

## Reversed sexual size dimorphism and parental care in the Red-footed Booby *Sula sula*

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The 'division-of-labour' hypothesis predicts that males and females perform different roles in parental care and that natural selection acts differently on each sex so as to produce different body size optima suited to their particular roles. Reversed sexual size dimorphism in avian species (females larger than males) may therefore be an adaptive consequence of different roles of males and females in parental care. We investigated patterns of nest attendance, brooding, foraging and provisioning rate in a tropical seabird, the Red-footed Booby *Sula sula*, a species showing a reversed sexual size dimorphism. During incubation, females attended the nest more often than males, and spent more time brooding the small chick than did males during daytime. Males and females did not differ in the average duration of their foraging trips. During incubation, there was a positive relationship between nest attendance and the duration of foraging trips in males, but not in females. During the small-chick stage, for the same time spent at the nest, males spent significantly more time than females at sea. On average, females fed the chick more often than did males. In males, there was a significant and positive relationship between the probability of feeding the chick and the duration of the foraging trip, whereas in females, this probability was much less dependent on the duration of the foraging trip. Overall, female Red-footed Boobies achieved slightly, but significantly, more parental commitment than did males. However, these sexual differences in parental participation were small, suggesting a minimal division of labour in the Red-footed Booby. Our results suggest that the division of labour hypothesis is unlikely to explain fully the adult size dimorphism in Red-footed Boobies.

Although the vast majority of male and female seabirds show similar body size (Lack 1968), a reversed sexual size dimorphism (RSD: females being larger than males) is found in skuas (*Catharacta* and *Stercorarius* spp.), boobies (*Sula* spp.) and frigatebirds (*Fregata* spp.). Why these species exhibit a reversed sexual size dimorphism is still open to debate (Schreiber & Schreiber 1988, Fairbairn & Shine 1993, Croxall 1995, Guerra & Drummond 1995, Shine & Fairbairn 1995, Phillips & Furness 1997). Studies on RSD have mainly considered sex-specific roles of raptors and owls (Andersson & Norberg 1981, Hedrick & Temeles 1989) in which females perform all or most of the brooding while males undertake most of the provisioning (Newton 1979); few studies have considered seabirds. Analysis of

RSD in seabirds might be illuminating because of the marked ecological and behavioural differences between them and the more commonly studied taxa.

As male and female parental roles differ in many dimorphic bird species, the 'division-of-labour' hypothesis holds that size dimorphism is an adaptive consequence of these different roles (Newton 1979, Lundberg 1986, Mueller 1990). This hypothesis implies that owing to sex-specific roles in parental care, males and females face different selection pressures. Natural selection therefore acts differently on each sex, so producing different body sizes suited to their particular role (Guerra & Drummond 1995). Sexual size dimorphism has also been explained by the intersexual competition hypothesis, which proposes that sex differences in size might evolve from niche partitioning between sexes as a mechanism to reduce intersexual competition for food (Fairbairn & Shine 1993, Gonzalez-Solis *et al.* 2000).

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Alternatively, Jehl and Murray (1986) emphasized that 'an important distinction should be made between origin and function: because sexual selection can result in ecological segregation, the differential habitat utilisation that might result from sexual dimorphism might be the result of sexual selection and not specific adaptation' (see also Székely *et al.* 2000). In the highly dimorphic Magnificent *Fregata magnificens* and Great Frigatebirds *F. minor*, there is a dramatic division of labour between the sexes in caring for the chick (Schreiber & Schreiber 1988, Osorno 1999, Lagarde *et al.* 2004). However, intrasexual competition is strong in male frigatebirds (Nelson 1981, 1983) and may markedly affect the evolution of RSD. Finally, behavioural differences between sexes, although subtle, have also been reported in monomorphic seabirds, such as the Northern Gannet *Morus bassanus*, which suggests that sex differences in parental behaviour may arise in the absence of any marked sexual size dimorphism (Lewis *et al.* 2002).

Because of the variety of processes potentially affecting RSD, additional detailed data are required on the relative roles of males and females in parental care, particularly in seabird species that exhibit a high diversity in sexual size dimorphism, ranging from monomorphism to either male-biased or female-biased dimorphism, but with relatively similar mating systems (Croxall 1995). For example, in sexually dimorphic boobies, in which all species share similar mating systems and are reputed to show a division of labour between males and females (Nelson 1978), the only detailed study conducted, on the Blue-footed Booby *Sula nebouxii*, revealed a minimal division of labour during the chick-rearing period (Guerra & Drummond 1995).

