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Overnight foraging trips by chick-rearing Nazca Boobies *Sula granti* and the risk of attack by predatory fish

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Most tropical booby species complete breeding foraging trips within daylight hours, thus avoiding nights at sea. Nazca Boobies *Sula granti* are unusual in this respect, frequently spending one or more nights away from the nest. We used GPS dataloggers, time-depth recorders, and changes in body weight to characterize foraging trips and to evaluate potential influences on the decisions of 64 adult Nazca Boobies to spend a night at sea, or to return to their chicks on Isla Española, Galápagos, in daylight hours. The tagged birds foraged east of Isla Española, undertaking both single-day (2–15 h, 67% of trips) and overnight trips (28 h–7.2 days, 33%), and executing 1–19 foraging plunge-dives per single-day trip. Birds might forage longer if they are in nutritional stress when they depart, but body weight at departure was not correlated with trip length. Birds might be expected to return from longer trips with more prey for young, but they returned from single-day and overnight trips with similar body weights, consistent with previous indications that Nazca Boobies forage until accumulating a target value of prey weight. Birds with a lower dive frequency during the first 5 h of a trip were more likely to spend the night at sea, suggesting that they might choose to spend the night at sea if prey capture success was low. At night, birds almost never dived and spent most of their time resting on the water's surface (11.8–12.1 h, > 99% of the time between civil sunset and civil dawn). Thus, the night is an unproductive time spent among subsurface predators under low illumination. The birds' webbed feet provided evidence of this risk: 24% of birds were missing > 25% of their foot tissue, probably due to attacks by predatory fish, and the amount of foot tissue lost increased with age, consistent with a cumulative risk across the lifespan. In contrast, other tropical boobies (Blue-footed *Sula nebouxii* and Brown Boobies *Sula leucogaster*), which do not spend the night on the water, showed no such damage. These results suggest that chick-rearing Nazca Boobies accept nocturnal predation risk on occasions of low prey encounter during a foraging trip's first day.

Keywords: at-sea movements, foot damage, GPS loggers, shark predation, *Sula granti*.

Boobies and gannets (Aves: Sulidae) are visual predators, foraging primarily or exclusively during daylight hours by plunge-diving for near- or subsurface prey (Nelson 1978). Most species forage hundreds of kilometres from their breeding colony, incurring commuting costs to varying degrees (Hamer *et al.* 2001, Grémillet *et al.* 2004, Weimerskirch *et al.* 2008). Central place foraging theory (Orians & Pearson 1979) predicts that long, unproductive commutes should extend the period of productive foraging, balancing a trade-off between diminishing returns at the foraging site and unproductive travel time. Higher-latitude

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breeding gannets (Cape *Morus capensis*, Northern *Morus bassana* and Australasian *Morus serrator*) often extend their feeding trips for more than 1 day by resting on the sea surface during the night. This foraging strategy probably compensates for the commuting cost incurred during long trips for successful feeding in highly predictable and profitable but distant prey patches (Garthe *et al.* 2003, Ropert-Coudert *et al.* 2004a, Bunce 2005, Pettex *et al.* 2010). Because the marine habitats of the tropics are less predictable and productive, and food is probably more patchy than in temperate and polar zones (Weimerskirch 2007), tropical boobies are expected to change flight direction in consecutive trips and travel to distant feeding areas, increasing the chances of spending a night at sea. Indeed, observations from a radiotelemetry study in 1986 revealed that although most breeding Nazca Boobies *Sula granti* from Isla Española, Galápagos, complete feeding trips during daylight hours, 8% of the trips span more than 1 day (Anderson & Ricklefs 1987). Likewise, breeding Masked Boobies *Sula dactylatra* from Latham Island, Tanzania, fitted with satellite transmitters occasionally forage in single trips of up to 7 days (Asseid *et al.* 2006). However, other tropical species (e.g. Brown *Sula leucogaster*, Red-footed *Sula sula* and Blue-footed *Sula nebouxii*) and Masked Boobies from other localities return to their nests in the same day that they depart, thereby avoiding a night at sea (Anderson & Ricklefs 1987, Lewis *et al.* 2004a, Weimerskirch *et al.* 2005, 2008, Young *et al.* 2010). The occurrence of both short and prolonged trips of some species of seabird during chick-rearing may be the result of temporal changes of prey distribution around their colonies (Rayner *et al.* 2010) or to a dual foraging strategy associated with parental decisions of maximizing food delivery rate to chicks through short trips or reducing the loss of adult body condition through long trips (Chaurand & Weimerskirch 1994, Baduini & Hyrenbach 2003). Northern Gannets from the Bass Rock, Scotland, do not exhibit an obvious bimodal pattern to trip duration and the decision to take a longer trip is not affected by an adult's initial rate of encounter with prey (Lewis *et al.* 2004b). Proximate factors such as adult's body condition or prey availability that might cause a bird's decision to undertake a long, overnight trip have not yet been examined in tropical boobies.

Many seabird species in the blue-water conditions of the tropical oceans feed in association with several species of tunas (Scombridae: *Thunnus* spp.) and dolphins (Delphinidae; Au & Pitman 1986, Jaquemet *et al.* 2004, Hebshi *et al.* 2008), exploiting the availability of bait fish driven to the surface by these sub-surface predators (Au & Pitman 1986, Au 1991). Foraging associations between marine mammals and seabirds also occur at higher latitudes (see review in Shealer 2002), but those catalysed by tunas and dolphins in the tropics are more conspicuous and recurrent, particularly in the Eastern Tropical Pacific (ETP; Au & Pitman 1986, Au 1991, Ballance *et al.* 2006). Tropical boobies and other seabirds attracted to these associations may spend the night near concentrations of these predators, risking becoming prey themselves. Sharks (Selachimorpha) are obvious candidates as predators of seabirds; Tiger Sharks *Galeocerdo cuvier* consuming albatrosses (Meyer *et al.* 2010) and White Sharks *Carcharodon carcharias* attacking penguins and cormorants (Johnson *et al.* 2006) provide well-known examples. Other possible predators also exist. It has been hypothesized that breeding tropical boobies may return to land at night to avoid sub-surface predators (Nelson 1978: 921, Schreiber & Chovan 1986, Weimerskirch *et al.* 2008). This potential cost of spending the night at sea has not been evaluated.

