Sex-specific foraging behaviour in northern gannets *Morus bassanus*: incidence and implications

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ABSTRACT: Sexual segregation in foraging and migratory behaviour is widespread among sexually dimorphic marine vertebrates. It has also been described for a number of monomorphic species, yet the underlying mechanisms are poorly understood. We examined variation among years, seasons and age-classes in sex-specific foraging and over-wintering behaviour in the northern gannet *Morus bassanus*, a species with slight sexual dimorphism. Our results revealed consistent sexual differences in the stable isotope ratios of breeding birds: over 3 different breeding periods, adult females consistently consumed prey with significantly lower $\delta^{13}C$ and $\delta^{15}N$ values than adult males. Additionally, GPS tracking data showed that breeding females foraged further offshore than breeding males (a result consistent with the $\delta^{13}C$ data), and the home ranges of the 2 sexes were distinct. Analyses of stable isotope ratios using a Bayesian mixing model (SIAR) revealed that breeding males consumed a higher proportion of fishery discards than females. Analysis of stable isotope ratios in red blood cells of immature gannets (aged 2 to 4) indicated that sexual segregation was not present in this age-class. Although sample sizes were small and statistical power correspondingly low, analysis of geolocator data and of stable isotope ratios in winter-grown flight feathers revealed no clear evidence of sexual segregation during the non-breeding period. Together these results provide detailed insight into sex-specific behaviour in gannets throughout the annual cycle, and although the mechanisms remain unclear they are unlikely to be explained by slight differences in size.

KEY WORDS: Sexual segregation · Stable isotope · Foraging ecology · Breeding season · Non-breeding · Fishery discards

INTRODUCTION

Many marine and terrestrial animals exhibit clear sex-related differences in foraging behaviour and distribution (e.g. Main et al. 1996, Conradt 1998, González-Solís et al. 2000, Bowyer 2004, Bearhop et al. 2006, Paredes & Insley 2010). These are often thought to be mediated via sexual size dimorphism, resulting in differences in dominance, foraging behaviour, flight efficiency and competitive ability (reviewed in Wearmouth & Sims 2008). However, focusing on size alone may impede our ability to fully understand the range of mechanisms that may underlie sexual segregation, since a number of studies

demonstrate gender-specific foraging behaviour and distribution in the absence of sexual dimorphism.

Sex-specific foraging has been described for a number of monomorphic birds, particularly seabirds (Wiggins & Morris 1987, Gray & Hamer 2001, Fraser et al. 2002, Lewis et al. 2002, Thaxter et al. 2009). While the underlying mechanisms are not fully understood, differences during the breeding season have been attributed to sex-specific provisioning behaviour and differential parental roles (e.g. Gray & Hamer 2001, Quillfeldt et al. 2004, Thaxter et al. 2009), inter-sexual competition (Peck & Congdon 2006), or sex-specific habitat specialisation (Phillips et al. 2004b). Moreover, nutritional investment by the female into the developing egg (Carey 1996, Mousseau & Fox 1998) could lead to sex-specific differences in prey choice during the breeding season (e.g. Nisbet 1997, Lewis et al. 2002).

Previous work studying sex-specific foraging behaviour of monomorphic seabirds has primarily focused upon differences among breeding adults. During this time of the year, the differing parental duties of males and females may do much to influence sex-specific foraging behaviour (Weimerskirch et al. 2009a,b). Moreover, foraging ranges are constrained, such that sex-specific foraging patterns may be dictated by intersexual competition for resources close to the colony (Peck & Congdon 2006, Phillips et al. 2011), by differing parental roles (Weimerskirch et al. 2009b), or nutritional investment (Lewis et al. 2002). In contrast, during the non-breeding season, seabirds are freed from reproductive constraints and often forage far offshore. Hence, only with the recent development of miniaturised tracking devices and forensic approaches to diet reconstruction has it become possible to examine sex-specific foraging behaviour during this time (Croxall et al. 2005, Phillips et al. 2005, 2009, 2011). These same techniques also provide an opportunity to study the large number of immature birds that are a feature of many seabird populations (Votier et al. 2008, 2011), but this age-class has not previously been studied with regard to sex-related differences in behaviour. To better understand the ecological and evolutionary importance of sex-specific foraging in the absence of clear dimorphism requires an understanding of segregation *throughout* the annual cycle and across multiple age-classes.

Understanding inter-sexual differences in behaviour has important implications for breeding biology and population ecology. If the sexes segregate into different areas, the key oceanographic processes and threats affecting each group could potentially be quite different. For example, this could lead to sex-

specific responses to climate change (Grosbois & Thompson 2005), or sex-specific differences in fisheries bycatch mortality (Gales et al. 1998).

