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The individual counts: within sex differences in foraging strategies are as important as sex-specific differences in masked boobies *Sula dactylatra*

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Understanding how animals allocate their foraging time is a central question in behavioural ecology. Intrinsic factors, such as body mass and size differences between sexes or species, influence animals' foraging behaviour, but studies investigating the effects of individual differences in body mass and size within the same sex are scarce. We investigated this in chick-rearing masked boobies *Sula dactylatra*, a species with reversed sexual dimorphism, through the simultaneous deployment of GPS and depth-acceleration loggers to obtain information on foraging movements and activity patterns. Heavier females performed shorter trips closer to the colony than lighter females. During these shorter trips, heavier females spent higher proportions of their flight time flapping and less time resting on the water than lighter females did during longer trips. In contrast, body mass did not affect trip duration of males, however heavier males spent less time flapping and more time resting on the water than lighter males. This may occur as a result of higher flight costs associated with body mass and allow conservation of energy during locomotion. Body size (i.e. wing length) had no effect on any of the foraging parameters. Dive depths and dive rates (dives h^{-1}) were not affected by body mass, but females dived significantly deeper than males, suggesting that other factors are important. Other studies demonstrated that females are the parent in charge of provisioning the chick, and maintain a flexible investment under regulation of their own body mass. Variation in trip length therefore seems to be triggered by body condition in females, but not in males. Consequently, shorter trips are presumably used to provision the chick, while longer trips are for self-maintenance. Our findings underline the importance of accounting for the effects of body mass differences within the same sex, if sex-specific foraging parameters in dimorphic species are being investigated.

Foraging behaviour in marine predators is intricately linked to extrinsic, environmental factors. For instance, the complex interactions between bathymetry and sea surface temperature (Yen et al. 2004, Hamer et al. 2009, Paiva et al. 2010) and other physical and biological processes promoting growth and retention of plankton, leading to higher productivity zones (Haury et al. 1978) and concentrations of prey. Yet factors intrinsic to the individual are also paramount in determining foraging performance and cannot be easily dissociated from extrinsic factors (Zimmer et al. 2011). Sex-specific foraging strategies in seabirds often result from intra-specific competition (Lewis et al. 2001, Phillips et al. 2004), sex-specific nutrient requirements (Lewis et al. 2002, Zavalaga et al. 2007) and/or sex-specific foraging abilities (Kato et al. 1999). But body mass and size also play important roles in dimorphic species (Kato et al. 1999, Velando and Alonso-Alvarez 2003, Lewis et al. 2005, Weimerskirch et al. 2009), with the larger sex being more competitive and dominant (reviewed for seabirds by Lewis et al. 2002). Flight performance is strongly constrained by body mass and size. As an illustration, flapping flight has been associated with high energy expenditure (Pennycuick 1989), which increases substantially with body mass (Pennycuick 1972), whereas gliding and soaring are considered to be energetically efficient flight methods (Norberg 1986). The energetic costs of locomotion are therefore likely to be an especially strong selecting force for efficient flight (Ballance 1995). This will be particularly important during the high-energy demanding chick-rearing period in which parents must sustain their chicks in addition to themselves.

Some seabird species adopt a bimodal foraging strategy during this high-energy demanding period (Chaurand and Weimerskirch 1994, Weimerskirch 1998, Weimerskirch and Cherel 1998, Sommerfeld and Hennicke 2010, Saraux et al. 2011). During short foraging trips, individuals forage near the colony to maintain a high feeding frequency of the chick at the expense of their own body mass, while longer foraging trips to more distant, but highly productive, areas are for self-provisioning (Granadeiro et al. 1998, Thalmann et al. 2009). In environments where resources are abundant, or in other seabird taxa (Lewis et al. 2004, Zavalaga et al. 2011), this alternation strategy disappears (Phillips et al. 2009).

Adult body mass further plays an important role in the regulation of parental effort (Chastel et al. 1995, Erikstad et al. 1997, Dearborn 2001). Sex-specific foraging strategies in species with reversed sexual dimorphism (RSD) often occur during the chick-rearing period as a result of differing parental roles – larger females exhibit a flexible breeding investment under regulation of their own body mass, whereas males present a fixed investment (Guerra and Drummond 1995, Velando and Alonso-Alvarez 2003, Weimerskirch et al. 2009b).

Deeper dives and consumption of different types and/or sizes of prey were found in individuals of the larger sex (Kato et al. 1999, Zavalaga et al. 2007), suggesting size-specific, vertical feeding niche segregation. Plunge-diving seabirds, such as Sulidae (gannets and boobies) use the momentum of their fall to attain depth (Ashmole 1971, Nelson 1978, but see Ropert-Coudert et al. 2004b, 2009 for alternative hunting strategies and use of wing flapping underwater). As such, heavy individuals are thought to attain deeper depths during plunge-diving from passive mechanisms mediated by gravitational acceleration (Ropert-Coudert et al. 2004b). Accordingly, the larger sex may be advantaged during diving (Kato et al. 1999, Lewis et al. 2005, Zavalaga et al. 2007), while the smaller sex may have higher flight efficiency in light winds (Shaffer et al. 2001). Consequently, the larger sex may dominate intra-specific competition near the colony, forcing the smaller and thus less competitive sex to use its higher flying efficiency to forage in more distant grounds. Such a case has for instance been found in northern giant petrels *Macronectes halli* (Gonzales-Solis et al. 2000) and brown boobies *Sula leucogaster* (Gilardi 1992).

