Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels, *Macronectes halli*, during incubation

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González-Solís, J., Croxall, J. P. and Wood, A. G. 2000. Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels, *Macronectes halli*, during incubation. – Oikos 90: 390–398.

Giant petrels (*Macronectes* spp.) are the most sexually dimorphic of all seabirds. We used satellite-tracking and mass change during incubation to investigate the influence of sexual size dimorphism, in terms of the intersexual food competition hypothesis, on foraging and fasting strategies of northern giant petrels at South Georgia. Females foraged at sea whereas males foraged mainly on the South Georgia coast, scavenging on seal and penguin carcasses. Foraging effort (flight speed, distance covered, duration of foraging trips) was greater for females than for males. In contrast, foraging efficiency (proportionate daily mass gain while foraging) was significantly greater for males than for females. Females were significantly closer to the desertion mass threshold than males and could not compensate for the mass loss during the incubation fast while foraging, suggesting greater incubation costs for females than for males. Both sexes regulated the duration and food intake of foraging trips depending on the depletion of the body reserves. In males the total mass gain was best explained by mass at departure and body size. We suggest that sexual segregation of foraging strategies arose from size-related dominance at carcasses, promoting sexual size dimorphism. Our results indicate that sex-specific differences in fasting endurance, contest competition over food and flight metabolic rates are key elements in maintenance of sexual size dimorphism, segregating foraging strategies and presumably reducing competition between sexes.

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Most seabirds are sexually monomorphic and we would expect, and find, that their foraging strategies and breeding duties are generally similar in both sexes. However, some seabirds, notably the great albatrosses (*Diomedea* spp.), giant petrels (*Macronectes* spp.) and snow petrel (*Pagodroma nivea*), are markedly sexually dimorphic in size (Croxall 1982a, González-Solís et al. 2000). Three main, non-mutually exclusive, hypotheses have been proposed to explain sexual size dimorphism: the sexual selection, the inter-sexual food competition and the dimorphic niche hypotheses (see review by Hedrick and Temeles 1989). The sexual selection hypothesis suggests that dimorphism evolved through mating preferences for larger individuals of the opposite sex as honest signs of their competitiveness. The inter-sexual food competition hypothesis proposes that sexual differences in size might evolve from niche-partitioning between sexes as a mechanism to reduce inter-sexual competition for food. The dimorphic niche hypothesis attributes dimorphism to differences in the reproductive roles of males and females. However, seabirds are monogamous and full biparental care is normal, so this last hypothesis is unlikely to apply. Although social monogamy and long-term mate partnership are typical, especially among large seabirds, this may not preclude the sexual selection hypothesis; inter-sexual food competition is, however, likely to be of particular potential importance in dimorphic species.

Observations of seabirds at sea have suggested sex-related foraging distributions in some species (Weimerskirch and Jouventin 1987, Gilardi 1992). Moreover, satellite tracking studies presented direct evidence of differences in foraging range for each sex of wandering albatrosses *Diomedea exulans* (Prince et al. 1992, Weimerskirch 1995), as well as sexual differences in foraging efficiencies (Weimerskirch et al. 1997a).

In addition to differences relating to resource acquisition strategies, sexual size dimorphism may also influence strategies of resource (energy) utilisation, particularly in relation to prolonged fasting (Croxall 1982b). In long-lived birds (like seabirds), the trade-off between present and future reproductions to maximise lifetime reproductive success involves decisions on how much to invest in current reproduction (Stearns 1992). In albatrosses and petrels, the implications of this trade-off on foraging strategies and allocation processes during the chick rearing period have been extensively studied (Chaurand and Weimerskirch 1994a, Chastel et al. 1995, Weimerskirch et al. 1995, 1997a, b, Weimerskirch 1998). The incubation period, however, has attracted less attention (Chaurand and Weimerskirch 1994b, Weimerskirch 1995, Tveraa et al. 1997). Petrels have long incubation periods with males and females alternating incubation and foraging, typically in shifts lasting one week or more while the partner fasts on the nest. The decision to cease incubation and start self-feeding is usually subordinate to relief by the partner, since the temporary desertion of the egg would increase the risk of nest predation (this is especially so in surface nesters, since unattended eggs are very conspicuous and immediately predated by scavengers such as gulls and skuas). However, the unpredictability of food resources and the distant location of feeding grounds of pelagic seabirds lead to a high variability in the duration of the foraging trips; foraging partners may, therefore, not return before incubating partners run out of reserves. In such circumstances, incubating birds have to decide when to stop fasting and desert the nest to replenish depleted body reserves before the return of the partner. Thus, they have a conflict of interest in determining the desertion threshold. If birds desert too early their fitness may be reduced through the loss of the breeding attempt. Conversely, if they fast too long they risk exhausting reserves before finding food, which may affect survival prospects. To minimise this threshold desertion conflict, birds must be able to cope with long fasting periods during incubation while waiting for the partner, which means the evolution of optimal life history traits, foraging strategies, and allocation processes.