Here we provide a detailed study of sexual segregation in the northern gannet *Morus bassanus*, hereafter gannet, a species with little or no dimorphism (Cramp et al. 1977), using a combination of stable isotopes as trophic markers in tandem with GPS and geo-location loggers to examine spatial segregation during the breeding and non-breeding periods. To determine the degree of sexual segregation during the breeding season we compare stable isotope ratios of red blood cells from incubating and chick-rearing adults (aged 5+) during 3 yr and also test whether there are sex-related isotopic differences in immature birds (aged 2 to 4) attending the colony. Using GPS loggers, we examine whether adult males and females are spatially segregated at sea during the breeding period. In addition, we use stable isotope ratios of primary feathers (grown during the winter) together with data from geolocators to examine the degree of sexual segregation of birds of breeding age during the winter period. To our knowledge, this is the first study to examine sexual segregation in a species with little or no dimorphism throughout the annual cycle, in multiple years and between different age-classes. Here we test a number of hypotheses regarding sexual segregation in gannets: (1) adult gannets exhibit sexual differences in stable isotope ratios and foraging locations during the breeding season; (2) sexual segregation during the breeding season is maintained across multiple years and thus is of ecological and evolutionary significance, and independent of inter-annual environmental variability; (3) there are sex-specific differences in the use of fishery discards (in light of recent evidence showing intra-population variation in scavenging behaviour; Votier et al. 2010); (4) adult gannets do not exhibit sex-specific foraging behaviour during the non-breeding period when there are no parental duties, foraging ranges are unconstrained and intra-specific competition is less intense; and (5) sex-specific foraging behaviour is absent in immature gannets during the breeding season because of the lack of parental duties.

MATERIALS AND METHODS

Study site and sampling

Work was conducted during June to August 2006, 2008 and 2009 at Grassholm, Wales (51° 43' N, 05°

28' W), which holds approximately 40 000 pairs of breeding northern gannets as well as several thousand immatures and other pre-breeders. Gannets return to the colony from early January, commence breeding from mid-April to mid-June, and depart in September to October (Kubetzki et al. 2009).

Gannets were caught using a brass noose attached to the end of a pole; breeding adults were caught at the nest during chick-rearing (and a single bird during incubation) (n = 36, 2006; n = 40, 2008; n = 27, 2009). Males and females were sampled in equal numbers throughout the breeding season (Table 1), which reduced any potentially confounding seasonal effects. During 2009, immature gannets, (aged 2 to 4 yr, n = 32) were caught while attending club sites (non-breeding aggregations) at the fringe of the colony and aged on the basis of plumage morphology (Votier et al. 2011). Under licence from the UK Home-Office, approximately 0.2 ml of blood was taken from the tarsal vein using 23 gauge needles. Shortly after sampling, blood samples were separated into red blood cells (RBC) and serum using a centrifuge. RBCs were stored frozen prior to DNA and stable isotope analysis.

DNA was extracted from freeze-dried RBCs (approximately 0.7 ± 0.1 mg) using an ammonium acetate protocol (e.g. see Nicholls et al. 2000). Gannets were genetically sex-typed by polymerase chain reaction (PCR) amplification of the sex-linked chromo-helicase-DNA-binding gene (CHD), using the primers 2550F and 2718R, by adapting methods from Fridolfsson & Ellegren (1999).

To investigate morphological differences between the sexes we took the following measurements in 2006; maximum flattened wing chord, bill length (to feathering), maximum tarsus (Redfern & Clark 2001) and body mass (to the nearest 50 g). These birds were sampled just before departure from the colony at the end of their incubation or brooding shift, and therefore are assumed to have empty stomachs.

Table 1. *Morus bassanus.* Northern gannet sampling during the breeding season in 2006, 2008 and 2009 on Grassholm, Wales, revealed no sex-related differences in sampling period

Year	Sampling period	Males (n)	Females (n)
2006	17–19 Jun	11	9
	12–13 Jul	9	7
2008	17–18 Jul	18	22
2009	23–25 Jun	2	0
	10 Jul	0	1
	12–13 Aug	15	9

Stable isotope analysis

In order to examine sex-specific dietary niches and prey preferences during the breeding and non-breeding periods, we analysed stable carbon and nitrogen isotope ratios in RBCs, and, for a subsample of birds with geolocators, the third outermost primary feather (P8). Avian erythrocytes have a lifespan of 28 to 45 d (Rodnan et al. 1957) and thus most likely represent assimilated prey over the previous 4 to 6 wk. Adult gannets undergo a complete postbreeding moult with primary feathers serially descendant (July to December; Cramp et al. 1977). P8 will be replaced late in the moult cycle and should therefore represent winter diet.

In general, the ratio of ^{15}N to ^{14}N (expressed as $\delta^{15}N$) increases by 3 to 5‰ with each trophic level (DeNiro & Epstein 1981, Hobson & Clark 1992, Bearhop et al. 2002). Although the ratio of ^{13}C to ^{12}C (expressed as $\delta^{13}C$) also increases with trophic level (approximately 1‰; Rau et al. 1992), the main causes of variation in $\delta^{13}C$ are differences in photosynthetic biochemistry within and among marine primary producer communities (Farquhar et al. 1989, Robinson 2001). Hence, in marine ecosystems, $\delta^{13}C$ signatures are used to infer the origin of a food item from the $\delta^{13}C$ gradients that exist between water masses, as well as gradients between inshore/offshore waters, and benthic/pelagic habitats (Cherel & Hobson 2007, Newsome et al. 2007).

