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Sex-specific foraging behaviour in a monomorphic seabird

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Sexual differences in the foraging behaviour of parents have been observed in a number of sexually size-dimorphic birds, particularly seabirds, and the usual inference has been that these sex-specific differences are mediated primarily by differences in body size. To test this explanation, we compared the foraging behaviour of parents in a monomorphic seabird species, the northern gannet *Morus bassanus*. Using specially designed instruments and radio telemetry we found that individuals of both sexes were consistent in the directions and durations of their foraging trips. However, there were significant differences in the foraging behaviour of males and females. Female gannets were not only more selective than males in the areas where they foraged, but they also made longer, deeper dives and spent more time on the sea surface than males. As the sexes are morphologically similar in this species, then these differences are unlikely to have been mediated by body size. Our work highlights the need to investigate sexual differences in the foraging behaviour of seabirds and other species more closely, in order to test alternative theories that do not rely on differences in body size.

Keywords: biparental care; sexual size dimorphism; diving; gannet; *Morus bassanus*

1. INTRODUCTION

In many animal species, care by both parents is required for successful rearing of offspring (Lack 1968; Clutton-Brock 1991). In these situations a common question is whether or not there are differences between parents in their foraging behaviour. This question is particularly relevant among birds, where biparental monogamy occurs in over 90% of species (Lack 1968).

Previous research, which has compared the foraging behaviour of the sexes during the breeding season, has concentrated almost exclusively on sexually size-dimorphic species, including species of passerines (e.g. Morse 1968; Aho *et al.* 1997) and raptors (e.g. Newton 1979; Marquiss & Newton 1982). These studies have reported some sexual differences in foraging behaviour, particularly the microhabitats and locations in which the two sexes tend to forage. More recently, the development of small, lightweight activity recorders and satellite tags has enabled researchers to investigate sex-specific foraging behaviour in seabirds. These studies have similarly reported sexual differences in foraging location, but also the times of day that birds forage, and the depths to which they dive (table 1). As the majority of these investigations were based on sexually size-dimorphic species, it is perhaps understandable that authors have argued that differences in foraging behaviour might be mediated by size-based mechanisms, such as asymmetrical competition or differences in foraging efficiency (e.g. Weimerskirch *et al.* 1997; Gonzalez-Solis *et al.* 2000).

If size was important in mediating feeding activities, then one would not expect to see sexual differences in foraging behaviour within monomorphic species. Indeed, even within a monomorphic seabird species that exhibited distinct parental roles, one might expect them to forage for food in a similar way. Yet, somewhat surprisingly, potential sexual differences in the foraging behaviour of monomorphic seabirds at sea have only rarely been investigated (table 1). While Gray & Hamer (2001) found that females of the sexually monomorphic manx shearwater *Puffinus puffinus* fed their chick less frequently than males, their study was unable to obtain any direct information on foraging. Similarly, common terns *Sterna hirundo* are monomorphic and exhibit distinct parental roles (Wiggins & Morris 1987) but, to our knowledge, no study has examined whether the two sexes actually forage for prey in different ways.

We present data to compare the foraging behaviour of the two sexes in a species with no size dimorphism. We have tested whether even phenotypically similar sexes can exhibit differences in foraging behaviour, and we explore the need to look beyond body size as an explanation for differences in the foraging behaviour of male and female

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Table 1. Studies that have investigated sexual differences in the foraging behaviour of seabird species at sea.
(Significant sex difference in foraging location (L), dive depth (D), time of day foraging (T); no sex difference in foraging location (no L).)

