Sex-specific foraging behaviour in tropical boobies: does size matter?

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Sex differences in the foraging behaviour of adults have been observed in a number of sexually size-dimorphic birds, and the usual inference has been that these sex-specific differences are driven primarily by differences in body size. An alternative explanation is that foraging differences result from sex differences unrelated to size, such as sex-specific nutritional requirements. To examine these alternative hypotheses, the foraging behaviour of parents was compared between two sympatric and congeneric species of seabird, the Brown Booby *Sula leucogaster*, which is highly sexually size-dimorphic (females 38% larger) and the Red-footed Booby *S. sula*, in which sex differences in body size are less marked (females 15% larger). Using temperature and depth loggers, we found that there were highly significant differences in the foraging trip durations and diving behaviour of male and female Brown Boobies. These sex differences were less marked in Red-footed Boobies. Thus, our interspecies comparison revealed that the magnitude of the difference between the sexes matched the sexual size dimorphism of the species, providing support for the size hypothesis.

Sex differences in foraging behaviour have been recorded in a number of sexually size-dimorphic birds, including passerines (Morse 1968, Gosler 1987, Aho *et al.* 1997), raptors (Newton 1979, Marquiss & Newton 1982) and seabirds (see Lewis *et al.* 2002). Differences in dominance, competitive ability, foraging efficiency and flight efficiency have been recorded, and the usual inference is that these differences are mediated through size (Weimerskirch *et al.* 1997, Gonzalez-Solis *et al.* 2000, Shaffer *et al.* 2001, Phillips *et al.* 2004). Thus, in seabirds, the larger sex may dominate intraspecific interactions close to the colony, forcing the smaller, less competitive sex to travel further away for food, as demonstrated in Giant Petrels *Macronectes* spp. (Gonzalez-Solis *et al.* 2000). Alternatively, the smaller sex may have a higher foraging and flight efficiency (Shaffer *et al.* 2001), and as such be able to use suitable wind currents to travel to more distant foraging areas that are

more profitable either due to prey density (Phillips *et al.* 2004) or due to a reduced level of intraspecific competition for food further away from the colony (see Lewis *et al.* 2001).

Foraging differences between the sexes may have been important in the evolution of size dimorphism (Andersson & Norberg 1981, Mueller 1986, Hedrick & Temeles 1989, Shine 1989, Mueller 1990). Large size may produce an advantage during foraging in one sex and/or small size an advantage during foraging in the other sex (Hedrick & Temeles 1989). However, sex differences in foraging behaviour have also been observed in species with no sexual size dimorphism, e.g. Manx Shearwaters *Puffinus puffinus* (Gray & Hamer 2001) and Northern Gannets *Morus bassanus* (Lewis *et al.* 2002). This suggests that differences in foraging behaviour of the sexes may arise independently of sexual dimorphism in body size, and as such may have little to do with the maintenance of size dimorphism.

An examination of two closely related sympatric species, which differ in their degree of sexual size

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dimorphism, is a useful approach to test the size hypothesis, in which sex-specific foraging behaviour is predicted to match the size dimorphism of the species, and the sex hypothesis, in which differences in foraging behaviour between the sexes do not match the size dimorphism of the species. We compared the foraging behaviour of two sympatric species of tropical booby (Pelecaniformes), the Brown Booby *Sula leucogaster*, which is markedly reverse size-dimorphic (females were 38% heavier than males in this study) and the Red-footed Booby *S. sula*, which is considerably less size dimorphic (females were 14% heavier than males in this study). Both species feed by plunge diving from the air, but it is not currently known whether there are any sex differences in prey type or prey size in either species; the main prey of boobies in this region are flying fish (Exocetidae) and squid (Omnastrephidae) (Schreiber *et al.* 1996, Schreiber & Norton 2002). We compared trip duration (a proxy for foraging range in other Sulid species; Hamer *et al.* 2000, 2001), dive rate (a measure of prey encounter rate in a plunge-diving species) and the proportion of trip time spent flying (a measure of prey search rate) of males and females in the two species.