Nazca Boobies are endemic to the ETP, with main populations on Malpelo Island and the Galápagos Archipelago (Pitman & Jehl 1998). Although chick-rearing Nazca Boobies from Isla Española, Galápagos, occasionally undertake overnight trips (Anderson & Ricklefs 1987), it is unknown whether birds spend nights away from land elsewhere in the archipelago, fly at night or rest on the sea. In this study, we characterized the foraging, especially regarding overnight trips, of chick-rearing Nazca Boobies from the colony of Punta Cevallos, Isla Española, Galápagos, in February/March 2007 using small GPS loggers, time-depth recorders and changes in body weight. We also examined injuries to the feet, as an index of predation attempts, to evaluate the relative risk of predation at sea for Nazca Boobies and two other tropical booby species in the ETP.

METHODS

Study site and period

The foraging behaviour of Nazca Boobies was studied at Punta Cevallos, Isla Española (1°22′S, 89°36′W, Fig. 1a) between 26 February and 15 March 2007. Approximately 3000 pairs breed seasonally in this colony, with most egg-laying occurring between October and January and chick-rearing between February and June (Maness & Anderson 2008). Foot damage was assessed in Nazca Boobies at Punta Cevallos (15–26 November 2000, D.J.A.), in Blue-footed Boobies from

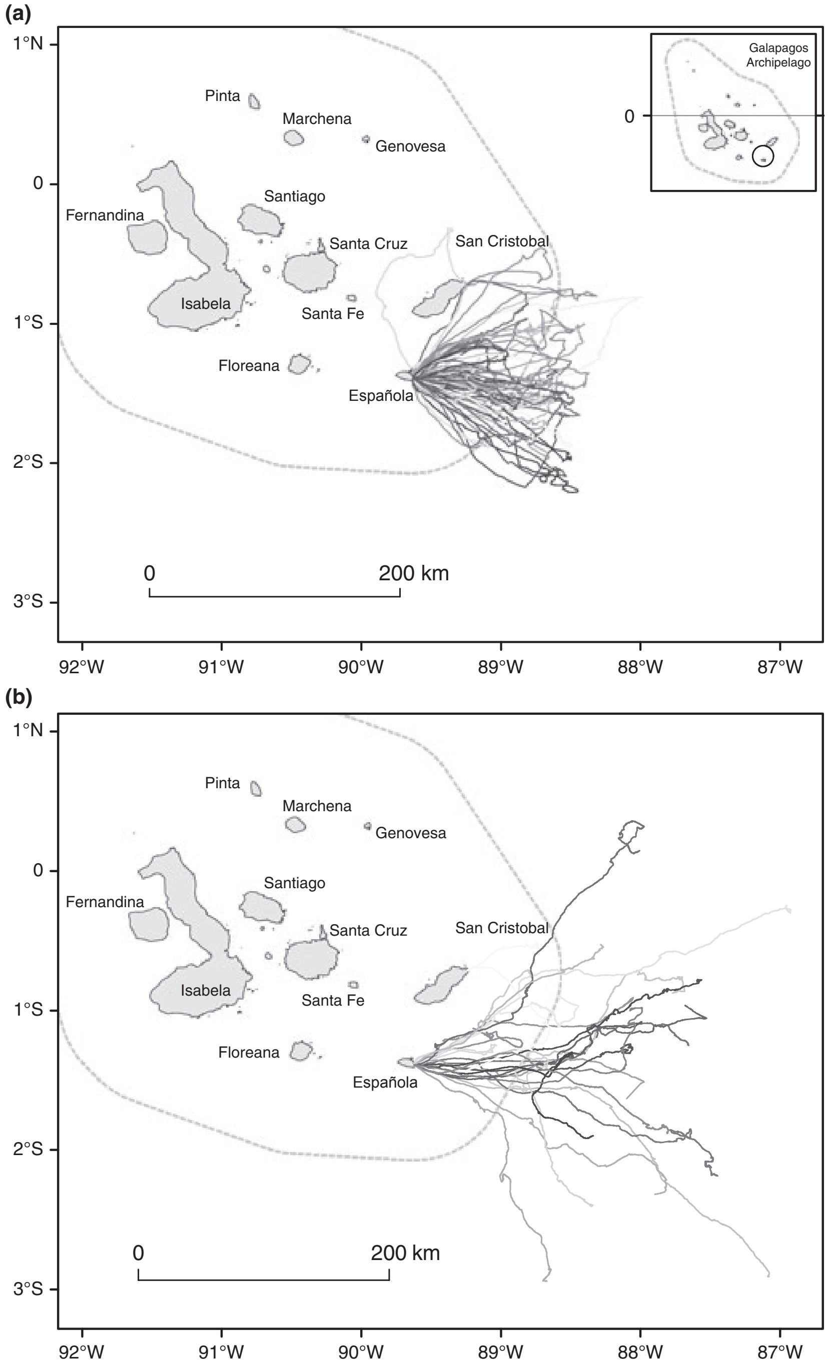

Figure 1. (a) Complete (n = 58) and (b) truncated (n = 15) tracks of chick-rearing Nazca Boobies from Punta Cevallos, Isla Española, Galápagos, as determined by GPS dataloggers. Individual trips are distinguished by different black and grey tones. The dashed line around the archipelago shows the boundaries of the Marine Protected Area.

photographs taken on Isla Lobos de Tierra, Peru (6°24′S, 80°51′W, 13–25 December 2006, M.S.M.), and in Brown Boobies from photographs taken on Isla Gorgona, Colombia (3°0′N, 78°10′W, 9–15 September 2007, F.A.E.).