species	size dimorphism	behaviour	study
wandering albatross	male > female	L	Weimerskirch & Jouventin (1987)
south Georgian shag	male > female	D	Croxall *et al.* (1991)
shag	male > female	no L	Wanless *et al.* (1991)
south Georgian shag	male > female	D	Kato *et al.* (1992)
wandering albatross	male > female	L	Prince *et al.* (1992)
wandering albatross	male > female	L	Salamolard & Weimerskirch (1993)
wandering albatross	male > female	L	Weimerskirch *et al.* (1993)
south Georgian shag	male > female	T	Wanless *et al.* (1995)
southern Buller's albatross	male > female	L	Sagar & Wiemerskirch (1996)
Japanese cormorant	male > female	D	Watanuki *et al.* (1996)
Japanese cormorant	male > female	D	Kato *et al.* (1999)
subantarctic cormorant	male > female	D	Kato *et al.* (1999)
thick-billied murres	male = female	T+D	Woo *et al.* (1999)
northern giant petrel	male > female	L	Gonzalez-Solis *et al.* (2000)
king cormorant	male > female	T+D	Kato *et al.* (2000)
grey-headed mollyhawk	male > female	L	Nel *et al.* (2000)
southern Buller's albatross	male > female	L	Stahl & Sagar (2000*a*)
southern Buller's albatross	male > female	L	Stahl & Sagar (2000*b*)
Antarctic shag	male > female	D	Casaux *et al.* (2001)
shy albatross	male > female	no L	Hedd *et al.* (2001)

parents. Our study species was the northern gannet, *Morus bassanus*, a sexually monomorphic species (mean culmen length (mm): male, 100.1 ($n = 66$); female, 99.2 ($n = 66$); mean tarsus length (mm): male, 58.8 ($n = 7$); female, 58.1 ($n = 5$); see Nelson 2002), where both parents help to rear the chick. Gannets have an expensive mode of flight (Birt-Friesen *et al.* 1989) and they capture prey by plunge and pursuit diving (Garthe *et al.* 2000). During chick rearing, parents generally alternate foraging trips with periods at the nest with the chick, such that when one parent arrives following a foraging trip and feeds the chick, its partner leaves almost immediately (Nelson 2002; this study). We investigated the foraging behaviours of males and females by simultaneously using (i) radio transmitters that provided foraging trip durations and departure directions, which are a good indicator of bearings to foraging locations (Hamer *et al.* 2000, 2001); and (ii) activity loggers that enabled us to distinguish four main activities during chick rearing (flying, diving, resting on the sea surface and attending the chick at the colony) and also record dive depth.

2. MATERIAL AND METHODS

The study was carried out between 19 June and 19 August 2001 at a breeding colony of *ca*. 40 000 pairs of northern gannets (Murray & Wanless 1997) at Bass Rock, southeast Scotland (56°6′N, 2°36′W). During the study, sunrise and sunset occurred at *ca*. 02.30 and 21.30 GMT (03.30 and 22.30 BST), respectively.

(a) *Radio transmitters*

Twenty-eight adults (from 14 pairs) with two-to-three-week-old chicks were caught at the nest using a roach pole. A VHF radio transmitter (Biotrack Ltd) weighing 20 g (less than 1% of adult mass) was attached to each bird with self-amalgamating tape and cable ties. To minimize drag during flight and prevent tags being displaced during plunge diving, tags were attached to the underside of the four central tail feathers, close to the base of the tail with the aerial pointing upwards through the feathers. Because the sexes are of similar size and cannot be reliably identified from plumage or soft-tissue coloration (Nelson 2002; Redman *et al.* 2002), a blood sample (less than 0.1 ml) was taken, under licence, from the tarsal vein of each bird, for subsequent sexing using two *CHD I* genes (see Griffiths *et al.* (1996) for details). The attachment of tags and collection of blood samples took *ca*. 10 min and after release every bird returned to the nest almost immediately (usually within 5 min). Birds were then tracked from a mainland station (*ca*. 1.5 km south of Bass Rock) during four tracking sessions. Each session ran continuously from dawn to dusk for several days (gannets are not active during the hours of darkness; see Garthe *et al.* 2000; Hamer *et al.* 2000), throughout a period of eight weeks (total tracking period of 40.5 days). The age of chicks during the study period ranged between 3 and 11 weeks. The receiving system consisted of two parallel eight-element Yagi aerials joined by a 2 m crosspiece, attached to a vertical 5 m mast, which allowed the aerials to rotate freely through 360°. The aerials were connected to an ATS R4000 scanning receiver, operating in the 173 MHz band. The different frequencies of the tagged birds were checked every 15 min. On the arrival of a bird in the colony, its arrival time and the departure time of its partner were both recorded, and the departing bird was tracked continuously to obtain the final bearing at the point of signal disappearance (on average, between 15 and 30 min after departure from the colony). At the end of the study period tags were removed. Previous research using satellite telemetry has shown that departure direction, coupled with trip duration, is a good indicator of where the birds forage, because they have a linear outward flight (Hamer *et al.* 2000, 2001).