In this study we investigated the foraging and fasting strategies of a large, long-lived, monogamous, surface-nesting seabird, the northern giant petrel, *Macronectes halli*, in relation to sexual size dimorphism. Sexual size dimorphism is greater (females 80% the mass of males) in giant petrels than in any other group of seabird

(Croxall 1982a, Hunter 1984). Our main questions were: (1) how do foraging area, effort and efficiency differ between sexes; (2) how are body reserves regulated and allocated during incubation in the two sexes; (3) how is sexual size dimorphism related to inter-sexual differences in foraging strategies and allocation processes; and (4) do these results support the inter-sexual food competition hypothesis?

Methods

Study species

Northern giant petrels have a sub-Antarctic distribution, breeding between 44°S (Chatham I.) and 55°S (Macquarie I.) (Carboneres 1992). They have a marked sexual size dimorphism (Table 1), with females being 75–80% of the mass of males (Hunter 1987). Northern giant petrels are thought to be the dominant scavengers in sub-Antarctic waters (e.g. Johnstone 1977, Hunter 1985, Voisin 1991). At our study site, Bird Island, South Georgia, the diet is mainly penguin and seal carrion, although sexual differences have been noted. Males are known to feed more extensively on penguin and seal carrion than females, which feed the chicks with a greater proportion of krill, squid and fish, presumably collected at sea (Hunter 1983).

The sub-Antarctic island of South Georgia is an important breeding site for both species of giant petrels. Hunter (1985) estimated that approximately 16% and 29% of the world breeding populations of southern *Macronectes giganteus* and northern giant petrel, respectively, occur there. At the beginning of the 1980s, Bird Island was estimated to hold about 9% (500–600 breeding pairs) and 52% (1000–1500 breeding pairs) of the South Georgia populations of southern and northern giant petrels, respectively (Hunter 1984).

Fieldwork

Fieldwork was carried out on Bird Island, South Georgia (54°, 03′ S, 38° 36′ W) between 1 November and 10 December 1998. This is during the second half of the incubation period, which lasts 60 d from a mean laying date of 2–3 October (Hunter 1984). By daily visits to

Table 1. Body measurements (mean ± s.d.) of male and female northern giant petrels of the study birds and percentage of difference between sexes for each measurement.

	Females (n = 35)	Males (n = 33)	Difference (%)
Mass (kg)	3.7 ± 0.2	4.6 ± 0.2	19.6
Culmen length (mm)	89.4 ± 2.1	103.5 ± 2.3	13.6
Wing length (mm)	501.8 ± 8.1	529.0 ± 11.6	5.2
Tarsus length (mm)	90.4 ± 2.0	100.1 ± 2.0	9.7

the nests, we studied the duration of the foraging trips and incubation shifts as well as changes in mass of 33 male and 35 female northern giant petrels from different nests. We measured changes in mass by weighing the birds every three days until departure for a foraging trip and on the arrival day after a foraging trip. Birds were weighed in a large bag using Pesola® spring balances. We measured culmen, tarsus and wing length of the study birds.

We deployed 30-g Platform Terminal Transmitters (PTTs) from Microwave, Columbia, MD, USA and 10-g radio transmitters on breeding northern giant petrels. PTT deployments were restricted to the period defined above. We tracked only one foraging trip per bird to ensure independence between trips. We removed birds from the nest for attaching PTTs, which were attached to the mid-dorsal feathers of the mantle using Tesa® tape (Wilson and Wilson 1989). To minimise nest desertion after PTT deployment we released the bird into a cage on the nest. The cage was $135 \times 84 \times 55$ cm, made of wooden sticks and 5×5 cm plastic mesh. Birds usually calmed down after one minute and proceeded with incubation. The cage was then removed. By using this method, we did not record any desertion in relation to the deployment of the PTT. Radio transmitters were always deployed together with PTTs. We installed an antenna on top of a hill in the middle of the breeding area to receive signals from radio transmitters deployed on each bird to record the precise times of departure and arrival of foraging trips.

