Flexible foraging patterns under different time constraints in tropical boobies

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The foraging behaviour of any animal is intricately linked to ecological constraints. Extrinsic factors, such as daylength, may limit the time available for foraging. Intrinsic factors, such as the coordination of mates at a nest site, may exacerbate this limitation. Using activity loggers, we examined the effects of extrinsic and intrinsic limitations on the foraging behaviour of the sympatric red-footed booby, *Sula sula*, and brown booby, *Sula leucogaster*, during incubation, and tested the prediction that individuals would work harder when time available for foraging was limiting. Both species share incubation duties and forage by day. Brown boobies made significantly shorter foraging trips than red-footed boobies, and thus, both parents could forage during the same day. Therefore, departure time and time available for foraging will also be influenced by when the partner returns to the colony. Overall foraging trip duration decreased linearly with respect to departure time. Our study suggests that the time available for foraging is limited by a combination of extrinsic and intrinsic processes in both species. Crucially, the rate of flying and diving, indicators of prey search and pursuit, respectively, increased with decreasing time available for foraging, whereas time spent inactive on the sea surface decreased, as did the time between departure and diving. Our data therefore suggest that boobies adjust their foraging behaviour according to extrinsic constraints.

Animals typically spend a large proportion of their time foraging (Drent & Daan 1980), and how individuals allocate time between foraging and other activities is an important feature of their behavioural ecology (Martin 1987; Roff 1992; Stearns 1992). In general, time allocated to foraging is thought to be constrained by behaviours such as predator avoidance, because in many cases the two activities cannot be carried out simultaneously (McFarland 1974; Krebs 1980; Yasue et al. 2003). In addition, extrinsic barriers to foraging are a fundamental feature of the ecology of most animals. When foraging time is reduced both by time allocation to other activities and by physical processes, for example the tidal cycle (Goss-Custard 1996),

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individuals are predicted to adjust their foraging behaviour to the time available (Swennen et al. 1989; Ydenberg et al. 1994; Ydenberg & Hurd 1998).

The cycle of night and day imposes a barrier to feeding in many species. Diurnal and nocturnal foragers alike must find enough food during the relevant foraging period of the light cycle. Thus, in temperate zones, diurnal foragers would be predicted to increase the proportion of the day spent feeding during winter, in part because they are constrained to find food in a shorter time. This prediction has been upheld in studies on mammals (Hill et al. 2003) and birds (Guillemette 1998; Cope 2003). Equally, within a single daily cycle, work rate on a foraging trip is predicted to reflect the time available for foraging. Among diurnal species, this should result in observable differences in foraging work rate between individuals that commence foraging earlier in the day and those commencing later in the day.

Within the temporal constraints of daylength, available foraging time of diurnal feeders may be further reduced by

intrinsic processes. One classic example of this is where two parents share breeding duties, with mates alternating foraging and breeding site duties (e.g. incubation of eggs, guarding of offspring). In many species, a parent on breeding site duty waits for the return of the mate before it leaves to forage. The time available to the departing individual for foraging depends upon both the fixed daily cycle and the timing of relief at the breeding site by the mate. Although interannual variability in extrinsic conditions is known to affect life history parameters (Pinaud & Weimerskirch 2002), to our knowledge, the combined effects of extrinsic and intrinsic limitations on foraging strategies at the foraging trip scale have not been examined.

We examined the effects of extrinsic and intrinsic constraints on the foraging strategies of two sympatric species of tropical seabird, the brown booby, *Sula leucogaster*, and red-footed booby, *Sula sula*. The study was carried out during incubation, which the parents share. Mates alternate incubation duties and may relieve the partner at any time during the day. In both species, a parent must attend the nest continuously because unattended eggs would be either subject to predation (B. Schreiber, personal communication) or likely to suffer thermal stress. Both species are diurnal feeders and predominantly spend the night on land (Schreiber et al. 1996; Schreiber & Norton 2002). Thus, our study animals were foraging for a duration limited by both extrinsic factors (remaining hours of daylight) and intrinsic processes (the requirement for a bird to be relieved by its mate before commencing a trip). The two study species offer an interesting comparison because brown boobies are believed to feed closer inshore than red-footed boobies (Nelson 1978), and, as such, the energy/time limitations of the two species are likely to differ.

