

Relationship between reversed sexual dimorphism, breeding investment and foraging ecology in a pelagic seabird, the masked booby

Henri Weimerskirch · Matthieu Le Corre ·
Hélène Gadenne · David Pinaud · Akiko Kato ·
Yan Ropert-Coudert · Charles-André Bost

Received: 3 November 2008 / Accepted: 15 May 2009 / Published online: 21 June 2009
© Springer-Verlag 2009

Abstract Reversed sexual dimorphism (RSD) may be related to different roles in breeding investment and/or foraging, but little information is available on foraging ecology. We studied the foraging behaviour and parental investment by male and female masked boobies, a species with RSD, by combining studies of foraging ecology using miniaturised activity and GPS data loggers of nest attendance, with an experimental study where flight costs were increased. Males attended the chick more often than females, but females provided more food to the chick than males. Males and females foraged during similar periods of the day, had similar prey types and sizes, diving depths, durations of foraging trips, foraging zones and ranges. Females spent a smaller proportion of the foraging trip sitting on the water and had higher diving rate than males, suggesting higher foraging effort by females. In females, trip duration correlated with mass at departure, suggesting a flexible investment through control by body mass. The experimental study showed that handicapped females and female partners of handicapped males lost mass compared to control birds, whereas there was no difference for

males. These results indicate that the larger female is the main provisioner of the chick in the pair, and regulates breeding effort in relation to its own body mass, whereas males have a fixed investment. The different breeding investment between the sexes is associated with contrasting foraging strategies, but no clear niche differentiation was observed. The larger size of the females may be advantageous for provisioning the chick with large quantities of energy and for flexible breeding effort, while the smaller male invests in territory defence and nest guarding, a crucial task when breeding at high densities. In masked boobies, division of labour appears to be maximal during chick rearing—the most energy-demanding period—and may be related to evolution of RSD.

Keywords *Sula dactylatra* · Experimental manipulation · Division of labour · Regulation · GPS

Introduction

Male birds and mammals are generally larger than the corresponding females, and this is commonly attributed to sexual selection acting on males as a result of competition for access to females (Andersson 1994). Reverse sexual dimorphism (RSD), where females are larger than males, occurs in several bird families. This has also been attributed to sexual selection in families where sex roles are reversed (jacanas or phalaropes), but in raptors or some seabirds, such as boobies or frigatebirds, no definitive answer has been proposed for the origin and maintenance of RSD (Mueller 1990). Larger size may be advantageous in terms of behaviour and dominance for access to a partner or to resources, but also in terms of foraging, nest protection, breeding investment and energetics or a combination

Communicated by Anssi Laurila.

H. Weimerskirch (✉) · H. Gadenne · D. Pinaud · C.-A. Bost
Centre d'Etudes Biologiques de Chizé, Centre National
de la Recherche Scientifique, 79360 Villiers en Bois, France
e-mail: henriw@cebc.cnrs.fr

M. Le Corre
Laboratoire d'Ecologie Marine, Université de la Réunion,
15 avenue René Cassin, BP 7151, 97715 Saint Denis,
Ile de la Réunion, France

A. Kato · Y. Ropert-Coudert
Institut Pluridisciplinaire Hubert Curien,
23 rue Becquerel, 67087 Strasbourg, France

thereof (Shine 1989). In particular, foraging differences between the sexes may be important for the evolution of size dimorphism (Andersson and Norberg 1981). One of the most popular hypotheses, the ‘division of labour’ hypothesis, which suggests that size dimorphism is an adaptive consequence of different roles, has received support in the best studied groups, i.e. raptors and owls. In these species, selection may lead to large females that incubate and guard the nest, and in small males that forage on agile prey (Newton 1979; Lundberg 1986).

However, this hypothesis might not apply to other groups, such as seabirds, where generally males and females share breeding duties equally. While RSD is rare in seabirds (Fairbairn and Shine 1993), it is found in several groups that show a lifestyle similar to owls or raptors. For instance, RSD in skuas may be related to the morphology or ecology of avian predators, and the division of labour hypothesis developed for raptors would apply regardless of its evolutionary origin in other taxa (Cathy et al. 1999), but no precise information on the foraging behaviour of skuas is available. In other seabird groups with RSD, the division of labour hypothesis has been often debated, with no clear trend being apparent within taxonomic groups (Nelson 1978; Guerra and Drummond 1995; Lormée et al. 2000). Jehl and Murray (1986) suggested that sexual selection in these groups might be important, with small size being attributed to selection for aerial agility and capture of different prey. Again, this hypothesis requires information on foraging abilities that are generally lacking. Sex-specific foraging differences are generally due to size dimorphism, although differences in foraging and provisioning may also exist in monomorphic species (see review in Lewis et al. 2002). Larger size may confer dominance on the smaller sex on feeding grounds (Gonzales-Solis et al. 2000), forcing males to forage further. Smaller size is associated with lower energy expenditure and requirement but, on a mass specific basis, energy expenditure is negatively correlated with body size (Shaffer et al. 2001). Similarly, because of this mass specific relationship, range could increase with body size (Lewis et al. 2005).

Seabirds are long-lived species, and life history theory predicts that parental investment in current reproduction should be balanced by costs in terms of residual reproductive value (Williams 1966; Stearns 1992). This balance is generally under the control of the parent’s body condition, monitoring of which should be essential in reproductive decisions (Drent and Daan 1980; Weimerskirch 1999). Since a larger size implies larger body reserves and therefore a better ability to regulate breeding investment (Weimerskirch 1999), the regulation of parental investment and foraging should be different between the sexes in species with high sexual size dimorphism, with an enhanced ability to regulate investment by the larger sex.

It could be predicted that larger sized females may be advantageous in species where regulation of investment by females is more important than that of males for breeding success. This might occur in species where division of labour is important.

Boobies show a more or less marked RSD according to species (Nelson 1978), and it is generally considered that ‘division of labour’ is minimal (Guerra and Drummond 1995; Lormée et al. 2005). However, in some species, females provision the chick to a larger extent than males (Anderson and Ricklefs 1992; Guerra and Drummond 1995; Simmons 1970; Tershy and Croll 2000). Small males could be more constrained energetically than larger females; breeding effort of the latter would be more flexible because of their large size, which would allow them to more easily buffer periods of food stress (Velando and Alonso-Alvarez 2003) and invest more in offspring provisioning (Anderson and Ricklefs 1992; Guerra and Drummond 1995). However, differences in size could have important implications in terms of foraging behaviour between the sexes. On the one hand, large females can dive deeper than males (Simmons 1970; Nelson 1978; Lewis et al. 2005; Weimerskirch et al. 2006), or forage at longer distances from the colony and therefore in different habitats (Gilardi 1992; Weimerskirch et al. 2006). Therefore, selection pressure on females for increased chick provisioning may result in larger size and increased foraging range, whereas smaller males would forage closer to the colony to maintain territories and prevent or acquire extra pair copulations (Gilardi 1992). In this hypothesis, sex-specific breeding investment results in the evolution of differential sizes with consequences on foraging abilities. However, studies on sex-specific breeding investment and foraging behaviour have so far been carried out independently. A combined approach is necessary to examine this hypothesis and the possible links between breeding investment, regulation abilities and foraging behaviour of the two sexes so as to better understand the possible reasons for sex-specific differences in size, and their possible link with the evolution of RSD.

Masked boobies (*Sula dactylatra* Milne Edwards) are the largest of all boobies and exhibit strong RSD. Although the clutch size is two, they rear a single chick (obligate siblicide) and are oceanic species, foraging far from their nest (Nelson 1978; Weimerskirch et al. 2008). The aim of our study is to examine whether the foraging behaviour and regulation of parental investment of masked boobies differs between the sexes, to test the hypothesis of a link between breeding investment, foraging ecology and the occurrence of RSD. In particular, we were interested in examining whether division of labour in breeding investment and foraging activities occurs: for this we test the predictions that the sexes perform different roles in parental care, with

possible consequences for foraging activities, and that a particular size may be optimal for each role. To examine this hypothesis, we combined a study of the foraging behaviour of masked boobies using miniaturised activity loggers and GPS telemetry systems with a study of nest attendance and breeding involvement by the two sexes. The study was carried out when adults were rearing large chicks, i.e. when energy requirement is highest. In addition, since larger size should confer better ability to regulate breeding effort, it should be found in the sex whose role requires this ability. The most straightforward way to measure regulation of reproductive effort is to manipulate reproductive effort experimentally (Reznick 1985). Therefore, we manipulated the flight costs of males and females to study sex-specific breeding investment and body mass regulation to test the prediction that the sex that invests most in the brood should be the one that has the best regulation abilities.