Data procedures

To analyse mass changes between departure and arrival of a foraging trip, we avoided pseudo-replication arising from the use of more than one foraging trip per bird by randomly selecting one trip per bird. Robustness of the results to random sampling was examined by producing and comparing ten random selections, which all gave very similar results.

For those birds that were weighed two or three days before departure, we estimated the mass at departure using the last mass recorded and the proportional daily loss of mass for the appropriate sex. To estimate body size, multivariate approaches with several representative measurements are preferable to univariate metrics (Freeman and Jackson 1990). Accordingly, we used Principal Component Analysis to combine the three linear measurements (culmen, tarsus and wing length) and extract the first principal component (PC1). This accounted for 51% of the variance in males and 46% in females. Female-male ratio of culmen length is from 0.86 to 0.87 in four localities (Hunter 1987) and culmen

length range does not overlap between sexes (Hunter 1984). Thus, we sexed the birds by culmen length measurement, birds with culmens shorter than 94 mm being females and larger than 98 mm being males. We verified the assigned sex by reference to the sex of the mate.

Data on the position of tracked birds were obtained from the ARGOS system. Initial data validation involved calculating velocities between successive satellite uplinks (ARGOS class A, B, Z and from 0 to 3), and rejecting those where the velocity exceeded a threshold of 30 m/s, and where a manual inspection of the data indicated an unlikely movement out and back from the normal track as defined by the preceding and following uplinks. This can remove up to 15% of uplinks per trip, all of which are the low quality, unclassifiable type according to the ARGOS system (class A, B, Z). Mean velocity for each trip was estimated by averaging the velocities between validated positions. Kernel analysis to characterise spatial distribution follows Wood et al. (in press). Validated positions from the same trip are not truly independent, but it should be noted that De Solla et al. (1999) show that assessing ranges using kernel density procedures does not require serial independence of data. We defined three different activity ranges as the areas encompassing 50%, 30% and 10% of locations.

Results are shown as mean ± standard deviation except as otherwise indicated. All tests are two-tailed and significance was set to $P < 0.05$. Multiple regression analyses were checked for normality.

Results

Foraging trip performance and foraging location

We satellite tracked eight foraging trips from females and nine from males. Examination of the foraging trip route indicates that all females foraged at sea, away from the South Georgia coast. In contrast, only two males foraged at sea, whereas seven foraged on the South Georgia coast (Fisher's exact test, $P = 0.002$). Validated positions received for all trips and activity ranges derived from kernel analyses are shown in relation to sex in Fig. 1. For females, activity ranges, as expressed by total area encompassed by 50%, 30% and 10% of locations was 151.4, 49.3 and 6.9 km^2, respectively. For males, total encompassed areas were 17.3, 7.1 and 2.0 km^2, which is about one-ninth, one-seventh and one-fourth of the activity ranges of females, respectively (Fig. 2). Flying speed was significantly greater for females than for males (Table 2). Maximum foraging range (the furthest point away from nest), total distance covered and daily distance covered were substantially greater for females than for males, although differences were not significant owing to the small sample size (Table 2).
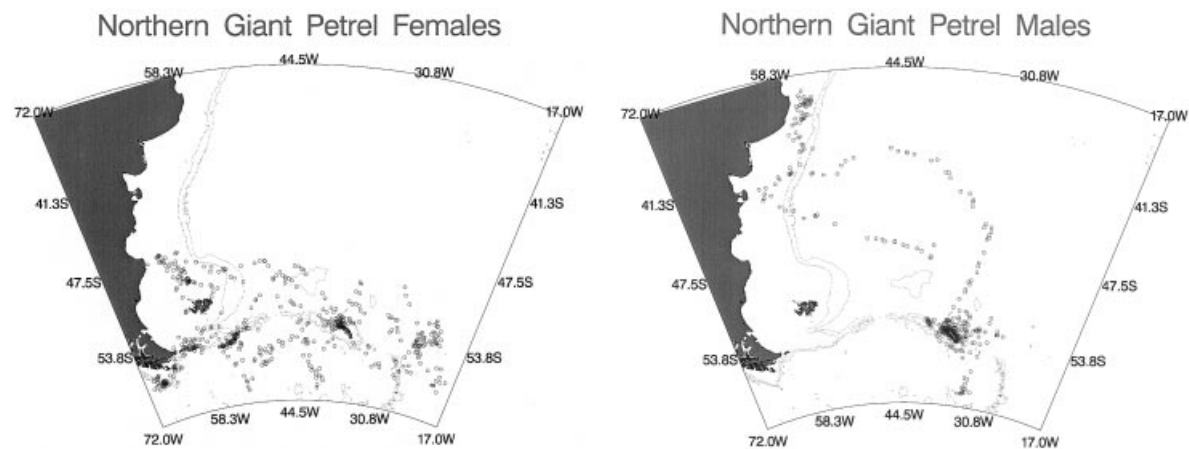
Fig. 1. Validated positions received from eight foraging trips of female northern giant petrels (left) and nine of males (right) during the incubation period.