In order to establish an effect of size, we tested the following two predictions: (1) owing to their larger size, female boobies will have a shorter trip duration than males, because they are able to dominate the foraging grounds close to the colony, thereby forcing the males to forage further away (Gonzalez-Solis *et al.* 2000). If the closer grounds are more productive, which is likely if they are dominating a resource, we predict a higher dive rate and lower proportion of time spent flying (searching for prey) in females. (2) Because of their small size, males have reduced flight costs (Shaffer *et al.* 2001), enabling them to access a broader range of habitats from which to select the most profitable areas, either due to higher prey densities or lower intraspecific competition, giving them access to less disturbed prey patches (Lewis *et al.* 2001). Thus, we would predict a higher trip duration in males, associated with lower flight costs, and a higher dive rate, because of an increased probability of prey encounter. Within both predictions, sex differences would be more apparent in Brown than in Red-footed Boobies, if size is more important than sex. If neither of the above predictions is upheld and sex differences in trip duration, dive rate and/or prey search rate are equally apparent in both species, it suggests that differences in the foraging behaviour are related to sex and not to size. Finally, if there are no effects of size or sex on any aspect of foraging behaviour measured then other factors are important.

METHODS

Study site

The study was carried out between 4 and 23 March 2003 at a colony of *c.* 450 breeding pairs of Brown Boobies and *c.* 1400 breeding pairs of Red-footed Boobies on Johnston Atoll (16°45′N, 169°30′W) in the central Pacific Ocean. Sunrise and sunset occurred at *c.* 07:30 and 19:30 h Pacific Time, respectively.

Temperature and depth loggers

We captured 56 incubating adults (25 Brown Boobies and 31 Red-footed Boobies) at the nest-site using a 2-m-long pole and net, and attached a rapid-response temperature and pressure logger (PreciTD, Earth & Ocean Technologies, Kiel, Germany) to the tail (see Daunt *et al.* 2003). We taped the logger to the underside of the four central rectrices, close to the base of the tail, using waterproof tape (Tesa AG, Hamburg, Germany). The logger dimensions are: length 80 mm, diameter 19 mm, maximum height 22 mm; mass 21–23 g (including the tape, *c.* < 2.5% of body mass, using the smallest body mass recorded in this study). Each bird was marked with a non-toxic dye that lasts for a few weeks, in order that it could be identified subsequently. Attachment of loggers took less than 5 min and after release every bird returned to the clutch immediately. The birds were recaptured at the nest in the same way and the device removed after their absence had been noted during twice-daily checks (*c.* 08:00 and 18:00 h), usually after 1–2 days. Culmen length was measured to the nearest 0.1 mm using Vernier callipers, wing length to the nearest 1 mm using a stopped rule and body mass to the nearest 10 g using a spring balance. The sexes of Red-footed Boobies cannot be determined reliably in the field, and so 3–4 body feathers were removed from each bird, for subsequent sexing based on analysis of two CHD I genes (Griffiths *et al.* 1996). These procedures again took fewer than 5 min and after release all birds again resumed normal incubation behaviour.

Temperature resolution of the PreciTDs was *c.* 0.005 °K (measurement uncertainty in the calibrated device is 0.03 °K), with a range of 15–35 °C. Two series of devices were used with pressure resolution of 1.5 and 2.5 mbar, corresponding to
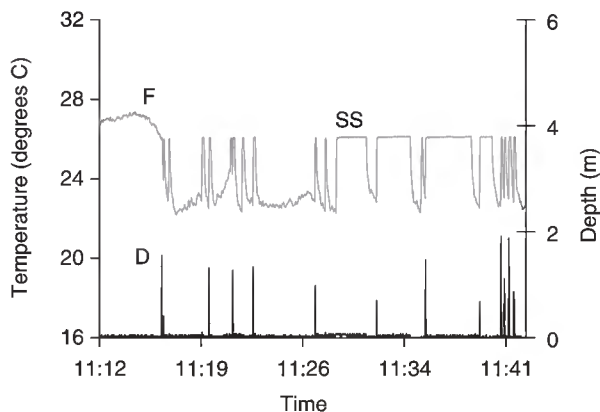
Figure 1. Data recorded from a temperature and pressure logger attached to a booby. Temperature (°C) is shown by the upper line and depth (m) is shown by the lower line. This trace illustrates how the different activities recorded during a typical foraging trip are distinguished where F = flying; SS = sea surface and D = diving.