(b) *Activity loggers*

Thirty different adults with chicks (age range of two to six weeks) were caught from the same area of the colony and each

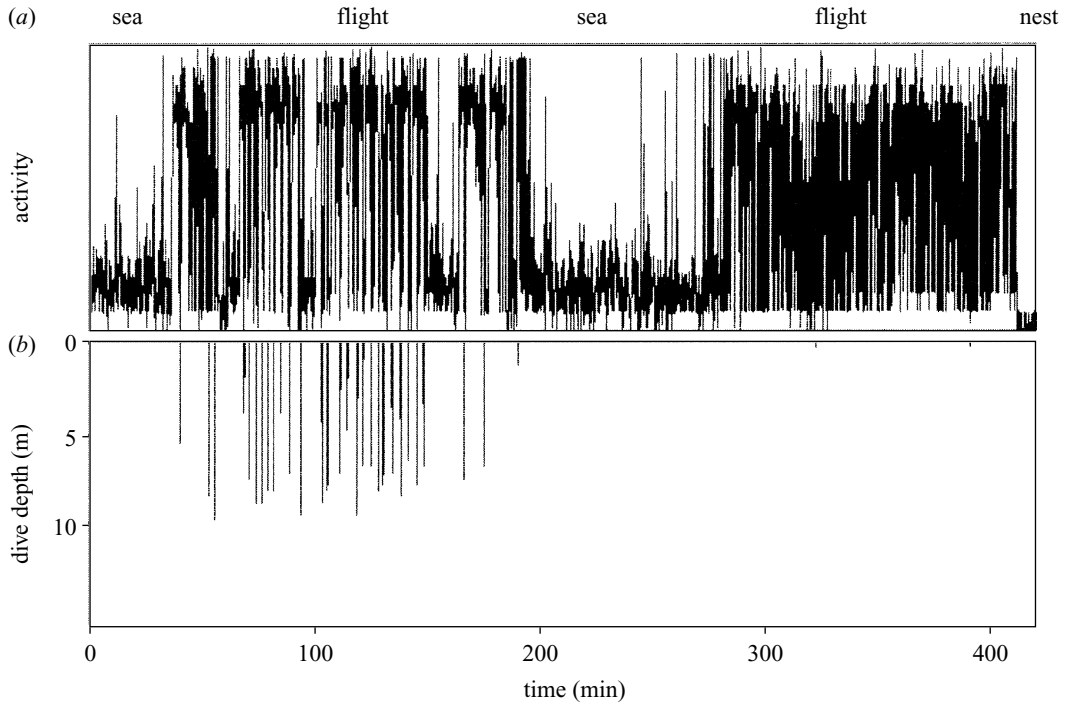

Figure 1. Data recorded from (*a*) a flight activity logger/motion sensor and (*b*) a depth meter attached to a chick-rearing northern gannet on Bass Rock in 2001. The trace is a sample taken during a foraging trip and lasts for 412 min. It shows a series of foraging flights during which the bird dived several times to a maximum depth of 10 m. Between the two flights the bird sat on the sea surface. The second flight includes two shallow dives ending with the bird back at the nest site.