Methods

The study was carried out on Clipperton Island (109.2°W, 10.3°N), in the eastern tropical Pacific between 4 and 28 January 2005. Clipperton is a circular, closed coral atoll, and hosts the world's largest masked boobies colony (120,000 individuals, R.L. Pitman et al. unpublished data). In January, birds were mainly rearing large chicks (age 30–60 days), with a few birds still incubating late eggs and brooding small chicks (chicks still protected under the adult). At first capture, each bird was banded with a stainless steel band, measured [culmen length (Cl; mm) using a caliper, and wing length (Wl; mm) using a ruler] and weighed in a bag using a Pesola balance. At second recapture for logger recovery, the birds were only weighed. An additional sample of individuals was captured specifically to measure wingspan (Ws; cm, $n = 20$) and wing area (Wa; cm², $n = 10$), according to methods developed by Pennycuik (1989), Hertel and Ballance (1999) and Shaffer et al. (2001). From these measurements and the body mass (BM; g), we calculated individually the wing loading, W_{load} (an index of force per unit wing area in g cm⁻²), as $W_{load} = BM \times g$ (gravitational acceleration, 9.81 m s⁻²)/Wa, and the wing aspect ratio (an index of wing shape), as $W_{ar} = Ws^2/Wa$. Adult boobies were sexed by voice (when approached or captured, males have a higher pitched voice than females, Nelson 1978), and by measurements (within a pair, females are larger than males).

Our main study plot included about 200 nests located on the western part of the atoll. At the beginning of the study period, nests were localised with numbered plastic tags fixed in the soil with metal pegs and the colony mapped. On each nest, one bird within the pair was colour

marked on the breast, without handling, using a sprayer, with a yellow patch of picric acid or with colour paint used for pigs (Raidex, France). With this method we could identify birds rapidly and from a distance for monitoring nest attendance. The study colony was systematically monitored at distance four to five times per day (at dawn and dusk, i.e. at 0600 and 1745 hours, and at 0900, 1200 and 1500 hours) to control for the presence of adults on the nest. To calculate meal mass delivered to chicks, chicks were weighed at each nest control in a subsample of 25 nests in the study colony, and the mass gain derived from mass increment attributed to the parent present. To either attach loggers, or to recover them on birds returning from a foraging trip, birds were captured at night (before dawn or after dusk) with a fishing rod. The exact duration of foraging trips was measured from GPS or accelerometer recordings.

To study the foraging movements of boobies we fitted 45 different individuals (24 males and 21 females) rearing chicks with a GPS receiver with integrated antenna and a 1-Mbyte flash memory operated by a rechargeable battery (Newbehavior, Zurich, Switzerland; Steiner et al. 2000) recording at 10 s intervals. The loggers were sealed into small polyethylene bags; the overall weight of the device and its waterproof package was 32 g. Loggers were left for 1–2 days on the birds before being retrieved, giving a total of 62 foraging trips. We studied the activity patterns, flight and diving behaviour of boobies using cylindrical, four-channel data-loggers (M190-D2GT, 12 bit resolution, 60 × 15 mm, 20 g, Little Leonardo, Tokyo, Japan) on 17 birds (9 males, 8 females) for one to three trips. The devices simultaneously monitored depth (every second), temperature (every minute) and acceleration (16 Hz) along two axes. The units contain a tilt sensor capable of measuring both dynamic (e.g. vibration) and static accelerations (e.g. gravity). Loggers were attached to the birds' tails so that acceleration was measured along the following two axes: surging acceleration measured along the longitudinal body axis of the birds, and heaving acceleration measured dorso-ventrally (Watanuki et al. 2003, see also Ropert-Coudert et al. 2004). The relative accuracy for the depth sensor was 0.1 m. Flapping frequency was calculated from dominant stroke cycle frequency as the Power spectral density (PSD). PSD was calculated from the entire acceleration dataset of each animal using a fast Fourier transformation (Sato et al. 2007).

GPS and accelerometers were taped under the three central tail feathers using Tesa tape. Only one logger type was attached to a bird (GPS represented a maximum of 3% of the bird's body mass and accelerometers 2%). GPS data were treated using a custom software package ('Diomedea', D. Filippi, see Weimerskirch et al. 2000, 2005 for details and other examples of its usage) to estimate

time spent per sector (unit of surface). The sections of the trip where satellite communication was lost were not included in the analysis. Speeds measured at 10 s intervals with GPS showed a bi-modal distribution, with speeds $<10 \text{ km h}^{-1}$ corresponding to birds sitting on the sea surface or diving, while speeds $>10 \text{ km h}^{-1}$ corresponded to birds travelling (Weimerskirch et al. 2005). The locations and duration of periods spent on the water were derived from GPS data when flight speeds were $<10 \text{ km h}^{-1}$.

Two methods were used to estimate the foraging areas of boobies. First, we used the kernel estimation technique to delineate foraging ranges and the core habitat areas used by birds (Worton 1995; Seaman and Powell 1996). For mapping purposes, we plotted the overall range and estimated contour levels including 50% (core area) and 95% of the locations distribution (Wood et al. 2000; Hyrenbach et al. 2002). Second, we used the first passage time (FPT) method to estimate the size of the zones of area restricted search (ARS), when birds decrease speed and increase sinuosity. ARS is generally considered as indicative of prey searching. The FPT method developed by Fauchald and Tveraa (2003) to identify the spatial scale (measured through a circle of a given radius) at which an animal increases its search effort, was adapted for GPS data (details in Pinaud 2008 and Weimerskirch et al. 2007). The sinuosity of the outbound flight tracks was estimated as the ratio of the actual distance covered to the straight-line distance covered between the nest and the most distant point in the track, so that a value of 1 would indicate a straight line.

Diet

Masked boobies regurgitate spontaneously their stomach contents when handled, and food samples were collected outside the study plots from breeding adults caught at nest just after returning from the sea. Food samples were frozen and returned to the laboratory for analysis. In the laboratory, each sample was weighed; items were then separated from each other and weighed separately. Identification of prey was made using Smith and Heemstra (1986) for fishes, Clarke (1986) and Nesis (1987) for squids, and our own reference collection. We measured fork length (FL, to the nearest 0.1 mm) and fresh mass (M to the nearest 0.1 g) of all intact fish, and dorsal mantle length (ML, to the nearest 0.1 mm), lower rostral length (LRL, to the nearest 0.01 mm) and fresh mass (M) of all intact squid. We used allometric relationships (see Le Corre et al. 2003) to reconstitute mass and length of partially digested items of the three main groups of preys (the fish Exocetidae and Hemiramphidae, and the squid Ommastrephidae).

Manipulation experiment

A total of 50 nests, located 100 m from the main study plot, i.e. with different individuals and nests, were marked with a numbered plastic label fixed to a stake planted in the soil. On the first day (14 January) of the experiment, the chick of each nest was banded with a metal band, marked on the breast with a coloured spot, weighed in a bag with a spring balance (accuracy $\pm 10 \text{ g}$), and its exposed culmen and wing length measured. A blood sample (0.5 ml) was taken from the wing for molecular sexing (see Lormée et al. 2000 for details of the sexing method). We selected chicks of approximately the same size (average mass: $1,612 \pm 248 \text{ g}$; wing length: $187 \pm 54 \text{ mm}$), corresponding to an age of ca. 60 days when they attain peak weight (Nelson 1978). The adults attending chicks were banded with a metal band, weighed in a bag and their wing length and exposed culmen measured. Nests were assigned by random choice to four treatment groups. In the first group, males and females were captured but not handicapped (controls, $n = 12$ nests). In a second group, both adults were handicapped ($n = 12$), and for the last two groups, either the male ($n = 13$) or the female ($n = 13$) was handicapped while the partner was used as a control. Seven days later (day +7), we searched marked adults in the colony without capturing them, weighed the chicks, and measured their culmen and wing length. Seven days later (day +14), we weighed and measured the chicks, captured and weighed all the adults present on the colony. Adults that could not be captured on day +14 were searched and captured during the subsequent 2 days (all except one individual).

