specific adaptations to unproductive tropical oceanic waters, and (2) if (or how) the birds adjust their foraging behaviour to inter-annually varying marine conditions. Abbott's boobies displayed a number of distinct characteristics in their foraging behaviour: flight velocities were slower and diving activity lower than in other booby species. Foraging efficiency was enhanced by distinct temporal tuning of diving activity and trip timing, peaking in the morning and again in the afternoon. The birds exhibited some flexibility in foraging behaviour: when conditions deteriorated (i.e. when waters became warmer and less productive), their diet composition changed, they increased their trip durations, trip range and maximum dive depth, although other parameters such as diving activity and sinuosity did not change. Remarkably, the time spent on the water increased simultaneously with trip length. By those adaptations, Abbott's boobies were able to keep their body condition (as well as that of their chicks) stable even under poor marine conditions.

KEY WORDS: Abbott's booby · *Papasula abbotti* · Tropical Indian Ocean · Marine variability · Foraging behaviour · Foraging flexibility · Prey availability · Christmas Island

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INTRODUCTION

Seabirds forage in a heterogeneous and variable environment in which prey abundance is patchy and ephemeral and varies considerably on a temporal and spatial scale (Ashmole 1971, Shealer 2002). This environmental variability and unpredictability has led to the evolution of foraging strategies and behavioural plasticity that enable seabirds to find enough food to sustain themselves and to reproduce successfully under challenging conditions (e.g. Furness & Monaghan 1987, Shealer 2002).

Tropical waters, as defined by Ashmole (1971) as having sea surface temperatures $\geq 23^{\circ}\text{C}$, are characterised by generally lower productivity than 'non-tropical' marine areas (i.e. waters of high latitudes or up-welling systems; Longhurst & Pauly 1987). As a result, tropical waters generally have a relatively low abundance and patchy distribution of seabird prey (Ainley & Boekelheide 1983, Ballance & Pitman 1999). Consequently, seabirds inhabiting those waters (i.e. tropical seabirds following the definition of Ashmole 1971 and Ballance & Pitman 1999), have evolved specific foraging behaviours in order to cope

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with these extreme conditions. For example, most species have a unique wing morphology for a highly proficient flight which enables them to search large marine areas for food while reducing energy expenditure (Flint & Nagy 1984, Ballance 1995, Spear & Ainley 1998, Ballance & Pitman 1999, Hertel & Ballance 1999). As a trade-off, those seabirds are generally poor divers (del Hoyo et al. 1992, Ballance & Pitman 1999), but they have compensated for this by feeding in aggregation with large sub-surface predators such as tuna that drive prey up to the surface and make it accessible (e.g. Au & Pitman 1986, Ballance & Pitman 1999). However, even though research efforts have increased over the last few decades, knowledge of the foraging behaviour of tropical seabirds is still relatively limited compared to that of non-tropical seabirds. For example, information about how they cope with the variability in their marine habitats is scarce, as the majority of studies that have examined the flexibility in foraging behaviour have been conducted on non-tropical seabirds. Those studies showed that non-tropical seabirds exhibit a high degree of phenotypic plasticity in order to adjust their foraging behaviour to varying oceanographic conditions and buffer the resulting variability in prey availability (e.g. Zador & Piatt 1999, Abraham & Sydeman 2006, Harding et al. 2007). Moreover, comprehensive studies that have investigated temporal as well as spatial (horizontal = displacement, vertical = diving) aspects of foraging behaviour and its flexibility are rare overall, but again particularly rare for tropical seabirds.

Boobies are medium-sized, pantropical seabirds belonging to the Family Sulidae, which also includes the gannets inhabiting higher latitudes (Nelson 1978, Carboneras 1992). Boobies occur in a wide variety of tropical and sub-tropical marine environments—from oceanic, oligotrophic waters to highly productive upwelling areas—and hence have evolved adaptations to cope with different oceanographic habitats (Nelson 1978, Carboneras 1992). The Abbott's booby *Papasula abbotti* differs from all other sulids as it has existed as a separate species for about 22 million years, before all other extant sulid species (Olson & Warheit 1988, Carboneras 1992, Patterson et al. 2011), and as it is thought to have predominantly inhabited islands in tropical oceanic waters (Bourne 1976, Nelson 1978). Therefore, Abbott's boobies might exhibit distinct foraging behaviours to cope with the especially oligotrophic characteristics of these habitats, although information on these potential behaviours is scarce.

This paper presents the first study on the foraging behaviour of Abbott's boobies, focusing on habitat utilization, activity patterns, diving behaviour and diet. In addition, the study covers a 7 yr period and is therefore the first to investigate in detail the foraging flexibility of a pelagic tropical seabird under varying oceanographic conditions. The aims of the study were (1) to investigate if Abbott's boobies show foraging behaviours that indicate specific adaptations to the relatively unproductive tropical oceanic waters, and (2) to examine if and how Abbott's boobies adjust their foraging behaviour to inter-annual variability in their marine habitat.

MATERIALS AND METHODS

Study animals, data loggers and sampling procedures

This study was carried out on Christmas Island (CI), in the Indian Ocean (10° 25' S, 105° 40' E), the only location in the world where Abbott's boobies are known to breed. CI is the emergent tip of a submarine mountain rising steeply from the surrounding 2000 m deep ocean floor (Gray 1995). Abbott's boobies nest in the canopy of the tropical rainforest that covers the island (Nelson 1978). Fieldwork was conducted on CI from late August until early October (when Abbott's boobies have small chicks) each year from 2004 to 2010. Nests were located in the primary rainforest by systematic ground searches in 2 areas of CI about 5 km apart where nest densities were known to be the highest: in the northwest (North-West-Point, NWP; 2004 to 2010) and in the southwest of the island (Eastern Circuit Track, ECT; 2005 to 2010). Nests were at heights of 12 to 40 m in the canopy, and were accessed by tree climbing. In 2004, nests alongside roads were also accessed using a 45 m mobile crane. Because of the difficulty involved in finding and accessing nests (nest search to logger retrieval took on average about 10 d per deployment), only a relatively small number of loggers were deployed each breeding season.

Birds were caught on their nest by hand or by using a ca. 1 m noose pole. Upon capture, birds were lowered to the ground in a bag for measurements and logger attachment/retrieval, and marked with colour paint on the lower abdomen for easier identification from the ground. At logger deployment and retrieval, birds were weighed to the nearest 10 g using a spring balance (Super Samson, Salter), and culmen length

was measured to the nearest 0.05 mm using calipers (except in 2004). Those 2 measurements were used to calculate body condition at deployment as scaled mass index (SMI) following Peig & Green (2009, 2010).

After handling, birds were taken back up into the tree in the bag and released on their nests, where they immediately resumed breeding duties. Logger attachment/removal took approximately 10 to 15 min; total time from catch to release was about 30 min. Attachment and retrieval times occurred randomly throughout the day.

All study birds had chicks, which were guarded by 1 adult at all times. If reachable by hand, chicks were measured (mass, culmen length) at logger deployment and/or retrieval and were aged by mass and culmen length following Nelson (1978). All chicks were between 1 and 8 wk of age. As with adults, body condition of chicks was calculated as SMI using mass and culmen length following Peig & Green (2009, 2010).