Foraging efficiency and incubation costs

The duration of the foraging trips was shorter for males than for females (and *vice versa* for the incubation shifts of their partners), although differences were not significant (median males: 3 d, range 2 to 13, $n = 33$, median females 5 d, range 2 to 12, $n = 35$, Mann-Whitney U test, $Z = -1.58$, $P = 0.11$). Duration of all incubation shifts recorded during the study period was significantly longer for males than for females (males 4.74 ± 0.16 d; females 3.81 ± 0.12 d; t-test for non-equal variances, $t = 4.55$, df $= 524.3$, $P < 0.001$). Foraging efficiency, measured as the proportionate daily mass gain while foraging, was significantly greater for males than for females (median males 2.46%, range -6.91 to 8.66, $n = 33$; median females 1.26%, range -5.35 to 7.23, $n = 35$; Mann-Whitney U test, $Z = -2.21$, $P < 0.05$). In males, efficiency decreased with the duration of the foraging trip, being greatest for foraging trips of three days duration (Fig. 3). In contrast, in females, efficiency increased with the duration of the foraging trip, reaching its greatest value in foraging trips lasting four to six days. Note that median values of foraging trip duration coincide with the optimum duration, as indicated by the highest efficiency, for each sex.

Mass on return decreased significantly with the progress of the incubation period for females ($n = 35$, $r^2 = 0.16$, $P < 0.001$) but not for males ($n = 33$, $r^2 = 0.02$, $P = 0.88$) (Fig. 4). Decisions to desert the nest seem to be closely related to a fixed mass threshold (Chaurand and Weimerskirch 1994a, b, Olsson 1997). To examine which sex was closer to the mass threshold at which the birds desert the nest, we compared the average mass when relieved by the partner to the threshold desertion values of 2.87 kg (Confidence Interval 95%: ± 0.12, $n = 4$) for females and 3.34 kg (± 0.15, $n = 2$) for males. Females were significantly closer to the desertion threshold than males (males $31.5\% \pm 9.9$, females

26.3% ± 10.5, $t = 2.1$, df $= 66$, $P < 0.05$). Mean fasting duration was 26.2 d (range $23-33$, $n = 4$) for females and 22 d for one male. Minimum mass recorded in natural circumstances during the study period was 2.99 kg per females and 3.59 kg for males; these values are close to the desertion mass thresholds (2.87 and 3.34 kg, respectively) found in the experimental study.

Regulation of the foraging trips

To investigate whether birds regulate foraging trips according to the depletion of the body reserves, we correlated the mass at departure with the duration of the foraging trips and the proportionate mass gain while foraging (Figs 5, 6). Mass at departure was significantly associated with the duration of the foraging trip as well as the proportionate mass gain in both males and females (males: $n = 33$, duration–mass at departure $r^2 = 0.14$, $P < 0.05$, mass gain–mass at departure $r^2 = 0.43$, $P < 0.001$; females: $n = 35$, duration–mass at departure $= r^2 = 0.14$, $P < 0.05$, mass gain–mass at departure $r^2 = 0.35$, $P < 0.001$). Proportionate mass gain while foraging was also significantly correlated with the duration of the foraging trips for females and marginally significant for males (males: $r^2 = 0.10$, $P = 0.07$; females: $r^2 = 0.39$, $P < 0.001$). Thus, to examine whether birds regulate the foraging trip according to the number of days spent foraging, or to the mass gained, or both, we performed stepwise multiple correlation analyses. In both males and females, mass at departure was best explained by the proportionate mass gained (males: $r^2 = 0.43$, $F_{1,31} = 23.3$, $P < 0.001$, females: $r^2 = 0.35$, $F_{1,33} = 17.9$, $P < 0.001$); number of days foraging did not improve the model significantly. However, the correlation coefficient was larger for males than for females, suggesting that the ability to regulate body reserves was greater for males than for females.