was equipped with an activity logger using the same handling, attaching and sexing techniques as for birds with radio transmitters. These instruments were modified versions of the loggers designed at the Istituto di Elaborazione dell'Informazione (Dall'Antonia *et al.* 1993; Benvenuti *et al.* 1998, 2001). Two types of loggers were used. Type 1 was equipped with a depth meter (operative range of 0–70 m, resolution of 0.3 m) and a flight sensor (a small modified microphone). The time between successive recordings was set at 4 s for the depth meter and 8 s for the flight sensor, which allowed continuous recording for *ca.* 3.8 days. In type 2 activity loggers the depth meter was replaced with two short electric wires emerging from the housing. The water switch was activated if the wires were submerged in the sea. The time between successive recordings was set at 4 s for the water switch and 6 s for the flight sensor, which allowed continuous recording for *ca.* 3.5 days. Type 1 and 2 loggers weighed 28 and 19 g, respectively. Each logger was deployed for two to four days on each bird, in order to record at least one foraging trip (mean trip duration at Bass Rock is *ca.* 24 h; see Hamer *et al.* 2000; Lewis *et al.* 2001). After this time the bird was recaptured and the device removed. Recorded data were downloaded from the loggers to a portable computer and analysed using specially designed software (A. Ribolini, unpublished data). Of the 29 retrieved loggers, data were successfully downloaded in 20 cases (type 1 logger: nine males (of which one failed to give depth data) and six females; type 2 logger: four males and one female). For type 1 loggers, four activities could be distinguished from the distinct signals that the sensors produced: (i) nest attendance: weak, variable signal from flight sensor; (ii) flight: strong, noisy signal from flight sensor; (iii) resting on sea surface: moderate signal from the flight sensor; (iv) diving: strong, noisy signal from flight sensor and activation of the depth sensor (figure 1). Dives of less than 1 m were not taken into account because such shallow dives often occur during bathing or other movements not related to feeding. Furthermore, the sampling interval (4 s) may have prevented recording of some of the 1–2 m dives. Garthe *et al.* (2000) provide further details of the methodology and accuracy of these instruments for northern gannets. For type 2 loggers, nest attendance and flight were distinguished in the same way as with type 1 loggers. Resting on the sea surface was characterized by a moderate signal from the flight sensor and activation of the water switch, and diving by a strong, noisy signal from the flight sensor and activation of the water switch. The distinction between resting on the sea and diving recorded by type 2 loggers was not always definitive, unlike with the type 1 logger, when dive duration could be recorded accurately. Therefore type 2 results were not used for dive data. However, results from the type 1 loggers showed that diving only represented *ca.* 0.2% of total time, so when comparing the time allocation to the different activities of male and female gannets, the time spent on the sea and time spent diving were combined, enabling us to use the data from both types of loggers.

(c) *Statistical analysis*

We compared bearings of foraging trips, trip duration and dive depths between males and females by fitting linear mixed models using residual maximum-likelihood analyses (REML; Patterson & Thompson 1971). We compared the number of dives per trip and per hour, between males and females by fitting a generalized linear mixed model (GLMM) with a Poisson error distribution and logarithmic link function (Schall 1991). In each case, we included sex as a fixed factor and bird identity as a random factor, to avoid problems of pseudo-replication. For bearings of foraging trips, we also fitted a model without bird as a random factor to compare the deviance values between models, using the χ^2-distribution. This allowed us to assess the significance of individual variation in bearings from one bird to

Table 2. Mean (± s.e.) trip duration, number of dives per trip and per hour, dive depth (m) and dive duration (s) for male and female northern gannets during early chick rearing on Bass Rock in 2001.

	males	females
trip duration (h)	20.88 (± 1.20)	22.34 (± 1.10)
dives per trip	25.92 (± 6.06)	47.75 (± 13.45)
dives per hour	1.35 (± 0.30)	1.50 (± 0.42)
dive depth (m)	3.24 (± 0.11)	4.71 (± 0.16)
dive duration (s)	7.36 (± 0.28)	10.01 (± 0.35)