In all years, adults were equipped with GPS loggers, temperature-depth-recorders (TDR) or both, to record foraging movements and diving behaviour. Logger models, attachment methods and sampling intervals varied between years (Table 1). The mass of loggers was always <5% of adult body mass (females: 1687 ± 98.7 g, $n = 26$; males: 1456 ± 96.3 g, $n = 27$), the weight limit for which loggers could potentially have adverse effects on bird behaviour (Phillips et al. 2003). Loggers were deployed for relatively short periods (1 to 10 d); the heaviest loggers used in the early years of the study (Table 1) were on the birds for a maximum of only 2 or 3 d.

GPS loggers were protected from water by an epoxy housing or by sealing them into a condom and a plastic bag. GPSs were attached to tail or back feathers, and TDRs to a plastic leg ring using Tesa Tape (Beiersdorf) (Table 1). In total, 54 birds (49 different individuals as some birds were equipped in several years) were equipped with GPS loggers from 2004 to 2010, and data on 134 foraging trips were recorded (Table 2). This yielded 1313.4 h of data on foraging movements with 128 619 location fixes. Data on diving behaviour were recorded for 49 birds (44 different individuals) during 95 foraging trips, yielding a total of 1077 dives (Table 2).

The GPS loggers recorded the birds' positions with a precision of ± 10 m (according to manufacturers). The sampling interval was 10 s or 3 min for all but 3 individuals in 2004 and 3 in 2010, for which the sampling interval was 15 min (Table 1). The resolutions

Table 1. *Papasula abbotti*. Details of loggers used on chick-rearing Abbott's boobies from 2004 to 2010

Year	GPS				TDR				Total logger weight as max. % of bird weight		
	Logger type	Weight incl. housing (g)	Sampling interval (s)	Attachment (with Tesa Tape)	No. of birds	Logger type	Weight (g)	Sampling interval (s)		Attachment (with Tesa Tape)	No. of birds
2004	GPS-log (Earth & Ocean Technologies)	65	900	On back, between wings	1	n/a	n/a	n/a	n/a	n/a	4.5
2007	GPS-log (Earth & Ocean Technologies)	45	180	Under tail	1	LAT 1110 (Lotek)	5	2	Leg ring	1	3.4
2004–2006	GPS-TDlog (Earth & Ocean Technologies)	70	180 (2 × 900)	On back, between wings	2004: 6 2005: 8 2006: 4	GPS-TDlog (Earth & Ocean Technologies)	see GPS	1	On back, between wings	2004: 6 2005: 7 2006: 4	4.8
2006–2008	GiPSy (Techno Smart)	42	10	Under tail	2006: 8 2007: 6 2008: 6	LAT 1110 (Lotek)	5	2	Leg ring	2006: 6 2007: 8 2008: 7	3.2
2009–2010	iGotU GT-120 (Mobile Action)	17	180 (3 × 900)	Under tail	2009: 6 2010: 8	LAT 1110 (Lotek)	5	2	Leg ring	2009: 5 2010: 5	1.5

Table 2. *Papasula abbotti*. Number of Abbott's boobies equipped with GPS and/or TDR loggers, and number of foraging trips recorded during the study years 2004 to 2010. GPS-TDR-combination: either 1 device, or 2 separate devices on the same bird (see Table 1)

Year	GPS & TDR combined	Foraging trips recorded with GPS	GPS trips also covered with TDR	Only GPS	Foraging trips recorded	Only TDR	Foraging trips recorded
2004	6	12	12	1	1	–	–
2005	7	20	20	1	2	–	–
2006	10	27	26	2	3	(2) ^a	2
2007	7	11	9	–	–	2	2
2008	5	9	7	1	1	2	3
2009	5	20	8	1	4	–	–
2010	5	12	6	3	12	–	–
Total	45	111	88	9	23	4	7

^aActually a GPS-TDR-combination, but GPS loggers failed after first trip in both animals while TDR loggers recorded another trip; individuals are taken into account in 'GPS & TDR combined'

of the pressure sensors of the GPS-TDlog and LTD 1110 (see Table 1) were 6 cm and 10 cm respectively, with a measurement accuracy of 20 cm and 12.5 cm (according to manufacturers).

When handled, adults occasionally (chicks rarely) spontaneously regurgitated their prey. From 2004 to 2008, regurgitates were collected in a sealable plastic bag and taken to the laboratory for analysis.

No negative effects of the investigations could be detected. Abbott's boobies are very calm birds compared to other Sulid species; they stayed on their nests as we approached (whether by tree climbing or by crane), remained calm during handling, and could easily be recaptured for logger retrieval. After release, all animals resumed their breeding duties. Treated nests were monitored until the end of the field season, and in all nests breeding was continued successfully. Birds exhibited no weight loss from logger deployment to retrieval (paired *t*-test, $t_{53} = -0.262$, $p = 0.794$, $n = 54$). Although the weights of GPS-log and GPS-TDlog loggers (used in 2004 to 2006, Table 1) were higher than that of the other logger types, foraging trip durations were not influenced by logger type (linear mixed model, LMM: $F_{3,58.4} = 0.715$, $p = 0.547$, $n = 134$), and the birds with the heavier loggers did not significantly lose weight during their trips (paired *t*-test, $t_{18} = -1.374$, $p = 0.186$, $n = 19$).

Foraging parameters

The start and end of foraging trips were determined using locational data of the GPS loggers (bird on nest vs. off nest), averaging the time of the last fix

on the nest and the first fix at sea, and vice versa. In 7 cases, GPS loggers failed or were lost, and therefore trip start and end times were determined by TDR temperature profiles — which showed clear temperature shifts when birds started from or arrived at the nest (as temperatures at the nests were higher and more variable than temperatures at sea). The validity of this approach was controlled by using trips with both GPS and TDR data. Some trips were not completely covered by GPS recording due to battery exhaustion. Data on those trips were only used in analyses when appropriate (e.g. time of trip start). Distances of birds from CI were calculated by using spherical trigonometry (arc distance formula; Robinson et al. 1978).

To distinguish between flying and floating/drift-ing/swimming on water, the frequency distribution of instantaneous displacement velocities (recorded by the GPS logger by Doppler shift at each location fix) was plotted. A local minimum at 7.0 km h^{-1} was found for both day and night. This velocity was considered to be the threshold between the bird being on the water surface and being in the air. All instantaneous displacement velocities $>7 \text{ km h}^{-1}$ were considered flight velocities, and were used to calculate the parameters of the birds' foraging trips.

To calculate time spent on the water, average displacement velocities were calculated for each sampling interval (i.e. the time between 2 location fixes), by dividing the distance between fixes by the time passed between fixes. If the velocity for a sampling interval was $<7.0 \text{ km h}^{-1}$, the interval was counted as time spent on water. For this calculation, only trips with complete GPS coverage were taken into account, and only data of loggers with 10 s and 3 min

sampling intervals were used to keep precision high. For the calculation of this parameter for 'day', overnight trips as well as their 'day parts' were excluded. 'Day' (i.e. hours of daylight), was defined as the time between the earliest departure of a bird from the nest (05:09 h) and the latest arrival time of a bird at the nest (18:16 h) during the study years; thus, day length was 13.1 h. For overnight trips, the night period (10.9 h) was subtracted from total trip duration to calculate diving activity (dives h^{-1}), since birds did not dive at night.