Isotope analysis was conducted at the Natural Environment Research Council (NERC) Life Sciences Mass Spectrometry Facility in East Kilbride, UK. Before analysis, primary feathers were washed in a detergent solution, and rinsed in a 2:1 chloroform:methanol solution (Paritte & Kelly 2009) and left to dry for 15 min. Only the first 1.5 cm of primary feathers (excluding material from the rachis) was cut up into fine fragments. RBC samples were freeze-dried and ground to powder. Approximately 0.7 mg (±0.1 mg) of each tissue was weighed into a tin capsule, combusted and oxidized in a Costech ECS 4010 elemental analyser, with the respective isotope ratios of carbon and nitrogen of the CO_2 and N_2 gas output measured by a Thermo Electron Delta Plus XP mass spectrometer. For both carbon and nitrogen, Alanine 14, Alanine 15, Tryptophan and in-house gelatine were used as standards. While the gelatine quantifies the size effect on uncorrected stable isotope ratios, tryptophan serves as a standard for elemental ratios. Precision was 0.1 and 0.2‰ for carbon and nitrogen isotope measurements, respectively.

Isotope ratios (R) of $^{15}N/^{14}N$ and $^{13}C/^{12}C$ are expressed in delta (δ) units, as parts per thousand (‰) difference from an international standard, where: $\delta^{13}C$ or $\delta^{15}N = [(R\,sample/R\,standard) - 1] \times 1000$. The international standards (= 0‰) for stable isotope analysis are atmospheric N_2 (AIR) for nitrogen and Pee Dee Belemnite (V-PDB) for carbon.

To estimate the relative contribution of different prey types to the diet of male and female gannets during 2006, we used the Bayesian stable isotope mixing model SIAR (Moore & Semmens 2008, Jackson et al. 2009, Parnell et al. 2010). We used the means and standard deviations of 4 food sources (Table 2), obtained from gannets that spontaneously regurgitated upon capture: (1) mackerel *Scomber scombrus* (n = 6), (2) garfish *Belone belone* (n = 6), (3) sprat *Sprattus sprattus* (n = 1; but made up of several animals) and (4) whitefish (n = 6) (haddock *Melanogrammus aeglefinus*, pollock *Pollachius pollachius*, red gurnard *Aspitrigla cuculus* and unidentified gadoid). Whitefish were assumed to be discards from fishing vessels because, after an initial planktonic phase during the first few years of life, these species occur at depths outside the known diving range of gannets. Gannets can only reach depths of ~11 m by plunge-diving, or ~24 m if wing-propulsion is used (Ropert-Coudert et al. 2009), and thus forage in areas too shallow for benthic prey. As there have been no controlled studies to determine gannet-specific trophic enrichment factors (TEFs), and TEFs can vary significantly between different orders and species (Caut et al. 2009), we calculated average values from multiple studies of piscivorous birds (Hobson & Clark 1992, Thompson et al. 1999, Bearhop et al. 2002, Forero et al. 2002, Cherel et al. 2005) to generate TEFs to inform our model: 2.25 (±0.61) for nitrogen and 0.24 (±0.79) for carbon. The intra-population differences in discard consumption have been published elsewhere (Votier et al. 2010), but not in relation to sex.

Table 2. Stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) of the 4 prey types (source values in the mixing model) of northern gannets sampled during 2006. Values are means ± SD

Prey	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Discarded whitefish	6	−17.03 ± 0.76	15.14 ± 0.64
Garfish	6	−17.28 ± 0.81	13.68 ± 1.34
Mackerel	6	−19.17 ± 0.34	11.89 ± 0.86
Sprat	1	−17.43	12.52

GPS tracking

During 2006, GPSlog loggers (Earth & Ocean Technologies) weighing 65 g were attached to the base of the tail feathers of 23 adult gannets (10 females and 13 males) using Tesa© tape, and retrieved following a single complete foraging trip. The loggers were programmed to record a fix every 2 min and in this mode; 90% of the fixes were within 19 m of the 'true' location (Earth & Ocean Technologies).

Duration and total distance travelled during foraging trips were compared between males and females. In addition, we examined sex-specific differences in home-ranges (95% volume contour) and core foraging areas (25% volume contour) from fixed kernel density estimation in a European Albers equal-area conic projection, using a smoothing parameter (h) of 10 km and a cell size of 1 km^2. This smoothing parameter was selected because the mean scale of area-restricted search behaviour in gannets is 9.1 ± 1.9 km (Hamer et al. 2009).

Geolocation tracking

During 2007 and 2009 we deployed 12 Earth & Ocean Technology (E&OT) and 20 mk5 British Antarctic Survey (BAS) geolocators on breeding gannets. We recovered 20 devices (6 E&OT and 14 BAS) during 2008, 2009 and 2010 (8 females and 12 males). Although devices were recovered across multiple years, gannets exhibit extremely high inter-annual over-winter site fidelity (Grecian 2011).