To increase the energetic cost of flight we reduced the wing length by clipping the tip of the feathers (Pennycuick 1989). This handicap disappears after the post-breeding moult and has a limited effect on flight performance (Cuthill 1991). Following Velando and Alonso-Alvarez (2003), we reduced the wingspan by 5 cm (the largest primary being cut 2.5 cm shorter from the tip of each wing and perpendicular to the wing length axis) to increase the cost of flight (by approximately 5%, calculations from Pennycuick 1989; Velando and Alonso-Alvarez 2003). To examine the consequences of this handicap, we handicapped three males by the same procedure and fitted each individual with an accelerometer for 2–3 successive trips on nests different from those of the experimental manipulation plot.

Statistical analyses were performed with STATISTICA 6.0. (StatSoft, Cary, NC). Average values are given with ± 1 standard deviation. Because the individuals were tracked for several successive trips, we analysed foraging parameters using mixed-model ANOVAs to take possible pseudo replication problems into account. Foraging

parameters were taken as dependent variables, whereas sex was added to the model as fixed factors and individual bird was included as a random factor. We included the mass of individuals as a covariate in all analysis to examine whether individual mass was important after controlling for sex: we report results for the effects of mass only when significant. Values for variables representing percentage were arcsine-transformed before performing ANOVAs.

Results

Size, mass, attendance pattern and food delivery

Females were 14.1% heavier and had longer wings and wingspans than males, with a higher wing loading (Table 1). Wing shape, as measured from the aspect ratio, as well as culmen lengths and heights were similar between the sexes (Table 1).

At night both parents were attending the nest together, whereas during the day, only one adult was present. Both sexes were observed attending chicks, but males did so more frequently than females (on average, when an adult was with a large chick, it was a male in 66.5% of the cases, Table 2), whereas for birds incubating or brooding small chicks the attendance pattern was different ($F_{2,30} = 8.9, P < 0.001$), with males and females sharing nest attendance equally (51.4 ± 6.0 and $52.4 \pm 4.1\%$ of observations with males on nest for incubating and brooding pairs, respectively). There was no influence of the mass of large chicks on the attendance pattern ($r = 0.089, P = 0.765$). The increase in chick mass (food load) was greater when the chick was fed by females than by males (Table 2).

Foraging duration

Departure times from the colony peaked at dawn and then declined progressively through the day and were similar between the sexes (Fig. 1). There was a negative

relationship between trip duration and departure time in both sexes (Fig. 1). Although the average duration of foraging trips was not statistically different between males and females (8.9 vs 7.3 h, Table 2), the frequency distribution of trip durations differed between the sexes: two peaks were observed in males and females at 0.3–2.5 h (short trips), 4–12 h (medium trips), a third peak for long trips >12 h in males only (Fig. 2), the frequency of occurrence of peaks being different between sexes ($\chi^2_2 = 7.9, P = 0.019$). Trips lasting 0.3–12 h were conducted during day time, while for trips >12 h males made part of the return flight at night. Thus, 12.1% of the foraging time of males was spent at night, whereas for females it was only 1.6% (Table 2). There was a negative relationship between the mass at departure and the duration of the foraging trip for females but not for males (Fig. 3), but there was no relationship between departure time and mass at departure ($P = 0.122$ for females and $P = 0.444$ for males).

Foraging range and zones

The foraging range was not different between males and females (Table 2; Fig. 2), but here again the frequency of occurrence was different between the sexes ($\chi^2_2 = 8.7, P = 0.013$), with longer ranges corresponding to night trips conducted by males. Trips of short range were also more common for males than for females (Fig. 2). There was a significant relationship between trip duration and foraging range for both males and females (Fig. 2); the slopes of the two regression lines were not significantly different ($P = 0.872$).

Trips consisted of relatively straight outward and return phases, separated by foraging bouts where the birds changed direction and landed frequently (Fig. 4). The zones of ARS estimated from FPT analysis were generally located at the extremity of the foraging trips (Figs. 4, 5). ARS zones were of similar size, at similar distances from the colony, and the time spent in ARS was similar between males and females (Table 2).

Table 1 Mass and morphometric measurements of male and female masked boobies from Clipperton Island

Values are presented as average \pm 1 SD (sample size in parentheses)

	Males	Females	<i>t</i> test
Culmen length (mm)	100.5 \pm 2.9 (26)	101.2 \pm 2.9 (22)	<i>t</i> = 0.7, <i>P</i> = 0.452
Culmen height (mm)	36.5 \pm 2.2 (11)	36.5 \pm 2.9 (10)	<i>t</i> = 0.1, <i>P</i> = 0.981
Wing length (mm)	424.3 \pm 10.6 (25)	431.7 \pm 8.5 (22)	<i>t</i> = 2.6, <i>P</i> = 0.012
Wing loading (N m ⁻²)	71.9 \pm 3.4 (5)	76.2 \pm 2.3 (5)	<i>t</i> = 2.34, <i>P</i> = 0.048
Aspect ratio	12.7 \pm 0.5 (5)	12.7 \pm 0.5(5)	<i>t</i> = 0.1, <i>P</i> = 0.932
Wing span (m)	1.631 \pm 0.25 (10)	1.680 \pm 0.17 (10)	<i>t</i> = 5.2, <i>P</i> < 0.0001
Weight (g)	1,555.0 \pm 84.8 (26)	1,744.9 \pm 152.2 (24)	<i>t</i> = 10.4, <i>P</i> < 0.0001

Table 2 Nest attendance and foraging parameters of male and female masked boobies rearing large chicks

	Males	Females	Statistics ^a	P value
Nest attendance (% of checks with:)	66.5 ± 12 (35)	34.5 ± 12.0 (35)	$t = 3.9$	0.001*
Meal mass delivered to chick (g)	188.6 ± 66.7 (29)	280.0 ± 105.2 (16)	$t = 3.6$	0.001*
Trip duration (h)	8.9 ± 3.8 (46)	7.3 ± 3.1 (24)	$U = 412$	0.084
Maximum foraging range (km)	90.9 ± 72.3 (21)	109.4 ± 44.3 (17)	$U = 229$	0.114
ARS size (km)	3.1 ± 3.1	4.3 ± 5.6	$F_{1,48} = 2.4$	0.132
Distance of ARS from colony (km)	83.1 ± 61.1	85.6 ± 38.3	$F_{1,48} = 0.01$	0.902
Time spent in ARS (h)	1.1 ± 1.4	1.3 ± 1.35	$F_{1,48} = 0.4$	0.535
Sinuosity during the outward movement	1.61 ± 0.34	1.40 ± 0.19	$F_{1,27} = 4.7$	0.045*
Instantaneous flight speed during trip (km h ⁻¹)	42.2 ± 5.7	44.1 ± 5.1	$F_{1,28} = 0.2$	0.940
Time spent at sea at night (%)	12.1 ± 18.2	1.6 ± 3.2	$F_{1,27} = 4.8$	0.040*
Foraging time spent on water (%)	29.8 ± 15.3	15.3 ± 13.2	$F_{1,28} = 6.9$	0.014*
Number of landing per hour	13.0 ± 4.9	11.5 ± 4.6	$F_{1,28} = 0.75$	0.393
Number of dives per hour	3.7 ± 1.4	8.2 ± 6.3	$F_{1,28} = 4.8$	0.009*
Flapping frequency (beats s ⁻¹)	3.83 ± 0.09	3.71 ± 0.11	$F_{1,26} = 8.8$	0.006*
Flight time spent flapping (%)	38.1 ± 15.1	46.7 ± 12.9	$F_{1,28} = 1.46$	0.237
Maximum dive depth (m)	2.03 ± 1.05	2.37 ± 1.12	$F_{1,35} = 4.2$	0.047*
Duration of dives (s)	2.8 ± 1.3	3.1 ± 1.3	$F_{1,35} = 2.7$	0.120
Number of prey per stomach content	5.4 ± 2.7	6.5 ± 3.2	$F_{1,43} = 1.6$	0.215
Length of <i>Exocetidae</i> fishes (mm)	193 ± 4	194 ± 4	$F_{1,53} = 0.2$	0.987
Length of <i>Hemiramphidae</i> (mm)	172 ± 6	183 ± 8	$F_{1,26} = 1.2$	0.384

Values are presented as average ± 1 SD (sample size in parentheses)

ARS area restricted search

* $P \leq 0.05$

^a T test, paired t test, Mann–Whitney test, Mixed ANOVA

Flight speed, activity, diving and diet

The average flight speeds were similar between males and females (Table 2). The overall sinuosity of the outward phase of the track until the bird reached its maximum range can be taken as an indicator of whether the bird left straight from the colony or not. This index was higher in males than in females (Table 2), suggesting that males took a less direct route than females when heading to foraging grounds.