Dive data were analysed with MultiTrace-Dive 4.0 (Jensen Software Systems). The minimum diving threshold was 30 cm, accounting for the resolution and measurement uncertainty of the pressure sensors (see logger specifications in the previous section). Locations of diving events were determined by interpolation between the GPS fixes preceding and following the dive event, assuming a constant flight velocity and a direct flight path between the fixes.

To determine the distribution of diving activity over the course of the day, numbers of dives per 30 min time slot were corrected for the number of birds at sea equipped with a TDR during any specific time slot. A bird was included for a given time slot if it spent at least 15 min at sea during that 30 min time slot. Only foraging trips that were completely covered by TDR recordings were included in analyses of diving activity (dives h^{-1} , timing of diving activity).

The distribution of dives over the course of the foraging trip was calculated as the ratio of the time of the dive since the start of the trip to the duration of the trip (i.e. a value of 0.5 indicates that the dive was conducted at the midpoint of the trip). Trips that were not completely covered by TDR recording were not included in this analysis. Only day trips were analysed, as overnight trips are likely to require different diving strategies than day trips and, in addition, dive data on overnight trips were only available for females.

To calculate sinuosity, positional data of 3 min sampling intervals were used as well as the positional data of 10 s intervals which were re-sampled at 3 min intervals. Sinuosity was calculated for each location fix as the ratio of the cumulative distance covered between 5 positions before and after the fix to the straight-line distance between the first and the last position within this 30 min sliding window. A value of 1 indicates a straight flight path.

For the calculation of foraging area sizes as well as for extraction of oceanographic parameters of the marine areas used by the birds, kernel density estimations were conducted with the R package 'ade-habitatHR' using positional lat/long data transformed

in UTM (Zone 48) and ad hoc h-values for kernel smoothing (Seaman & Powell 1996, Wood et al. 2000). Trajectories of the 15 min sampling intervals were interpolated to locations every 3 min, assuming a constant flight speed and direct flight path between fixes, and were then combined with the positional data used for sinuosity and travelling speed; i.e. all trips (sampling intervals of 10 s, 3 min and 15 min) were divided into 3 min intervals to make them comparable. A 95% fixed kernel density estimation was used to determine total foraging areas, while 50% kernel estimations were considered core areas. The core areas of each foraging trip were subsequently used to extract the oceanographic parameters of the marine habitat used by the birds. To obtain meaningful results, positional fixes were taken into account for the analyses instead of only dive locations (i.e. actual hunting events) as dive frequencies were low (see Results) and oceanographic data coarse (see below). Core areas were used instead of all fixes or total foraging areas to exclude marine areas that were only used for commuting.

Diet

A total of 37 regurgitates containing 131 prey items of 26 different chick-rearing Abbott's boobies were collected from 2004 to 2008. Complete spines, spine fragments, and vertebrae were cleaned of remaining flesh using Bio-tex[®] (Blumøller) following Watt et al. (1997). Digested chyme was dispersed in water in a Petri dish and searched for diagnostic prey remains such as otoliths and vertebrae of fish, and/or squid beaks.

For intact fish, identification keys of the Food and Agriculture Organization (FAO identification sheets; www.fao.org), open source data of Fishbase (Froese & Pauly 2013), and literature sources (Harrison et al. 1983, Smale et al. 1995, Rivaton & Bourret 1999) were used. A reference collection was compiled for otoliths and vertebrae to identify incomplete prey items. Squid species were identified using the identification key of Clarke (1986) and Lu & Ickeringill (1999) as well as the reference collection of Dr. U. Piatkowski, Institute for Marine Sciences, Kiel, Germany.

The length of intact fish was determined to the nearest mm as total length (TL) following Froese & Pauly (2013) using a ruler, and mass was determined to the nearest g using a digital balance. Otolith size was measured to a precision of 0.1 mm and size of vertebrae to a precision of 0.05 mm using calipers or a binocular dissecting microscope with scaled ocular

(Wild M 7 S, Heerbrugg). To determine the length and mass of incomplete prey items, various regression equations between otolith and vertebra size with fish length and mass were used, which were derived from intact fish collected in this study or taken from the literature following Härkönen (1986) and Watt et al. (1997).

The dorsal mantle length (ML) of intact squid was determined to the nearest mm using a ruler, and mass was determined to the nearest g using a digital balance. Rostral lengths of upper and lower beak were measured to a precision of 0.05 mm using calipers or a binocular dissecting microscope. If the upper and lower beak of the same individual were present, measurements were derived from the lower beak. As for fish, length and mass of incomplete squid were calculated using regression equations derived from intact squid collected in the study, following Clarke (1986) and Croxall & Prince (1996).

Loose otoliths, vertebra and squid beaks were grouped according to species/family and size to determine the actual number of prey items for the analyses. For length and mass determination, the same methods were used as for intact prey items.

All prey items were identified to species or family level, and were subsequently pooled into different groups of prey (i.e. flying fish, non-flying fish or squid), to allow more meaningful and sound statistical analyses. Frequency of occurrence was calculated on the basis of individual birds (not on the number of regurgitates), as several birds regurgitated at both logger deployment and retrieval.

Oceanographic parameters

Sea surface temperature (SST) and chlorophyll *a* (chl *a*) concentration were chosen as parameters to characterise the oceanographic conditions around CI, as it has been shown in various seabird studies that they are suitable proxies for prey availability, and consequently have the potential to influence various parameters of seabird foraging behaviour (e.g. Peck et al. 2004, Weimerskirch et al. 2005a, Erwin & Congdon 2007). Other parameters, such as bathymetry, sea level height or gradients of any of the oceanographic parameters — which have also been shown to potentially affect seabird foraging behaviour — were not included in the analyses due to the small foraging range of the boobies (see Results) combined with the low temporal resolution of the oceanographic data (see below). SST and chl *a* data were compiled from NASA, through its GIOVANNI data gateway (<http://disc.sci.gsfc.nasa.gov/giovanni/overview/index.html>). MODIS Aqua data were used for both parameters with a spatial resolution of 9 km. For SST, daytime 11 micron data were used. As daily and weekly data coverage within the study area was poor due to substantial cloud coverage, available data were averaged over the month of September for each year according to the yearly study period. For the general description of the marine habitat around CI, an area of $4 \times 4^\circ$ with CI in the middle was chosen, as that size corresponds approximately to the boobies' maximum foraging range (248.3 km; excluding the outlier of over 550 km in 2005). In addition, SST and chl *a* values of this $4^\circ \times 4^\circ$ area were linked to the birds' body condition at de-

Table 3. *Papasula abbotti*. Correlations of adult and chick body condition with SST and chl *a* in the $4 \times 4^\circ$ area around Christmas Island, and of foraging parameters with SST and chl *a* of each respective foraging trip (**bold**: significant)