Surprisingly, although sex-specific and species-specific foraging strategies due to body mass and size differences have been found in several species, studies investigating the effects of individual differences in body mass and size within the same sex still remain scarce (but see Kato et al. 2008, Zimmer et al. 2011). This is an important component of intrinsic influences on behaviour as it helps to disentangle the potentially confounding effects of body mass, size and sex.

We investigated this in masked boobies *Sula dactylatra* breeding on Phillip Island (Norfolk Island Group) in the southwestern Pacific. Masked boobies are the largest of all boobies and display a moderate RSD (Nelson 1978). The aim of the study was to examine the effects of individual differences in body mass and size within the same sex on four key foraging parameters: 1) foraging trip duration, 2) flight time spent flapping, 3) foraging time spent sitting on the water surface, and 4) dive depth and dive rate (dives h^{-1}).

Methods

Study site and species

Masked boobies were studied on Phillip Island (29°02’S, 167°57’E) in the south-west Pacific Ocean. Phillip Island (190 ha) is part of the Australian Norfolk Island Group, located approximately 1670 km north-east of Sydney, Australia and 1070 km north-west of Auckland, New Zealand. The study took place between 12 February 2010 and 3 March 2010 and 27 October 2010 and 10 November 2010, corresponding to late and early breeding seasons, respectively.

Approximately 300 masked booby pairs breed on Phillip Island (Garnett et al. 2010, Priddel et al. 2010). Females lay two eggs, but generally only one chick is reared through obligate siblicide (Dorward 1962). All individuals in the present study were rearing chicks between three and 11 weeks of age during February and March 2010 and between two and seven weeks of age during October and November 2010.

Data loggers and deployment

Activity patterns and time budgets of masked boobies were studied using cylindrical, four channel data-loggers (53 × 15 mm, 17 g), which simultaneously recorded depth (1 Hz), temperature (1 Hz) and acceleration (16 Hz) along two axes. The relative accuracy for the depth sensor was 0.1 m. The loggers contain an acceleration sensor measuring both dynamic (vibration) and static (gravity) accelerations. The depth-acceleration loggers were attached using TESA tape, positioned underneath three central tail feathers in order to measure acceleration along two axes: surging acceleration along the longitudinal body axis and heaving acceleration dorso-ventrally.

Individuals were simultaneously equipped with GPS data loggers (46 × 32 mm, 20 g) to study foraging movements. GPS loggers were attached on top of three central tail feathers using TESA tape. Total attachment weight including tape was approximately 55 g (range 45–60 g, n = 27), corresponding to 2.2% and 2.7% of female and male mean body mass respectively. This was below the generally accepted 3% of mean body mass threshold for attachment of GPS loggers (Phillips et al. 2003, Wilson and McMahon 2006, but see Vandenabeele et al. 2012).

Adults were sexed by voice and by measurements: males have a distinctive higher pitched voice than females and are the smaller bird within a pair (Nelson 1978). Either the female or the male of a chick-rearing pair was captured with a noose-pole and weighed using a spring balance (maximum deviation ± 0.3% of load). Prior to deployments, nests were monitored throughout the day (or during the previous day, if deployments occurred at night). This maximised our chances of attaching data loggers on individuals that spent the day at the nest and were thus likely to depart on a foraging trip and, to avoid potential biased body masses due to full stomach contents. Birds were colour-marked on the breast with a green or blue biological dyer (sheep crayon) at first capture. Non-banded adults were banded with a metal leg band. After attachment of the data loggers, individuals were released immediately onto their nests. Loggers were retrieved after 1–4 d, recording 1–4 successive foraging trips. Wing length, an index for body size (see Weimerskirch et al. 2009a for the use of wing length as an index of body size in brown and blue-footed boobies *Sola nebouxii*), was