c. 1.5 and 2.5 cm of the water column (measurement uncertainty 10–15 mbar, range 0–5 bar and 0–10 bar above atmospheric pressure, which corresponds to 0–50 and 0–100 m depth, respectively). The sampling interval was set at 1 s in order to record even the rapid shallow plunges that boobies are known to carry out (E.A.S. pers. obs.).

Logger analyses

Data were downloaded and analysed using Multi-trace (Jensen Software System, Kiel, Germany). Figure 1 shows a sample of data obtained from a Brown Booby. Resting on the sea surface was characterized by a very stable body temperature around *c*. 26 °C, a value that closely corresponds to sea-surface temperature in this region (http://www.cpc.noaa.gov/data/indices). Flight was characterized by a more variable temperature signal and dives by positive pressure signals. We set the threshold depth for a dive at 0.3 m. Thus by identifying when a change in signal occurred we were able to estimate (1) trip duration, (2) the number (and depth) of dives, (3) time spent flying and (4) time spent sitting on the sea surface, while on a trip. Time spent diving during a trip only represented *c*. 0.3% of total trip time, and so we only examined time spent flying during a trip because time spent on the sea surface approximated to the reciprocal of time spent flying, and is therefore non-independent. For eight birds, it was not possible to determine the total time spent flying and sitting on the sea surface because the

temperature traces became unstable as the trip progressed. However, it was possible to use the pressure data to determine the number and depth of dives in these cases, and for four of these individuals we could also determine when the trip began and ended, and thus determine trip duration.

Statistical analyses

In 13 cases, more than one trip was recorded per bird. Therefore, in order to prevent pseudoreplication, trip duration, proportion (arcsine transformed) of time spent flying and sitting on the sea surface while on a trip, dive rate (dives per hour on a trip) and dive depth were compared between male and female Brown and Red-footed Boobies by fitting linear mixed models using residual maximum likelihood analyses (REML), including bird identity as a random factor (Patterson & Thompson 1971). We also included mass as a covariate in all analyses, to investigate whether individual mass was important, after controlling for sex. Sex differences matching the dimorphism in size in Brown and Red-footed Boobies would support the size hypothesis, while effects of sex in both species not matching the size differences would support the sex hypothesis. In all REML models, the significance of each variable or interaction was determined by comparing Wald statistics with chi-squared percentiles (Elston *et al.* 2001). Results are given as means ± sd unless otherwise indicated.

RESULTS

Body size and mass

Table 1 shows the sex differences in culmen length, wing length and mass for Brown and Red-footed Boobies. Females of both Brown and Red-footed Boobies are larger than males, although the extent of sexual size dimorphism is much greater in Brown Boobies (38%) than in Red-footed Boobies (14%).

Foraging behaviour

Male Brown Boobies made significantly longer trips than females (Fig. 2, $\chi^2 = 7.15$, *df* = 1, *P* = 0.007), but this was not so in the Red-footed Booby (Fig. 2, $\chi^2 = 0.17$, *df* = 1, *P* = 0.7). Trip duration was also related negatively to mass in the Brown Booby (Fig. 3, $\chi^2 = 8.48$, *df* = 1, *P* = 0.004), but there was no relationship between mass and trip duration in

Table 1. Comparison of culmen, wing and mass for male and female Brown and Red-footed Boobies using an independent samples t-test for each species. Data shown as mean ± sd and significance levels indicated as ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$.