Males spent a greater proportion of the foraging trip sitting on the water compared to females (Table 2). They also showed a lower rate of dives per hour but had similar numbers of landings on the sea-surface per hour (Table 2). The flapping frequency was higher in males than in females (Table 2), and there was a significant negative effect of mass on flapping frequency ($F_{1,20} = 6.9$, $P = 0.016$), but the percentage of flight time spent flapping was similar between the sexes (Table 2). The distribution of diving depths was similar between the sexes (Fig. 6), females diving slightly deeper than males (Table 2). Both sexes showed similar dive durations (Table 2).

The number of prey per stomach content was similar between males and females (Table 2). Masked boobies preyed essentially on flyingfish (mainly *Exocetidae*), other

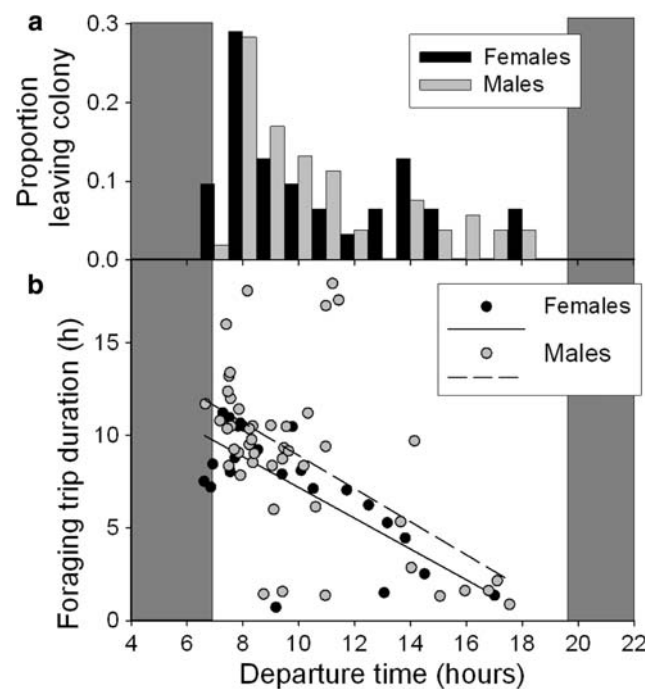
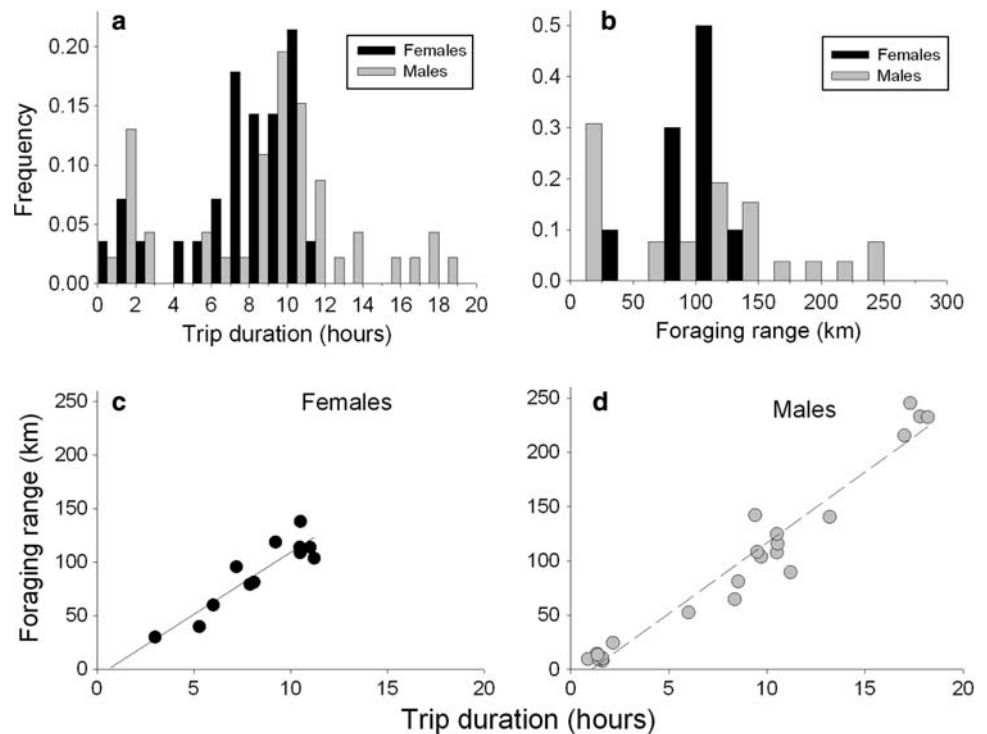


Fig. 1 **a** Frequency distribution of departure time of males and females. **b** Relationship between trip duration and departure time of male and female masked boobies (males $y = -0.894 + 17.8$, $r^2 = 0.318$, females $y = -0.831 + 15.5$, $r^2 = 0.546$). Grey boxes Night

Fig. 2 Frequency distribution of **a** trip duration and **b** maximum foraging range in male and female masked boobies. Relationship between trip duration and foraging range in **c** females (black dots, $r^2 = 0.842$, $y = 11.6x - 6.7$, $P < 0.001$) and **d** males (grey dots, $r^2 = 0.949$, $y = 13.0 - 1.4$, $P < 0.001$)



fish species and flying squids (Ommastraphidae) (Table 3). There were no differences in the prey composition ($\chi^2_5 = 1.1$, $P = 0.894$) or size of the flyingfishes taken by males and females (Tables 2, 3; Fig. 7).

Experimental manipulation

Female chicks were heavier than male chicks at the beginning and end of the experiment ($F_{1,45} = 8.1$, $P = 0.007$ and $F_{1,44} = 7.7$, $P = 0.008$, respectively), and chicks of both sexes lost a similar amount of mass (females: -126 ± 180 g; males: -107 ± 207 g; $F_{1,44} = 0.1$, $P = 0.729$) or relative mass (-6.1 ± 7.1 and $-6.1 \pm 9.2\%$ of total mass, $F_{1,44} = 0.1$, $P = 0.771$). There was no significant difference between the mass loss of chicks from the four experimental groups (control -45 ± 139 g, both adults handicapped -123 ± 167 g, female handicapped -160 ± 212 g, male handicapped -130 ± 236 g, $F_{3,42} = 0.7$, $P = 0.534$). Although chicks from a nest where at least one adult was handicapped lost a greater mass than those from other nests (control nests: -45.4 ± 130.1 g, manipulated nests: -139.4 ± 204.4 g), a two-way ANOVA of the effect of treatment and sex of chick indicated that the handicapping of parents had a marginal effect on changes in the mass of male and female chicks (treatment $F_{1,44} = 2.0$, $P = 0.160$; sex of chick $F_{1,44} = 0.12$, $P = 0.729$; Interaction $F_{1,42} = 0.020$, $P = 0.890$).

Overall, adult males and females lost mass between the start and end of the experiment (Fig. 8). The manipulation of flight costs of male parents did not produce significant differences in body mass changes between the handicapped and control birds ($F_{1,37} = 0.078$, $P = 0.780$). When considering males whose female partner was handicapped, handicapped and control males, we also found no difference between groups ($F_{2,36} = 0.179$, $P = 0.837$). In contrast, a similar test carried out for females indicates that there was a significant differences between groups ($F_{2,30} = 4.9$, $P = 0.014$); handicapped females and non-handicapped females with a handicapped partner lost a similar amount of mass ($F_{1,25} = 0.35$, $P = 0.557$), but this loss was significantly greater than the mass loss of the control females ($F_{2,30} = 4.92$, $P = 0.014$, Fig. 8).

The three handicapped males fitted with accelerometers behaved similarly to other males but we observed two differences, which, although non-significant, we consider worth reporting here. Handicapped males tended to dive more frequently ($F_{1,14} = 3.7$, $P = 0.076$, Levene Test for homogeneity of variance, $F = 0.4$, $P = 0.396$; handicapped males: 4.6 ± 1.5 dives per hour, controls: 3.1 ± 1.2 dives per hour), and to spend more time flapping than control males ($F_{1,14} = 1.9$, $P = 0.157$ Levene Test, $F = 0.2$, $P = 0.665$; $46.7 \pm 9.9\%$ and $38.1 \pm 15.1\%$, respectively). There was no trend in flapping frequency between the sexes ($3.80 \pm$ and 3.83 ± 0.09 beats s^{-1} , respectively, $P = 0.736$).