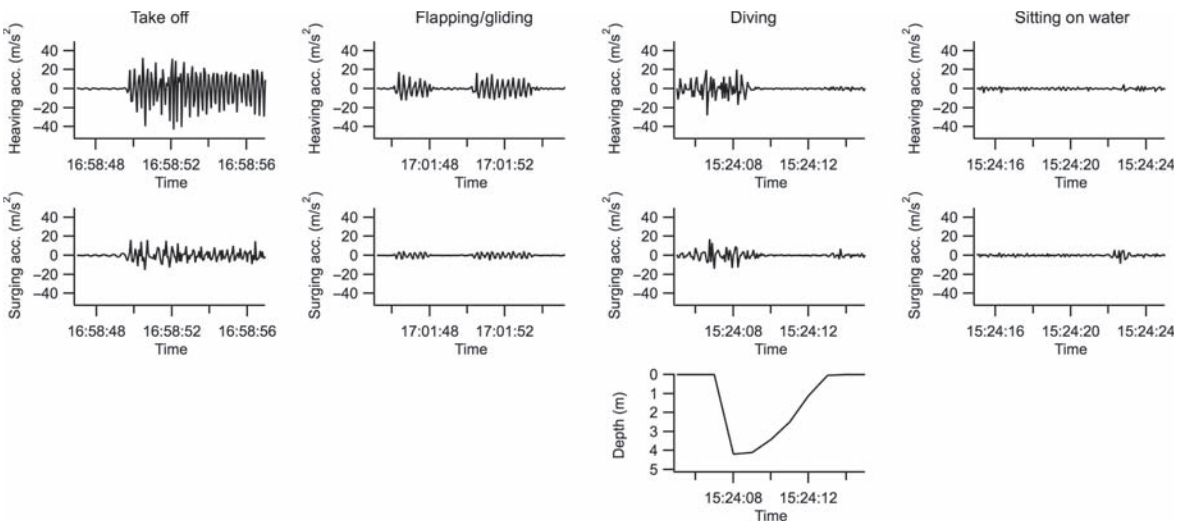

Figure 1. Dive depth, high-frequency components of heaving and surging acceleration data recorded for take-off, flapping and gliding flight, plunge-diving and sitting on the water surface in a masked booby.

measured as the distance from the distal portion of the carpus to the tip of the longest primary feather, using a ruler to the nearest 1 mm, upon retrieval of the data loggers. To minimise disturbance and possible device-related effects, only one adult of a pair was instrumented with data loggers and individuals were never studied twice within or between seasons. No nests were deserted during the entire duration of the study.

Data analysis

Depth-acceleration data were analysed with IGOR Pro 6.21. First, the component of the gravity acceleration along the surging and heaving axes was separated from the high-frequency component resulting from wing beat activity, using a low-pass filter (Tanaka et al. 2001). Next, the following types of behaviour were identified from the depth-acceleration logger signals: 1) on land, 2) take-off, 3) in flight (flapping/gliding), 4) sitting on the water surface and 5) plunge-diving (Fig. 1). Diving threshold was set to 0.2 m. Flapping activity within each flight session was identified as an oscillating pattern present simultaneously on both axes, with each propulsive stroke recorded on the heaving axis resulting in a forward acceleration recorded on the surging axis (Fig. 1, see Ropert-Coudert et al. 2004b for details). Birds were considered to be gliding when these distinctive oscillation patterns within a flight bout were absent. On-land behaviours were excluded from the analysis.

Flight time was calculated as the sum of the total time spent flapping and gliding per foraging time (total trip duration minus nocturnal time). The proportion of flight time spent flapping was accordingly the amount of time spent flapping within the total flight time. The proportion of time spent sitting on the water was the time sitting at the water surface within the total foraging time. Dive rates were calculated as the total number of dives within an hour of the total foraging time (dives h^{-1}). For statistical analysis, foraging time, foraging trip duration (used as a continuous variable), body mass, wing length and dive rates were $\log_{10}$ transformed. Proportion values were logit transformed.

Statistical analysis

All statistical analyses were performed using R ver. 2.15.0. Non-linear mixed models (Faraway 2006) were applied using the function lme in R package nlme (ver. 3.1-104, Pinheiro et al. 2012), with respective foraging parameters as response variables and interactions sex × body mass and sex × wing length as fixed effects to account for individual differences in body mass and wing length within the same sex. As several foraging trips were recorded for the same individual, and data were collected over two breeding seasons, bird ID nested within season was included as a random effect to account for pseudoreplication. When effects of interactions were not significant, we tested whether any of the single terms sex, body mass or wing length had a significant effect on respective foraging parameters. We further tested, in two separate models, whether the interaction sex × flapping × body mass and sex × sitting × body mass had an effect on foraging time.

To test the influence of single terms or interactions in a model, the function drop1 in R was used. This function tests every term in the model as if it is the last entering the model, so that it omits every term in the model in turn. The reduced model was then compared with the full model using a likelihood ratio test under 1 degree of freedom (test Chisq in R). Before drawing inference, model assumptions were checked following Crawley (2007).

Significant interactions were plotted using function allEffects of package effects in R (Fox et al. 2012). From these interaction plots, we drew inference about the directions of the significant interactions. Correlations were calculated using Spearman's rank correlation or Pearson's product moment correlation. To test for body mass and wing length differences between sexes, a Welch's t-test was

Table 1. Body mass and wing length of male and female masked boobies from Phillip Island. Values are presented as mean ± SD. Ranges in parentheses. Sample sizes (n).

	Males	n	Females	n	Welch's t-test
Body mass (g)	2059.1 ± 225.8 (1685–2465)	17	2470.2 ± 220.2 (2120–2870)	10	$t = 7.13$, $p < 0.001$
Wing length (mm)	460.3 ± 6.0 (443–474)	17	469.5 ± 5.3 (460–479)	10	$t = 6.05$, $p < 0.001$

performed. All tests were two-tailed, with a significance level of $p < 0.05$. Mean (SD) results are reported.