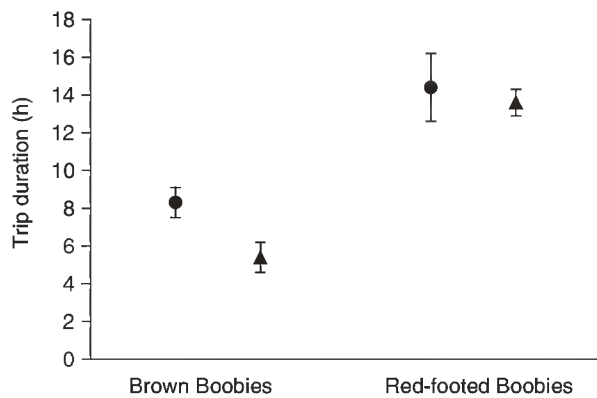|	Brown Booby				Red-footed Booby			
	Male ($n = 12$)	Female ($n = 13$)	t	P	Male ($n = 16$)	Female ($n = 15$)	t	P
Culmen (mm)	97 ± 3	103 ± 3	−4.9	***	81 ± 3	84 ± 4	−3.1	**
Wing (cm)	415 ± 11	427 ± 11	−2.9	**	405 ± 10	417 ± 11	−2.9	**
Mass (g)	1077 ± 78	1491 ± 76	−13.4	***	1035 ± 70	1182 ± 86	−5.6	***

Figure 2. Mean (± se) foraging trip duration (h) of Brown Boobies (males: circles, $n = 11$; females: triangles, $n = 12$) and Red-footed Boobies (males: circles, $n = 16$; females: triangles, $n = 13$).
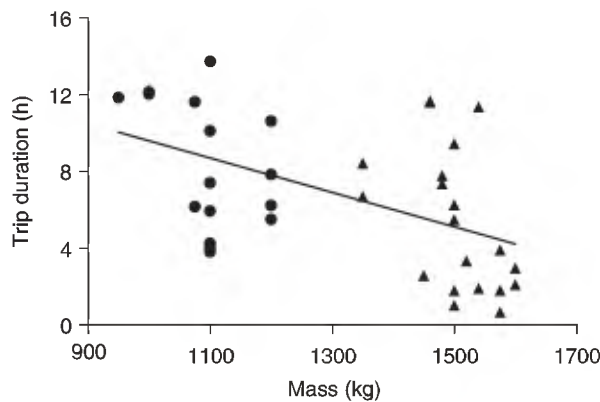

Figure 4. Mean (± se) proportion of foraging trip time (h) spent flying and sitting on the sea surface of male (grey bars) and female (white bars) Brown Boobies (males: $n = 10$; females: $n = 11$) and Red-footed Boobies (males: $n = 16$; females: $n = 11$).

Figure 3. The relationship between foraging trip duration (h) and mass (kg) of Brown Boobies (males: circles, $n = 11$; females: triangles, $n = 12$).

Figure 5. Mean (± se) dive rate per trip (dives per hour) of Brown Boobies (males: circles, $n = 11$; females: triangles, $n = 12$) and Red-footed Boobies (males: circles, $n = 16$; females: triangles, $n = 13$).