The aim of this paper is to provide additional data on the relative roles in parental care of males and females in a tropical pelecaniform showing RSD, the Red-footed Booby *Sula sula*, with the main goal of investigating whether the sexual size dimorphism is associated with a division of labour as pronounced as found in raptors. In this study we compare nest attendance, brooding, duration of foraging trips and provisioning rate in male and female Red-footed Boobies.

## MATERIALS AND METHODS

The study was carried out from September to October 1998 (45 days) at Europa Island, Mozambique Channel, Western Indian Ocean (22°20'S, 40°22'E)

in a large colony of Red-footed Boobies (3000 pairs; Le Corre & Jouventin 1997). At Europa, Red-footed Boobies breed from July to December in trees and the parental phase (incubation + chick rearing) lasts for 145 days (Lormée *et al.* 2000).

### Sexual size dimorphism

Birds were captured on the nest by hand or with a landing net and ringed with a metal ring. Boobies were sexed using a molecular method (Fridolfsson & Ellegren 1999, Lormée *et al.* 2000, 2003). Wing length was measured to the nearest millimetre with a steel rule, and culmen length, culmen depth, tarsus length and sternum length to the nearest millimetre with a pair of callipers. Birds were also weighed to the nearest 5 g using a Pesola balance. All the individuals were measured by the same researcher (H.L.).

### Nest monitoring

Nest monitoring was conducted on three categories of nest: (1) nests with an egg, in the late part of incubation (hereafter 'incubation',  $n = 10$  nests); (2) nests with a 1–19-day-old chick (mean 6.15 days, hereafter 'small chick',  $n = 20$  nests); and (3) nests with a 29–49-day-old chick (mean 37.8 days, hereafter 'large chick',  $n = 10$  nests). Because of the loosely seasonal breeding pattern shown by Red-footed Boobies on Europa Island, all three breeding stages could be monitored simultaneously. Within each pair, one of the adults was dyed with picric acid on the crown and belly, to allow individual observation from a distance, thereby reducing disturbance at the nest. Each category of nest was monitored continuously for 5 days. Observations were made each day from dawn (06:00 h) to dusk (19:00 h), by checking the nest hourly.

### Nest attendance and diurnal brooding

At each check, we recorded adult presence, and when the two adults were present we noted which one was on the nest. If a bird departed from or arrived at the nest between two successive checks, we considered that the relief occurred at the midpoint between the two time checks. Incomplete nest attendance bouts, i.e. bouts beginning before the start of the 5 days' monitoring or ending after the end of the 5 days' monitoring, were excluded from the analyses (number of nest attendance bouts used: incubation 32, small chick 123, large chick 71).

During the small-chick stage, we recorded which adult was brooding the chick from dawn to dusk (in hours): brooding is when the parent is sitting on the chick to protect it from heat, cold or predators (Howell & Bartholomew 1962).

### Foraging trips and chick feeding

We observed eight nests continuously for 48 h and confirmed that Red-footed Boobies return daily to the nest-site at or before dusk (19:00 h) and spend the entire night on or near the nest. During this survey we never observed adults departing for or returning from a foraging trip at night. We were therefore confident that by observing the nests from dawn to dusk, we correctly monitored the presence and absence of the parent birds. As in Masked and Blue-footed Boobies (*Sula dactylatra* and *S. nebouxii*, respectively), adult Red-footed Boobies foraged only during daylight hours and remained at the nest-site when not on foraging trips (Anderson & Ricklefs 1992, Schreiber *et al.* 1996). Thus absence from the nest-site estimates the maximum time spent foraging (Anderson & Ricklefs 1992). Absences from the nest lasting less than 2 h were never followed by chick feeding. Consequently, such absences were not considered to be foraging trips, and were removed from the analysis (number of foraging trips used: incubation 56, small chick 161, large chick 88).

We estimated the probability of adults provisioning their chick in relation to the duration of their foraging trip at sea. Thus, in a subsample of nests (small-chick stage  $n = 6$ , large-chick stage  $n = 6$ ), chicks were regularly weighed every 4 h, from dusk to dawn (07:00 h, 11:00 h, 15:00 h, 19:00 h) and we determined whether adults had fed their chick at least once between the successive weighings.