Dataloggers

In 2007, adults were tagged either with a GPS datalogger (GPS, Gipsy-1, 33 g; 5 × 3 × 1 cm; http://www.technosmart.eu, October 2011) only, or with a GPS in conjunction with a time-depth recorder (TDR, Lotek LTD1110; 5 g; 1.1 × 3.2 cm, http://www.lotek.com, October 2011). The GPS units were powered with 700 mA.h rechargeable batteries and set to record one position every 10 or 20 s (accuracy of < 10 m in > 95% of location fixes) for a maximum deployment time of 36 h. The GPS units were protected in two heat-sealed waterproof polyethylene bags (1 g) before deployment. The TDRs collected data every second for approximately 18 h after initialization. The pressure sensor recorded depths with an accuracy of ±0.3 m (depth range: 0–30 m). Dive events were identified by immersions > 0.3 m and extracted for each trip using MULTITRACE MT-dive software (Jensen Software Systems, Kiel, Germany). The GPS units were attached to the dorsal base of four central tail feathers using waterproof Tesa® tape (product 4651; Tesa, Charlotte, NC, USA). The TDRs were attached to a metal leg band with three small plastic cable ties. The loggers and their accessories (plastic bags, band, tape and cable ties) added a burden of approximately 50 g, representing < 3.5% of the tagged bird's weight (range = 1425–2100 g, see Results). Attachment of the loggers was completed in < 10 min, and adults returned to their nests and resumed their activities after handling.

Capture and handling of birds

Birds were captured at their nests between 05:00 and 06:30 h local time, when the gut contents were minimized. Only one member of a breeding pair was selected, removed from the nest by hand, and held by one member of a two-person team. At first capture, each bird was weighed in a bag using a 5-kg Pesola® balance (accuracy ± 25 g; Pesola AG, Baar, Switzerland) and banded on one leg with a uniquely numbered stainless steel ring. This adult body weight was considered the minimum daily weight without any payload. The nests were marked with numbered vinyl flagging. At recapture upon return from a trip, and before any food weight was lost by feeding a nestling, the loggers were removed and birds were weighed and measured with a rule (±1 mm) to record wing chord (WC) and ulna length (UL), and with a digital calliper (±0.01 mm) to record culmen length (CL). Chicks from tagged birds were also weighed and measured to estimate their age using weight and wing chord growth curves derived from known-aged chicks (Nelson 1978). The feeding trip length was used as a proxy of foraging effort and defined as the time elapsed between departure and arrival to the nest as indicated by the GPS unit.

Controls and monitoring of nests

Fourteen tracking sessions were conducted, with each session using birds nesting near one another to facilitate simultaneous observation. Each session used birds from a previously unused part of the colony. In each session, half of the adults were fitted with loggers, and the other half were treated as control birds to detect any handicapping effect of the loggers. For comparisons of tagged and control birds, trip length was measured by visual observations of departures and arrivals. We assumed that any adverse effect of loggers would be reflected in an increased trip length. GPS data indicated that the shortest successful trip (adult's body weight increase ≥ 50 g) of tagged birds was 2 h (see Results) and that boobies immediately returned and remained at their nest-sites when not on foraging trips. Thus, nest absences of < 2 h were excluded from analyses. Control birds were captured and measured as were tagged birds, but they did not carry any added weight. Nests of tagged birds were monitored continuously from 06:30 to 18:30 h, with an additional check at 20:00 h. Birds recaptured at 20:00 h were assumed to have arrived at the midpoint between the last two checks (birds outfitted with GPS showed that arrivals stopped at 20:00 h; see Results).

Spatial data analysis

The spatial data from loggers were mapped and analysed using ARCGIS 9.2 Geographic Information System software (ESRI Inc., Redlands, CA, USA). The positions were projected to the Miller Cylindrical coordinate system for all spatial analysis. A detailed description of the analysis of foraging variables is given in Zavalaga *et al.* (2010). Briefly, all positions on land were excluded from analysis, and instantaneous speeds were calculated from the distance and time elapsed between two consecutive positions. An inspection of the frequency distribution of speeds revealed a clear bimodality, with a minimum value of 10 km/h between the two modes. For the calculations of the proportion of time spent on water (sitting or diving), we used values < 10 km/h, and consequently the proportion of time spent flying was calculated from speeds > 10 km/h (mean flight speed = 45.3 ± 2.75 km/h, with a burst speed of 87 km/h). Individual tracks were reduced to three main components: (1) the bearing between the nest and outmost foraging point; (2) the maximum foraging range, defined as the straight line distance between the nest and the furthest position in the route; and (3) the cumulative distance travelled during the foraging trip.

The TDRs were synchronized with the GPS units before deployment to the nearest 1 s using the satellite-time read from a conventional hand-held GPS. Thus, all dives were geo-referenced and their locations used to identify foraging areas (Fig. 2).

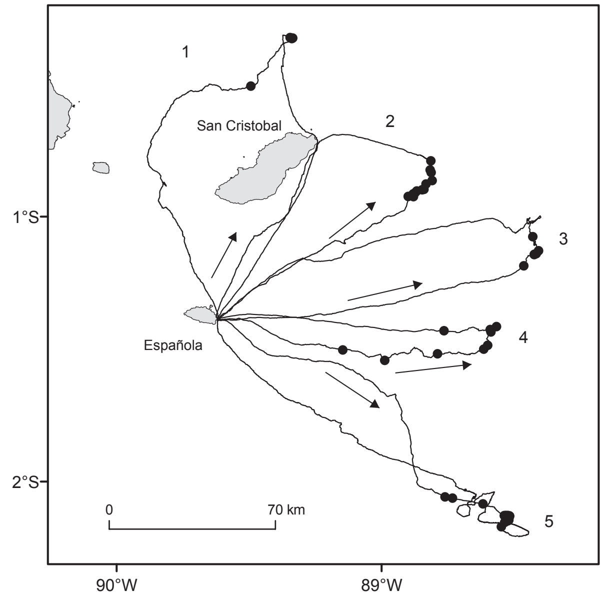

Figure 2. Foraging single-day trips of five chick-rearing Nazca Boobies from Isla Española tracked with GPS loggers and time-depth recorders. The locations of dives in the foraging paths are shown by closed circles. The direction of outbound paths is indicated by arrows.