Positional information was calculated from logger data following standard methods (Wilson et al. 1992, Phillips et al. 2004a). Briefly, geolocation relies on estimating the timings of sunset and sunrise using set thresholds in the light curves recorded by the datalogger. Latitude can be derived from day length and longitude from the timing of local mid-day and midnight, with respect to Greenwich Mean Time and the day of the year, providing 2 positions per day with an accuracy of circa 186 ± 114 km (Phillips et al. 2004a). However, around the vernal and autumnal equinoxes, day and night are of equal length, and so it becomes impossible to estimate latitude.

Light curves were analysed for BAS loggers using BAS TransEdit and BirdTracker software and for E&OT loggers using Multitrace Geolocation from Jensen Software Systems. Light thresholds and elevation angles were estimated on the basis of calibration data from fixed points and knowledge of likely wintering areas relative to major land masses. We

removed obviously erroneous locations associated with interference in light curves around the time of sunset and sunrise. Location errors can occur through shading of the tag sensor and during equinox periods. All positions recorded up to 10 d either side of the equinox were removed, as well as any fix obviously affected within 4 wk of the equinox. Validated data were smoothed twice to reduce the error associated with geolocation (Phillips et al. 2004a).

We also used kernel density estimation to identify the wintering ranges of adult males and females, using a cell size of 25 km^2 and a smoothing factor (h) of 200 km, which reflects the estimated error associated with geolocation (Phillips et al. 2004a). All kernel density estimation was carried out in ArcGIS 9.3 (ESRI) using the Spatial Analyst Toolbox and Hawth's Tools (Worton 1989).

Statistical analysis

We examined the isotope data for evidence of sexual segregation using multivariate analysis of variance (MANOVA Pillai's trace; V) for RBC, in breeding (5+ yr) and immature (2 to 4 yr old) gannets separately. The dependent variables were δ^{15}N and δ^{13}C, and fixed factors were year (for breeders only) and sex. Although δ^{13}C data for adults had unequal variances, analytical residuals did not deviate from expectation and thus MANOVAs were performed without transformation. If overall differences were detected we conducted post hoc univariate general linear models (GLMs). For MANOVAs we included an estimate of power (based on an alpha of 0.05) as a measure of the likelihood of falsely accepting the null hypothesis.

For breeders captured in 2006 we tested for differences between sexes in morphology, trip duration and distance travelled using t-tests. We also examined the proportion of breeders wintering in 1 of 3 core areas, based on their wintering destination relative to the Straits of Gibraltar (36°N meridian): to the north

(northern), south (southern), or to the east (Mediterranean) using contingency tables. Moreover, we tested for qualitative differences in stable isotope values in P8 among males and females that wintered in these different areas. All data were normally distributed. Data analysis was carried out using SPSS 18.0.

RESULTS

Morphological comparisons

In general, there was little sexual dimorphism in the length of the tarsus, bill, or wing of breeding gannets (Table 3). However, females were significantly heavier than males, by an average of approximately 250 g (Table 3).

Stable isotope ratios in tissues of breeding birds

Analysis of RBC from breeding gannets indicated that there were statistically significant differences between sexes and among years in their isotopic values (Sex: $V = 0.376$, $F_{2,96} = 28.904$, p < 0.001, power = 100%; Year: $V = 0.845$, $F_{4,194} = 35.476$, p < 0.001, power = 100%). Post hoc GLMs for δ^{15}N revealed significant Sex and Year effects, with no interaction (Sex effect: $F_{1,102} = 50.441$, p < 0.001, power = 100%; Year effect: $F_{2,102} = 14.809$, p < 0.001, power = 100%; Sex × Year effect: $F_{2,102} = 1.477$, p = 0.233; power = 30.9%). Males had significantly higher δ^{15}N values compared with females (Fig. 1). Post hoc GLMs for δ^{13}C also showed significant Sex and Year effects, as well as a significant interaction (Sex effect: $F_{1,102} = 50.589$, p < 0.001, power = 100%; Year effect: $F_{2,102} = 14.956$, p < 0.001, power = 99.9%; Sex × Year effect: $F_{2,102} = 4.944$, p = 0.009, power = 79.8%). Males had significantly higher δ^{13}C values compared with females, although the extent of this difference varied across years (Fig. 1).

Stable isotope mixing models

Based on SIAR outputs for breeders sampled in 2006, there were differences between males and females in the relative contribution of the 4 main prey types to the diet (Fig. 2). In general, males consumed higher proportions of discards and garfish, and lower proportions of mackerel, compared with females.

Table 3. *Morus bassanus.* Comparison of body measurements of male and female northern gannets breeding on Grassholm, Wales, in 2006. Values are means ± SD. *** p < 0.001

	Males (n = 20)	Females (n = 16)	t-statistic
Tarsus length (mm)	73.1 ± 1.54	74.2 ± 2.58	−1.49[a]
Bill length (mm)	98.5 ± 3.75	100.9 ± 3.33	−2.02
Wing length (mm)	496.9 ± 8.68	496.2 ± 10.41	0.22
Mass (g)	2956.0 ± 140.24	3209.4 ± 211.52	−4.12***