Northern Giant Petrel Females
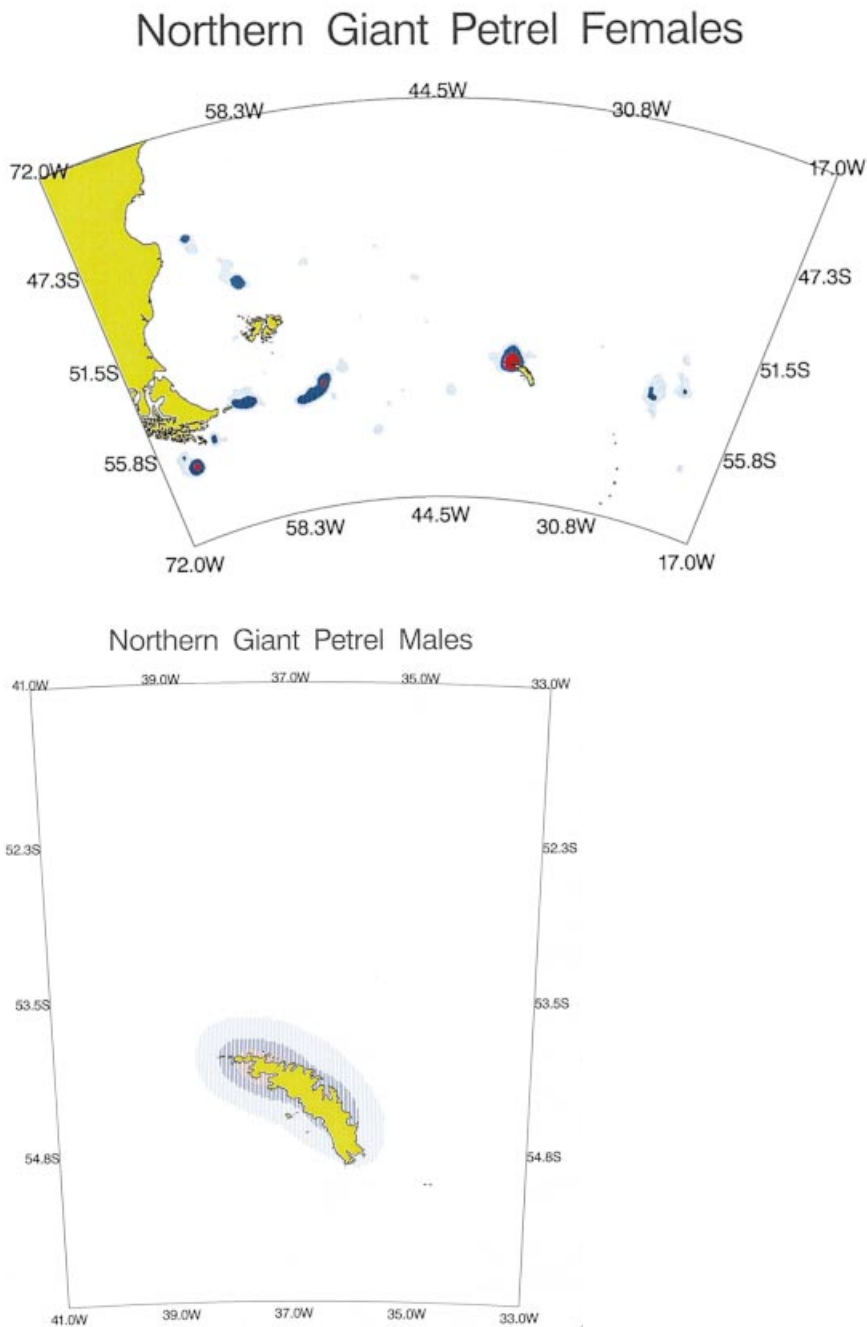

Northern Giant Petrel Males

Fig. 2. Activity ranges derived from kernel analyses on the validated positions for females (top) and males (bottom). Activity ranges encompassed 50%, 30% and 10% of locations as indicated by green, blue and red colours, respectively.

Factors affecting total mass gain at sea and resource predictability.

To investigate the factors affecting the total mass gain per foraging trip, we performed a stepwise multiple regression with duration of the trip, mass at departure and body size of the birds. In males the total mass gain was best explained by the mass at departure and the body size (mass at departure, $\beta = -0.62$, body size, $\beta = 0.30$, $r^2 = 0.46$, $F_{2,30} = 13.0$, $P < 0.001$). In contrast, in females the total mass gain was best explained by the duration of the foraging trip and the mass at departure (days, $\beta = 0.46$, mass at departure, $\beta = -0.36$, $r^2 = 0.48$, $F_{2,32} = 14.7$, $P < 0.001$). Total mass gain while foraging was significantly correlated with the duration of the trip for females but not for males (males: $n = 33$,

Table 2. Median and range of the speed, maximum foraging range, distance covered of foraging trips by males and females northern giant petrel during incubation.