To detect nocturnal feeding events from adults arriving just after the last diurnal weighing, we first estimated mass loss due to respiration and defecation of small and large chicks separately, by regressing body mass loss on time since last feeding observed ( $n = 7$  small chicks and 14 large chicks): small chicks exhibited a  $1.64 \pm 0.08\%$  mean ( $\pm$  se) hourly body mass loss from 0 to 5 h after feeding, and a  $0.5 \pm 0.09\%$  hourly body mass thereafter. Large chicks exhibited a  $1 \pm 0.11\%$  hourly body mass loss from 0 to 5 h after feeding,  $0.77 \pm 0.05\%$  from 5 to 15 h and  $0.41 \pm 0.04\%$  thereafter. From the last weighing at 19:00 h, we estimated what the chick's body mass should have been the following morning at 07:00 h if no feeding had occurred during the night. If the

measured body mass was above the predicted body mass  $\pm$  se, we concluded that a feeding event had occurred during the night (especially when the chick is young, parents may give several small feeds from a large meal collected during a foraging trip). When we detected a feeding event that we could not attribute with confidence to the male or the female (e.g. when both mates arrived at the nest at the same time), the corresponding trip at sea was eliminated from the analysis.

### Statistics

All behavioural data were transformed with decimal logs to fit the assumptions for parametric tests (Sokal & Rohlf 1981). We analysed the effect of sex, breeding stage and individual treated as a random factor on nest attendance and foraging trips, using Generalized Linear Mixed Models (GLMMs; Littell *et al.* 1996), which represent an extension of Generalized Linear Models (McCullagh & Nelder 1989). Because diurnal brooding was recorded only during the small-chick stage, we only tested the effect of sex. GLMMs allow incorporation of independent variables or random effects in the models. In our case, because a given individual could present different durations of nest attendance, diurnal brooding and foraging trips, we fitted individual as a random term in GLMMs using the SAS MIXED procedure.

Because incubating or chick-rearing birds alternate nest attendance bouts during which they fast with foraging trips at sea during which they feed for themselves and also bring back food for the chick, we examined how long a bird had to forage at sea in relation to the time it has spent attending the nest, i.e. we investigated how birds 'regulate' their time spent at sea. Thus, we analysed for each breeding stage the relationship between the average duration of foraging trips and the average duration of nest attendance bouts (including the time spent roosting/incubating or brooding at night), following the same procedure as described above.

Finally, we also used GLMMs to examine whether the probability that a chick was fed by its parents was influenced by the duration of trips at sea, controlling for the effect of sex and chick stage. The probability of feeding the chick was modelled as a binomial response variable using the logit function  $\log[\pi/(1 - \pi)]$  where  $\pi$  is the probability of feeding the chick. For all analyses, we started model selection with a full model (i.e. all factors and their interactions), and selected for the most parsimonious model using the Akaike Information Criterion with small-sample

**Table 1.** Measurements of male and female Red-footed Boobies from Europa Island. Values are means  $\pm$  se. Numbers in parentheses refer to sample size.

	Males	Females	<i>T</i>	<i>P</i>
Body mass (g)	840 $\pm$ 7 (64)	987 $\pm$ 7 (66)	217	< 0.001
Wing length (mm)	387 $\pm$ 0.9 (61)	400 $\pm$ 0.8 (65)	82	< 0.001
Culmen length (mm)	78.90 $\pm$ 0.30 (65)	81.06 $\pm$ 0.33 (66)	48.8	< 0.001
Culmen depth (mm)	12.52 $\pm$ 0.07 (60)	13.08 $\pm$ 0.07 (65)	29.5	< 0.001
Sternum length (mm)	94 $\pm$ 0.3 (65)	100 $\pm$ 0.4 (66)	135	< 0.001
Tarsus length (mm)	35.47 $\pm$ 0.15 (58)	37.00 $\pm$ 0.16 (60)	42	< 0.001

bias adjustment (AICc). The model with the lowest AICc is the one to be selected. Values were expressed as mean  $\pm$  se and presented in all figures without being log-transformed. All computations were performed using the SYSTAT and SAS statistical packages (SAS 1994, Wilkinson 1997).