[a]t-test on unequal variances
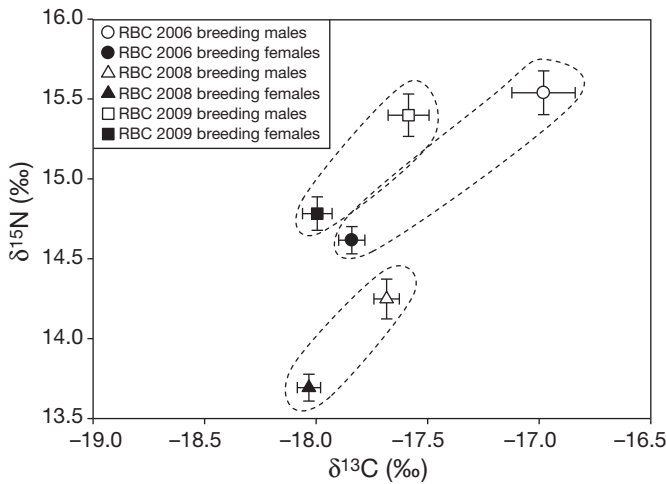
Fig. 1. *Morus bassanus.* Mean (±SE) $\delta^{13}C$ and $\delta^{15}N$ values in red blood cells (RBC) of breeding northern gannets. Males showed consistently higher $\delta^{13}C$ and $\delta^{15}N$ than females (ellipses enclose data collected in the same year). A significant Year × Sex interaction revealed that the extent but not the direction of the effect of sex varied among years (2006: n = 16 females, n = 20 males; 2008: n = 22 females, n = 18 males; 2009: n = 10 females, n = 17 males)

Stable isotope ratios of immature birds

Analysis of $\delta^{13}C$ or $\delta^{15}N$ values in RBCs of immature birds caught in 2009 revealed no difference between the sexes during the breeding season (RBC: $V = 0.021$, $F_{2,29} = 0.323$, p = 0.738, power = 9.4%). Immature gannets were isotopically segregated from breeding birds (Fig. 3).

GPS tracking

There was clear segregation between the 95% kernel density distributions (representing home ranges) and 25% kernel density distributions (representing foraging locations) of males and females tracked in 2006 (Fig. 4). Females mainly foraged in offshore/pelagic waters (Fig. 4) and travelled significantly further than males (females: 519.17 ± 226.97 km, n = 10; males 265.63 ± 122.21 km, n = 13; $t = 3.19$, df = 12.98, p = 0.007). Males typically foraged near the colony (Fig. 4) and in inshore waters along the coast of Wales and southern Ireland. Although the foraging trip durations of females were on average longer than those of males, this difference was not statistically significant (females: 31.22 ± 12.20 h, n = 10; males 21.93 ± 16.09 h, n = 13; $t = 1.52$, df = 21, p = 0.14).
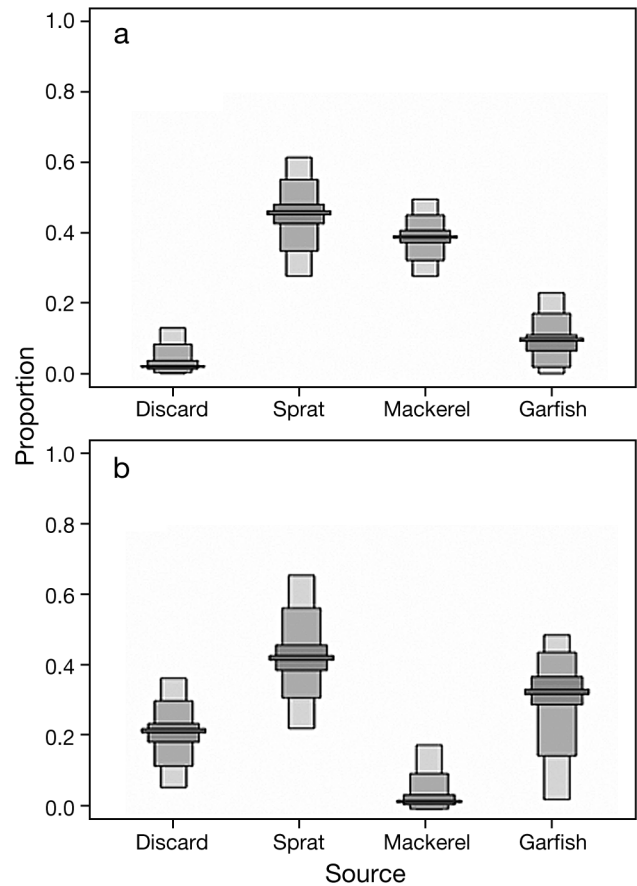