Parameter	n	SST		chl <i>a</i>	
		Kendall's τ -b	p	Kendall's τ -b	p
Adult body condition (SMI)	48	-0.060	0.574	0.126	0.239
Chick body condition (SMI)	44	-0.061	0.584	0.061	0.584
Trip duration (h)	114	0.194	0.003	-0.170	0.008
Max. foraging range (km)	115	0.198	0.003	-0.185	0.003
Total distance travelled (km)	114	0.168	0.011	-0.173	0.006
Avg. flight speed day (km h^{-1})	118	-0.003	0.957	-0.065	0.295
Avg. flight speed night (km h^{-1})	17	-0.150	0.407	0.185	0.303
Time spent on water, day (% of trip)	106	0.162	0.019	-0.133	0.087
Total foraging area (km^2)	118	0.170	0.009	-0.154	0.014
Sinuosity	118	-0.039	0.533	0.067	0.290
Dives h^{-1}	69	-0.047	0.595	0.087	0.302
Avg. dive depth (m)	78	-0.030	0.711	0.020	0.799
Max. dive depth (m)	78	0.175	0.030	-0.132	0.089
Dive pause (s)	78	-0.078	0.331	0.017	0.829
Closest dive to island (km)	78	0.167	0.038	-0.137	0.076

ployment (see Table 3), as it also integrates the marine conditions before the study (i.e. the conditions that determined the body condition of the birds at deployment). To determine the oceanographic conditions of the marine areas chosen by the birds, average SST and chl *a* values for each foraging trip were calculated by overlaying the oceanographic data with the core areas of the trips.

SST anomalies in the $4 \times 4^\circ$ area around CI during September were compiled for the study years, with the lowest and highest SSTs from the NASA POET data gateway (<http://thredds.jpl.nasa.gov/las/getUI.do> [original link was <http://poet.jpl.nasa.gov>, now retired]) using the Reynolds Optimally Interpolated SST dataset, to obtain a relative measure of 'how low/high' the SST was.

Statistical analyses

Statistical analyses were performed with SPSS 11.5 (SPSS), and R Studio (Version 0.94.92) using R version 2.13.0 (R Development Core Team 2010) and the R packages 'nlme' and 'circular'.

Normality of response variables were checked by Q-Q-plots or, in case of small sample sizes, with application of the Shapiro-Wilks test. If necessary, appropriate transformations were performed to gain normality, e.g. \ln -transformations of trip duration, dives h^{-1} , and dive duration. Sinuosity values were transformed using the logit (\ln) of the inversed sinuosity. Heteroscedasticity was checked using plots of residuals over fitted values or, in case of small sample sizes, with Levene's test for heteroscedasticity. If necessary, test statistics and degrees of freedom were adjusted appropriately.

To determine the influence of bird sex and study year and their interaction on foraging parameters, LMMs were fitted with sex and year as fixed factors. Bird identity was included as a random factor to avoid pseudo-replication, since, for most individuals, data on several foraging trips were recorded. Significance of models was determined by *F*-statistics using a backward stepwise testing procedure based on Akaike's information criterion values. As there were no significant effects of sex or the interaction of sex and year on any foraging parameter, data from both sexes were pooled for all further analyses.

Depending on sample size, either Kendall's τ -b or Spearman's rank correlations

were used to examine correlations between foraging parameters (e.g. trip duration vs. trip range), and to investigate the effect of year on foraging behaviour (i.e. if and how the oceanographic variability between years influenced foraging parameters).

For all tests, the threshold for significance was $p < 0.05$, and all tests were 2-tailed. Means are given \pm SD, and medians with minimum and maximum values.

RESULTS

Foraging movements and activity patterns

Abbott's boobies foraged over deep oceanic waters around Christmas Island, covering a total area of 108 503 km² (90% kernel of all location fixes) with a core area of 12 186 km² (50% kernel; Fig. 1)

The median duration of foraging trips was 6.2 h ($n = 133$), with the shortest trip being 0.4 h and the longest, 152.8 h. The frequency distribution of trip durations showed 3 peaks: short single-day trips, intermediate trips including 1 night at sea, and long trips including 2 ($n = 2$), 3 ($n = 1$) and 6 ($n = 1$) nights at sea (Fig. 2). Most trips (88.0%) were single-day trips (<12.2 h), while the remaining were overnight trips.

On their foraging trips, birds travelled a median distance of 154.3 km, with the shortest trip covering 12.4 km and the longest, 2218.3 km ($n = 126$ trips). The median foraging range (= max. distance from nest) was 56.8 km, ranging from 3.6 to 556.7 km ($n = 127$ trips). Foraging trip duration was significantly

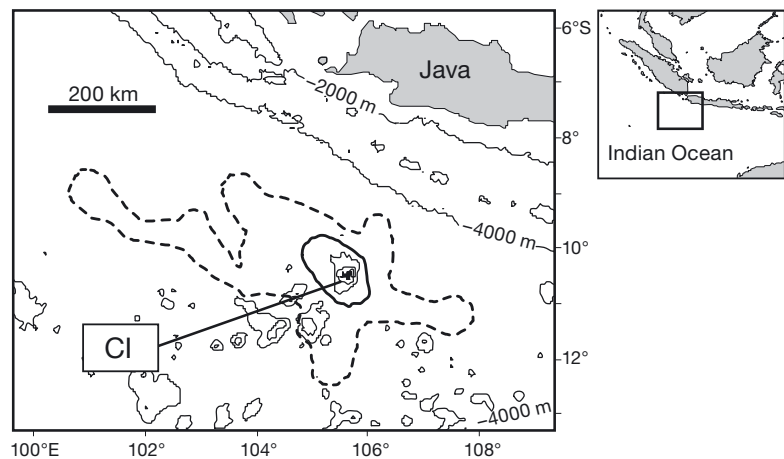


Fig. 1. *Papusa abbotti*. Eastern Indian Ocean (including isobaths), showing the location of Christmas Island (CI) and foraging areas of Abbott's boobies around the island from 2004 to 2010 — dotted line = 95% kernel, solid line = 50% kernel

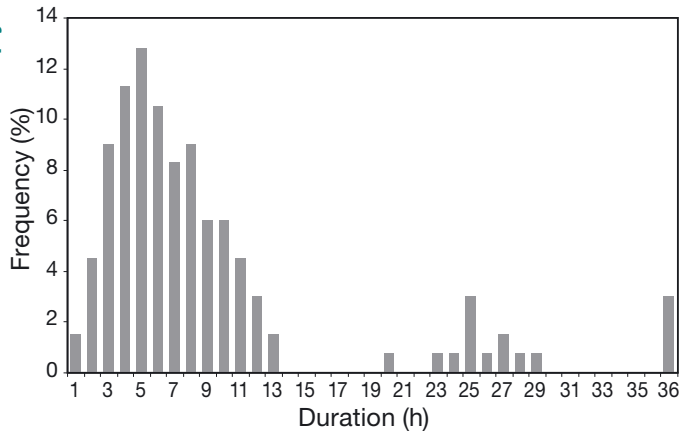


Fig. 2. *Papasa abbotti*. Frequency distribution of foraging trip durations of Abbott's boobies from 2004 to 2010 (n = 133)