Results

A total of 61 foraging trips from 27 individuals (17 males and 10 females) containing both position and activity data were recorded. Of the 27 birds, three females and four males stayed overnight at sea (one male spent two nights at sea). Three of these foraging trips were excluded from the data analysis because battery-exhaustion of the depth-acceleration loggers occurred before the birds returned to the colony. Our sample size was too small to test whether birds staying overnight at sea differed from birds that made single-day trips, therefore the nocturnal portions of the overnight trips were excluded (birds spent most of the nocturnal period sitting on the water surface for long hours without any significant activity). Overnight trips – without the nocturnal period – were subsequently pooled with single-day trips. Consequently, foraging time as used in the present study corresponded to the total foraging trip duration minus the nocturnal period.

Morphological comparison

Females were on average 16.6% heavier than males, but only 2% larger in terms of wing length (Table 1). Mean body mass and wing length differed significantly between males and females (Welch's t-test $t = 7.13$, $DF = 45.21$, $p < 0.001$ and $t = 6.05$, $DF = 43.45$, $p < 0.001$, respectively). Body mass and wing length showed a significant positive correlation in males (Spearman $r_s = 0.50$, $S = 5732.61$, $p = 0.001$, $n = 17$), but not in females (Spearman $r_s = -0.39$, $S = 810.01$, $p = 0.088$, $n = 10$).

Foraging trip duration and range

Both mean foraging trip duration and total distance travelled were highly variable, but not significantly different between males and females ($\chi^2_1 = 1.93$, $p = 0.165$, $\chi^2_1 = 2.92$, $p = 0.093$, respectively) (Table 2). Mean maximum distances from the colony were greater in females than males (Table 2), but the difference was not significant ($\chi^2_1 = 1.76$, $p = 0.185$). Not surprisingly, foraging trip duration was strongly and positively correlated with both the total distance travelled (Pearson $r = 0.91$, $t_{56} = 16.11$, $p < 0.001$) and the maximum distance from the colony (Pearson $r = 0.86$, $t_{56} = 12.62$, $p < 0.001$). Foraging movements of both sexes showed considerable overlap (Fig. 2).

The interaction sex × body mass on foraging trip duration was significant ($\chi^2_1 = 4.46$, $p = 0.034$), indicating that the effect of sex on foraging trip duration changed with individual body mass (Table 3). Heavier females conducted shorter foraging trips, while lighter females performed longer foraging trips (Fig. 3). Males showed a weak and opposing effect, with heavier males undertaking longer foraging trips and lighter males shorter foraging trips (Fig. 3). The interaction sex × wing length had no effect on foraging trip duration ($\chi^2_1 = 2.61$, $p = 0.106$), as was also the case for the single term wing length ($\chi^2_1 = 0.72$, $p = 0.393$).

Flight

The percentage of foraging time spent in flight and the total flight time spent flapping was similar between males and females (Table 2). The two-way interaction sex × bird mass was highly significant ($\chi^2_1 = 11.05$, $p < 0.001$), indicating that the effect of sex on the flight time spent flapping changed with individuals' body mass (Fig. 3, Table 3). Heavier females spent more time flapping than lighter females, whereas the opposite was observed in males: heavier males spent less time flapping than lighter males (Fig. 3). The interaction sex × wing length, as well as the single term wing length did not significantly improve the fit of the models ($\chi^2_1 = 0.09$, $p = 0.758$ and $\chi^2_1 = 0.10$, $p = 0.744$, respectively), indicating that wing length did not affect the amount of time individuals spent flapping (Table 3).

The effect of the three-way interaction sex × flapping × body mass on foraging time was significant ($\chi^2_1 = 4.81$, $p = 0.028$), indicating that heavier females spent more time flapping during shorter foraging trips than lighter females during longer foraging trips, but this effect was not evident in males.

Table 2. Foraging parameters of male and female masked boobies during chick-rearing. Values are presented as mean ± SD. Ranges in parentheses. Sample sizes (n).

Foraging parameters	Males	n	Females	n
Trip duration (h)	7.03 ± 8.16 (0.15–41.79)	41	8.18 ± 7.61 (0.52–37.19)	20
Total distance travelled (km)	148.6 ± 143.4 (3.2–577.7)	39	213.9 ± 174.0 (10.4–602.3)	19
Maximum distance from colony (km)	57.9 ± 54.9 (2.2–226.7)	39	77.6 ± 64.4 (4.5–230.8)	19
Foraging time spent in flight (%)	67.9 ± 17.0 (19.9–95.9)	41	63.5 ± 17.9 (13.9–83.9)	20
Flight time spent flapping (%)	57.5 ± 8.3 (38.8 78.7)	41	48.3 ± 12.9 (20.9–71.5)	20
Foraging time spent sitting on water (%)	28.0 ± 15.6 (2.8–62.6)	41	34.7 ± 18.1 (12.2–84.8)	20
Dive depth (m)	2.5 ± 1.4 (0.2–6.0)	540	2.9 ± 1.4 (0.2–6.3)	256
Dive rate (dives^{-h})	0.88 ± 1.0 (0.2–4.7)	35	1.4 ± 1.9 (0.2–6.5)	19