the Red-footed Booby ($\chi^2 = 0.87$, $df = 1$, $P = 0.4$). There were no sex differences in the proportion of time spent flying (and consequently sitting on the sea surface) in either the Brown Booby (Fig. 4, $\chi^2 = 0.55$, $df = 1$, $P = 0.5$) or the Red-footed Booby (Fig. 4, $\chi^2 = 0.12$, $df = 1$, $P = 0.7$). There was also no
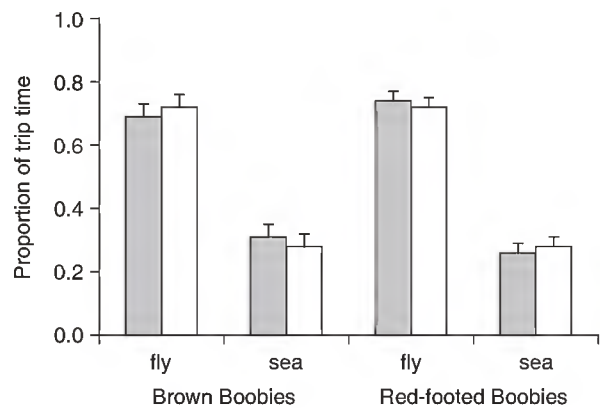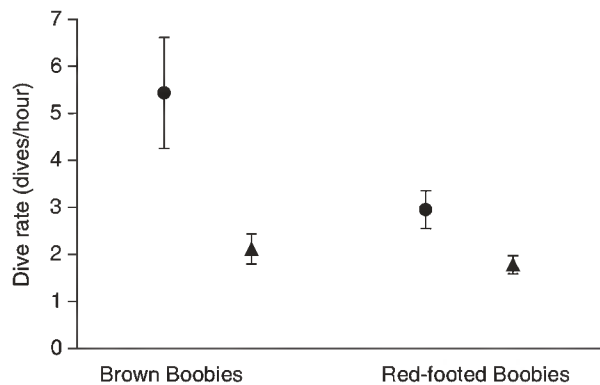
relationship between time spent flying and individual mass in either the Brown Booby ($\chi^2 = 0.74$, $df = 1$, $P = 0.4$) or the Red-footed Booby ($\chi^2 = 0.83$, $df = 1$, $P = 0.4$). However, male Brown Boobies had a significantly higher dive rate (dives per hour on a trip) than females (Fig. 5, $\chi^2 = 6.53$, $df = 1$, $P =$
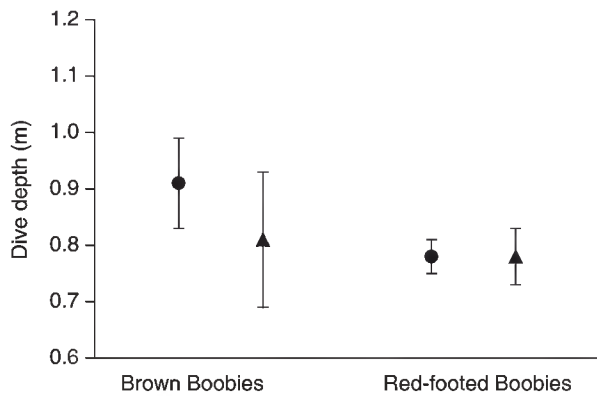
Figure 6. Mean (± se) dive depth (m) of Brown Boobies (males: circles, *n* = 12; females: triangles, *n* = 13) and Red-footed Boobies (males: circles, *n* = 16; females: triangles, *n* = 15).

0.011), whereas there was only a marginally significant sex difference in the Red-footed Booby (Fig. 5, χ^2 = 3.72, *df* = 1, *P* = 0.054). There was, however, no relationship between dive rate and individual mass in either the Brown Booby (χ^2 = 0.54, *df* = 1, *P* = 0.5) or the Red-footed Booby (χ^2 = 0.23, *df* = 1, *P* = 0.6). There were no sex differences in dive depth in either species (Fig. 6, Brown Booby χ^2 = 0.11, *df* = 1, *P* = 0.7; Red-footed Booby χ^2 = 1.18, *df* = 1, *P* = 0.3). There was also no effect of individual mass on dive depth in either species (Brown Booby χ^2 = 0.09, *df* = 1, *P* = 0.8; Red-footed Booby χ^2 = 2.70, *df* = 1, *P* = 0.1).

DISCUSSION

We have shown that sex differences were much more apparent in the Brown Booby, in which sexual size-dimorphism is more extreme (38%) than in the Red-footed Booby (14%), adding support for the hypothesis that sex differences in the foraging behaviour of boobies are related to differences in body size rather than to sex. Male Brown Boobies made significantly longer trips than females, and smaller birds made longer trips independent of sex, further highlighting that size is important. Hamer *et al.* (2000, 2001) have demonstrated a linear relationship between foraging trip duration and foraging range in the closely related Northern Gannet. If this pattern is also consistent in the Brown Booby, then males should have a greater foraging range than females. There was no evidence for a sex difference in trip duration in the Red-footed Booby, suggesting that both sexes were using a similar radius of sea around the colony. Male and female Red-footed