Foot damage

During annual ring-resighting surveys, all leg-banded Nazca Boobies at Punta Cevallos were captured and examined. During the 2000 session, D.J.A. evaluated injuries to the feet of the entire banded population of 1852 adults while each bird was in the hand. D.J.A. also evaluated photographs of the feet of 26 adult Brown Boobies and 116 adult Blue-footed Boobies; in these cases, the feet were flattened against a transparent plastic plate and photographed through the plate. The age of many of the Nazca Boobies, but not the other species, was known. However, the random sampling of Brown and Blue-footed Boobies probably included individuals from different age-classes. For all birds, the area of the foot that was missing was estimated and the damage was classified into five categories:

Category 0: 0% damage; intact web and foot.

Category 1: < 1% damage; pin hole(s) in web or small scallop(s) in margin of web. These injuries were consistent with punctures from stepping on sharp seeds or fish bones in the colony, or possibly bites on the foot margin during fights with conspecifics.

Category 2: 1–5% damage; holes larger than 2 mm diameter, missing web(s) and/or larger scallop(s) in margin of web, end of a toe missing. These were generally consistent with both fight injuries and predator attacks.

Category 3: 6–25% damage; web between two adjacent toes mostly missing, one or more phalanges missing from a toe. These injuries were probably caused by a predator, and often left evenly spaced shreds of tissue on the foot, consistent with a row of sharply pointed teeth.

Category 4: > 25% damage; substantial part of foot including toe missing, such as all web between adjacent toes. These injuries were almost certainly all from predators with powerful mouths and teeth. No plausible alternative explanation exists for these injuries that usually severed at least one bone.

Figure 3 shows examples of Nazca Booby feet in each damage category. For inter-specific comparisons, we selected categories 3 and 4 as evidence of bites of sub-surface toothed predators. In this case,

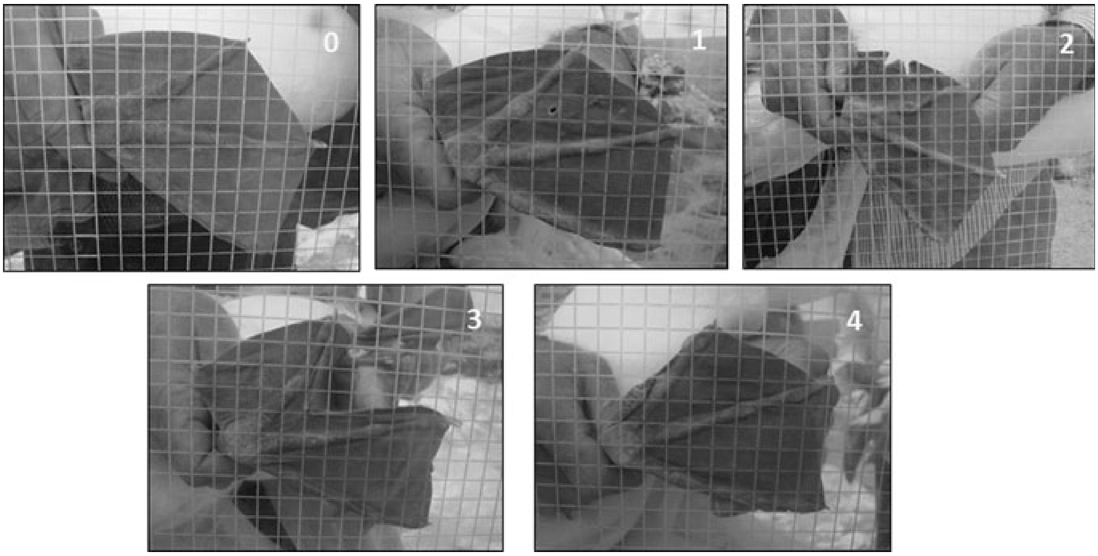

Figure 3. Comparison images of foot damage in Nazca Boobies from Isla Española, Galápagos. Damage was divided into five categories based on the foot area that was missing: (0) intact foot web, (1) small pin hole in the web, (2) large scallop in margin of web, (3) web between digits 2 and 3 mostly missing, and (4) all web between digits 1 and 2 missing.

the highest score of the two feet of each individual was included in the analysis.

Statistical analysis

Where necessary, data were arcsin- or log-transformed to meet normality requirements before statistical analysis. The dataset compiled for each bird included multiple sequential data values within a trip and occasionally more than one trip during one deployment. To avoid data autocorrelation at the bird level, general linear mixed models were applied with restricted maximum likelihood estimations (REML) for comparisons of foraging variables of categorical data (e.g. tagged vs. control birds), covariates, and their respective interactions. In this model, bird identity was fitted as a random factor. General linear models (GLM) were used for data comprising single observations per bird. The mean directional vector (*r*) was used to measure bearing dispersion, with *r* values close to 1 indicating that headings were highly concentrated to a specific location (Batschelet 1981). Comparisons of categorical data (foot damage) were evaluated with log-linear analysis. Statistical Analysis Systems (SAS) was used for all statistical tests of linear variables (SAS Institute 2004). Descriptive statistics of circular data (angles and time) were performed using ORIANA 2 software (Kovac Computing Service, Pentraeth, Wales, UK). Means are expressed ±1 sd unless otherwise indicated, and differences were considered significant at $\alpha < 0.05$.

RESULTS

The recovery rate of dataloggers was 100%. We obtained data from 64 birds (52 fitted with GPS and TDR loggers and 12 with GPS only) for a total of 73 trips. However, 15 of these trips were truncated during the outbound path due to battery depletion of either the GPS (maximum deployment time = 36 h) or the TDR (maximum = 18 h) and, as a result, the sample size (number of trips or number of birds) varied with the foraging variable and the type of trip measured (single-day or overnight, complete or truncated, or a combination of both). The age of chicks of tagged birds was estimated to be between 8 and 14 weeks (range body weight = 1100–2250 g; range wing chord = 120–385 mm). Adults were provisioning chicks in this age range at the peak rate (Anderson & Ricklefs 1992), leaving the nest unattended for most of the day.