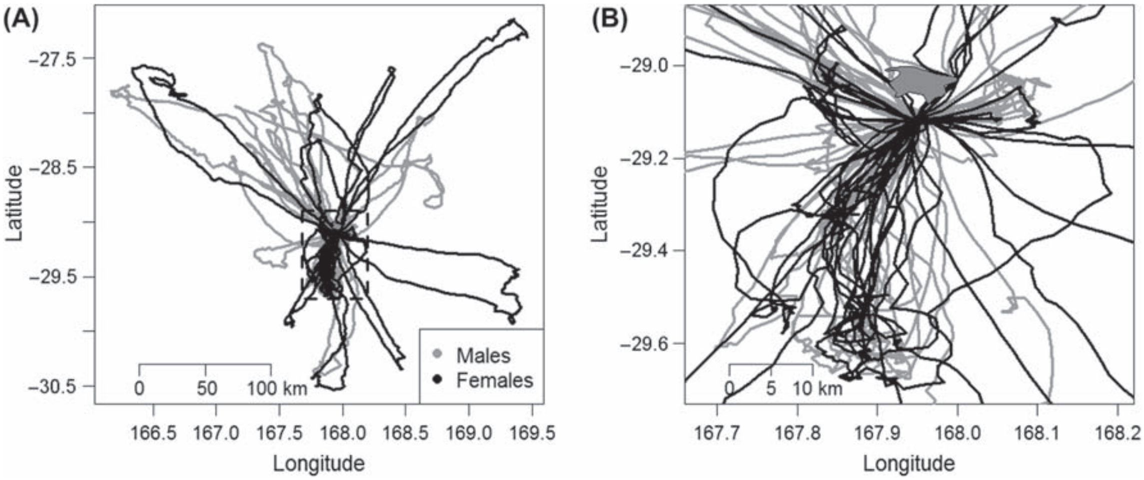

Figure 2. Foraging movements of male and female masked boobies recorded by GPS at 4 min intervals. (A) All foraging movements, and (B) short foraging movements within the black rectangle. Black lines correspond to female tracks, grey lines to males. Dark grey area represents Norfolk Island, Australia.

Resting at the water surface

Males and females spent similar proportions of their total foraging time sitting at the water surface (Table 2). The two-way interaction sex × body mass was statistically significant ($\chi^2_1 = 8.40$, $p = 0.003$) (Table 3). Heavier females spent less time sitting at the water surface than lighter females, while heavier males spent more time sitting at the water surface than their lighter counterparts (Fig. 3). Again, sex × wing length or the single term wing length were not significant ($\chi^2_1 = 1.44$, $p = 0.229$ and $\chi^2_1 = 0.66$, $p = 0.414$, respectively). Surprisingly, the three-way interaction sex × sitting × body mass had no effect on foraging time ($\chi^2_1 = 0.15$, $p = 0.697$), indicating that the time heavier or lighter individuals spent resting on the water was similar in both sexes during shorter trips in close proximity to the colony, as well as in longer, more distant trips.

Dive behaviour

A total of 796 dives were recorded. Overall, diving accounted for less than 1% of the time budget of masked boobies. Dive depth was not affected by the two-way interactions sex × body mass or sex × wing length ($\chi^2_1 = 0.19$, $p = 0.662$ and $\chi^2_1 = 0.01$, $p = 0.904$, respectively) (Table 3). The single term wing length did not influence dive depth ($\chi^2_1 = 0.37$, $p = 0.548$). However, the difference of distribution of diving depths was statistically significant between sexes ($\chi^2_1 = 6.31$, $p = 0.012$), with greater depths more common in females than in males (Fig. 4).

Dive rates were not explained significantly better by the interaction sex × body mass ($\chi^2_1 = 0.25$, $p = 0.614$) or sex × wing length ($\chi^2_1 = 0.24$, $p = 0.624$) (Table 3) or wing length ($\chi^2_1 = 1.84$, $p = 0.174$) and did not differ between sexes ($\chi^2_1 = 1.52$, $p = 0.218$) (Table 2).

Discussion

This study examined the effects of individual differences in body mass and wing length within and between sexes on several foraging parameters. Most importantly, individual differences in body mass led to contrasting foraging behaviours in males and females. Consequently, the interpretation of sex-specific foraging behaviour would be overall misleading in this species (except in dive depth and dive rate), because the effect of sex changes with individual body mass.

Wing length

Wing length did not affect foraging trip duration or any of the other foraging parameters in our study, either because there was no effect or, more likely, because wing length is not an ideal descriptive parameter for body size in this species, as indicated by the minimal differences within and between sexes. On Palmyra Atoll in the

Table 3. Non-linear mixed models of foraging parameters explained by sex × body mass and sex × wing length. Chi-square under 1 degree of freedom for maximum likelihood analysis (χ^2_1). Akaike's information criterion (AIC). Significant results in bold.