Our aim was to examine the effect of departure time on work rate in both the brown booby and the red-footed booby, and test the prediction that work rate will increase when time available for foraging decreases. Our measures (currencies) of work rate were (1) the dive rate during a foraging trip (dives/h on a trip, hereafter called total dive rate), (2) the dive rate during the time between the first and last dive (dives/h, hereafter called foraging dive rate), (3) the number of dives carried out during a trip, (4) the total time spent flying while on a trip, (5) the proportion of time spent flying while on a trip, (6) the flight time between departing and making the first dive (log-transformed data), (7) the flight time between the last dive and the return to the colony, and (8) the rate of energy expenditure during a foraging trip. These currencies were examined in relation to foraging trip departure time.

METHODS

We carried out the study from 4 to 23 March 2003 at a colony of ca. 450 breeding pairs of brown boobies and ca. 1400 breeding pairs of red-footed boobies on Johnston Atoll (16°N, 169°W) in the central Pacific Ocean. The study site was close to the equator with approximately 12 h of daylight each day. Sunrise and sunset occurred at ca. 0730 and 1930 hours Pacific Time, respectively. The U.S. Fish and Wildlife Service granted access to the Atoll and permission to attach loggers to boobies.

Using a 2-m-long pole and net, we caught 56 incubating adults (25 brown boobies and 31 red-footed boobies) at the nest site. A rapid response temperature and pressure logger (PreciTD, earth & OCEAN Technologies, Kiel, Germany; see Daunt et al. 2003 for details) was attached to the underside of the four central rectrices, close to the base of the tail, using waterproof tesa tape (Tesa AG, Hamburg, Germany). The logger dimensions were: length 80 mm; minimum diameter 19 mm; maximum diameter 22 mm; mass 21–23 g (including the tape, <2.5% body mass, using the smallest body mass recorded in this study). The attachment of loggers took less than 5 min and after release every bird returned to its nest immediately. The birds were recaptured at the nest in the same way after their absence had been noted during twice daily checks (ca. 0800 and 1800 hours). The device was removed, usually after 1–2 days, to record at least one foraging trip per bird, and body mass was measured. These procedures took less than 5 min and after release all birds resumed normal incubation behaviour.

Temperature resolution was ca. 0.005 K (measurement uncertainty in the calibrated device is 0.03 K, range 15–35°C); two series of devices were used with pressure resolution being 1.5 and 2.5 mbar, respectively, corresponding to ca. 1.5 and 2.5 cm of the water column (measurement uncertainty 10–15 mbar, range 0–5 bar and 0–10 bar above atmospheric pressure, which corresponds to 0–50 and 0–100 m water depth, respectively). The time between successive recordings was set at 1 s to record even the rapid shallow plunges that boobies are known to carry out.

Data were downloaded and analysed using Multitrace (Jensen Software System, Kiel, Germany). Figure 1 shows a sample of data obtained from a brown booby. Resting on
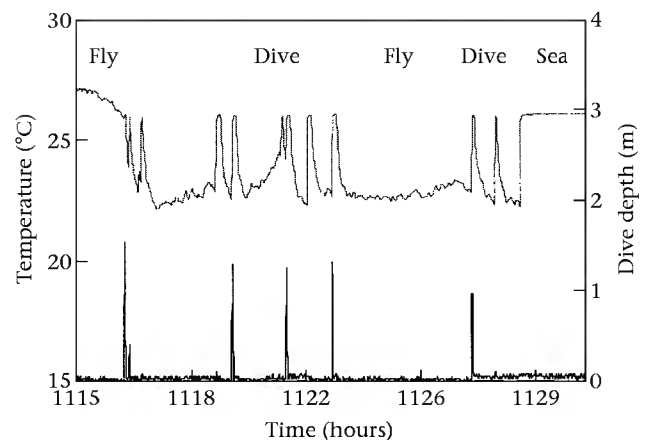