	Males ($n = 9$)	Females ($n = 8$)	Mann-Whitney U test
Speed (m/s)	4.0 (2.7–10.9)	8.2 (5.5–11.8)	$Z = -2.31$; $P = 0.02$
Maximum foraging range (km)	180 (127–2396)	1226 (950–2073)	$Z = -1.06$; $P = 0.32$
Distance covered (km)	1524 (396–10630)	5159 (419–9342)	$Z = -0.77$; $P = 0.48$
Daily distance covered (km)	173 (89–609)	389 (150–584)	$Z = -1.64$; $P = 0.11$

$r^2 = 0.10$, $P = 0.08$; females: $n = 35$, $r^2 = 0.36$, $P < 0.001$). In addition, the correlation coefficient was larger for females than for males, suggesting that predictability of resources used by females is greater than those used by males (Fig. 7).

Discussion

Male northern giant petrels foraged mainly on the South Georgia coast whereas females foraged at sea. This difference agrees with previous observations on diet and on attendance at seal carcasses, which suggested that, during this period, males feed mainly on seal and penguin carcasses whereas females prey chiefly on krill, squid and fish (Hunter 1983). Thus, overall, male and female giant petrels clearly exploited different food resources during incubation, males scavenging on beaches and females foraging at sea. However, males also had the capacity to switch search modes, as shown by two males foraging at sea. Similarly, carrion is known to occur in female diet and some females have been observed attending at carcasses (Hunter 1983), showing that both sexes can change the search mode when necessary.

The exploitation of different food resources by males and females involved important differences in foraging strategies for each sex (Table 3). Scavenging on beaches or foraging at sea imply searching in different areas, involving a fundamental decision on where to direct search effort before starting foraging. Foraging effort, measured as the duration of foraging trips and flight velocities, was clearly greater for females than for males. Potential predictability of resources, as suggested by the correlation between the duration of the foraging trip and the total mass gain, was greater for females than for males. Optimum foraging duration, expressed as the number of days that maximise the quantity of mass gained per unit time, was shorter for males than for females.

During the incubation period, foraging petrels and albatrosses have to recover from the previous fasting period and need to store new reserves for the next incubation shift. Therefore, if birds are able to regulate body reserves, we would expect a relationship between the degree of depletion in body reserves when leaving the colony and the restored reserves when returning for the incubation shift. Thus the mass gained at sea and the duration of the trip are usually inversely related to the body mass at departure (Chaurand and Weimerskirch 1994b, Weimerskirch 1995). Male and female giant petrels also regulated their body reserves. Mass at departure was primarily related to the subsequent mass gain, suggesting that the time spent at sea is mainly dependent on the restoration of body condition. Although both sexes regulated body mass, this ability, expressed as the degree of correlation between the mass when relieved and the proportionate mass gain in the subsequent foraging trip, was greater for males than for females.

However, the fact that some birds return to undertake the next incubation shift after losing mass, suggests that mass gain alone does not explain the decision to return to the colony. Birds appear to take into account the increased probability of partners deserting the nest with the duration of the foraging trip and/or the proximity of hatching and return to the colony without completely restoring their reserves. For instance, Tveraa et al. (1997), found that experimentally handicapped female Antarctic petrels, *Thalassoica antarctica*, spent more time at sea but also had lower body condition on return to the colony than controls; prolonged foraging trips were associated with higher desertion rates than controls.
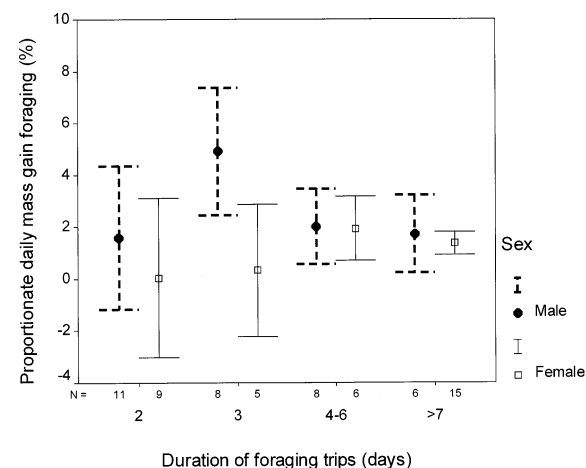