	Foraging trip duration			Flapping			Sitting on the water			Dive depth			Dive rate (dives^{-h})		
	AIC	χ^2_1	p	AIC	χ^2_1	p	AIC	χ^2_1	p	AIC	χ^2_1	p	AIC	χ^2_1	p
Full model	89.82			47.35			172.71			2721.6			57.96		
Sex × body mass	92.28	4.46	**0.034**	56.40	11.05	**< 0.001**	179.11	8.40	**0.003**	2719.8	0.19	0.662	56.21	0.25	0.614
Sex × wing length	92.43	2.61	0.106	45.45	0.09	0.758	172.15	1.44	0.229	2719.7	0.01	0.904	56.19	0.24	0.624

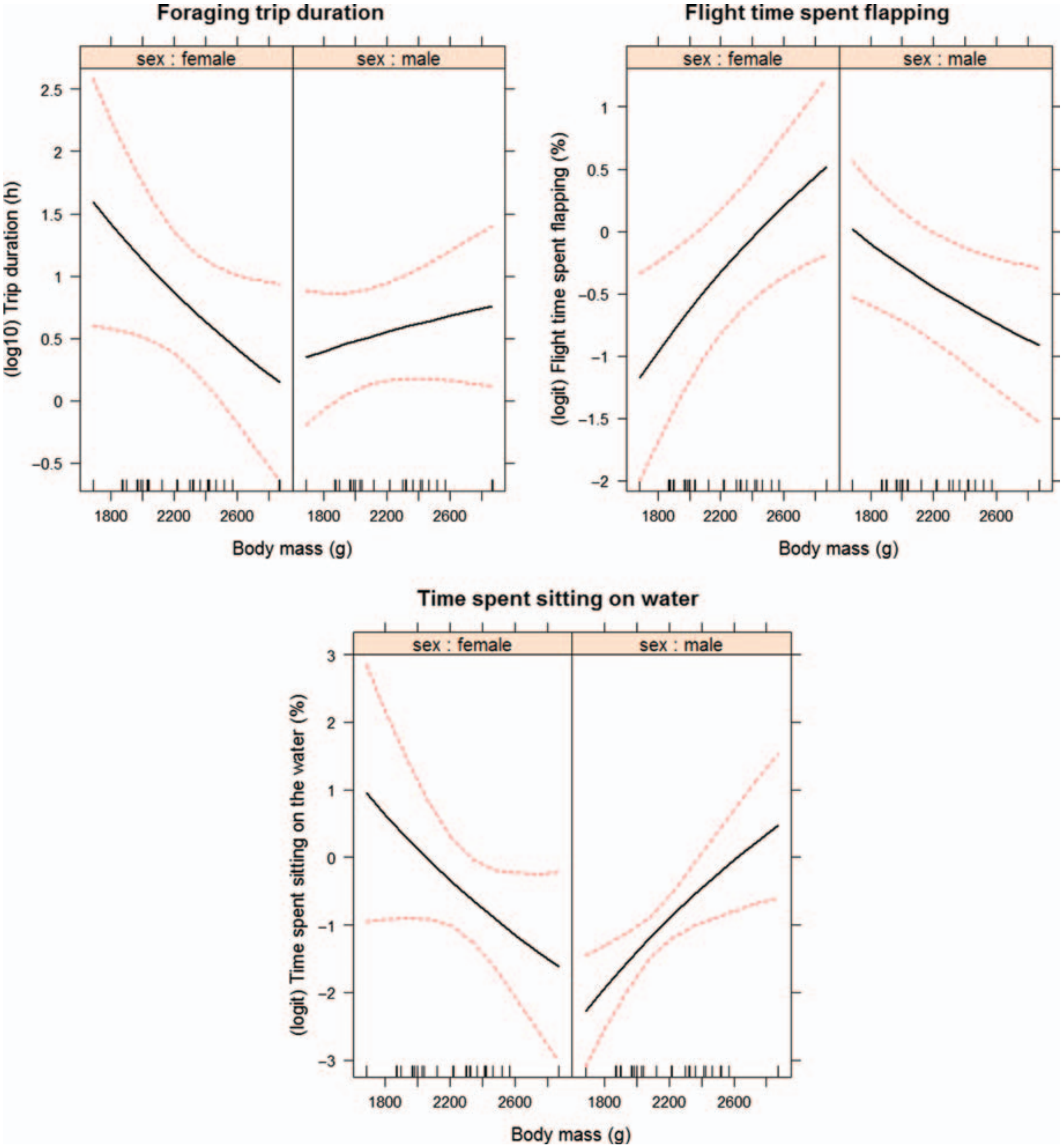

Figure 3. Effect display for the interaction sex × body mass on (top left) $\log_{10}$ foraging trip duration (h), (top right) logit transformed flight time spent flapping (%) and (bottom) foraging time spent sitting on the water surface (%). Red-dashed line represents the 95% pointwise confidence interval around the estimated effect.

Pacific Ocean, male and female masked boobies differed with respect to body mass, as well as head-to-bill length, while culmen and tarsus lengths were similar between sexes (Young et al. 2010). However, wing measurements were not taken in this study. In blue-footed and brown boobies, wing length used as an index of body size, had a significant effect on maximum foraging range and total distance covered, which in turn were further positively correlated with foraging trip duration (Weimerskirch et al. 2009a). However, differences between female and male wing lengths were considerably greater than in our study species (5 and 6% larger in female blue-footed and brown boobies, respectively).