Boobies may nonetheless have foraged in different locations, if they left the colony in different directions, as previously shown in the sexually monomorphic Northern Gannet (Lewis *et al.* 2002), although spatial data are required to confirm this. In neither species did the sexes differ in the proportion of time spent flying or sitting on the sea surface during a foraging trip. This indicates that in both species the sexes did not differ in the time spent searching for prey on the trip. However, the dive rate of male Brown Boobies was 2.6 times higher than that of females, compared with only 1.6 in Red-footed Boobies. Finally, unlike in many size-dimorphic seabird species in which the larger sex dives deeper (e.g. Croxall *et al.* 1991, Casaux *et al.* 2001), in these booby species the sexes did not differ in dive depth.

Unlike the pattern observed in the Giant Petrel *Macronectes halli* (Gonzalez-Solis *et al.* 2000), we suggest that males are not being out-competed in productive coastal waters. Rather, the higher trip duration and dive rate of males may reflect the fact that they are foraging in areas of higher productivity, due to increased prey abundance or reduced disturbance from conspecifics, but which are further from the colony (Lewis *et al.* 2001). As such, we believe that our data support our second prediction, i.e. that males are able to fly further to exploit potentially more productive foraging grounds because of lower flight costs (Shaffer *et al.* 2001). Flight performance may also dictate to where birds can fly, particularly if they make use of wind patterns that minimize the costs of flying (Weimerskirch *et al.* 2000, Phillips *et al.* 2004). A smaller bird may also be able to make use of particular wind currents to take them to specific hot spots. Part of the difference in dive rate may also be associated with differing diving costs of the two sexes. Dive costs, in particular post-dive take-off, will be higher in larger individuals (Weimerskirch *et al.* 2000). Thus, there may be sex differences in the decision to make a dive. For example, female Brown Boobies may require a higher probability of prey capture to initiate a dive, to balance the increased cost of diving, thereby leading to their dive rate being lower than in males, as we observed.

Sex differences in foraging behaviour during the breeding season may be one component of the evolution of reverse size dimorphism in socially monogamous species with biparental care (Andersson & Norberg 1981, Mueller 1986, 1990). Large size in females may have evolved through a selective advantage in dominating foraging areas closer to the colony. Equally, selection could favour small males

because small size would be advantageous to males if it reduced their foraging costs (Shaffer *et al.* 2001) and increased their flight efficiency (Phillips *et al.* 2004). Alternatively, nutritional niche divergence between the sexes may be an important factor responsible for reversed size dimorphism in this species, particularly if different foraging methods linked to size are implicated. For example, the sexes may differ in their nutritional requirements, and so need to forage in different areas (Lewis *et al.* 2002). This requirement might increase the selection pressure for greater size in females, if they require specific nutrients post-laying (Nisbet 1997) that are only present close to the colony, and large size is advantageous in intrasexual competition (Gonzalez-Solis *et al.* 2000). However, nutritional niche divergence may operate irrespective of dimorphism, as has been suggested in the sexually monomorphic Northern Gannet (Lewis *et al.* 2002).

Size dimorphism may have evolved from sex-specific reproductive role specialization. In birds of prey, several authors have argued that larger females play a more active role in nest defence and smaller males are better able to provision offspring (Storer 1966, Snyder & Wiley 1976, Andersson & Norberg 1981). However, male Rough-legged Buzzards *Buteo lagopus* carry out all nest defence, presumably because of their increased aerial agility, which results from their smaller size (Andersson & Wiklund 1987). Alternatively, females may be larger to enhance their ability to produce larger eggs (Reynolds 1972), incubate the eggs more efficiently (Snyder & Wiley 1976) and carry out longer incubation shifts because of their greater ability to withstand starvation (Reynolds 1972, Snyder & Wiley 1976, Korpimäki 1986, Lundberg 1986, Mueller 1989). As such, large size would be selected for in females. A greater commitment at the nest-site by females may enable males to forage for longer and collect more food, and being smaller would facilitate this. However, we were not able to measure incubation shifts directly from our data, and trip duration in one parent may not correspond to incubation in the other.