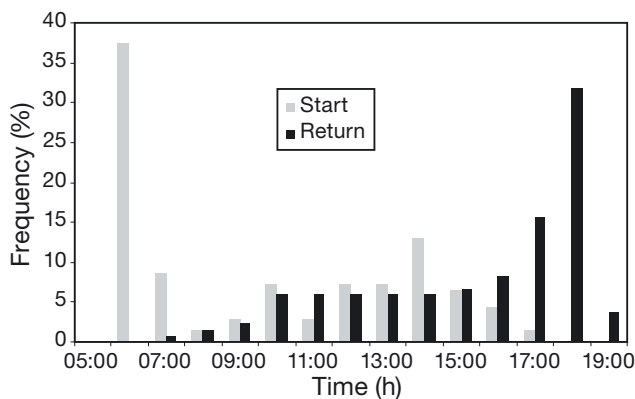


Fig. 3. *Papasa abbotti*. Departure (n = 139) and return times (n = 135) of Abbott's boobies from 2004 to 2010

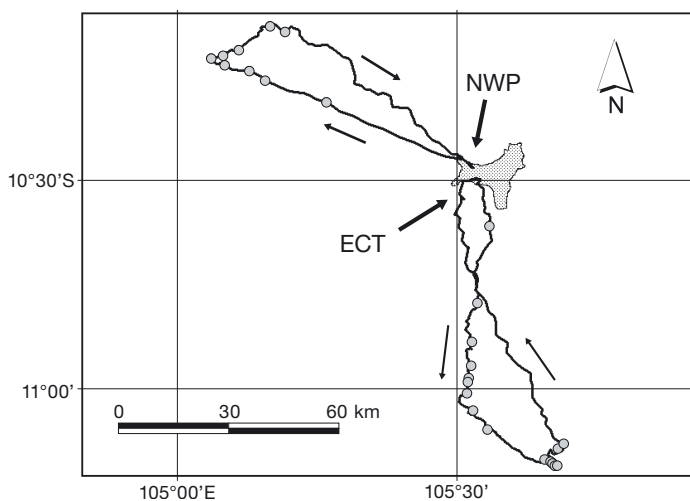


Fig. 4. *Papasa abbotti*. Typical tracks of foraging trips of Abbott's boobies of the North West Point (NWP) and Eastern Circuit Track (ECT) colonies on Christmas Island. Circles represent dives and thin arrows show flight directions (examples from 2005)

correlated with maximum foraging range, total trip distance, and total foraging area ($\tau = 0.749, 0.826, 0.726$, respectively; for all parameters: $p < 0.001$, $n = 126$).

Departure times showed a bimodal distribution (Fig. 3). The majority of trips (46.0%) started between 05:00 h and 07:00 h. The start of the remaining the trips varied over the day, with a second peak around 14:00 h. The latest departure was at 16:36 h. Birds returned to the island from 06:53 h onwards. Return times varied over the entire day, although returns were most common in the late afternoon, with 59.3% occurring after 16:00 h.

Median flight velocities during the day were 30.0 km h^{-1} ($n = 79\,690$ velocity recordings). At night, velocities were lower, with a median of 20.0 km h^{-1} ($n = 19\,523$ velocity recordings). During the day, birds spent only a small proportion of the foraging trip on the water surface (median = 5.9%, range = 0.0 to 31.9%, $n = 102$ trips), while at night a mean of 49.1% (± 27.71 , $n = 15$) was spent on the sea surface. The paths of foraging trips were typically linear to curvilinear, and for the most part lacked major directional changes, showing a relatively low sinuosity with a median of 1.19 (range = 1 to 191.5, $n = 22\,345$; Fig. 4).

Diving behaviour

Dives were shallow and short, with a mean dive depth of $2.21 \pm 1.04 \text{ m}$ ($n = 1077$, max. = 9.51 m; Fig. 5a) and a median duration of 5 s (range = 2 to 23 s, $n = 1077$). Dive depth was significantly correlated with dive duration ($\tau = 0.334$, $p < 0.01$, $n = 1077$). Birds dove infrequently, with a median of 1.7 dives h^{-1} at sea (range = 0.0 to 5.0, $n = 84$) and a median duration between dives of 10.4 min (range = 0 to 370 min, $n = 978$). The first dives during a foraging trip were 4.6 to 93.2 km away from CI (median = 22.6 km, $n = 85$).

Diving occurred throughout the foraging trip (including the outbound leg), but during the last 20% (inbound leg) only few dives were performed (Figs. 4 & 5b). The distribution of dives over the course of the day was bimodal, with peaks occurring in the morning (06:30 to 07:00 h) and in the afternoon (14:00 to 15:00 h; Fig. 5c). No dives were performed at night.

Diet

The diet of chick-rearing Abbott's boobies consisted mainly of flying fish, with non-flying fish species and squid as secondary prey. The tropical two-

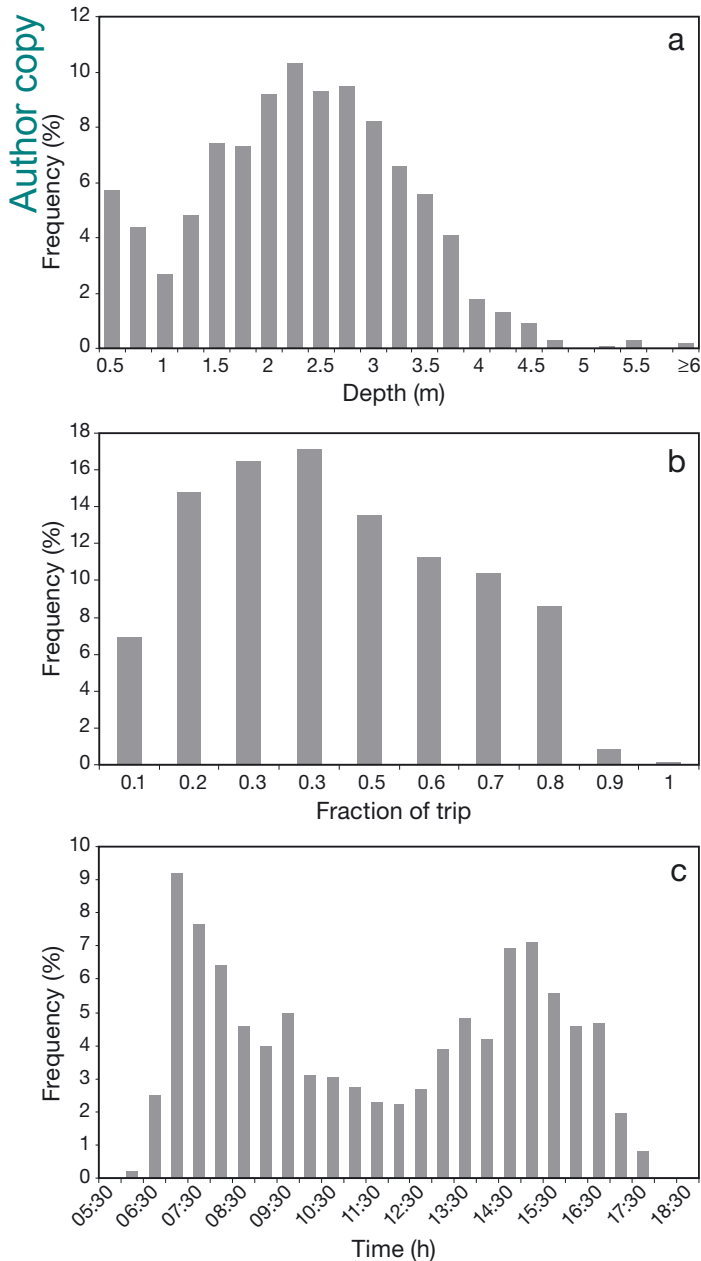


Fig. 5. *Papasula abbotti*. Characteristics of the diving behaviour of Abbott's boobies from 2004 to 2010: (a) frequency distribution of dive depths, (b) distribution of dives over the course of the foraging trip (fraction of 0.5 = midpoint of trip, 1 = end of trip), (c) frequency distribution of diving activity over the course of the day; (n = 1077 for all graphs)