Flight orientation, trip duration and foraging range

Foraging flights were predominantly oriented in an arc from the northeast to southeast of Punta Cevallos (mean vector bearing $\mu = 85.5°$, vector length $r = 0.89$, 93% of the trips oriented between 40° and 140°, Fig. 1a,b) with only one excursion occurring inside the archipelago (within the envelope connecting the outer points of islands), around Isla San Cristóbal (Figs 1a and 2). Trip length of tagged birds followed a positively skewed distribution, with 67% of the trips ($n = 73$) completed between 2 and 15 h, and the remaining trips completed between 28 h and 7.2 days (Fig. 4). Thirty-one per cent of the birds ($n = 64$) took overnight trips. Based on this distribution, feeding trips were categorized into single-day trips (< 15 h, completed in the day of departure, mean = 8.48 ± 2.78 h, median = 8.8 h, $n = 48$) and overnight trips (> 28 h, birds spent one or more nights at sea, mean = 57.52 ± 39.83 h, median = 35.3 h, $n = 25$). The maximum foraging range and the total distance travelled of birds with single-day trips did not exceed 193 km (mean = 98 ± 39 km, $n = 48$) and 464 km (mean = 257 ± 92 km, $n = 48$), respectively. Nevertheless, outbound tracks from incomplete overnight trips revealed that the furthest distance recorded from the colony was 329 km.

Effects of instrumentation

A two-way mixed model revealed that tagged and control birds had similar trip duration (log-x, REML, $F_{1,116} = 0.03$, $P = 0.86$). The instrumentation by trip type interaction was also non-significant (log-x, REML, $F_{1,2} = 0.01$, $P = 0.95$), indicating that the average trip length of single-day and overnight trips was similar between tagged and control birds (trip length controls: single-day = 8.32 ± 2.32 h, $n = 39$; overnight = 57.06 ± 31.69 h, $n = 15$).

At-sea activities during single-day and overnight trips

The timing of foraging of birds with single-day (departures: mean = 08:28 h, range = 03:18–15:35 h, $n = 48$; arrivals: mean = 16:57 h, range = 13:47–19:40 h, $n = 48$) and overnight trips (departures: mean = 08:31 h, range = 04:54–13:48 h, $n = 25$; arrivals: mean = 16:07 h, range = 11:30–20:00 h, $n = 25$) was similar (departures: REML, $F_{1,61} = 0.001$, $P = 0.96$; arrivals: REML, $F_{1,61} = 3.38$, $P = 0.16$). First departures generally started between 05:18 and 06:03 h, before civil sunrise (06:03 h). Only 9.5% of the trips ($n = 73$) finished after civil sunset (18:10 h). Birds on overnight trips spent a much larger proportion of the trip's duration resting on the sea than did birds on single-day trips (single day: mean = 33 ± 11% of the total trip length, range = 10–61%, $n = 48$ birds; overnight: mean = 62 ± 4% of the total trip length, range = 59–65%, $n = 2$ birds with complete overnight trips). An inspection of tracks of birds with overnight trips showed clearly that birds rest on the sea surface during the hours of darkness. During overnight excursions, birds landed on the water just before sunset or twilight (17:15–18:15 h) and

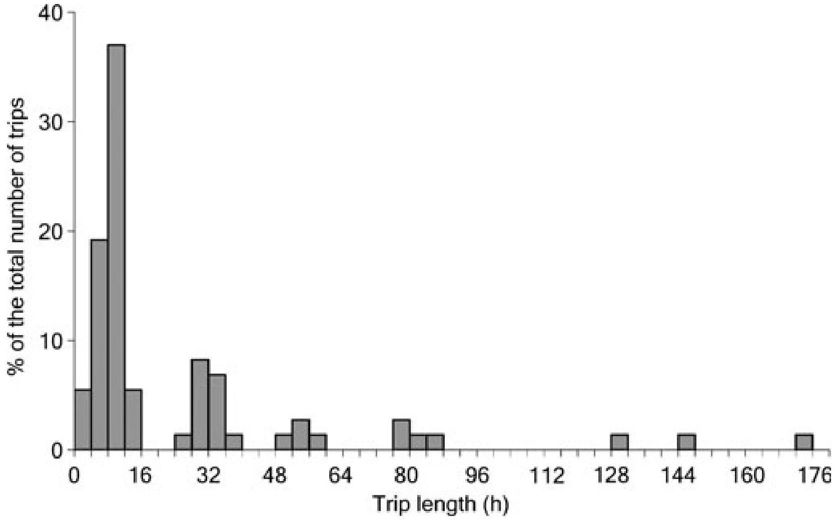

Figure 4. Frequency distribution of foraging trips of tagged ($n = 73$) chick-rearing Nazca Boobies from Punta Cevallos, Isla Española, Galápagos, in February–March 2007.

resumed flight after dawn the next day. During inactive nocturnal periods on the water, birds occasionally left the water (number of events = 3–16 per night) for short flights (modal flying time = 20 s, $n = 4$ trips for four birds with complete and truncated tracks between departure from the colony and the next morning). The tracks of these short flights showed rectilinear displacement (modal distance = 300 m) and not a sinuous path typical of food searching; thus, these short nocturnal flights were probably not related to foraging. Furthermore, the median distance travelled between the last dive during daylight and settling on the water for the night was 10.85 km (range = 0.15–78 km, $n = 16$ birds with TDR and GPS with overnight trips), indicating that birds did not necessarily stay overnight close to the foraging patch for surface seizing prey during darkness or resuming plunge-diving the next morning. Overall, birds spent 11.8–12.1 h sitting on the water during the night (> 99% of the time between civil sunset and civil sunrise), drifting a total mean distance of 19.3 ± 7.1 km (range = 11.1–30 km, $n = 4$ birds with complete and truncated tracks between departure from the colony and the next morning) at a constant modal speed of 0.55 m/s. Four birds visited the Nazca Booby colony at Punta Pitt, Isla San Cristóbal (Fig. 1a,b), of which two birds spent the night in this colony (3% of the total number of tagged birds) and two birds passed by.