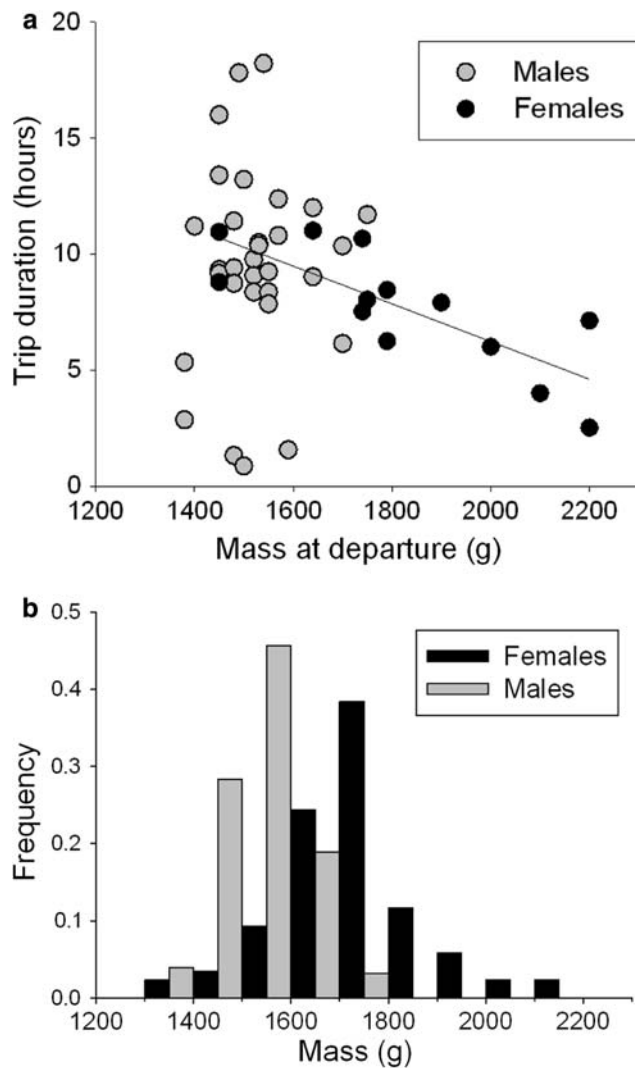


Fig. 3 **a** Relationship between the duration of foraging trips and the mass at departure of males and females adult masked boobies (females $r^2 = 0.617$, $y = -7.6x + 2.4$, $P = 0.007$, males $P = 0.707$). **b** Frequency distribution of the mass of adult male and female masked-boobies

Discussion

This study is the first, to our knowledge, to examine sex-specific differences in the breeding effort of a seabird by combining a study on foraging ecology at sea (using high precision activity and telemetry loggers, as well as diet analysis) and the attendance pattern on land together with an experimental manipulation of flight costs in the two sexes. Generally, such approaches are carried out independently, especially foraging studies, which furthermore remain rare. However, foraging and breeding involvement are intimately connected and should ideally be studied jointly (Boggs 1992).

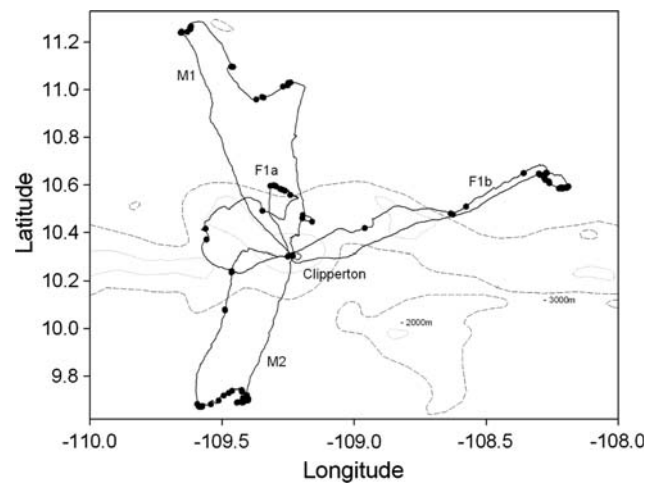


Fig. 4 Examples of foraging of masked boobies fitted with GPS recording at 10-s intervals. *Black dots* Speed $<10 \text{ km h}^{-1}$, i.e. foraging activity (landing, diving, etc.). Four trips of two males (M1 and M2) and two successive trips of the same female (F1a and F1b) are shown. *Dashed lines* Isobaths

Sex-specific differences in breeding investment

During the period of rearing of the large chick, which is considered to be a period of high-energy demand for adult seabird parents (Ricklefs 1983), male masked boobies attended the chick a much greater proportion of the time than females. Higher nest attendance by males is generally considered to improve defence of the territory (Nelson 1978) and favours extra pair copulation during the earlier stages of the breeding season (Tershy and Croll 2000). At Clipperton, nest density is high and the presence of males on the nest plays an important role in protecting the chicks from the attacks of other males, unattended chicks being attacked regularly and often injured by non-breeding birds wandering in the colonies and trying to occupy a territory (personal observation). Females provisioned the chick to a much larger proportion than males, and consequently spent less time at the colony and delivered larger meals. Thus, the two sexes take on different roles in breeding investment when they rear large chicks, indicating a clear division of labour during chick rearing, probably because it is the most energy-demanding period. During incubation and the period of brooding, males and females share nest attendance equally. This difference in breeding investment during chick rearing contrasts with the behaviour of most other seabird species, which share breeding duties equally, including chick provisioning. In species with RSD such as boobies, different roles in nest attendance by each sex have long been suspected in several species (Nelson 1978), but it was later suggested that division of labour was minimal in boobies with marked (blue-footed boobies *Sula nebouxii* Milne Edwards) and limited (red-footed boobies *S. sula*

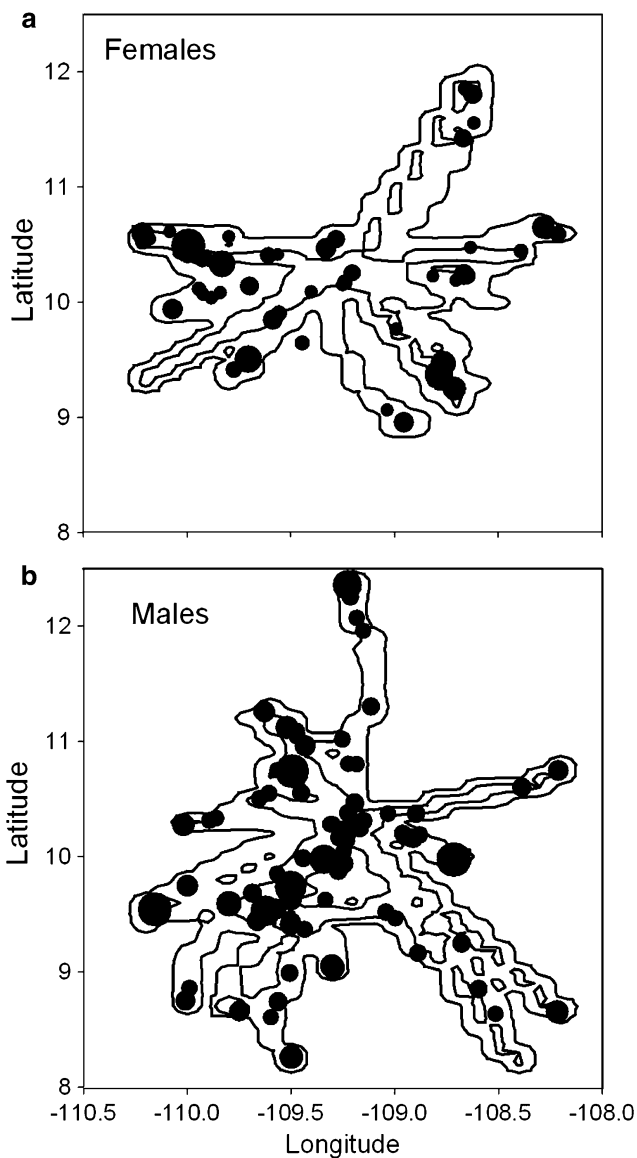


Fig. 5 Foraging areas as shown by density contour plots from kernel estimates of the amount of time spent at sea, for **a** female and **b** male masked boobies. *Dotted line* Range, *solid line* 95% density level, *bold line* 50% core area, *circles* zone of ARS (size of circle is proportional to time spent in ARS)