wing flyingfish *Exocoetus volitans* was the most numerous prey item overall, although within the flying fishes (family Exocoetidae) other species were also found, such as margined flyingfish *Cheilopogon cyanopterus* and manyspotted flyingfish *C. spilopterus*. Non-flying fish belonged to the families Coryphaenidae (dolphin fishes), Hemiramphidae (half-

bills), Scombridae (mackerels, tunas, bonitos), and Carangidae (jacks and pompanos), such as the mackerel scad *Decapterus macarellus*. The squids found in regurgitates were all purple-back (flying) squid *Sthenoteuthis oualaniensis* of the family Ommastrephidae (flying squids).

Over the 5 study years, flying fish contributed the most to the total prey biomass ($81.5 \pm 12.7\%$), followed by non-flying fish ($15.5 \pm 11.8\%$) and squid ($2.9 \pm 2.7\%$). Within the group of flying fish, *Exocoetus volitans* made up on average 37.5% (± 12.2).

Inter-annual differences in oceanographic conditions, foraging behaviour, diet and body condition

Oceanographic conditions in the foraging zone of Abbott's boobies around CI (i.e. the $4 \times 4^\circ$ area) varied among years (Fig. 6). In 2006, SST was the lowest, at 25.3°C (± 0.25 ; -0.77°C SST anomaly) and chl a concentration was the highest at $0.433 \pm 0.358 \text{ mg m}^{-3}$, almost twice as high than the average of the 7 yr study period ($0.235 \pm 0.104 \text{ mg m}^{-3}$). The warmest year was 2010, with a mean SST of 27.9°C (± 0.48 ; $+1.44^\circ\text{C}$ SST anomaly), 1.7°C higher than the mean temperature of the study period ($26.2 \pm 0.83^\circ\text{C}$). During this year, chl a concentration was the lowest at $0.092 \pm 0.018 \text{ mg m}^{-3}$, about 2.5 times lower than the average concentration during the study period.

The foraging behaviour of Abbott's boobies was influenced by the varying oceanographic conditions. When waters were warmer and less productive, birds went on longer foraging trips, had larger ranges and covered longer distances and areas (foraging trip duration, foraging range, total distance travelled and

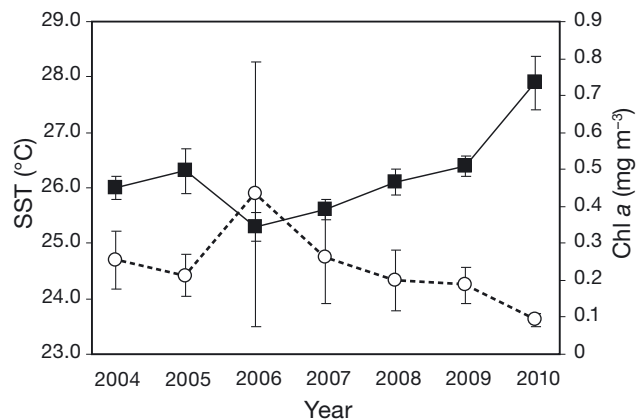


Fig. 6. Sea surface temperature (SST, solid line) and chlorophyll a concentrations (chl a, dashed line) in a $4 \times 4^\circ$ area around Christmas Island. Error bars show \pm SD

total foraging area all correlated positively with average SST in the core foraging area and negatively with chl *a*; Table 3). Relative time spent on water, maximum dive depth, and closest dive to CI did not correlate with chl *a*, but were positively correlated with SST (Table 3). Other parameters such as body condition, diving activity, sinuosity, and flight speeds were not influenced by SST or chl *a* (Table 3).

Prey composition (i.e. relative numbers, number of occurrence and relative biomass of flying fish, non-flying fish and squid) varied among years, but no coherent relationships of those parameters with SST or chl *a* were found, apart from in the frequency of occurrence of non-flying fish. This parameter increased with increasing SST ($r_S = 0.9$, $p = 0.037$, $n = 5$) and decreasing chl *a* ($r_S = 1.0$, $p < 0.001$, $n = 5$). Prey lengths within the different prey groups were affected by the marine conditions: the lengths of flying fish correlated negatively with SST ($\tau = -0.295$, $p < 0.001$, $n = 95$) and positively with chl *a* ($\tau = 0.174$, $p = 0.023$, $n = 95$). In contrast, squid length correlated positively with SST ($r_S = 0.594$, $p = 0.019$, $n = 15$) but not with chl *a* ($r_S = -0.465$, $p = 0.081$, $n = 15$). The length of non-flying fish did not correlate with either SST ($r_S = -0.084$, $p = 0.807$, $n = 11$) or chl *a* ($r_S = 0.502$, $p = 0.115$, $n = 11$).

Body condition of adults and chicks did not differ among years (ANOVA, $F_{5,47} = 0.907$, $p = 0.486$, $n = 48$, and $F_{5,43} = 1.007$, $p = 0.427$, $n = 44$) and did not correlate with either SST or chl *a* (Table 3).

DISCUSSION

The present study is the first to gather detailed data on the foraging ecology of Abbott's boobies as well as, to our knowledge, the first that investigates the foraging behaviour and flexibility of a pelagic tropical seabird using data loggers over several subsequent breeding seasons.

Foraging behaviour of Abbott's boobies

Abbott's boobies exhibited several foraging behaviours that reflect adaptations to their oligotrophic marine habitat, some of which differed from findings in other booby species. The average flight speed of 30.0 km h^{-1} during daytime foraging was considerably lower than that of other booby species, for which average speeds of about 38 km h^{-1} have been recorded (38.3 km h^{-1} in masked/Nazca booby *Sula dactylatra* and 39.1 km h^{-1} in blue-footed booby

S. nebouxii, Anderson & Ricklefs 1987; and 38 km h^{-1} in red-footed booby *S. sula*, Weimerskirch et al. 2005b). Those species have broader wings and flap often when flying (Nelson 1978, Weimerskirch et al. 2005b), whereas Abbott's boobies have long and narrow wings that are generally assumed to have evolved for a gliding and hence generally slower flight—which can substantially reduce the energetic costs of foraging. Thus, the slow flight speeds might be related to this morphological difference, but differences in prevailing wind speeds between the respective foraging habitats might also contribute. Comparative investigation between the other CI booby species (brown and red-footed booby) would help to clarify this point.