Figure 1. Data recorded over a 15-min period from a temperature and pressure logger attached to a booby. Temperature (°C) is shown by the upper line and depth (m) by the lower line. This trace illustrates how the different activities recorded during a typical foraging trip are distinguished where Fly = flying (a variable temperature signal), Sea = sea surface (a stable temperature signal) and Dive = diving (a positive pressure signal).

the sea surface was characterized by a stable temperature around ca. 26°C, a value that closely corresponds to sea surface temperature in this region (http://www.cpc.noaa.gov/data/indices/). Flight was characterized by a much more variable temperature signal and dives by positive pressure signals (Fig. 1). Thus by identifying when a change in signal occurred, we were able to estimate trip duration, the number and depth of dives and time spent flying and sitting on the sea surface while on a trip. Time spent diving represented only ca. 0.3% of total trip time, and so when comparing time activity during a trip we examined only time spent flying, because time spent on the sea surface approximated to trip duration minus time spent flying. For eight of the 56 birds studied, we could not determine the total time spent flying and sitting on the sea surface because the temperature traces became unstable as the trip progressed. However, we used the pressure data to determine the number of dives and, for four of these birds, we could also determine when the trip began and ended, and therefore trip duration.

To estimate the energy expenditure during a foraging trip for each bird, we substituted metabolic rate of resting on the sea surface and flight (which account for 99.7% of time activity during a foraging trip) from doubly labelled water trials on freeranging red-footed boobies at the same study colony (Ballance 1995):

$$\text{Mean resting metabolic rate} \pm \text{SD} = 9.7 \pm 0.7 \text{ W}$$
$$(N = 8; \text{ mean mass} \pm \text{SD} = 1039 \pm 25.8 \text{ g}) \tag{1}$$

$$\text{Mean power required for flight} \pm \text{SD} = 19.0 \pm 3.4 \text{ W}$$
$$(N = 6; \text{ mean mass} \pm \text{SD} = 1014 \pm 42 \text{ g}) \tag{2}$$

For each bird, we calculated the costs of each activity (incorporating the individual's body mass), summed the cost of flying and sitting on the sea surface, and divided by trip duration to calculate the energy expenditure for the trip in W/kg. Although there may be some error associated with the absolute values, the patterns will reflect a reliable index of energy expenditure in our two study species.

In 13 cases, we recorded more than one trip per bird. Therefore, to control for potential pseudoreplication, we fitted linear mixed models to the work rate currencies being examined (total dive rate (log transformed), foraging dive rate (log transformed), total number of dives, total time spent, proportion of trip spent flying (arcsine transformed), flight time to first dive, flight time after last dive and the rate of energy expenditure) using a combination of residual maximum likelihood analyses, (REML; Patterson & Thompson 1971) and generalized linear mixed models (GLMM) to our data, with bird identity as a random factor, using Genstat Release 6.1, Lawes Agricultural Trust (Rothamsted Experimental Station, U.K.). All models included departure time as a covariate, species as a fixed factor and the interaction between departure time and species. The GLMM model used a Poisson error distribution with a logarithm link function for the count data (Schall 1991). To establish whether any effects of departure time were due to time of day per se, we carried out an additional analysis on dive rate (recalculated as hourly dive rates), with both hour of day and time of departure. In the REML and GLMM

analyses, the significance of terms was assessed by the Wald statistic at the final iteration of the algorithm, for each term when fitted last in the model with percentiles of chi-square distributions (Elston et al. 2001). Nonsignificant terms were dropped sequentially from the model in reverse order of significance, commencing with the highest order interaction term, until the most parsimonious model was obtained. Means ± SD are given unless otherwise indicated.