Proximate causes for the occurrence of overnight trips

To examine the effects of body condition on the duration of feeding trips, a principal component (PC1) derived from body measurements (culmen, ulna and wing chord) of 64 tagged birds was calculated (82% of the variance explained by the standardized PC1 = 0.0072*CL + 0.39*UL + 0.92*WC). Seven of these birds departed the day after attachment and weighing (mean = 27.8 ± 1.48 h, range = 25.9–29.7 h), whereas 57 birds departed within a few hours of attachment and weighing (mean = 3.07 ± 2.24 h, range = 0.066–9.63 h). An analysis of covariance with the complete dataset revealed that the index of body size was highly correlated (GLM, $F_{1,60} = 67.9$, $P < 0.0001$) with body weight in the early morning (mean = 1717 ± 171 g, range 1425–2100 g, $n = 64$) and that initial body weights of birds that performed single-day and overnight trips did not differ after controlling for the effect of body size (GLM, intercept: $F_{1,60} = 0.02$, $P = 0.88$, slope: $F_{1,60} = 0.01$, $P = 0.93$). Therefore, initial body weight did not influence the bird's decision to take a single-day or overnight trip. When the analysis was restricted to only those birds that departed soon after attachment and weighing, the result was similar (GLM, intercept: $F_{1,53} = 0.001$, $P = 0.96$, slope: $F_{1,53} = 0.09$, $P = 0.77$). Adult body weight increment after a feeding trip varied between 50 and 700 g (mean 344 ± 142 g, $n = 35$) and was not correlated with the body size index (GLM, $F_{1,33} = 0.253$, $P = 0.618$). The weight increase after a feeding trip in relation to the initial body weight was similar for birds with single-day (median = 17%, range = 3–29%, $n = 22$) and overnight trips (median = 23%, range = 0–40%, $n = 11$; arcsin-x, GLM, $F_{1,33} = 1.834$, $P = 0.185$).

To assess whether low prey encounter rates at distances close to the colony influenced the decision of birds to carry out overnight trips, we compared the dive frequency of birds with single-day and overnight trips in the first 5 h of a trip which corresponded to the initial, outward phase of the trip. Diving rates were significantly higher in birds that undertook single-day trips (mean = 0.93 ± 0.67 dives per hour, $n = 34$) than in birds that chose overnight trips (0.61 ± 0.42 dives per hour, $n = 15$; GLM, $F_{1,47} = 4.08$, $P = 0.04$). Dives were shallow (mean = 1.6 ± 1.1 m, maximum = 4.6 m, $n = 405$ dives for 52 birds) and of short duration (mean = 3.2 ± 1.1 s, maximum = 8 s, $n = 405$ dives for 52 birds). The dive depth was similar for single-day and overnight trips (REML, $F_{1,50} = 2.15$, $P = 0.148$). No immersions were detected in two of 35 birds that foraged successfully in single-day trips (confirmed by the foraging track pattern and body weight increase), suggesting that 'aerial dives' or very shallow dives (< 0.3 m) may occur. The total number of dives in single-day trips varied between 1 and 19 (mean 6.7 ± 4.3 dives per trip, $n = 33$ birds with TDR and GPS in single-day trips).

Foot damage

The log-linear analysis of damage categories (0–4) and booby species revealed that the species by damage interaction was significant ($\chi^2 = 1311$, df = 2, $P < 0.0001$), with severe foot damage (category 4) observed only in Nazca Boobies (24% of the birds; Fig. 5). Overall, the majority of individuals had feet that were intact or nearly so (categories 0–2:

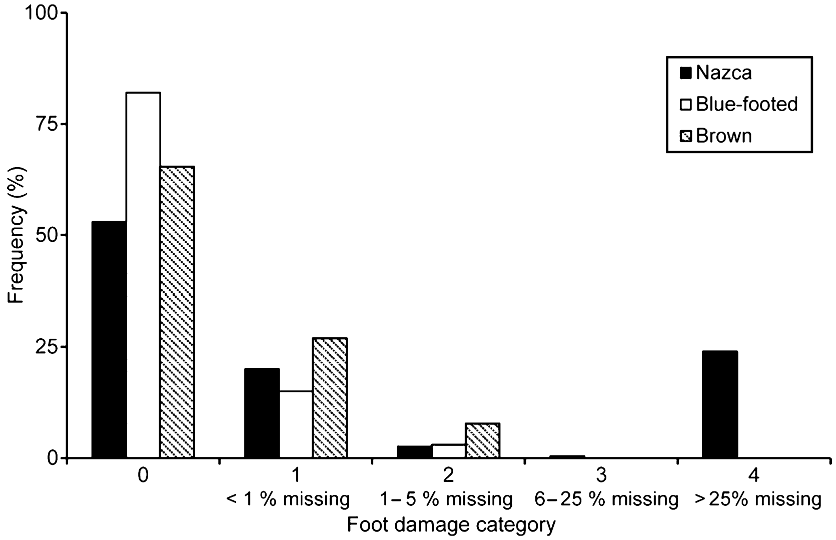

Figure 5. Frequency (proportion of the total number of inspected feet) of foot damage of three species of booby (Nazca Boobies from Isla Española, Galápagos, $n = 1852$; Blue-footed Boobies from Isla Lobos de Tierra, Perú, $n = 116$; Brown Boobies from Isla Gorgona, Colombia, $n = 26$). Foot damage was categorized into five categories based on the area of the foot that was missing (see Fig. 3).