Our data support the hypothesis that size is an important factor explaining sex differences in foraging behaviour. However, the observation that in some sexually monomorphic species the sexes differ in foraging behaviour (Gray & Hamer 2001, Lewis *et al.* 2002) does indicate that size may not explain these differences fully. Unfortunately, we cannot unequivocally separate the effects of sex and size, and a growing number of studies reveal support for

both the size and sex hypotheses. Thus, a comparative study, using simple estimates of foraging specialization, but with a phylogenetic context (Nunn & Stanley 1998) would be informative. Such a study would establish whether variation in competitive ability and foraging efficiency can be explained by sexual size dimorphism alone. Finally, although we have identified a proximate association between sexual size dimorphism and sex-specific foraging behaviour using two species, further investigation is required to establish the ultimate cause of reverse sexual size dimorphism.

REFERENCES

Aho, T., Kuitunen, M., Suhonen, J., Hakkari, T. & Jantti, A. 1997. Effects of male removal on female foraging behavior in the Eurasian Treecreeper. *Behav. Ecol. Sociobiol.* **41**: 49–53.

Andersson, M. & Norberg, R.A. 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.

Andersson, S. & Wiklund, C.G. 1987. Sex-role partitioning during offspring protection in the Rough-legged Buzzard *Buteo lagopus*. *Ibis* **129**: 103–107.

Casaux, R., Favero, M., Silva, P. & Baroni, A. 2001. Sex differences in diving depths and diet of Antarctic Shags at the South Shetland Islands. *J. Field Ornithol.* **72**: 22–29.

Croxall, J.P., Naito, Y., Kato, A. & Rothery, P. 1991. Diving patterns and performance in the Antarctic blue-eyed shag *Phalacrocorax atriceps*. *J. Zool. (Lond.)* **225**: 177–199.

Daunt, F., Peters, G., Scott, B., Gremillet, D. & Wanless, S. 2003. Rapid-response recorders reveal interplay between marine physics and seabird behaviour. *Mar. Ecol. Prog. Series* **255**: 283–288.

Elston, D.A., Horgan, G.W. & Hunter, E.A. 2001. *Introduction to REML for Scientists*. Edinburgh: Biomathematics & Statistics Scotland.

Gonzalez-Solis, J., Croxall, J.P. & Wood, A.G. 2000. Sexual dimorphism and sexual segregation in foraging strategies of Northern Giant Petrels, *Macronectes halli*, during incubation. *Oikos* **90**: 390–398.

Gosler, A.G. 1987. Pattern and process in the bill morphology of the Great Tit *Parus major*. *Ibis* **129**: 451–476.

Gray, C.M. & Hamer, K.C. 2001. Food-provisioning behaviour of male and female Manx Shearwaters, *Puffinus puffinus*. *Anim. Behav.* **62**: 117–121.

Griffiths, R., Daan, S. & Dijkstra, C. 1996. Sex identification in birds using two *CHD* genes. *Proc. Royal Soc. Lond. B.* **263**: 1251–1256.

Hamer, K.C., Phillips, R.A., Hill, J.K., Wanless, S. & Wood, A.G. 2001. Contrasting foraging strategies of Gannets *Morus bassanus* at two North Atlantic colonies: foraging trip duration and foraging area fidelity. *Mar. Ecol. Prog. Series* **224**: 283–290.

Hamer, K.C., Phillips, R.A., Wanless, S., Harris, M.P. & Wood, A.G. 2000. Foraging ranges, diets and feeding locations of Gannets *Morus bassanus* in the North Sea: evidence from satellite telemetry. *Mar. Ecol. Prog. Series* **200**: 257–264.

Hedrick, A.V. & Temeles, J.E. 1989. The evolution of sexual dimorphism in animals: hypotheses and tests. *Trends Ecol. Evol.* **4**: 136–138.