RESULTS

In both species, activity showed a strong diurnal pattern with foraging occurring during the day and birds incubating at the nest or roosting in the colony at night (Fig. 2). No individual left the colony before ca. 0500 hours and only one of the 56 birds, a red-footed booby, spent the night sitting on the water, returning to the colony the next evening after 2 full days at sea foraging. The mean trip duration of brown boobies was significantly shorter than that of red-footed boobies (Table 1), which contributed to differences in diurnal patterns between the species in the length of time a bird was at sea. Brown booby trips starting later than 1100 hours were negatively related to trip duration (general linear model, GLM: $F_{1,12} = 538.91$, $r^2 = 0.978$, $P < 0.001$; trip duration = −0.983 departure time ± 0.042 + 19.293 ± 0.664 h), whereas trips starting before 1100 hours were not (GLM: $F_{1,20} = 0.045$, $r^2 = 0.002$, $P = 0.834$; Fig. 3a). In contrast, among
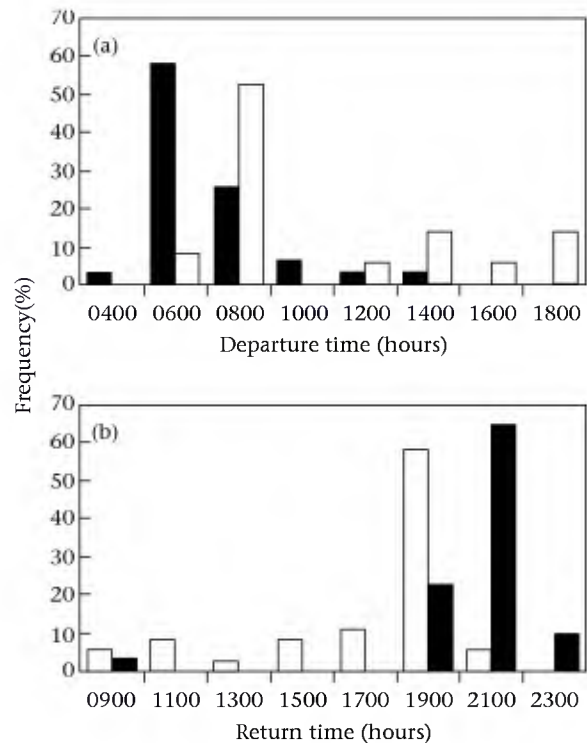

Figure 2. Frequency distribution (%) of (a) departure times and (b) return times of foraging trips made by brown boobies (□; $N = 23$) and red-footed boobies (■; $N = 29$).

Table 1. Work currencies of incubating brown and red-footed boobies during foraging trips

Work currency	Brown booby $N=23$	Red-footed booby $N=29$	χ^{2*}_1	P
Trip duration (h)	6.7 ± 3.8	14.0 ± 5.7	15.70	<0.001
Total dive rate	3.8 ± 4.1	2.4 ± 1.5	0.39	0.53
Foraging dive rate	6.1 ± 4.8	3.5 ± 1.8	0.66	0.42
Number of dives	25.3 ± 32.0	31.7 ± 19.0	0.36	0.55
Total flight time (h)	4.4 ± 2.5	9.9 ± 2.8	35.26	<0.001
Percentage trip time in flight	78	89	3.86	0.05
Departure to first dive (h)	1.1 ± 0.7	1.8 ± 1.1	1.82	0.20
Last dive to return (h)	1.0 ± 0.7	2.0 ± 1.3	10.19	<0.001
Energy expenditure (W/kg)	15.65 ± 1.44	16.45 ± 1.02	5.80	0.016

Total dive rate is the number of dives per total trip duration, and foraging dive rate is the number of dives divided by the time from the first to the last dive. Mean values are given $\pm$ SD.
*Chi-square for residual maximum likelihood analyses or, for number of dives, a generalized linear mixed model.

red-footed boobies, there was a negative relation between trip duration and departure time across all trips (GLM: $F_{1,28} = 21.877$, $r^2 = 0.439$, $P < 0.001$; trip duration = -1.108 departure time $\pm 0.237 + 21.134 \pm 1.759$ h; Fig. 3b).