Abbott's boobies were hitherto thought to be one of the most pelagic booby species, foraging at long distances from CI (Becking 1976, Hirons et al. 1976, Nelson 1978, Reville et al. 1990, van Balen 1996). Unexpectedly, although the furthest foraging location was over 550 km away from CI, Abbott's boobies foraged relatively close to the island, with an average foraging range of <60 km. In comparison to other booby species, this is an intermediate foraging range. Chick-rearing Peruvian boobies *Sula variegata* and blue-footed boobies *S. nebouxii* were found to have average foraging ranges of 25 km (Zavalaga et al. 2010) and 39 km (Zavalaga et al. 2008), respectively; brown boobies *S. leucogaster* between 17 and 39 km (Weimerskirch et al. 2009b), and red-footed boobies *S. sula* of 39 km (Weimerskirch et al. 2005a), while Nasca boobies *S. granti* and masked boobies *S. dactylatra* had larger foraging ranges than Abbott's boobies, with average ranges of 98 km (Zavalaga et al. 2012) and 103 km (Weimerskirch et al. 2008), respectively. The relatively small foraging range of Abbott's boobies that was recorded in this study, in contrast to previously published information, might be because the data for this study was collected during the early chick-rearing period. At this breeding stage, seabirds have relatively limited foraging ranges in order to provision their chicks frequently and relieve their partners regularly from brooding the young on the nest. During incubation, Abbott's boobies forage much further away from CI with a median range of 169.6 km ($n = 8$, J. C. Henricke unpubl. data). Thus, Abbott's boobies might show foraging ranges that match those previously assumed during other breeding stages (such as late chick-rearing or post-fledging care) when chicks can be left alone on the nest.

Like all other boobies, Abbott's boobies are diurnal foragers, typically leaving the nest in the morning

and returning before nightfall. A second peak of trip departures, however, occurred around the middle of the day. As only 1 partner is at the nest during the day guarding the chick, the other partner appears to do a change-over around midday, rather than switching over the course of the entire day as it has been found in other booby species (e.g. Zavalaga et al. 2007, 2010, Weimerskirch 2009a). This distinct behaviour is highly adaptive as it allows both partners not only to forage on the same day, and consequently to reduce the duration of fasting stints for the adult on the nest, but also gives both partners the opportunity to increase foraging efficiency—as both can take advantage of one of the 2 peaks of high prey availability generated by sub-surface predators early in the morning and late in the afternoon (see below).

Although spending the night at sea is generally a rare behaviour in boobies (Nelson 1978, Carboneras 1992), it was not rare in Abbott's boobies—with 12% of all trips being overnight trips. Masked boobies have been found to make parts of their return flights back to the colony at night (Weimerskirch et al. 2009a), red-footed boobies have been recorded to make overnight trips in the Galapagos (Nelson 1978, H. Weimerskirch unpubl. data), but only recently have frequent overnight trips been observed in Nazca boobies (Zavalaga et al. 2012). Sulids are visual hunters, and hence depend on light to capture prey (Nelson 1978). During their overnight trips, Abbott's boobies did not dive, and therefore most likely no feeding took place—probably because darkness prevented prey capture. In addition to the decreased energy intake, foraging at night increases the risk of attack by predatory fish such as sharks, which are common in tropical waters and often hunt from dusk to dawn (cf. Nelson 1978, Weimerskirch et al. 2005b, Zavalaga et al. 2012). Indeed, Abbott's boobies spent only about 50% of their time on the water surface, flying at low velocities for the rest of the night, in contrast to the behaviour of Nazca boobies that rest on the water most of the night (Zavalaga et al. 2012). However, despite the decreased energy intake and reduction in chick provisioning frequency, it was found, unexpectedly, that Abbott's boobies made many overnight trips. Most likely, these trips allowed the birds to increase their foraging range and hence search larger marine areas for food.

The present study shows that Abbott's boobies are shallow divers, with an average dive depth of only 2.2 m. This depth corresponds well to findings in other booby species that feed on similar prey (i.e. flying fish) and depend strongly on sub-surface predators driving prey species to the water surface. Red-

footed boobies dove on average only 0.9 m (Weimerskirch et al. 2005b), Nazca boobies had a mean dive depth of 1.1 m (Zavalaga et al. 2012), and brown boobies of 1.1 to 1.3 m (Weimerskirch et al. 2009b), while masked boobies and Peruvian boobies had similar average dive depths to Abbott's boobies at 2.2 m (Weimerskirch et al. 2008) and 2.5 m (Zavalaga et al. 2010), respectively. In plunge-diving boobies, dive depth is strongly linked to body mass—which determines the bird's momentum when plunging (cf. Ropert-Coudert et al. 2004). This is well reflected in Abbott's boobies, which dive deeper than smaller species and reach comparable depths as species of similar weight.

Diving took place during the entire foraging trip, including the outbound leg. This spatial distribution of dives matches the assumed homogeneous distribution of prey patches in tropical oceanic waters, and reflects the highly opportunistic foraging behaviour of Abbott's boobies. However, this behaviour contrasts with that of other boobies that forage mainly at the maximum range of their trips using extensive area-restricted search (e.g. brown and blue-footed booby, Weimerskirch et al. 2009b; Peruvian booby, Weimerskirch et al. 2012). In general, the sinuosity in the foraging paths of Abbott's boobies was relatively low, suggesting the potential use of a different search strategy—but only comparative investigations of several booby species within the same marine habitat could elucidate this question further.

Abbott's boobies exhibited a relatively low diving frequency of 1.7 dives h^{-1} . In other booby species feeding on similar prey, higher dive rates have been recorded. Lewis et al. (2004) reported 3.8 dives h^{-1} and 2.4 dives h^{-1} for brown and red-footed boobies, respectively, and Weimerskirch et al. (2005b) recorded 4.5 dives h^{-1} for red-footed boobies, while masked boobies made 3.7 to 8.2 dives h^{-1} (Weimerskirch et al. 2009a). Only Nazca boobies in the Galapagos had similarly low diving rates (Zavalaga et al. 2012). It is possible that Abbott's boobies are using foraging techniques other than diving which were not detectable with the methodologies used in this study; either taking prey in flight (like red-footed boobies; Weimerskirch et al. 2005b) or catching prey from the water surface. The main prey of Abbott's boobies are flying fish, which are fast moving, agile prey that are unlikely to be caught often by a booby sitting on the water, whereas prey capture in flight would certainly be possible. Also, Abbott's boobies may have generally higher prey capture rates than other boobies, reducing their requirement for more frequent diving. On the other hand, the low diving

activity might simply reflect low prey availability in their foraging habitat. Thus, further studies using additional techniques such as accelerometers would be necessary to clarify this point.

Diving activity changed substantially over the course of the day. The majority of dives were performed in the morning and afternoon, a behaviour which has also been found in other boobies (e.g. Weimerskirch et al. 2005b). These peaks of diving activity can be associated with the feeding activity of large predatory fish, such as tuna or billfish. These predators mainly feed during the morning and afternoon, and hunt flying fish and squid—which are also prey for Abbott's boobies (Weimerskirch et al. 2005b, Froese & Pauly 2013). Due to their limited diving capabilities, Abbott's boobies can only catch prey that is found close to the surface. However, the prey species of Abbott's boobies frequently occur at deep depth (Froese & Pauly 2013). As such, Abbott's boobies, like many other tropical seabirds, seem to depend strongly on sub-surface predators to drive prey up to the surface and make it accessible to the birds (Au & Pitman 1986, Anderson and Ricklefs 1987, Balance & Pitman 1999). By foraging during periods when sub-surface predators are most likely to provide enhanced access to prey, Abbott's boobies can increase their foraging efficiency.