Fig. 2. *Morus bassanus.* Estimated contribution of 4 prey types (fishery discards, sprat, mackerel and garfish) to the diet of (a) female and (b) male northern gannets during the breeding season in 2006. Central horizontal line is the median value; bars represent 50, 75 and 95% credibility intervals from Bayesian mixing models (SIAR)
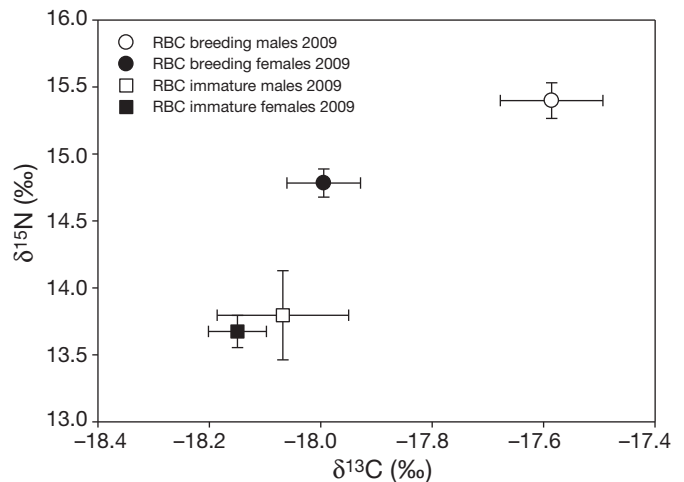

Fig. 3. *Morus bassanus.* Mean (±SE) $\delta^{13}C$ and $\delta^{15}N$ values in red blood cells (RBC) of immature and breeding northern gannets by sex during 2009 (immatures: n = 23 females, n = 9 males; breeders: n = 10 females, n = 17 males)
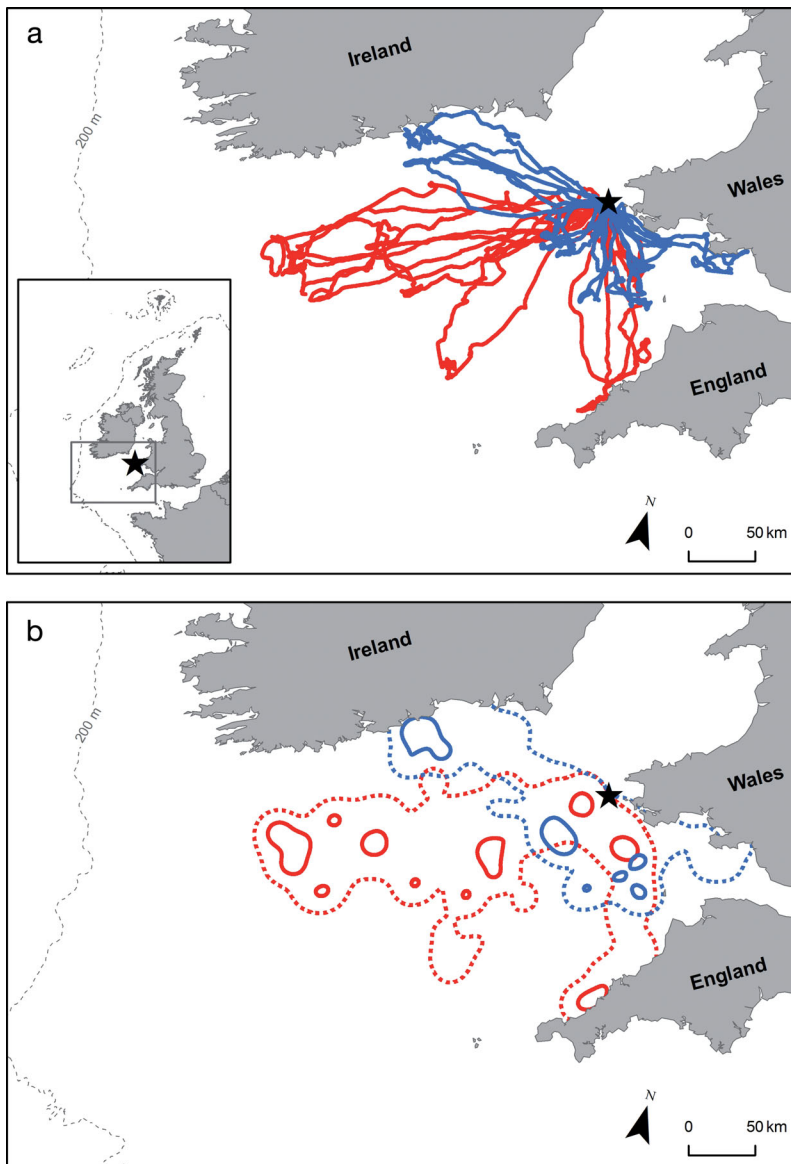
areas categorised as northern, southern, or Mediterranean (Table 4c χ^2_1 = 1.033, p = 0.309). Although sample sizes were small, there was no obvious difference between males and females in stable isotope values in flight feathers grown in different regions (Fig. 6).

DISCUSSION

The present study is the first to investigate sex-specific foraging behaviour in immature (2 to 4 yr old) and breeding (5+ yr old) gannets during both the breeding and interbreeding periods, and in multiple years. Several clear results emerged, key amongst which was that spatial and dietary sexual segregation is evident among adult gannets during the breeding season, and that these behavioural strategies were maintained across years. In contrast, we found no evidence for sexual segregation during the non-breeding period, nor among immature birds.