The 'total' dive rate and the 'foraging' dive rate increased significantly with departure time (REML: total: $\chi^2_1 = 20.40$, $P < 0.001$; foraging: $\chi^2_1 = 11.59$, $P < 0.001$; Fig. 4), but there was no significant difference in the number of dives on trips with respect to departure time (GLMM: $\chi^2_1 = 2.07$, $P = 0.15$). There was, however, no difference in the total dive rate, the foraging dive rate or the number of dives between species (Table 1). The total time spent flying was significantly longer in trips leaving earlier in the day than in trips leaving later (REML: $\chi^2_1 = 19.59$, $P < 0.001$). However, birds departing on a foraging trip later in the day spent proportionally more time flying on a trip than those leaving earlier (GLMM: $\chi^2_1 = 17.59$, $P < 0.001$; Fig. 5), and therefore spent proportionately less time on the sea surface. As a consequence of their longer trip durations, red boobies spent significantly more time flying than brown boobies, and there was a marginally significant difference in the proportion of time spent flying during foraging trips between the species (Table 1). The interval between departure and the first dive was significantly negatively related to departure time (REML: $\chi^2_1 = 20.21$, $P < 0.001$), and the return flight was significantly longer for trips starting earlier in the day (REML: $\chi^2_1 = 14.26$, $P < 0.001$). There were no differences between the species in time between departure and the first dive, but red-footed boobies had a longer commute back to the colony (Table 1). The rate of energy expended (W/kg) on a foraging trip increased significantly with departure time (REML: $\chi^2_1 = 18.12$, $P < 0.001$; Fig. 6), and was also greater for red-footed boobies (Table 1), which is in part explained by their proportionately longer flights. Finally, in a model including both departure time and time of day, there was a significant effect of the former, but not of the latter (REML: departure time: $\chi^2_1 = 15.36$, $P < 0.001$; time of day: $\chi^2_1 = 2.69$, $P = 0.10$). No interaction terms were significant in any of the above analyses.

DISCUSSION

Boobies had a flexible daily foraging strategy that was linked to the time available to forage. In both species of booby, foraging behaviour during incubation was strongly influenced by daylight. Both measures of dive rate and the proportion of time spent in flight increased as the number of hours of daylight available decreased. The flight duration before the first dive of a trip and the return flight home after the last dive were significantly shorter in
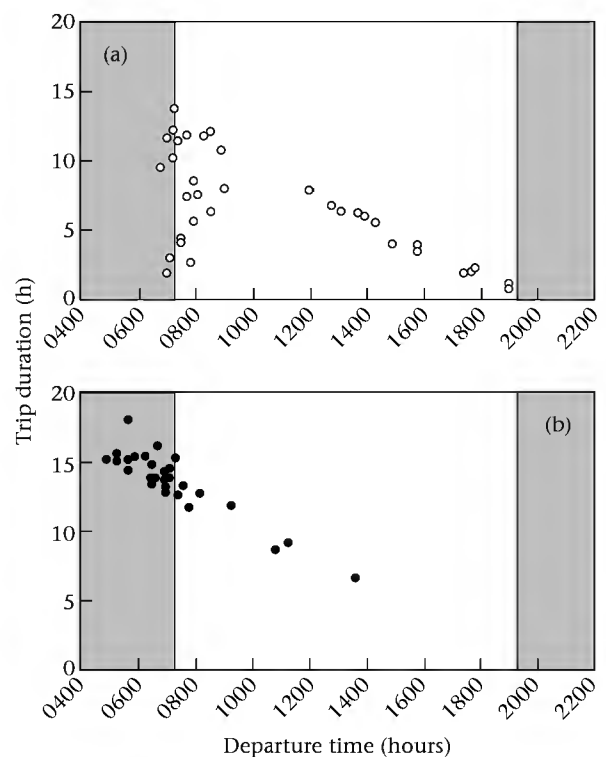