Linnaeus) RSD, even during chick rearing (Guerra and Drummond 1995; Lormée et al. 2000; Weimerskirch et al. 2006). However, although male and female blue-footed boobies share duties equally during incubation and the brooding phase, when chicks are larger, females provisioned the chick more than males (Guerra and Drummond 1995), similar to our results on masked boobies. In red-footed boobies, where sex dimorphism is less marked, studies were carried out during brooding (Weimerskirch et al. 2006). Therefore, when examining breeding investment and testing the division of labour hypothesis, it is very important to take into account the stage of the

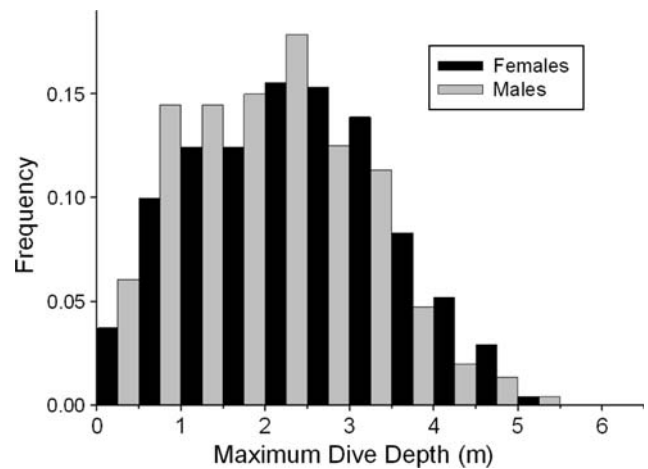


Fig. 6 Frequency distribution of dive depths attained by male and female masked boobies

Table 3 Comparison of the diet of 32 male and 28 female masked boobies (number of individual prey in parentheses) according to prey type (by numbers)

Class	Family	Males	Females
Squid	Ommastrephidae	4.9% (7)	3.2% (4)
Fish	Exocoetidae	77.8% (112)	79% (98)
	Hemiramphidae	11.1% (16)	9.7% (12)
	Scombridae	5.5% (8)	6.4% (2)
	Coryphaenidae	4.9% (7)	3.2% (4)

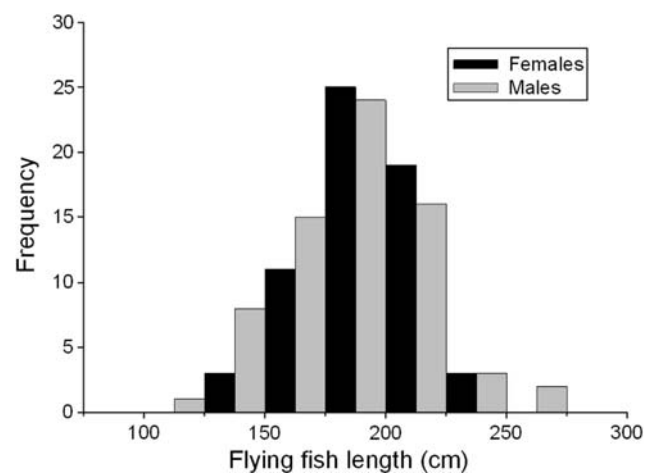


Fig. 7 Frequency distribution of flyingfish fork length caught by male ($n = 69$) and female ($n = 61$) masked boobies

breeding season—some periods being potentially critical, especially those where energy demand is at its highest. In addition, Clipperton is the largest colony of boobies in the world, with high densities of birds in the colony, which could be an additional constraint to a clear division of labour—the role of males in protecting chicks from

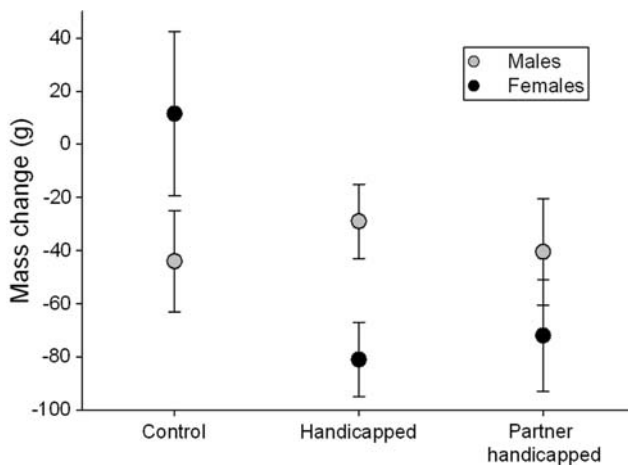


Fig. 8 Mean (\pm SE) mass changes of adult male and female masked boobies according to the treatment: control, handicapped (wing tip clipped) and mate of a handicapped bird

congeners probably being as critical as provisioning by the female for breeding success.

Foraging and breeding investment

Sex differences in foraging behaviour are generally considered as being mediated through size differences—larger sex being more competitive and dominant, flying faster with higher costs (Newton 1979, reviewed for seabirds in Lewis et al. 2002). However, our analysis, which takes into account mass after controlling for sex, shows that there was an effect of individual mass in only one parameter, i.e. the flap frequency, which is known to be strongly influenced by mass (Sato et al. 2007). We even found no effect of the mass on some parameters that could be related directly to mass or size, such as diving depth of plunge-diving birds (Ropert-Coudert et al. 2004) or flight speed (Pennycuik 1989). Therefore, most differences cannot be explained by size difference. Sex differences have also been found in the foraging behaviour of species with no sexual dimorphism (Gray and Hamer 2001; Lewis et al. 2002; Phillips et al. 2004), indicating that factors other than size influence sex-specific foraging performance.

From the observed sex-specific breeding investment, we might expect that division of labour between the sexes could result in differences in foraging strategy, or alternatively is the result of different foraging skills or sexual segregation at sea. Our results show that foraging niche divergence between the sexes is very limited. The two sexes fed on the same prey type of similar size, and foraged in approximately the same areas, although males can access more distant waters during their longer trips. Overall, both sexes showed similar patterns in the timing of departure from the colony, most birds leaving the colony

early in the morning. Furthermore, later departures resulted in shorter foraging trips. As boobies generally avoid foraging at night (Weimerskirch et al. 2005), the timing of departure directly influences the time spent foraging and imposes strong constraints on the birds (Lewis et al. 2004). Surprisingly the higher nest attendance by males does not result in shorter foraging trips. Although there are a greater proportion of short foraging trips by males, average values were similar between the two sexes because males were the only sex to display protracted foraging trips, which included part of the night spent in flight at sea. Although males leave much of the provisioning to the females, they exhibit a strategy whereby they can leave the nest for short periods to forage in the vicinity of the island—probably to ensure maximum nest attendance—but at some stage they leave for longer periods, with part of the return trip spent in flight at night, so as to forage farther than the females. These long trips, which include night flight, do not decrease nest attendance, since at night females are on the nest anyway. The decision to conduct a short or long trip is not related to the mass at departure for males, as it is in females. The decision of females to perform a long or a short foraging trip is under the control of their body mass, which suggests strongly that females, but not males, regulate their foraging effort, as also suggested by the results of the experimental study. Furthermore, foraging male masked boobies spent a larger proportion of their trip time at the sea surface and dived much less frequently than females, indicating a higher foraging effort by females.

Experimental manipulation

The handicapping of birds by clipping of flight feathers has been used extensively (e.g. Cuthill 1991; Mauck and Grubb 1995; Saether et al. 1993; Weimerskirch et al. 1999). Based on theoretical calculations of flight costs (Pennycuik 1989), it is generally considered that reducing wingspan or wing surface increases wing loading and therefore the cost of flight. However, so far no study has tried to estimate the actual consequences of clipping on flight efficiency. Although our experiment was based on a small sample size and did not yield significant statistical results, it is of interest for future studies to note that handicapped birds tended to dive more frequently and spent more time flapping than non-handicapped birds. An increase in the time spent flapping following a reduction in wingspan or surface would be logical in accordance with flight theory (Pennycuik 1989), and supports the assumption that clipping flight feathers increases flight costs. Theoretical calculations based on average values give an increase in 5% in flight costs for a reduction of 5 cm in wingspan, corresponding to an increase in 6% of wing loading (Pennycuik 1989; Velando and Alonso-Alvarez 2003), which is in

accordance with the measured increase in time spent flapping of 8% estimated in our study using accelerometers. The increased dive rate by handicapped birds is more difficult to interpret. It may be the result of a lower efficiency of aerial dives, which would impose more frequent dives on handicapped birds, or, by diving more birds potentially try to catch more prey to compensate for the increased costs associated with the handicap, but more data are required to distinguish between these possibilities.