Sexual segregation among breeders

During the breeding season, male gannets had significantly higher $\delta^{13}C$ and $\delta^{15}N$ values than females, and, although the extent of segregation varied, this pattern remained consistent in 3 breeding seasons (Fig. 1). This inter-annual variation does not necessarily represent a change in the trophic level of prey, but is instead likely to reflect variation in the baseline isotopic signatures arising from ecosystem-wide changes such as shifts in primary production or nutrient inputs (Yoshioka et al. 1994). Alternatively, it could represent a change in the types of fish caught and subsequently discarded by fishermen that are then eaten by gannets.

Female gannets had lower $\delta^{13}C$ values in RBCs compared with males, which may arise because of spatial or trophic differences in diet. Compared to coastal waters, offshore areas tend to be more depleted in ^{13}C (Hobson et al. 1994, Cherel & Hobson 2007, Graham et al. 2010). Although we cannot

Fig. 4. *Morus bassanus*. Foraging ranges of male (blue, n = 13) and female (red, n = 10) northern gannets with eggs (1 bird) or chicks during the breeding season in 2006: (a) raw GPS tracks and (b) kernel density volume contours (dotted lines: 95%; solid lines: 25%). Breeding colony is indicated with a star. Kernel smoothing parameter (*h*) = 10 km, cell size = 1 km

Geolocator tracking

Gannets from Grassholm wintered in a range of different regions, including the Celtic Sea, English Channel, Bay of Biscay, Mediterranean, Iberian Peninsula and the Canary Current upwelling region (Fig. 5). There was no clear difference in the broad-scale distribution of male and female gannets during this period (Fig. 5). Moreover, there was no difference in the distribution of the sexes by wintering

Fig. 5. *Morus bassanus*. Wintering distributions of male (blue, n = 12) and female (red, n = 8) northern gannets tracked from Grassholm, Wales, during 2007/2008 (n = 7) and 2009/2010 (n = 13); kernel density volume contours (dotted lines: 95%; solid lines: 25%). Breeding colony is indicated with a star. Kernel smoothing parameter (*h*) = 200 km, cell size = 25 km

Table 4. *Morus bassanus*. Wintering locations of male and female northern gannets tracked using geolocators (in percent of total number of each sex). Wintering areas were categorised in relation to the Straits of Gibraltar (36°N meridian): northern, southern and Mediterranean

Wintering region	Males	Females
Northern	25%	37.5%
Mediterranean	8%	0
Southern	67%	62.5%
Total no. of birds	12	8

exclude the possibility that the lower $\delta^{13}C$ values found in RBCs of females relate to differences in prey trophic levels, the likelier explanation based on the GPS-tracking data from 2006 is that this isotopic difference reflects the greater time that females spend foraging in waters further from the colony (Fig. 4).
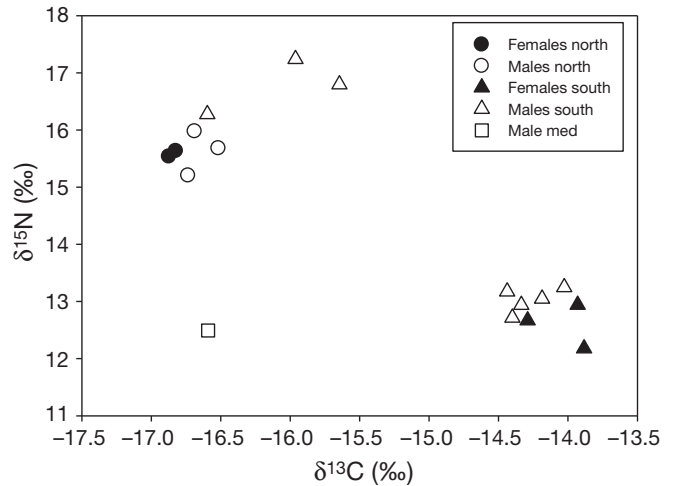

Fig. 6. *Morus bassanus*. $\delta^{13}C$ and $\delta^{15}N$ values in wintergrown primary feathers (P8) of male and female breeding northern gannets. All birds have been grouped by wintering location determined using geolocators. North and south categories represent the core wintering areas relative to the Straits of Gibraltar (36°N meridian), and 'med' represents 1 male wintering in the Mediterranean

Differences in $\delta^{15}N$ suggest that male gannets feed at a higher trophic level than females. Inshore waters tend to have longer food-chains because of stronger benthic–pelagic coupling compared with the open ocean (Forero et al. 2004), which would generate higher $\delta^{15}N$ values in the more inshore foraging males (Fig. 4b). While this is possible, it is not clear whether this would apply in the study region because the offshore waters used by females are still on the continental shelf. A more likely explanation for sex differences in trophic level in gannets may therefore be that males eat a greater proportion of fishery discards (Fig. 2). Differences in discard use could reflect the relative density of fishing vessels within the respective home ranges of males and females (Witt & Godley 2007, Votier et al. 2010), or that females preferentially feed on oily fish such as mackerel and sprat instead of low-fat, discarded whitefish, perhaps to replace nutrients lost during egg formation. However, given the proportionately small size of the single gannet egg and that egg-laying occurred several months prior to blood sampling, this latter option seems unlikely. Alternatively, sex-related differences in competitive ability could favour males behind fishing vessels if it influences the outcome of scramble competition.