Figure 3. Relation between trip duration (h) and departure time for (a) brown boobies (○; $N = 23$) and (b) red-footed boobies (●; $N = 29$), excluding one overnight trip. The hours of darkness are shown as shaded bars.
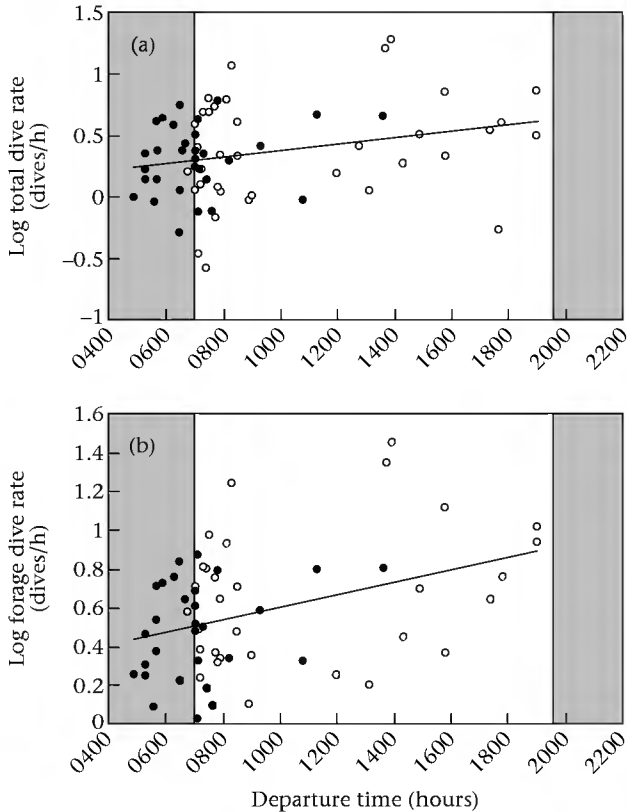
Figure 4. Relation between (a) log total dive rate per trip (dives/h) and departure time and (b) log foraging dive rate per trip (dives/h) and departure time for brown (○; N = 23) and red-footed boobies (●; N = 29). The hours of darkness are shown as shaded bars.

Figure 5. Proportion of total trip time spent flying with respect to departure time for brown (○, - - -; N = 21) and red-footed boobies (●, —; N = 27). The hours of darkness are shown as shaded bars.

trips that departed later in the day. The net result was that the number of dives made on a trip did not differ between early and late departures. Overall, this suggests that birds departing on foraging trips later in the day have a higher prey encounter rate than birds on trips starting earlier in the day. Therefore, these data support our prediction that dive rate would increase during trips commencing later in the day to ensure that enough food is obtained in the shorter time available for foraging. This daily pattern corresponds to the seasonal patterns observed in diurnal species, which increase their foraging effort during winter when the hours of daylight are reduced (Guillemette 1998; Cope 2003; Hill et al. 2003). We also show that these data have large energetic implications because both diving and flying are much more energetically costly than sitting on the sea surface (Birt-Friesen et al. 1989; Ballance 1995; Jodice et al. 2003). Boobies expended energy at a significantly higher rate during trips that started later in the day than during trips that started earlier in the day.

Boobies are plunge divers and forage in the first few metres of the water column, as supported by our data (maximum depth was ca. 6 m). The main prey of boobies in this region are flying fish (Exocetidae) and squid (Omnastrephidae; Schreiber et al. 1996; Schreiber & Norton 2002). A positive relation between dive rate and time of day might indicate that particular prey species were more available (e.g. higher densities within the
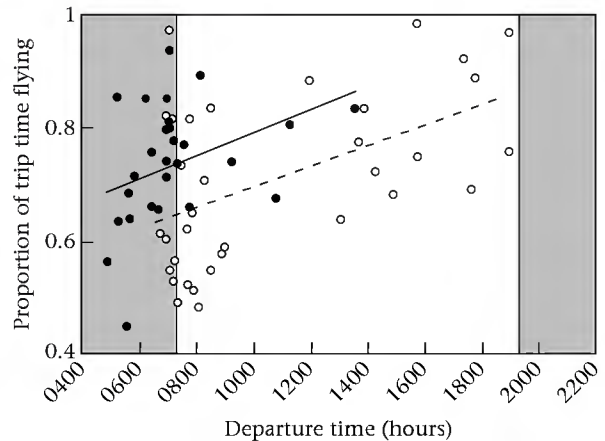
foraging range or more accessible in surface waters) later in the day. However, our model incorporating both departure time and time of day showed that the increase in dive rate was dependent on departure time and not time of day per se. Therefore, we have no evidence that our results reflect extrinsic differences in prey availability.