Nazca = 55.5%, Blue-footed = 97%, Brown = 92%; Fig. 5). Foot damage of Nazca Boobies increased significantly with age in males between 2 and 16 years old (right foot: Spearman $r = 0.238$, $P < 0.05$, $n = 669$; left foot, Spearman $r = 0.172$, $P < 0.05$, $n = 669$) and in females between 4 and 16 years old (right foot, Spearman $r = 0.195$, $P < 0.05$, $n = 485$; left foot, Spearman $r = 0.099$, $P < 0.05$, $n = 485$). Only seven of 101 (7%) Nazca Booby males aged 4–5 years had category 4 damage to at least one foot, but 11 of 40 (28%) males aged 15–16 years did; one male in this age class had category 4 damage to both feet. For Nazca Booby females, the parallel results were 13 of 100 (13%) 4–5-year-olds, and 10 of 27 (37%) 15–16-year-olds had category 4 damage; two females in this age class had category 4 damage to both feet.

DISCUSSION

Effects of tagging

Nazca Boobies from Punta Cevallos, Isla Española, tolerate human presence, which facilitated the capture of birds and recovery of the loggers. An increase in trip length of tagged seabirds has been generally attributed to handicapping effects of external devices (Paredes *et al.* 2005, Passos *et al.* 2010). We found no evidence that the simultaneous use of GPS loggers and TDRs had short-term consequences for the foraging performance of Nazca Boobies. The mean trip duration and the distribution of single-day and overnight trips were similar for equipped and non-equipped birds, with no significant differences by group. Furthermore, no tagged birds deserted their nest during the study period and we did not observe any evident change of behaviour of tagged birds in the nest after attachment of loggers and handling.

Foraging range

This study showed that chick-rearing Nazca Boobies are one of the most pelagic of all boobies studied so far during the breeding period. This finding is supported by inter-specific comparisons of the maximum foraging range of breeding boobies obtained with dataloggers or telemetry at different colonies: 70 km from Palmyra Atoll, Equatorial Pacific Ocean (derived from Young *et al.* 2010), 245 km from Clipperton Island, ETP (Weimerskirch *et al.* 2008), and 367 km from Latham Island, Tanzania (Asseid *et al.* 2006), for Masked Boobies; > 329 km from Isla Española, Galápagos (this study), for Nazca Boobies; 148 km from Europa Island, Indian Ocean (Weimerskirch *et al.* 2005), and 160 km from Palmyra Atoll (derived from Young *et al.* 2010) for Red-footed Boobies; 109 km from Isla San Idelfonso, the Gulf of California (derived from Weimerskirch *et al.* 2009), and Isla Lobos de Tierra, Peru (Zavalaga *et al.* 2008), for Blue-footed Boobies; 96 km from Isla San Idelfonso (derived from Weimerskirch *et al.* 2009) for Brown Boobies; and 21 km from Isla Pájaros, Chile (Ludynia *et al.* 2010), and 68 km from Isla Lobos de Tierra, Peru, for Peruvian Boobies *Sula variegata* (Zavalaga *et al.* 2010). The furthest distance recorded for a Nazca Booby from Punta Cevallos in 2007 was 329 km, which was obtained from an outbound commute truncated 1.5 days after the bird left the nest. Thus, we believe that in longer trips (up to 7 days recorded in this study), chick-rearing Nazca Boobies may have travelled longer distances. Indeed, in 2008 we documented a tagged Nazca Booby raising a small chick travelling 912 km east of the Punta Cevallos colony, returning to its nest 9 days after departure (C.B. Zavalaga, S. Emslie, S. Cruz, C. Proaño, J. Grace, D.J. Anderson unpubl. data). Shorter foraging trips and lower occurrence of overnight trips of chick-rearing Nazca Boobies from Punta Cevallos have been observed in previous years (Anderson & Ricklefs 1987, 1992), suggesting that adjustments in the foraging range of these birds probably occur as a result of local oceanographic conditions. The waters east of Isla Española, where Nazca Boobies usually feed (Anderson & Ricklefs 1987, this study), vary on annual and inter-decadal scales, related in part to El Niño conditions (Pennington *et al.* 2006), which influence the breeding phenology and diet of Nazca Boobies (Anderson 1989).

Spending the night at sea

Thirty-one per cent of Nazca Boobies spent a night at sea, sitting on the water and occasionally making brief, non-foraging flights. Birds passively drifted with ocean currents during this long period (approximately 12 h), probably digesting food ingested during the day (Garthe *et al.* 2003), recovering from the energy costs incurred during the first part of the foraging trip (Ropert-Coudert *et al.* 2004b), and possibly resting and sleeping (Shamoun-Baranes *et al.* 2011). Because tracks in these long trips were truncated during the outward section, it can be argued that adults also may have been resting in other places on Isla Española or on other islands within the Galápagos archipelago. We can rule out these possibilities as Nazca Boobies stay in their nests when not foraging (Anderson & Ricklefs 1987, this study), and although a small number of birds stayed overnight on Isla San Cristobal (two of 64), the majority travelled hundreds of kilometres east and southeast of Punta Cevallos where there are no islands for landing. Likewise, the complete long track recorded in 2008 (see above) suggests that it is likely that during prolonged absences from the nest, Nazca Boobies in 2007 travelled far to the east of the colony.

In some species of tubenose seabirds (Procellariiformes), breeding adults alternate or mix short and long trips during the chick-rearing period as a strategy to maximize food delivery rate to chicks and reduce the risk of depleted adult body condition (Chaurand & Weimerskirch 1994, Baduini & Hyrenbach 2003). Short trips maximize provisioning rates to chicks, but adults typically lose body weight as a result of higher energy requirements to find food during short trips, and the mix is thought to balance the food requirements of parent and offspring. Although Nazca Boobies undertook single-day and overnight trips, we recorded no clear separation or bimodal distribution in the duration of feeding trips that could suggest a dual foraging strategy. More importantly, our data indicate that the occurrence of short and long forays was not related to adults' body condition, contrary to the predictions of the dual foraging strategy hypothesis. Finally, body weight increment was similar for birds with single-day and overnight trips, suggesting that the net profit of the trip was not higher as a result of long trips.