## RESULTS

### Sexual size dimorphism

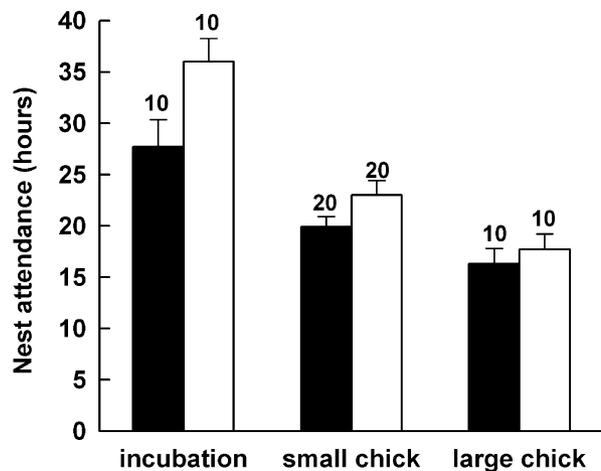
For all measurements, females were significantly larger than males (Table 1). This sexual dimorphism was most noticeable for body mass (females 15% heavier), then sternum length (6%), culmen depth and tarsus length (4.3 and 4.1%, respectively), wing length (3.2%) and finally culmen length (2.7%).

### Nest attendance and brooding

According to model selection, nest attendance was affected by sex and breeding stage. On average, females attended the nest more than did males ( $F_{1,146} = 6.17$ ,  $P = 0.014$ ; Fig. 1) and nest attendance decreased from incubation to the large-chick stage ( $F_{1,146} = 18.80$ ,  $P < 0.0001$ ). If taking each breeding stage separately, sex significantly differed only during the incubation stage ( $F_{1,12} = 5.39$ ,  $P = 0.038$ ; Fig. 1). However, females with a small chick spent significantly more time during the day brooding than did males (females  $7.2 \pm 0.42$  h, males  $5.8 \pm 0.42$  h;  $F_{1,158} = 4.41$ ,  $P = 0.037$ ).

### Foraging trips and chick feeding

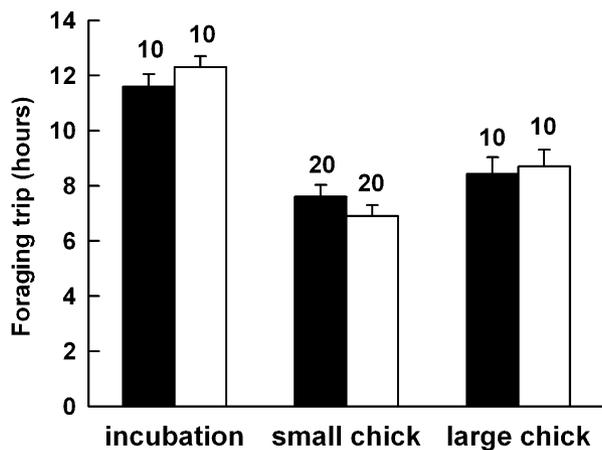
The selected model retained only a breeding stage effect on the duration of foraging trips ( $F_{2,221} = 23.95$ ,  $P < 0.0001$ ). Trip duration decreased from the incubation to the small-chick stage ( $F_{1,154} = 56.05$ ,  $P < 0.0001$ ; Fig. 2) and remained unchanged thereafter (small- vs. large-chick stage:  $F_{1,189} = 2.54$ ,  $P = 0.11$ ; Fig. 2).



**Figure 1.** Nest attendance in male (black bars) and female (white bars) Red-footed Boobies. Data are means  $\pm$  se. Sample sizes (number of individuals) are given above the bars.

During incubation, the best model selected suggested that the average duration of foraging trips was significantly correlated with average nest attendance ( $F_{1,16} = 5.22$ ,  $P = 0.03$ ; Fig. 3). However, there was a difference between sexes ( $F_{1,16} = 10.26$ ,  $P = 0.006$ ), with a positive relationship only for males (interaction sex  $\times$  log nest attendance,  $F_{1,16} = 10.24$ ,  $P = 0.006$ ). During the chick rearing period, there was a positive relationship between average nest attendance and the average duration of foraging trips (small chick  $F_{1,37} = 38.39$ ,  $P < 0.001$ , large chick  $F_{1,17} = 4.20$ ,  $P = 0.056$ ; Fig. 3). During the small-chick stage, for a similar time spent at the nest, males spent significantly more time at sea than did females ( $F_{1,37} = 10.36$ ,  $P = 0.003$ ). This difference was not observed during the large-chick stage ( $F_{1,11} = 0.02$ ,  $P = 0.88$ ).