Until now, knowledge of the diet of Abbott's boobies has been limited to flying fish and cephalopods (Nelson 1978); prey upon which the majority of all tropical seabirds feed (Nelson 1978, Schreiber et al. 1996, Schreiber & Norton 2002). In the present study the main prey of Abbott's boobies was indeed flying fish. This prey group, comprised mainly of *Exocoetus volitans*, was dominant in the prey spectrum with respect to numbers, biomass and frequency of occurrence. Non-flying fish and flying squid played only a minor role in those 3 parameters. This prey composition matches the prey spectrum of other boobies foraging in tropical pelagic marine environments (Nelson 1978, Schreiber et al. 1996, Schreiber & Norton 2002, Weimerskirch et al. 2009a).

Variation in oceanographic conditions and flexibility in foraging behaviour

CI has neither a shelf nor a considerable sublittoral zone, but the seafloor drops off to about 2000 m close to the shore and is not exposed to pronounced upwellings, currents, or water influx of rivers or surface water (Gray 1995). Thus, the foraging habitat of chick-rearing Abbott's boobies represents a tropical

oceanic marine environment of deep waters. This type of marine environment is generally low in productivity (Longhurst & Pauly 1987). Consistently, the oceanographic conditions around CI during the study years were characterised by generally high SST and low concentrations of chl *a*. However, there was variability in those parameters among years, with 2006 being the coldest and most productive year, while in 2010 SST was highest and chl *a* lowest during the 7 yr study period; this variability significantly affected the foraging behaviour of Abbott's boobies.

In studies on seabirds of higher latitudes, birds were found to buffer food shortages caused by unfavourable oceanographic conditions by adjusting parameters such as time spent at the colony (e.g. Harding et al. 2007), trip duration (e.g. Welcker et al. 2009), diving activity (e.g. Ronconi & Burger 2008), prey selection (e.g. Abraham & Sydeman 2006, Erwin & Congdon 2007), meal size and feeding rates (e.g. Peck et al. 2004). Abbott's boobies used some of those behavioural adjustments, and managed to keep their body condition, as well as that of their chicks, stable despite varying marine conditions. Foraging trips became longer in duration and further from the nest, and covered more distance and larger areas when SST increased and chl *a* decreased. In addition, when SST increased, birds spent more time on the water's surface, and maximum dive depths were deeper than under colder conditions. On the other hand, diving activity, sinuosity, flight speeds, and pauses between dives were not affected by either SST or chl *a*.

To counterbalance decreased prey availability, birds must intensify foraging effort. As such, increasing trip duration (and thus foraging time) is an often observed behaviour in seabirds in order to adjust to lower prey densities (e.g. Peck et al. 2004, Hamer et al. 2007, Welcker et al. 2009). Accordingly, trip duration of Abbott's boobies correlated positively with SST and negatively with chl *a*. However, the longer trip durations not only resulted in more time at sea, but also led to an increase in foraging range. Faced with the widely distributed and rare prey patches (as indicated by the low diving activity and long pauses between dives), Abbott's boobies increased their foraging range to cover a larger marine area in search of prey. Obviously, staying longer in the same impoverished marine area would not have resulted in increased prey capture.

Another often observed adjustment by seabirds in areas of poor prey densities is a change in time allocation. To compensate for lower prey availability, seabirds reduce their time spent at the nest and/or

increase their time at sea, both of which results in more foraging time (e.g. Harding et al. 2007, Piatt et al. 2007, Ronconi & Burger 2008). During early chick-rearing, Abbott's booby partners do not spend extended periods together at the nest during the day (Nelson 1978, J. C. Hennicke unpubl. data), and no time is spent elsewhere on the island (this study). This suggests that there is not a lot of 'loafing' time that the birds could reduce in order to increase foraging time. Accordingly, Abbott's boobies increased their time at sea, but surprisingly, the time spent on the water's surface relative to foraging trip duration also increased. If anything, the reverse would have been expected intuitively. At the moment, we cannot offer a conclusive explanation for this finding. Birds may also simply spend less time searching if feeding opportunities (such as the presence of sub-surface predators) are rarer, which should have resulted in longer pauses between dives. Potentially, this unusual behaviour is a unique constraint in the foraging plasticity of Abbott's boobies, although further investigations on other pelagic tropical seabirds are needed to explain the finding.

While several foraging parameters were affected by the varying marine conditions, trip sinuosity, flight speeds, pauses between dives and diving activity did not change with SST and chl *a*. This suggests that birds had similar search strategies during the different oceanographic conditions and, in addition, that the spatial dispersion and temporal occurrence of the ephemeral prey patches remained similar. Under varying oceanographic conditions, the prey spectrum was similar whereas prey lengths changed. Notably, the average length of the main prey, flying fish, decreased by 12.6% (2.9 cm) with rising SST and decreasing chl *a*. Consequently, the energy gain per flying fish may have decreased under unfavourable conditions. To compensate for this potential reduction in energy gain per prey item, the boobies shifted to non-flying fish, which showed no changes in body size between varying marine conditions. Shifts in diet composition have often been observed in seabirds as a means to successfully buffer unfavourable oceanographic conditions (e.g. Erwin & Congdon 2007). However, it seems that Abbott's boobies were not able to fully buffer a reduced energetic value of smaller flying fish by consuming more non-flying fish, as the contribution to total biomass of both prey groups did not change according to marine conditions. In addition to the prey size, diving depth was affected by marine conditions. When SST increased, maximum dive depth also increased—and in 2010 (the year with the highest SST), the deepest dives

were recorded. The deeper dive depths might have reduced the success rate of prey capture per dive, but certainly have increased energy expenditure per dive—both of which will have decreased the birds' diving efficiency. Thus, changes in both prey energy content and diving efficiency are likely to have affected the foraging success of Abbott's boobies under poor conditions, resulting in the observed longer and more distant foraging trips.

Conclusions

Abbott's boobies have adapted to the oligotrophic conditions of their marine environment by a suite of foraging behaviours that reduce foraging costs and enhance foraging success. However, the species exhibits only a few foraging behaviours that differ from other tropical booby species, despite their presumably more intensive exposure to tropical oceanic waters. Most remarkable are their low flight speeds, change-over patterns and frequent overnight trips—all of which seem to enhance the Abbott's boobies' gross foraging efficiency. With regard to the variability in their marine habitat, those behaviours will also contribute to the birds' remarkable ability to keep their body condition, and that of their chicks, stable even under unfavourable oceanographic conditions, at least during the early chick-rearing period. However, Abbott's boobies have one of the longest chick-rearing periods of all seabirds: up to 14 months (Nelson 1978), thus the birds may not be able to buffer low prey availability over this extended period, despite the manifold adaptations to their challenging marine habitat.

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