Fig. 3. Efficiency, as indicated by the proportionate daily mass gain while foraging, depending on the total duration of the foraging trip for male and female northern giant petrels. Values are means ± 95% confidence interval.
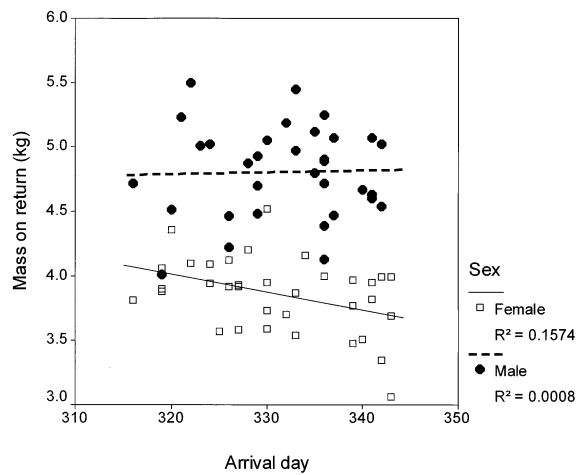
Fig. 4. Mass on return to the breeding area after a foraging trip in relation to the arrival day, expressed as the day of the year from the first of January, for female and male northern giant petrels during the incubation period.

Fig. 6. Proportionate mass gain while foraging, in relation to the mass at departure from the breeding area for female and male northern giant petrels.

Thus, the decision to return to the colony without completely restoring fat reserves to avoid partner desertion or to allow for feeding chicks rapidly and efficiently after hatching can lead to reproductive costs through progressive depletion of body reserves over the incubation period. Giant petrel males seem to have a more profitable foraging strategy than females. Males were more efficient when foraging and were able to undertake longer incubation shifts than females and simultaneously to maintain body condition. In contrast, females were less efficient, were closer than males to the desertion mass threshold when relieved and could not compensate while foraging for the mass loss during the incubation fast. Thus, differences in foraging strategies resulted in inter-sexual differences in foraging efficiencies and probably explain differences in reproductive costs incurred by each sex.
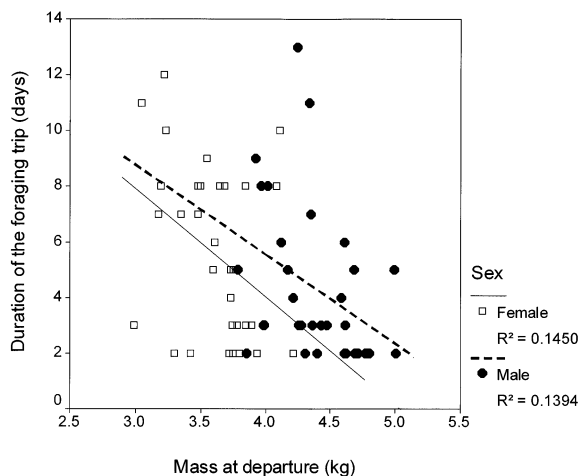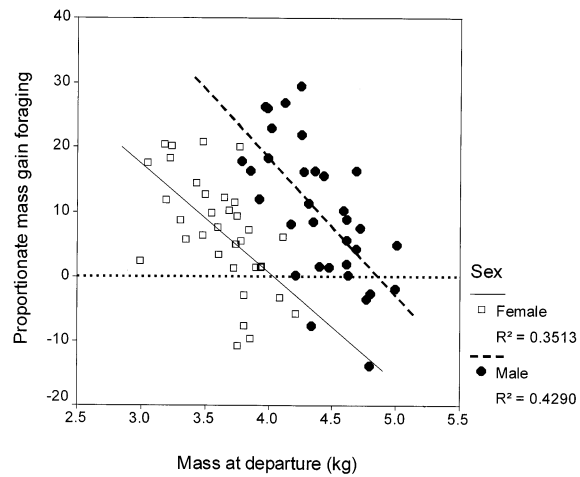
From a life history perspective, allocation of effort to current reproduction in order to minimise the desertion threshold conflict can generate reproductive costs, which differed between sexes and may result in reduced adult survival prospects for females.

In giant petrels, the adaptive basis of sexual dimorphism is not clear (Hunter 1987, Fairbairn and Shine 1993, Croxall 1995). The important difference in foraging strategies between sexes is possibly related to the substantial sexual dimorphism in body size, with females being only 80% the mass of males. Body size is subject to various selective pressures, which may differ between sexes (see review in Andersson 1994). Particularly, fasting endurance, contest competition over food and flight metabolic rates are likely to differ between sexes in giant petrels and relate to their differences in foraging strategies.