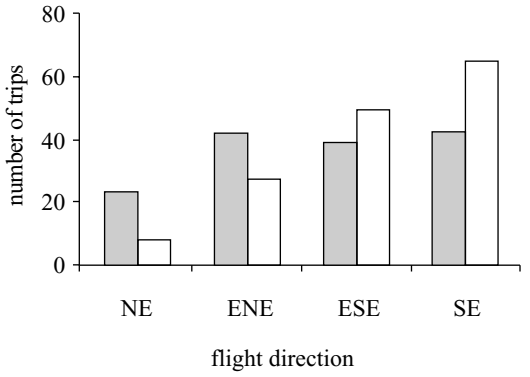

Figure 2. Frequency distribution of foraging trip departure directions ($n = 294$) of 14 pairs of northern gannets during chick rearing on Bass Rock in 2001. (Shaded bars, males; open bars, females.)

another. There was a highly significant positive correlation between dive depth and dive duration (Spearman correlation: $r = 0.95$, $n = 720$, $p < 0.001$), so only dive depth was compared statistically between sexes. Previous studies have found evidence of diel patterns in dive depths of seabirds (Wilson *et al.* 1993; Wanless *et al.* 1999; Benvenuti *et al.* 2001; Dall'Antonia *et al.* 2001). To test for this effect in northern gannets we included time of day (split into four 6 h periods: 01.00–06.59, 07.00–12.59, 13.00–18.59, 19.00–00.59 GMT) as a fixed factor in the analysis of dive depth. We also included the interaction between sex and time of day in this analysis. In all REML and GLMM models, the significance of each variable or interaction was determined by comparing Wald statistics with percentiles of χ^2- or F-distributions (Elston *et al.* 2001).

3. RESULTS

(a) *Directions of foraging trips*

The final flight directions that birds took when departing the colony differed significantly between sexes (table 2; REML, flight direction: Wald statistic $\chi^2 = 4.98$, d.f. = 1, $p = 0.026$, $n = 293$). Females flew mainly south-east, whereas males went in all directions equally frequently (figure 2). Comparison of the deviances between models, with and without bird identity as a random factor, showed that individual effects were highly significant, indicating that individual birds tended to head in similar directions on their foraging trips ($\chi^2 = 62.93$, d.f. = 1, $p = 0.001$, $n = 293$).

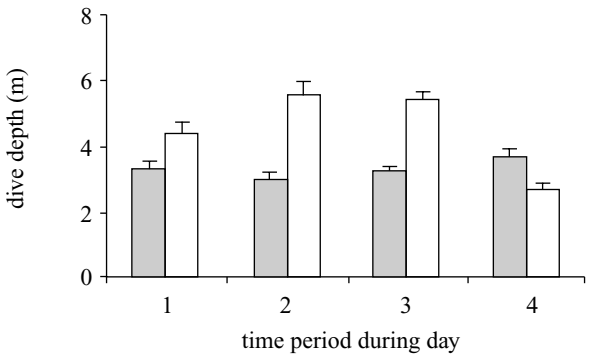

Figure 3. Mean dive depths (± s.e.) of male (shaded bars; $n = 8$) and female (open bars; $n = 6$) northern gannets at different periods of the day (period 1, 01.00–06.59; 2, 07.00–12.59; 3, 13.00–18.59; 4, 19.00–00.59), during chick rearing on Bass Rock in 2001.

(b) *Duration of foraging trips*

There was no significant difference in trip duration between the sexes (table 2; REML, square root of trip duration: Wald statistic $\chi^2 = 0.82$, d.f. = 1, $p = 0.366$, $n = 348$). Comparison of the deviances between models, with and without bird identity as a random factor, showed that individual effects were significant, indicating that individual birds tended to make foraging trips of similar duration ($\chi^2 = 4.09$, d.f. = 1, $p = 0.043$, $n = 348$).