Korpimäki, E. 1986. Reversed size dimorphism in birds of prey, especially in Tengmalm Owl *Aegolius funereus*: a test of the starvation hypothesis. *Ornis Scand.* **17**: 326–332.

Lewis, S., Benvenuti, S., Dall'Antonia, L., Griffiths, R., Money, L., Sherratt, T.N., Wanless, S. & Hamer, K.C. 2002. Sex-specific foraging behaviour in a monomorphic seabird. *Proc. Royal Soc. Lond. B.* **269**: 1687–1693.

Lewis, S., Sherratt, T.N., Hamer, K.C. & Wanless, S. 2001. Evidence of intra-specific competition for food in a pelagic seabird. *Nature* **412**: 816–819.

Lundberg, A. 1986. Adaptive advantages of reversed sexual size dimorphism in European owls. *Ornis Scand.* **17**: 133–140.

Marquiss, M. & Newton, I. 1982. Habitat preference in male and female Sparrowhawks *Accipiter nisus*. *Ibis* **124**: 324–328.

Morse, D.H. 1968. A quantitative study of foraging of male and female spruce-woods warblers. *Ecology* **49**: 779–784.

Mueller, H.C. 1986. The evolution of reversed sexual dimorphism in owls: an empirical analysis of possible selective factors. *Wilson Bull.* **98**: 387–406.

Mueller, H.C. 1989. Evolution of reversed sexual size dimorphism: sex or starvation? *Ornis Scand.* **20**: 265–272.

Mueller, H.C. 1990. The evolution of reversed sexual dimorphism in size in monogamous species of birds. *Biol. Rev. Cambridge Phil. Soc.* **65**: 553–585.

Newton, I. 1979. *Population Ecology of Raptors.* Berkhamsted: Poyser.

Nisbet, I.C.T. 1997. Female Common Terns *Sterna hirundo* eating mollusc shells: evidence for calcium deficits during egg laying. *Ibis* **139**: 400–401.

Nunn, G.B. & Stanley, S.E. 1998. Body size effects and rates of cytochrome b evolution in tube-nosed seabirds. *Mol. Biol. Evol.* **15**: 1360–1371.

Patterson, H.D. & Thompson, R. 1971. Recovery of inter-block information when block sizes are unequal. *Biometrika* **58**: 545–554.

Phillips, R.A., Silk, J.R.D., Phalan, B., Catry, P. & Croxall, J.P. 2004. Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? *Proc. Royal Soc. Lond. B.* **271**: 1283–1291.

Reynolds, R.T. 1972. Sexual dimorphism in accipiter hawks: a new hypothesis. *Condor* **74**: 191–197.

Schreiber, E.A. & Norton, R.L. 2002. Brown Booby (*Sula leucogaster*). In Gill, F.B. & Poole, A. (eds) *The Birds of North America* no. **649**: 1–28. Philadelphia: The Academy of Natural Sciences, and Washington, DC: The American Ornithologists' Union.

Schreiber, E.A., Schreiber, R.W. & Schenk, G.A. 1996. Red-footed Booby (*Sula sula*). In Gill, F.B. & Poole, A. (eds) *The Birds of North America* no. **241**: 1–24. Philadelphia: The Academy of Natural Sciences, and Washington, DC: The American Ornithologists' Union.

Shaffer, S.A., Weimerskirch, H. & Costa, D.P. 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.

Snyder, N.F.R. & Wiley, J.W. 1976. *Sexual Dimorphism in Hawks and Owls of North America.* Ornith. Monog. **20**: 1–96.

Storer, R. 1966. Sexual dimorphism and food habits in three North American accipiters. *Auk* **83**: 423–436.

Weimerskirch, H., Cherel, Y., CuenotChaillet, F. & Ridoux, V. 1997. Alternative foraging strategies and resource allocation by male and female wandering albatrosses. *Ecology* **78**: 2051–2063.

Weimerskirch, H., Guionnet, T., Martin, J., Shaffer, S.A. & Costa, D.P. 2000. Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proc. Royal Soc. Lond. B.* **267**: 1869–1874.