With regard to the probability of feeding the chick, the best model selected showed a positive effect of the 'log duration of foraging trip' ( $F_{1,91} = 29.76$ ,  $P < 0.0001$ ), sex ( $F_{1,91} = 9.32$ ,  $P < 0.003$ ), with



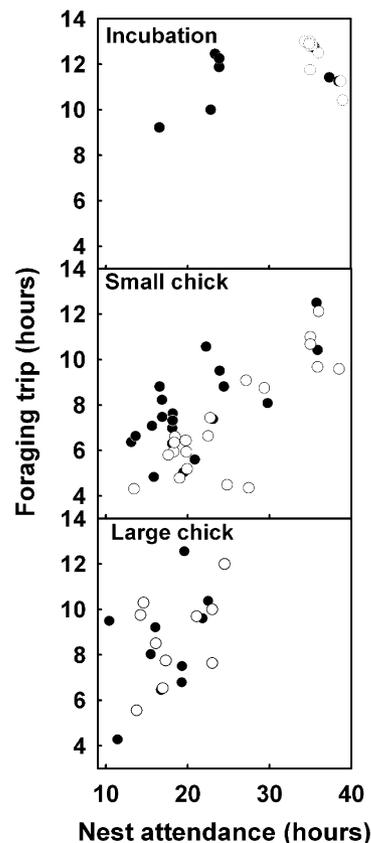
**Figure 2.** Duration of foraging trips in male (black bars) and female (white bars) Red-footed Boobies. Data are means  $\pm$  se. Sample sizes (number of individuals) are given above the bars.

females feeding the chick more often than did males, and interaction sex  $\times$  'log duration of foraging trip' ( $F_{1,91} = 7.13$ ,  $P = 0.009$ ). Therefore, to determine how feeding probability differed in relation to the duration of foraging trips between sexes, we ran a GLMM separately on each sex, with log trip length as a factor. In males, there was a significant and positive relationship ( $F_{1,49} = 34.69$ ,  $P < 0.001$ ; Fig. 4), much stronger than in females, in which this relationship was only close to being significant ( $F_{1,41} = 3.73$ ,  $P = 0.065$ ; Fig. 4): thus males had a lower probability than females of feeding the chick as foraging trips became shorter.

## DISCUSSION

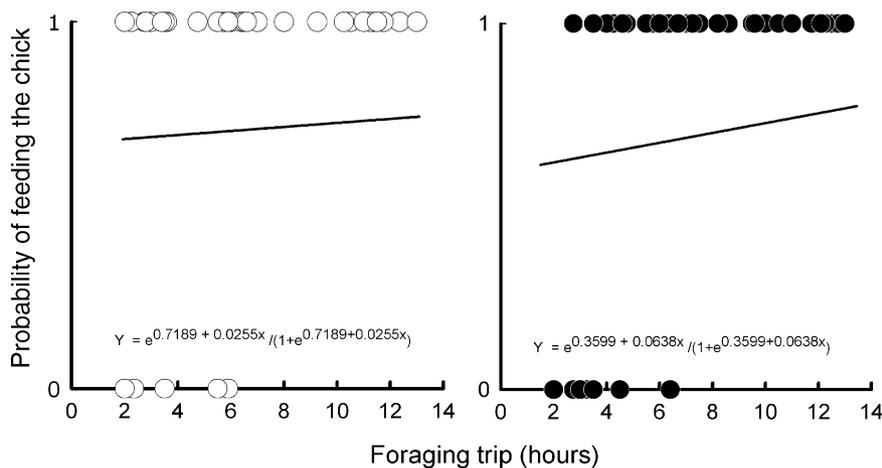
### Nest attendance, brooding and sexual size dimorphism

In our study of the Red-footed Booby, the larger female attended the nest slightly more often during incubation, and spent more time brooding the small chick during the daytime. Female-biased brooding commitment has been documented in two other dimorphic tropical sulids: in Masked Boobies, which show a similar RSD, Anderson and Ricklefs (1992) reported that during the daytime, females spent more time than males at the nest during early chick-rearing. In the Blue-footed Booby, which exhibits the strongest RSD of any sulid (females 25–30% heavier), females performed 30% more brooding than males when chicks were 5–10 days old (Guerra & Drummond 1995).