(c) *Activity and time allocation*

During a total of 1429 h of recording, we obtained data on the time allocation of 13 males and 7 females over 29 complete foraging trips. There was no difference in the mean time spent flying per trip by males and females, where means per individual were used when more than one trip was recorded (male: 10.9 h, $n = 13$, s.d. ± 4.7; female: 13.2 h, $n = 7$, s.d. ± 4.8; $t_{18} = 1.034$, $p = 0.315$). However, females spent significantly longer than males on the sea surface (male: 10.8 h, $n = 13$, s.d. ± 3.2; female: 17.6 h, $n = 7$, s.d. ± 7.3; $t_{18} = 2.891$, $p = 0.010$). Birds did not fly at night (see Garthe *et al.* 1999, 2000; Hamer *et al.* 2000, 2001) and after removing hours of darkness from the data, females still spent a greater proportion of daylight hours than males on the sea surface (male: 0.18 h; female: 0.28 h; t-test with arcsine-transformed data; $t_{18} = 2.562$, $p = 0.020$).

(d) *Diving behaviour*

A total of 720 dives was recorded from 14 birds (eight males and six females; one depth meter failed). There were no significant differences between males and females in the mean number of dives made per trip or per hour on a trip (table 2; GLMM, dives per trip: Wald statistic $\chi^2 = 2.68$, d.f. = 1, $p = 0.120$, $n = 22$ trips; dives per hour: Wald statistic $\chi^2 = 0.08$, d.f. = 1, $p = 0.777$, $n = 22$). However, females consistently made deeper and thus longer dives than males (table 2; REML (log-transformed depth), sex: Wald statistic $F_{1,12} = 7.19$, $p < 0.025$, $n = 720$). The deepest and longest dives recorded were 11 m and 28 s for males, compared with 18 m and 37 s for females. From the same test, there was also a significant effect of time of day on dive depth (figure 3; Wald statistic $F_{3,10} = 21.21$, $p < 0.001$, $n = 720$) and a significant interaction between

sex and time of day (Wald statistic $F_{3,10} = 19.57$, $p < 0.001$, $n = 720$), indicating no difference between sexes in dive depth during the first and last periods of the day (figure 3). Finally, there was a significant positive correlation between dive depth and the subsequent inter-dive duration (time spent between successive dives) in females, but not in males (Spearman correlation: females: $r = 0.197$, $p < 0.001$, $n = 374$; males: $r = 0.028$, $p < 0.616$, $n = 323$).

4. DISCUSSION

To our knowledge, attaching devices caused no adverse effects for study birds or their chicks. All study nests contained a healthy chick at the end of the study period, and the mean trip durations from radio tags and loggers (tags: 22 h ± 14.9 s.d.; loggers: 25 h ± 9.5 s.d.) were consistent with two recent studies that recorded trip durations at Bass Rock from direct observations at the nest (27 h in 1998, Hamer *et al.* 2000; 19 h in 2000, Lewis *et al.* 2001).

Satellite telemetry of northern gannets at Bass Rock in 1998 (Hamer *et al.* 2000) showed that 71% of birds foraged southeast of the colony, although these authors did not consider sex in their analyses. We found a similar proportion (66%), but we also showed that it was females that were largely responsible for this bias in directions of trips (figure 2). Individuals tended to be consistent in their departure directions, as also found from satellite telemetry of northern gannets (Hamer *et al.* 2001) and radio tracking of black-legged kittiwakes (Irons 1998), suggesting that bearings of foraging trips may have been influenced by birds' prior experience. Individuals were also consistent in the duration of their trips (and thus foraging range; see Hamer *et al.* 2000), providing further evidence that individual birds tended to return to familiar foraging locations. Our results indicate that although there were no significant differences between the sexes in trip duration, or the time spent flying on a trip, females spent more time on average on the sea surface in-between foraging bouts. Females also dived significantly deeper than males during the middle of the day, but at dawn and dusk they dived at the same shallower depths as males. These temporal patterns in dive depth may be related to changes in light penetration into the water column through the diel cycle, influencing where birds can forage and/or the vertical migration of their prey (Wilson *et al.* 1993; Wanless *et al.* 1999). In particular, low light penetration at dawn and dusk may have forced females to forage at the same shallow depths as males did during these periods. Woo *et al.* (1999) similarly reported a difference in dive depths between male and female thick-billed murres *Uria lomvia*, also a monomorphic species. Females made deeper dives than males, yet in this species females are diurnal foragers whereas males are nocturnal. In our study, we found differences in dive depth between the sexes operating under the same light conditions, in the middle of the day.