Birds making overnight trips were apparently not driven to do so by late departures on the first day of the trip, or by poor nutritional status at the beginning of the trip. Instead, a low prey encounter rate on the first day of the trip preceded a night at sea, suggesting that overnight trips are a compensatory strategy of poorly foraging birds attempting to acquire a target amount of prey far from the colony. Anderson and Ricklefs (1992) also documented variable trip lengths but consistent amounts of food delivered to the nest in this same population. Long excursions of Northern and Cape Gannets were related to the exploration of more predictable and profitable offshore areas (Lewis *et al.* 2004b, Ropert-Coudert *et al.* 2004b, Pettex *et al.* 2010), but the high variability in length of overnight trips and longer duration than their temperate relatives (Northern and Cape Gannets usually travel < 48 h, Garthe *et al.* 2003, Grémillet *et al.* 2004), and wide dispersion of their destinations (Fig. 1) suggest that food patches within the foraging range of Nazca Boobies are relatively unpredictable, at least in a coarse (1-100 km) spatial scale. Although the decisions of chick-rearing Nazca Boobies about foraging destination are not associated with their body condition, they also may be influenced by age and individual foraging skills (Zimmer *et al.* 2011), sex (González-Solís *et al.* 2000), chick condition (Ochi *et al.* 2010) and success in locating prey during the previous trip (Hamer *et al.* 2001), all variables that should be included in future studies.

Risk of predation by sub-surface predators

Sharks are obvious potential predators of Nazca Boobies because they are known to attack seabirds (Johnson *et al.* 2006, Meyer *et al.* 2010) and are relatively abundant in and around Galápagos (Hearn 2009). However, we cannot rule out other toothed sub-surface predators, such as tunas and marine mammals, because their foraging grounds east of Española overlap with those of Nazca Boobies (Au & Pitman 1986, Ballance *et al.* 2006). Our observations of foot damage indicate that Nazca Boobies are attacked sporadically by toothed sub-surface predators. The birds' webbed feet provide evidence of the risk of attack: 24% of birds had lost > 25% of their foot tissue and a remarkable 28–37% of 15–16-year-old Boobies had incurred serious damage to their feet. This age-related increase in foot injury, for which predators at sea are the only plausible cause, suggests a cumulative risk across the lifespan. In addition to damaged feet, we have observed more severe injuries to adult Nazca Boobies returning from the sea, including loss of the entire body posterior to the legs, and missing legs and feet. We do not know when Nazca Boobies incur these injuries, but the fact that such damage is rare in another two tropical booby species that avoid spending the night on the water suggests that the risk is nocturnal. This argument is supported by sporadic, short flights during long nocturnal floating bouts, which indicate that birds are probably disturbed from underneath by sub-surface predators. They may have little need to do so during the day, with better illumination and most time spent in the air.

Nazca Boobies may prefer to return to the colony before nightfall to reduce encounters with predators, and indeed, the majority of trips (67%) occur within one daylight period, but our data indicate that poor foraging success drives the decision to accept the risk of being prey in order to offset unproductive commuting. But why do Nazca Boobies accept this predation cost, whereas other species of tropical boobies do not? One possibility is that tropical boobies that are reluctant to spend a night at sea experience favourable food conditions relatively close to their colonies (at least within the maximum foraging range that can be attained within a round trip restricted to approximately 13 h of useable daylight in the tropics) that allow them to return before or around sunset, and thus to avoid sub-surface predators at night. However, marine productivity in the feeding zones of Nazca Boobies from Punta Cevallos during the study period (0.2 and 0.64 mg of chlorophyll-*a*/m^3; extracted from http://coastwatch.pfeg.noaa.gov) was similar to or higher than that estimated in the feeding areas of tropical boobies with strict diurnal at-sea activities: 0.2–0.3 mg of Chl-*a*/m^3 around Clipperton Island for Masked Boobies (Weimerskirch *et al.* 2008), 0.1–0.2 mg of Chl-*a*/m^3 around Palmyra Atoll for Masked and Red-footed Boobies (Young *et al.* 2010), and an average of 0.165 mg of Chl-*a*/m^3 around Europa Island for Red-footed Boobies (Weimerskirch *et al.* 2005).

Another possibility involves flight aerodynamics and associated costs of flight. Masked and Nazca Boobies both make long foraging flights; these two are also the largest of the boobies, and Masked Boobies exhibit a higher wing loading (an index of body weight per unit wing area) than expected if scaled by body weight (Hertel & Ballance 1999, Brewer & Hertel 2007). Although we lack published data on wing morphometry of Nazca Boobies, wing loading probably resembles that of Masked Boobies because body sizes of these two species are more similar to each other than to other species of boobies (Pitman & Jehl 1998). Greater wing loads require faster gliding flights to keep the bird aloft, and offer some locomotion advantages only in regions of high wind speeds (Hertel & Ballance 1999, Shaffer *et al.* 2001). Winds in the tropical oceans are typically lighter (wind speed = 5–6 m/s) than are winds in higher latitudes (9–11 m/s, Suryan *et al.* 2008) and could be exploited with rather reduced energetic costs by boobies with small wing loadings such as Brown, Red-footed and Blue-footed Boobies (Hertel & Ballance 1999, Brewer & Hertel 2007). Thus, the commuting flight of Nazca Boobies could be more costly compared with that of smaller tropical boobies. Under central place foraging theory, this extra travel expense should be linked to an extension of the productive feeding period, making the entire trip longer and increasing the probability that a trip will extend into the next daylight period.

Other authors have also interpreted the return to land at night of some species of tropical booby as avoidance of sub-surface predators (Nelson 1978: 921, Schreiber & Chovan 1986, Weimerskirch *et al.* 2008). Our results also support this hypothesis, as we found evidence of foot damage in Nazca Boobies, but not in Brown and Blue-footed Boobies, species that do not rest on the sea at night. As discussed above, greater wing loadings in a region of relatively light tropical winds may increase the energetic costs of commuting flights, forcing chick-rearing Nazca Boobies to extend their foraging trips for several days by sitting on the water at night when prey encounter is low around their colonies. The nocturnal resting period on the water surface may then expose Nazca Boobies to the attack of predators.

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