Fig. 5. Duration of the foraging trip in relation to the mass at departure from the breeding area for female and male northern giant petrels.
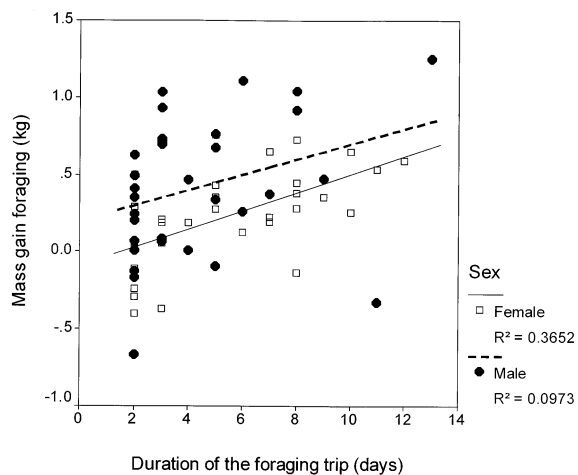

Fig. 7. Mass gain while foraging in relation to the duration of the trip for female and male northern giant petrels.

Table 3. Main differences in foraging strategies between male and female giant petrels during the second half of the incubation period.

	Females	Males
Foraging habitat (% of birds)	At sea (100%)	In coast (78%)
Activity range (km^2)	151.4	17.3
Foraging effort	High	Low
Median trip duration (d)	5	3
Optimum foraging trip duration (d)	4–6	3
Mean incubation shift duration (d)	3.8	4.7
Foraging efficiency	Low	High
Mass average loss in 30 d	0.4 kg	No loss
Average proximity to desertion mass threshold	26.3%	31.5%
Predictability of resources	High	Low

Fasting endurance increases rapidly with body size in petrels (e.g. Warham 1990) because capability to store energy reserves increases with body size faster than do metabolic costs (Calder 1984, Millar and Hickling 1990, 1992). Thus, larger body size can be advantageous to minimise the desertion threshold conflict as well as to overcome fasting periods produced by environmental fluctuations in food resources. The former may explain why incubation shifts are longer for males than for females (Hunter 1984, this study). The latter may create advantages for larger males, given the low resource predictability found for this sex.

Contest competition over food is likely to increase with male size. When males feed at carcasses, at any one time a single feeding male appears to dominate the others (Johnstone 1979). Males at carcasses are continually interacting agonistically and it is reasonable to believe that the outcome of the encounters is related to the size of the bird. For instance, the larger southern giant petrel is more successful than the smaller northern giant petrel in inter-specific disputes at carcasses (Johnstone 1979). In our study, larger males tended to gain more mass per trip than smaller males, suggesting that size of the meal may be related to dominance at carcasses, which may produce further selection for larger male size.

Flight energetics may partly explain the smaller size of giant petrel females. Flight costs increase with body mass (e.g. Norberg 1990), and sexual dimorphism in some wader species has been related to sexual differences in flight displays and other active flights (e.g. Jönsson and Alerstam 1990). Foraging strategies of female giant petrels involve much higher foraging effort than males, which may favour smaller female than male size.

The origin of sexual size dimorphism in giant petrels may be the result of trophic niche divergence between sexes, so that feeding efficiency and reproductive success could be maximised by sexual segregation of forag-

ing niche (Darwin 1871, Selander 1972, Shine 1989). Even if sexual selection was responsible for the initial morphological differences between sexes, the strong difference in foraging strategies between sexes in giant petrels was probably important in the evolution of dimorphism. Generally, sexual foraging differences in size dimorphic bird species do not involve different search modes or foraging strategies but are usually related to partitioning resources based on prey size, so selective pressures on body size do not greatly differ between sexes. In this study, we showed that males and females have consistently different foraging strategies, at least during the incubation period. It is difficult to know whether foraging differences are the cause of sexual dimorphism or the consequence of sexual selection of females choosing larger males (Hedrick and Temeles 1989, Shine 1989), since larger males may show better foraging performance and provide better resources than smaller males and therefore may be preferred by females. However, the importance of sexual selection on dimorphism seems particularly relevant among lekking and other polygynous birds (Payne 1984, Björklund 1990), rather than on monogamous species as giant petrels.

The greater difficulties in coping with the energy requirements of reproduction, the higher foraging effort and the lower foraging efficiency of females when compared to males, suggest that sexual segregation of foraging strategies is a product of the size-related male dominance at carcasses. Thus females may be forced to take alternative foraging strategies, incurring a higher cost of reproduction; however this may confer benefits as a consequence of the reduction in competition for food. We do not know the origin of the sexual dimorphism in giant petrels, but sexual foraging difference is probably an important factor in its evolution and maintenance.

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