The fact that we have observed sexual differences in the foraging behaviour of a monomorphic seabird raises the possibility that differences reported in sexually dimorphic species (table 1) are not mediated exclusively by differences in body size. Sexual differences in foraging behaviour could have arisen for a number of other reasons, which are not necessarily independent. Moreover, different components of foraging behaviour may be related. For instance, sexual differences in foraging location may have an impact on dive depth, if prey associated with different foraging locations have different vertical distributions. Similarly, in this study, females that dived deeper also had greater inter-dive periods (probably because diving is energetically and physiologically demanding; Schmid *et al.* 1995), and this may have accounted, to some extent, for the longer total time that females spent on the sea surface. In the following paragraphs, we briefly discuss several potential proximate explanations for the sex-specific foraging patterns we have observed.

One possible explanation for the difference in foraging behaviour of males and females is that regardless of them being the same size, males are more effective than females at exploiting fish close to the sea surface, for instance by outcompeting females within the same feeding group. Such interference competition would force females to dive deeper or forage elsewhere. Despite behavioural differences between the sexes at the colony (Nelson 2002), there are no obvious morphological asymmetries that might give one sex a competitive advantage over the other while feeding at sea. Furthermore, our radio tracking data show that females do not forage exclusively in areas that are not used by males, which might be expected if competition were driving these differences. Another possibility is that the two sexes differ in their abilities to capture prey at particular depths. If females are better able to exploit deeper-swimming fishes which are found in particular areas of sea, then not only would the sexes tend to show different diving behaviour, but they might also tend to feed in different areas. Clearly, to test this idea one would need to examine the diving abilities of the two sexes in more detail.

Our results suggest that females are more restricted than males in the areas where they forage, and one possibility is that this is driven by sexual differences in energy or nutrient requirements. These differential requirements could arise, for instance, from differences between sexes in the timing or extent of feather moult (Hemborg *et al.* 1998; Hemborg 1999*a*, 1999*b*). Moulting is an energetically expensive process (Hull *et al.* 2001), which begins at the onset of hatching in northern gannets, and continues until late autumn (Nelson 2002). It is not known whether there are sex-specific differences in moult in gannets, but such differences do occur in other seabirds (Weimerskirch 1991) and could potentially create temporary sex differences in dietary needs and/or foraging abilities. Alternatively, the need for nutrients related to reproduction has been shown to influence females' dietary requirements (Carey 1996). For example, calcium deficiency greatly limits eggshell quality and even reproductive success in great tits *Parus major* (Graveland & Drent 1997), and prior to egg laying both female common terns and magellanic penguins *Spheniscus magellanicus* ingested more mollusc shells than males (Nisbet 1997; Boersma & Stokes 1999), presumably from the area around their nests, to improve their calcium nutrition. If female gannets do not have access to such a food source at their colonies then, despite the fact that they lay only one small egg (Nelson 2002), females may still need to restore their calcium levels post-laying by some means, for example, by selecting prey species with a high calcium content. Thus, if nutritionally

important prey species were found at specific areas and/or depths, then selection for these species by one sex in particular, might lead to the observed sex differences in foraging behaviour. Unfortunately, there are currently no data available on the diets of northern gannets that would allow us to compare intakes of key nutrients between the sexes.

By using specially designed instruments to monitor the foraging behaviour of northern gannets at sea, we have shown that even monomorphic seabirds can exhibit significant sexual differences in their foraging characteristics. In particular, females tended to forage in a more restricted location than males, made deeper dives and spent longer resting on the sea surface. As this is one of the first studies to look at the foraging behaviour of monomorphic seabirds, we do not know how general our results are. However, we have demonstrated significant sexual differences in foraging behaviour in the absence of sexual-size dimorphism, and this in itself raises some important questions, which may have implications for our understanding of the foraging ecology of seabirds and other species.

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