Foraging trip duration and body mass

Lighter individuals within a sex often perform longer foraging trips, reaching more distant foraging grounds due to lower flight costs, as it was found in brown boobies, a species with marked RSD (Lewis et al. 2005). In our study, variations in body mass in males had no evident effect on foraging trip duration, indicating that factors other than lower flight costs led males to determine the duration of their foraging trips. Weimerskirch et al. (2009b), as well as studies on blue-footed boobies (Guerra and Drummond 1995, Velando and Alonso-Alvarez 2003), demonstrated that a division of labour occurred within a

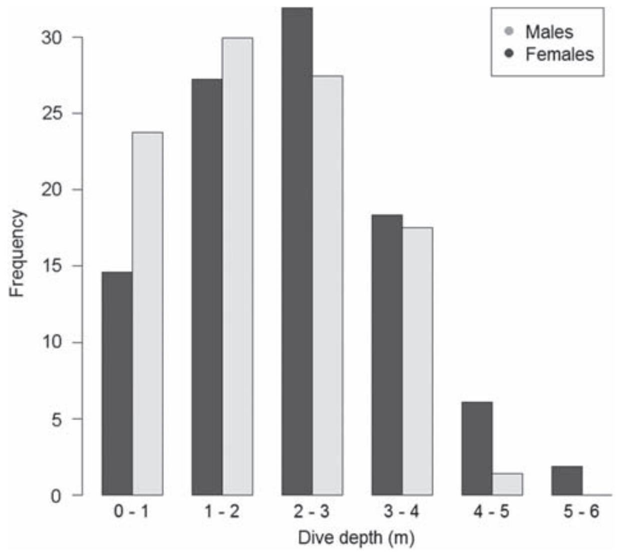

Figure 4. Frequency distribution of diving depths of male and female masked boobies.

pair. Females had a flexible investment under regulation of their own body mass, while males had a fixed investment. In the study from Weimerskirch et al. (2009b), body mass at departure was negatively correlated with foraging trip duration in females, but not in males, as also found in our study. Weimerskirch et al. (2009b) further showed that females were the main provisioning parent of the larger chick, i.e. females delivered larger meal masses (i.e. large quantities of energy) and spent more time at sea foraging. Smaller males in contrast, delivered smaller meal masses, but attended the nest significantly more often, suggesting that males invest more in territory defence and nest guarding (Weimerskirch et al. 2009b). Meal masses delivered by adults were not measured in our study due to logistical constraints, but similar attendance patterns were observed in masked booby pairs breeding on Phillip Island (H. McCoy pers. comm.).

From the above, we consider it very likely that masked boobies at Phillip Island also exhibit such a sex-specific division of labour. Shorter foraging trips undertaken by heavier females are likely to provision the chick at the expense of their body mass. In contrast, lighter females undertake longer foraging trips at greater distances from the colony to replenish their own body reserves. The evident limitation of our results is that we could not weigh the birds after their return from a foraging trip. We unfortunately cannot ascertain whether heavier females lost weight during those shorter foraging trips, closer to the colony, and if lighter females gained weight after longer foraging trips, further away from the island. However, based on results recorded in masked boobies from Clipperton Island (Weimerskirch et al. 2009b), as well as in other seabird species (Clarke 2001, Ropert-Coudert et al. 2004b, Kato et al. 2008, Saraux et al. 2011), this seems a plausible explication.

Two hypotheses have been proposed to explain why foraging trip duration is independent of body stores in males (Weimerskirch et al. 2009b). Firstly, males may have a lower body mass safety margin than the larger females, before reaching a critical threshold under which an individual limits its mortality by deserting its nest or by reducing parental effort (Weimerskirch 1998, Weimerskirch et al. 1999, 2009b). Secondly, males may be unwilling, irrespective of body mass, to invest more in provisioning their chicks as their primary role is nest defence, which is safer and more predictable in terms of energy expenditure than foraging (Weimerskirch et al. 2009b).

Time budget

In birds, flapping costs increase with body mass (Pennycuick 1972). In addition, higher proportions of flapping have been associated with foraging flight, while there is generally a lower proportion of flapping during travelling flight (Ropert-Coudert et al. 2006). Because the functions of the foraging trips were different within females, as well as between sexes, time budget changed according to body mass. Each sex regulated differently their time budget to optimize their foraging trips. Heavier females increase their energy expenditure during shorter trips in order to maintain a high provisioning rate of the chick (i.e. more time spent flapping/foraging and less resting), while lighter females restore their body reserves during longer trips (i.e. less costly flapping flight and more resting periods). Time spent resting at the water surface might further allow lighter adults to digest and, at least to some extent, assimilate already ingested food. These physiological processes would reduce the total mass of food individuals have to carry back, or alternatively, would make space in the stomach for storing more food for their chicks, before returning to the colony (Sibly 1981, Jackson 1992, Guillemette 1994, Ropert-Coudert et al. 2004a).