The mass changes of handicapped males or of males with a handicapped partner, were similar to those of control males, suggesting that male boobies were not affected in their energy budget when foraging costs increased. Conversely, handicapped females were significantly affected by the clipping as they lost mass compared to control females. Mass loss by handicapped females may be the result of the increased cost of flight, but could also be adaptive as an adjustment of wing loading to the reduced wing area by adaptive mass loss (Lind and Jakobsson 2001). However, since males did not show increased mass loss, the first hypothesis seems more likely. Furthermore, the response of females with a handicapped partner was similar to that of handicapped females, females apparently compensated for the reduced investment by their handicapped partner. Our results are similar to those observed by Velando and Alonso-Alvarez (2003) following a manipulation of male and female blue-footed boobies, suggesting similar constraints for these two species. The differential response between males and females may have several origins. Males, being lighter than females, may be less flexible in their capacity to decrease their body mass to compensate for an increased foraging cost. This is consistent with the reduced mass range observed in males compared to females. In addition, males invest naturally less in offspring provisioning than females, spend more time on land and may be, therefore, less affected by a handicap affecting their flight abilities than females. Alternatively, males may have different foraging strategies, and could be less affected than females by a handicap, but this is not confirmed by our data on foraging. Thus, the larger females appear to be more capable of adjusting foraging effort than males, a critical advantage for the sex that is the main provisioner in the pair where division of labour is maximal.

The manipulation of parents had no significant effects on chicks of either sex. Velando (2002) found that larger female chicks of the blue-footed booby were more affected by the handicapping of parents, whereas we found no sex differences. Our experiment was carried out over a relatively short time period, which may not be long enough to detect the differential consequences of a parental handicapping on the growth of male and female chicks observed in blue-footed boobies.

Conclusions

Because pelagic seabirds such as masked boobies are long-lived, they should limit the risk of increased mortality during a breeding event because of the high residual reproductive value (Williams 1966). Ways to optimise the balance between current and future reproductive effort in boobies has been much debated, and two non-exclusive mechanisms have been proposed: a fixed investment, independent of chicks needs, or a flexible investment in reproduction (Ricklefs 1987; Saether et al. 1993). Recent studies suggest that a combination of the two hypotheses is more likely because decisions to allocate to the offspring depend on food availability (Erikstad et al. 1998; Weimerskirch et al. 2001). In addition, there is a consensus that allocation decisions are under the control of the body condition of adults, especially in long-lived species such as seabirds (Monaghan et al. 1989; Chaurand and Weimerskirch 1994; Weimerskirch 1999).

Our simultaneous investigations of nest attendance, foraging effort, regulation abilities related to body mass and experimental manipulation of flight costs suggest that males and females have contrasting breeding investment strategies when energy requirement is highest. Females invest much more in offspring provisioning than males, which show a lower foraging effort (dive rate) than females. The female—the main provisioner of the chick in the pair—appears to regulate breeding effort in relation to its own body mass. In addition, if foraging costs are increased, females use their body reserves to compensate for this increased cost. Consequently, the duration of female foraging trips is directly under the control of body mass. Several factors could explain why smaller-sized males do not regulate their breeding effort. First, being lighter, males could have a lower safety margin before reaching a critical body mass threshold under which seabirds have been shown to modify their behaviour to limit mortality cost, either by stopping reproduction or by reducing their breeding investment in offspring (Weimerskirch 1999). Alternatively, males may be unwilling to invest more energy in the offspring, independently of body mass. Males could be working at a fixed level because they favour defence of the territory and of the chick, an activity that is more predictable in terms of energy expenditure than foraging. Thus, the division of labour may favour the evolution of contrasting strategies. Division of labour between the sexes implies that each sex plays a different role in parental care, and that natural selection acts differently on the male and female to ensure that each is the optimal size to play a particular role. This argument has been applied successfully to explain RSD in raptors (Lundberg 1986). Sexual selection in species with RSD could be an alternative hypothesis (Jehl and Murray 1986)

but has received little support (Guerra and Drummond 1995), and has been put forward for species for which division of labour between sexes was not apparent. The division of labour that we observed in masked boobies is, however, different from that observed in raptors, where larger females guard the nest (Newton 1979; Lundberg 1986), indicating that the evolution of RSD in raptors and sulids is related to different selection pressures. Although our results indicate division of labour between the sexes, we cannot distinguish at this stage if this is a cause or a consequence of RSD.

In masked boobies, each sex uses a specific breeding strategy, i.e. a flexible investment by the female, and a fixed investment by the male (Velando and Alonso-Alvarez 2003). These different strategies influence the foraging ecology of the two sexes, although they use the same niche at sea. We thus suggest that differences in foraging strategies between the sexes are only partly explained by size differences, and that it is primarily the difference in investment strategies that drives sex-specific foraging differences. Why would natural selection lead to large females provisioning the chick, and small males protecting the chick? In the case of raptors, the small size of the male is advantageous in the capture of agile prey (Lundberg 1986). In masked boobies, nest attendance by males is probably important for chick survival, in addition to territory defence and the possibility of extra pair copulation. These last two functions are male specific, and, together with chick defence, do not require selection for large size. Conversely, a larger size for masked boobies may be advantageous for the parent providing the major provisioning to the chick, since it allows the transport of a greater amount of food (see also Anderson and Ricklefs 1992) and is associated with a high variability in mass that allows flexibility for regulation of provisioning.

Acknowledgments We would like to address our special thanks to Dr. Jean Louis Etienne for organising the expedition to Clipperton Island, and for the logistical and financial support of the study. We thank the Conseil Régional Poitou Charentes, Université de la Réunion for additional financial support. We also extend our gratitude to all the participants of the expedition for their help during the fieldwork. We finally thank S. Ruault for molecular sexing of the boobies. We thank R. Mullers and Lisa T. Ballance for extensive comments and suggestions on an earlier version of the manuscript.

References

- Anderson DJ, Ricklefs RE (1992) Brood size and food provisioning in masked and blue-footed boobies (*Sula* spp.). *Ecology* 73:1363–1374
- Andersson M (1994) Sexual selection. Princeton University Press, Princeton
- Andersson M, Norberg RÅ (1981) Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biol J Linn Soc* 15:105–130
- Boggs CL (1992) Resource allocation, exploring connections between foraging and life histories. *Functl Ecol* 6:508–518
- Catry P, Phillips RA, Furness RW (1999) Evolution of reversed sexual size dimorphism in skuas and jaegers. *Auk* 116:158–168
- Chaurand T, Weimerskirch H (1994) The regular alternation of short and long trips in the Blue petrel *Halobaena caerulea*, a previously undescribed strategy of food provisioning in a pelagic seabird. *J Anim Ecol* 63:275–282
- Clarke MR (1986) A handbook for the identification of cephalopods beaks. Clarendon, Oxford
- Cuthill I (1991) Field experiments in animal behaviour, methods and ethics. *Anim Behav* 42:1007–1014
- Drent RH, Daan S (1980) The prudent parent, energetic adjustment in avian breeding. *Ardea* 68:225–252
- Erikstad KE, Fauchald P, Tveera T, Steen H (1998) On the cost of reproduction in long-lived birds: the influence of environmental variability. *Ecology* 79:1781–1788
- Fairbairn J, Shine R (1993) Patterns of sexual size dimorphism in seabirds of the southern hemisphere. *Oikos* 68:139–145
- Fauchald P, Tveraa T (2003) Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology* 84:282–288
- Gilardi JD (1992) Sex-specific foraging distributions of brown boobies in the eastern tropical Pacific. *Colon Wat* 15:148–151
- Gonzales-Solis J, Croxall JP, Wood AG (2000) Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels *Macronectes halli* during incubation. *Oikos* 90:390–398
- Gray CM, Hamer KC (2001) Food-provisioning behaviour of male and females Manx shearwaters. *Anim Behav* 62:117–121
- Guerra M, Drummond H (1995) Reversed sexual size dimorphism and parental care : minimal division of labour in the blue-footed booby. *Behaviour* 132:479–496
- Hertel F, Ballance LT (1999) Wing ecomorphology of seabirds from Johnston Atoll. *Condor* 101:549–556
- Hyrenbach KD, Fernandez P, Anderson DJ (2002) Oceanographic habitats of two sympatric North Pacific albatrosses during their breeding season. *Mar Ecol Prog Ser* 233:283–301
- Jehl JR Jr, Murray BG Jr (1986) The evolution of normal and reverse sexual size dimorphism in shorebirds and other birds. In: Johnston RF (ed) Current ornithology, vol 3. New York, Plenum, pp 1–86
- Le Corre M, Chérel Y, Lagarde F, Lormée H, Jouventin P (2003) Seasonal and inter-annual variation in the feeding ecology of a tropical oceanic seabird, the red-tailed tropicbird *Phaethon rubricauda*. *Mar Ecol Progr Ser* 255:289–301
- Lewis S, Benvenuti S, Dall'Antonia L, Griffiths R, Money L, Sherratt TN, Wanless S, Hamer KC (2002) Sex-specific foraging behaviour in a monomorphic seabird. *Proc R Soc Lond B Biol Sci* 269:1687–1693
- Lewis S, Schreiber EA, Daunt F, Schenk GA, Wanless S, Hamer KC (2004) Flexible foraging patterns under different time constraints in tropical boobies. *Anim Behav* 68:1331–1337
- Lewis S, Schreiber EA, Daunt F, Schenk GA, Orr K, Adams A, Wanless S, Hamer KC (2005) Sex-specific foraging behaviour in tropical boobies: does size matter? *Ibis* 147:408–414
- Lind J, Jakobsson S (2001) Body building and concurrent mass loss: flight adaptations in tree sparrows. *Proc R Soc Lond B Biol Sci* 268:1915–1919
- Lormée H, Jouventin P, Lacroix A, Lallemand J, Chastel O (2000) Reproductive endocrinology of tropical seabirds, sex specific patterns in LH, steroids and prolactin secretion in relation to parental care. *Gen Comp Endocrinol* 117:413–426