**Figure 3.** Relationship between the average nest attendance and the average duration of foraging trips in male (black dots) and female (white dots) Red-footed Boobies. Each point represents a mean individual value.

The observed greater brooding commitment of female Red-footed Boobies implies, at least during incubation, and probably the small-chick stage also, that they fast slightly more than males. A larger body size in birds is predicted to promote a lower mass-specific metabolic rate (Calder 1984). Thus, in boobies the larger females probably benefit from improved fasting abilities compared with the smaller males. However, a larger body size, and hence probably also better fasting ability, is not always associated with greater brooding commitment in other sulid species. In the sexually dimorphic Brown Booby *Sula leucogaster* (females being 20–29% heavier), Tershy and Croll (2000) found no difference between sexes, but data on brooding and incubation were pooled. Conversely, in the monomorphic Northern Gannet (males only 4% larger), Montevecchi and Porter (1980) reported that females performed significantly longer brooding shifts than did males. It seems therefore that a greater brooding commitment by



**Figure 4.** Relationship between the probability of feeding the chick and the duration of foraging trip in male (black dots) and female (white dots) Red-footed Boobies. Equations of the curves are indicated below. Predicted values (line) for the probability of feeding the chick were estimated from the link functions given in the figures. The probability of feeding the chick was modelled as a binomial response variable using the logit function  $\log[\pi/(1 - \pi)]$  where  $\pi$  is the probability of feeding the chick.

female Red-footed Boobies cannot be explained solely by their better fasting abilities resulting from their larger body size.

### Foraging trips and feeding probability

Because we did not use an activity recorder, we cannot be sure that all the time spent by boobies at sea was strictly devoted to foraging and not to other activities such as resting on water. However, Ballance (1995), using an activity recorder, showed that Red-footed Boobies spent  $84\% \pm 4.1$  (se) of their total time at sea in flight: an activity which can be associated with foraging. We are therefore confident that, although probably overestimated (although for both sexes similarly), the measure of time spent at sea was a reliable approximation of foraging time.

In our study, sexes did not differ in the average duration of their foraging trips. Similarly, studies on the sexually dimorphic Masked, Blue-footed and Brown Boobies did not reveal sexual differences in average foraging trip duration (Anderson & Ricklefs 1987, 1992, Tershy & Croll 2000).

As documented in the Wandering Albatross *Diomedea exulans* (Weimerskirch 1995) and the Northern Giant Petrel *Macronectes halli* (Gonzalez-Solis *et al.* 2000), there was a positive and significant relationship between the duration of foraging trips and nest attendance in Red-footed Boobies (incubation: males, chick stages: both sexes). During the small-chick stage, for an equivalent amount of time spent at the nest, males spent more time at sea than

did females. This suggests that although the average duration of foraging trips of males and females was similar, males may be less efficient foragers, i.e. they need more time to gather food. Such a sex difference in the regulation of foraging trips has been found in the Wandering Albatross and the Northern Giant Petrel, in which females are 10–20% smaller than males and have lower foraging efficiency during incubation (Weimerskirch 1995, Gonzalez-Solis *et al.* 2000).

Metabolic considerations might be invoked to explain differences in the regulation of foraging trips between the sexes in the Red-footed Booby. As the rate of energy expenditure per unit mass declines with increasing body mass (Peters 1983), one might expect that the smaller males would use relatively more energy than the larger females during their foraging trips and, consequently, would need more time to forage for the chick and for themselves (Barbraud *et al.* 1999). These higher energetic constraints are also suggested by physiological observations made in the Red-footed Booby: unlike females, in males a deterioration in body condition associated with elevated corticosterone levels (a hormone associated with stress and foraging effort, Wingfield 1994) is observed during chick rearing (Lormée *et al.* 2003). This probably results from higher energetic flight costs and/or a lower foraging efficiency imposed by the smaller body size of males (Lormée *et al.* 2003).