Morphological comparisons

Despite no statistically significant differences in body measurements, female gannets tended to be

larger and were significantly heavier than males by an average of 250 g (Table 3). It is not clear whether these slight differences are maintained throughout the annual cycle or arise because of differences in body condition. For instance, males may be in poorer condition because they spend more time on land in nest defence (Nelson 2002), because of more intense competition closer to the colony, or because of a diet with a higher proportion of lean discarded whitefish or a combination of these. Previous work has shown that female gannets dive deeper than males (Lewis et al. 2002), and, in other seabirds, the heavier sex also tends to dive deeper (Phillips et al. 2011). However, even if differences in mass do represent a dimorphic trait, they do not explain all sex-specific differences in gannet foraging — normally the larger or heavier birds forage close to the colony (e.g. González-Solís et al. 2000), the reverse of what is reported here.

Sexual segregation during the non-breeding period

Our analysis of tracking data collected using geolocators shows that gannets breeding at Grassholm exhibit wide inter-individual variation in wintering regions, with no clear broad-scale differences between sexes (Table 4, Fig. 5). There was a suggestion that birds wintering in southern regions had different isotope values in winter-grown feathers, but there was no evidence of sex-related differences within wintering regions (Fig. 6). However, sample sizes were small, and collection spanned multiple years; hence, we cannot completely exclude the possibility that sex-specific foraging segregation exists during the winter period.

Sexual segregation among immatures

Immature gannets (aged 2 to 4 yr) sampled during summer 2009 showed no evidence of sexual segregation based on stable isotope ratios in RBC (Fig. 3). Immature gannets travel much more widely than breeders during the summer (Votier et al. 2011), and are likely to feed in waters with a wider range of baseline isotope signatures. Testing for inter-sexual differences using isotopes is therefore problematic; statistical power was low (9.4%), and so we cannot completely exclude the possibility that sex differences in diet or location exist. Further work combining tracking data and isotopes would be required to study this in more detail.

Potential mechanisms underlying sexual segregation

Factors driving sexual segregation in breeding gannets are poorly understood. The slight dimorphism reported here suggests different drivers compared with other seabird taxa which seem to relate mainly to sexual size dimorphism (Phillips et al. 2009, 2011). Female gannets may choose to feed in different areas from males to satisfy particular dietary needs, as suggested by Lewis et al. (2002); however, there are currently no data on the fine-scale distribution of different prey to test this. Alternatively, females may be displaced by inter-sexual competition, but there is no evidence that males are able to out-compete the similarly sized (yet heavier) females either at fishing vessels or at-sea. Different parental roles could lead to sexual segregation as in other dimorphic Sulidae (Weimerskirch et al. 2006, 2009a,b). Male gannets invest more in nest defence than females (Nelson 2002), which could in theory reduce time available for feeding and lead to differences in foraging ranges. However, despite the longer distances travelled by females, they did not spend significantly more time away from the nest than males. Further work investigating sex-specific provisioning rates, meal sizes and nest attendance is required to better understand how parental roles may influence sex-specific differences in gannets.

Conservation implications

Sexual segregation may lead to differences in the risk of exposure to a wide range of potential environmental impacts such as oil pollution (Votier et al. 2005, 2008), offshore renewable energy installations (Grecian et al. 2010), climate variation (Grosbois & Thompson 2005), or fisheries bycatch (Gales et al. 1998). Currently, levels of gannet bycatch are thought to be very low in the NE Atlantic; nevertheless, an estimated 1331 gannets per year were caught by the Gran Sol Fishery during 2006/2007 (BirdLife International 2009). Differences in discard use by male and female gannets (Fig. 2) suggest that males will be more susceptible to this type of negative fishery interaction. Forthcoming reforms of the EU Common Fisheries Policy (OCEAN '2012' 2010) are expected to significantly reduce discarding levels, which may have a disproportionate impact on males either reducing an important resource or decreasing bycatch risk. Further work is therefore required to

better understand the ecology of scavenging and also to investigate both the positive and negative effects of this food subsidy (Grémillet et al. 2008, Votier et al. 2010).

Conclusions

The sex differences described here for the breeding season are consistent with previous work on this species (Lewis et al. 2002), but the tendency for females to travel longer distances during foraging trips has not been reported previously. Overall our results suggest that parental roles influence sexual segregation in breeding gannets, but more accurate and detailed assessment of adult time budgets, provisioning rates and fine-scale foraging behaviour at sea are required. We found no evidence of sexual segregation during the non-breeding season or for immature gannets, hinting that reproduction is a key driver of sexual segregation in this species. However large variation in isotopic baselines over the very broad foraging ranges of these gannets means that these conclusions are tentative, pending the collection of further isotope and tracking data. Sex-specific differences in discard use suggested by the analysis of blood isotope levels could be confirmed by integrating fine-scale foraging behaviour collected using GPS, dive, immersion, accelerometer, or camera loggers with data from vessel monitoring systems. By integrating these results with information on feeding frequency, meal mass and energy content it will be possible to understand in detail the likely consequence of these different behaviours.

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