Traditionally, tropical seabirds have been regarded as being under severe energy limitation because of the low and highly variable productivity of tropical marine environments compared with temperate waters (Ashmole 1971). However, our results add to a growing body of evidence that question the general assertion that tropical seabirds operate under more challenging environmental conditions than their temperate counterparts (Schreiber 1996; Shea & Ricklefs 1996). The boobies in this study, at least during incubation in one year, had the flexibility to adjust their daily work rate considerably in relation to different time regimes. Repeating this study during the chick-rearing period, when total energy expenditure by
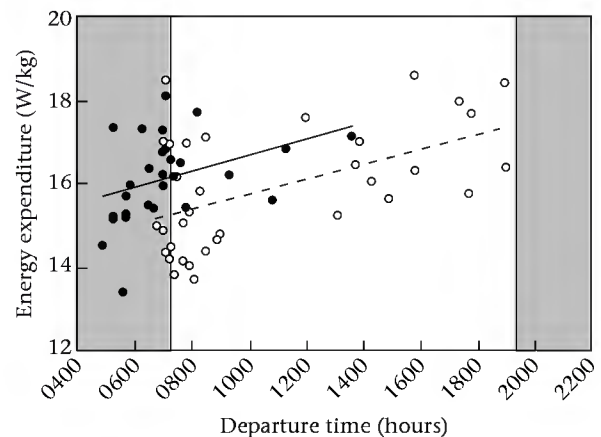

Figure 6. Relation between rate of energy expenditure (W/kg body mass) and departure time for brown (○, - - -; N = 21) and red-footed boobies (●, —; N = 27). The hours of darkness are shown as shaded bars.

adults is expected to be higher, would therefore be of great interest.

While we have shown that both species were able to adjust their foraging effort with respect to departure time, there were distinct behavioural differences between the species, notably longer trip duration (an index of foraging range in Sulids, Hamer et al. 2000, 2001), the total and proportion of time spent flying, and the greater rate of energy expenditure in red-footed boobies. However, whether extrinsic or intrinsic effects are driving this species difference remains unclear. Foraging range may be greater in red-footed boobies to minimize the impact of interspecific competition with brown boobies, which are larger and therefore potentially more dominant at feeding sites closer to the colony. This mirrors the foraging segregation demonstated in giant petrels *Macronectes* spp., but with males (the larger sex in this species) dominating the coastal foraging grounds (Gonzalez-Solis et al. 2000). Alternatively, the observed interspecific differences in trip duration may be linked to intrinsic processes at the colony, such as different incubation patterns. Our data are consistent with brown boobies alternating shifts within a single day, with one member of the pair departing on a foraging trip at dawn and returning to the colony in the middle of the day to relieve its mate from nest duties, thereby enabling the partner to forage until dusk. In red-footed boobies in the majority of cases, only one member of a pair makes a trip each day. Incubation regimes may differ between the species for energetic reasons. Brown boobies have a dark plumage, and so they may absorb the sun's heat at a higher rate than red-footed boobies (Hochscheid et al. 2002). Lustick (1984) suggested that behavioural adjustments can be made to compensate for thermoregulatory properties of different plumage colour. Conceivably, brown boobies would suffer thermal stress if incubating throughout the day without nest relief, hence the strategy of alternating shifts within a day in this species.

Limitations on the time available for foraging can arise from numerous extrinsic and intrinsic mechanisms. Here, we have demonstrated behavioural adjustments that individuals make in association with such limitations. For a more complete understanding of the precise mechanisms dictating foraging behaviour, data are required on the biology and physics of the environment where the birds are feeding, coupled with an experimental approach to disentangle the causes of the strategies of the two species in this study.

Acknowledgments

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