Foraging trip duration of males, in contrast, is independent of body mass, suggesting that males are not willing to increase chick provisioning under expense of their own body mass. Differences observed between lighter and heavier males might thus be primarily related to an energy-efficient foraging strategy due to prevailing body mass, as we would have expected. Heavier males spent less time flapping (i.e. more time gliding) and more time resting on the water to save energy, while lighter males are already flying in an energy-efficient mode. For example, within the Sulidae, the larger and heavier gannets (Lewis et al. 2004, Ropert-Coudert et al. 2004a, Garthe et al. 2007, Green et al. 2010) spend considerably more time sitting on the water than lighter, smaller boobies (Lewis et al. 2005). Resting for prolonged periods at the water surface probably allows the larger and heavier birds to recover from their energetically more costly flight in comparison with lighter birds (Ropert-Coudert et al. 2004a, Green et al. 2010).

Diving behaviour

Body mass and size differences between sexes and specific nutritional requirements may facilitate feeding niche segregations, including underwater niches, in seabirds with regard to foraging areas and/or diet (Kato et al. 1999, Lewis et al. 2005, Zavalaga et al. 2007). Foraging ranges overlapped extensively between sexes, and body mass, regardless of sex, had no effect on dive depths and rates in masked boobies.

However, females dived on average deeper than males, indicating that factors other than body mass play an important role in dive depth. Such a sex-based segregation may not be so surprising since different dive depths between sexes have also been documented in monomorphic species, such as northern gannets, where females dive deeper than males (Lewis et al. 2002). By diving deeper, females may have access to different prey as shown in blue-footed boobies breeding on Isla Lobos de Tierra (Peru). These females dive deeper and consume larger prey, primarily peruvian anchovies *Engraulis ringens*, than do males (Zavalaga et al. 2007). However, such segregation may not be always observed: male and female blue-footed boobies, breeding on Isla San Ildefonso in the Gulf of California (Mexico), dive to similar depths (Weimerskirch et al. 2009a). In our study, females may dive deeper to catch different prey types or sizes due to differing nutritional requirements compared to males and/or to deliver different prey items to the chick. Although we were not able to collect prey samples here, dietary analyses of masked boobies breeding on Lord Howe Island (Priddel et al. 2005), approximately 900 km southwest of Phillip Island, and of birds breeding on Raine Island in the far northern Great Barrier Reef (Blaber et al. 1995), showed that these birds feed almost exclusively on flying fish (*Cheilopgon* spp. and Exocetidae, respectively), with fewer squid samples (Ommastrephidae). It is therefore reasonable to assume that masked boobies of Phillip Island feed on similar prey. Flying fish generally occur near the surface (Cervigón et al. 1992), but it is unknown whether larger individuals occur at greater depths. The depth at which flying fish occur may further be influenced by the presence of subsurface predators such as tuna or dolphins, which drive them to the surface, where they become accessible to seabirds (Frimodt 1995, Ballance and Pitman 1999). Foraging in association with subsurface predators is an important foraging strategy in tropical seabirds (Ballance et al. 1997, Ballance and Pitman 1999), including masked boobies (Ballance et al. 1997, Mills 1998, Weimerskirch et al. 2008).

Conclusions

Our findings reveal that a combination of differences in individual body masses and parental roles (but the latter was not explicitly tested) influences the foraging behaviour of chick-rearing masked boobies. As such, individual characteristics, such as body mass, are as important as sex-specific foraging strategies. This underlines the need to account for intrinsic factors when examining the effects of extrinsic, environmental factors in sexually dimorphic species.

It has been shown in several species that parents adjust their foraging strategies according to changes in the availability and distribution of prey (Croxall et al. 1999, Burke and Montevecchi 2009, Garthe et al. 2011). However, despite such behavioural adjustments, changes in prey availability often lead to a dramatic decrease in reproductive success (e.g. by 50% in grey-headed albatrosses *Diomedea chrysostoma* and by 90% in black-browed albatrosses *D. melanophris* and gentoo penguins *Pygoscelis papua*; Croxall et al. 1999). This suggests that at least some individuals are restrictive in the increase of their parental effort. For example, the ability of Antarctic petrels *Thalassoica antarctica* to adjust their parental effort depends upon their own body condition (Tveraa et al. 1998). Parents deserted the egg when their body mass reached some critical lower threshold (Tveraa et al. 1997). In this context, effects of changes in the temporal and spatial availability and distribution of prey could have different effects upon individuals of varying body masses within the same sex.

For example, in species exhibiting RSD and a division of labour, heavier individuals with a fixed breeding investment (e.g. male masked and brown boobies) may be unable or unwilling to modify their time budgets at sea (e.g. spend more time in flight/flapping in search of food and less time resting) than their lighter counterparts. The latter, on the other hand, may have a lower critical body mass threshold. Conversely, individuals with a flexible breeding investment (e.g. female masked and brown boobies) may cope better with changes in food availability. Nevertheless, they may be unable to maintain their role as the main parent provisioning the chick once a critical lower body mass threshold is reached and/or males abandon offspring. However, these hypotheses need to be confirmed in further studies. Studies investigating the effects of individual body mass differences within a sex in species where no division of labour occurs would further help to disentangle the confounding effects of body mass and sex on foraging strategies.

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