- Lormée H, Barbraud C, Chastel O (2005) Reversed sexual size dimorphism and parental care in the Red-footed booby (*Sula sula*). *Ibis* 147:307–315
- Lundberg A (1986) Adaptive advantages of reversed sexual dimorphism in European owls. *Ornis Scand* 17:133–140
- Mauck RA, Grubb TC Jr (1995) Petrel parents shunt all experimentally increased reproductive costs to their offspring. *Anim Behav* 49:999–1008
- Monaghan P, Uttley JD, Burnes MD, Thaine C, Blackwood J (1989) The relationship between food supply, reproductive effort and breeding success in Arctic terns *Sterna paradisae*. *J Anim Ecol* 58:261–274
- Mueller HC (1990) The evolution of reversed sexual dimorphism in size in monogamous species of birds. *Biol Rev* 65:553–585
- Nelson B (1978) The Sulidae: gannets and boobies. Oxford University Press, Oxford
- Nesis KN (1987) Cephalopods of the World. Squids, cuttlefishes, octopuses and allies. TFH Publications, Neptune City, NJ
- Newton I (1979) Population ecology of raptors. Poyser, Berkhamsted
- Pennycuik CJ (1989) Bird flight performance: a practical calculation manual. Oxford Science Publications, Oxford University Press, Oxford
- Phillips RA, Silk JRD, Phalan B, Catty P, Croxall JP (2004) Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence. *Proc R Soc Lond B Biol Sci* 271:1283–1291
- Pinaud D (2008) Quantifying search effort of moving animals at different spatial scales using first passage time analysis: effect of structure of the environment and tracking system. *J Appl Ecol* 45:91–99
- Reznick D (1985) Cost of reproduction: an evaluation of empirical evidence. *Oikos* 44:247–267
- Ricklefs RE (1987) Response of adult Leach's storm petrel to increase food demand at nest. *Auk* 104:750–756
- Ricklefs RE (1983) Some considerations on the reproductive energetic of pelagic seabirds. *Stud Avian Biol* 8:84–94
- Ropert-Coudert Y, Grémillet D, Ryan P, Kato A, Naito Y, Le Maho Y (2004) Between air and water, the plunge dive of the Cape Gannet *Morus capensis*. *Ibis* 146:281–290
- Saether BE, Andersen R, Pedersen HC (1993) Regulation of parental effort in a long-lived seabird: an experimental manipulation of the costs of reproduction in Antarctic petrels *Thalassoica antarctica*. *Behav Ecol Sociobiol* 33:147–150
- Sato K, Watanuki Y, Takahashi A, Miller PJO, Tanaka H, Kawabe R, Ponganis PJ, Handrich Y, Akamatsu T, Watanabe Y, Mitani Y, Costa DP, Bost CA, Aoki K, Amano M, Trathan P, Shapiro A, Naito Y (2007) Stroke frequency, but not swimming speed, is related to body size in free-ranging seabirds, pinnipeds and cetaceans. *Proc R Soc London B Biol Sci* 274:471–477
- Seaman DE, Powell RA (1996) An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77:2075–2085
- Shaffer SA, Weimerskirch H, Costa DP (2001) Functional significance of sexual dimorphism in Wandering albatrosses *Diomedea exulans*. *Funct Ecol* 15:203–210
- Shine R (1989) Ecological causes for the evolution of sexual dimorphism, a review of the evidence. *Q Rev Biol* 64:419–461
- Simmons KEL (1970) Ecological determinants of breeding adaptations and social behaviour in two fish-eating birds. In: Crook JH (ed) Social behaviour in birds and mammals. Academic, London, pp 37–77
- Smith MM, Heemstra PC (1986) Smith's sea fishes. Springer, New York
- Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford
- Steiner I, Bürgi C, Werffeli S, Dell'Omo G, Valenti P, Tröster G, Wolfer DP, Lipp HP (2000) A GPS logger and software for analysis of homing in pigeons and small mammals. *Physiol Behav* 71:589–596
- Tershy BR, Croll DA (2000) Parental investment, adult sex ratios, and sexual selection in a socially monogamous seabird. *Behav Ecol Sociobiol* 48:52–60
- Velando A (2002) Experimental manipulation of parental effort produces differential effects in sons and daughters, implications for adaptive sex ratios in blue-footed boobies. *Behav Ecol* 13:443–449
- Velando A, Alonso-Alvarez C (2003) Differential body condition regulation by males and females in response to experimental manipulations of brood size and parental effort in the blue-footed booby. *J Anim Ecol* 72:846–856
- Watanuki Y, Niizuma Y, Gabrielsen GW, Sato K, Naito Y (2003) Stroke and glide of wing-propelled divers, deep diving seabirds adjust surge frequency to buoyancy change with depth. *Proc R Soc London B Biol Sci* 270:483–488
- Weimerskirch H (1999) The role of body condition in breeding and foraging decisions in albatrosses and petrels. In: Adams NJ, Slotow RH (eds) Proceedings of the 22nd International ornithological congress, Johannesburg: Birdlife South Africa, Durban, pp 1178–1189
- Weimerskirch H, Fradet G, Chérel Y (1999) Natural and experimental changes in provisioning in a long-lived seabird, the Antarctic Prion. *J Avian Biol* 30:165–174
- Weimerskirch H, Guionnet T, Martin J, Shaffer SA, Costa DP (2000) Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proc R Soc London B Biol Sci* 267:1869–1874
- Weimerskirch H, Prince PA, Zimmermann L (2001) Influence of environmental variability on breeding effort in a long-lived seabird, the yellow-nosed albatross? *Behav Ecol* 12:22–30
- Weimerskirch H, Le Corre M, Ropert-Coudert Y, Kato A, Marsac F (2005) The three-dimensional flight of red-footed boobies: adaptations to foraging in a tropical environment. *Proc R Soc London B Biol Sci* 272:53–61
- Weimerskirch H, Le Corre M, Ropert-Coudert Y, Kato A, Marsac F (2006) Sex-specific foraging behaviour in a seabird with reversed sexual dimorphism, the red-footed booby. *Oecologia* 146:681–691
- Weimerskirch H, Pinaud D, Pawlowski F, Bost CA (2007) Does prey capture induce area-restricted search? A fine scale study using GPS in a marine predator, the wandering albatross. *Am Nat* 170:734–743
- Weimerskirch H, Le Corre M, Bost CA (2008) Foraging strategy of masked boobies from the largest colony in the world: relation with environmental conditions and fisheries? *Mar Ecol Prog Ser* 362:291–302
- Williams GC (1966) Natural selection, the cost of reproduction and a refinement of lack's principle. *Am Nat* 100:687–690
- Wood AG, Naef-Daenzer P, Prince PA, Croxall JP (2000) Quantifying habitat use in satellite tracked pelagic seabirds: application of the kernel estimation to albatross locations. *J Avian Biol* 31:278–286
- Worton BJ (1995) Using Monte Carlo simulation to evaluate kernel-based home range estimators. *J Wildl Manage* 59:794–800