In sulids, adults appear to forage until a set meal mass has been captured per trip (Montevecchi & Barrett 1987). Anderson and Ricklefs (1992) showed that in male Masked Boobies, meal mass delivered to

the chick was positively correlated with the duration of foraging trips, whereas in females, meal mass was independent of the duration of the foraging trip. As in the Masked Boobies in the Galapagos (Anderson & Ricklefs 1992), Red-footed Boobies at Europa Island did not forage at night and therefore have a maximum of roughly 13 h per day to forage. As males appeared to forage less efficiently than females they may be forced, for a given time spent attending the nest, to devote a larger proportion of daytime to foraging. Consequently, males could not afford to spend a lot of time brooding at the nest during the daytime because they would not have sufficient time to collect food for the chick and for themselves before nightfall. This hypothesis is supported further by our results showing that males fed their chick less often than did females, and that their ability to deliver a meal was influenced much more by the duration of foraging trips than in females: the shorter the trip the less males are likely to feed their chick. This suggests that, as in female Masked Boobies (Anderson & Ricklefs 1992), female Red-footed Boobies gathered food for the chick and for themselves in a more time-efficient manner than males.

Similarly, in the highly dimorphic Blue-footed and Brown Boobies, Guerra and Drummond (1995) and Tershy and Croll (2000) found that females fed their chicks at similar frequency during the first 10 days, but during the next 50 days females fed chicks more often than did males. Further, experimental manipulations of parental effort conducted on breeding Blue-footed Boobies revealed that whereas males worked at some physiological maximum, females exercised more flexibility in their effort, and worked with a buffer of nutritional reserves that they used when necessary (Velando & Alonso-Alvarez 2003). However, in the monomorphic Northern Gannet, despite similar trip durations (Lewis *et al.* 2002), males fed neonatal chicks more than did females, and females fed older chicks more than did males (Montevecchi & Porter 1980).

### **Sexual size dimorphism and the division of labour in sulids**

Division of labour implies that each sex outdoes the other in at least one component of parental care. In its most extreme form, males and females perform different activities (e.g. females brood and males provision), but such a division can be more subtle with greater sharing of activities (females do most of the brooding and males do most of the provisioning).

In our study, females of the dimorphic Red-footed Booby incubated more and spent slightly more time brooding the chick, and males were less prone to feed the chick than were females. Overall, these sex differences in parental participation were relatively weak, suggesting a minimal division of labour in the Red-footed Booby, as found in the Blue-footed Booby (Guerra & Drummond 1995).

Contrary to what has been documented in raptor species (Wheeler & Greenwood 1983, Mueller & Meyer 1985), it seems therefore that in boobies smaller males have not specialized into provisioning, in contrast to larger females which have been shown to deliver much more food to chicks than males (two- to three-fold in Blue-footed Boobies: Anderson & Ricklefs 1992, Guerra & Drummond 1995; 1.2-fold in Masked Boobies: Anderson & Ricklefs 1992; up to four-fold in Brown Boobies: Simmons 1970, Tershy & Croll 2000).

In fact, instead of the dramatic division of labour predicted from observation of raptors and owls (Lundberg 1986), it seems that in tropical sulids the larger females achieve more of the parental effort than males (she broods more and delivers most of the food to the chick). Alternatively, the potential for extra-pair copulation and its resulting reduction in the male's likelihood of paternity may also affect parental investment by males and females differentially; it has been shown in the Blue-footed Booby that males may drastically reduce their parental investment when paternity is in doubt (Osorio-Beristain & Drummond 2001). Although we have no data on extra-pair copulation in Red-footed Boobies breeding on Europa Island, the greater parental effort in females is consistent with the fact that during the whole breeding cycle, female Red-footed and Masked Boobies show consistently higher levels of prolactin (Lormée *et al.* 2000), a hormone involved in the expression and maintenance of parental care (Buntin 1996).

To conclude, our observations on Red-footed Boobies suggest that RSD is unlikely to be an adaptive result of different roles of the sexes in parental care. The origin of RSD might be linked to a partition of foraging niches in order to optimize the foraging profitability of both males and females (Selander 1966, 1972, Fairbairn & Shine 1993). Indeed, ecological segregation between sexes (foraging area or diet) has been documented in some sexually dimorphic seabirds (Wandering Albatross: Prince *et al.* 1992, Weimerskirch *et al.* 1993; Northern Giant Petrel: Gonzalez-Solis *et al.* 2000). In tropical sulids, a

sex-specific foraging distribution has already been observed in Brown Boobies (Gilardi 1992), in which males forage closer to the coast than females. There is therefore a need to explore the respective distributions at sea and foraging ecology of males and females in dimorphic and monomorphic seabirds, and the development of technologies such as loggers, satellite tracking or GPS (Weimerskirch *et al.* 2002) should help to attain this goal.

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