Testing for sub-colony variation in seabird foraging behaviour: ecological and methodological consequences for understanding colonial living

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ABSTRACT: Intraspecific interactions have important roles in shaping foraging behaviours. For colonial species such as seabirds, intense competition for prey around colonies may drive differences in foraging behaviour between age-classes and sexes or lead to individual specialisation. While much research has focussed on understanding these differences in foraging behaviour, few studies have investigated the possibility of sub-colony foraging asymmetries within colonies. Such knowledge could improve our understanding of the ecological processes associated with colonial living. It may also have important methodological implications in studies where the foraging behaviours recorded from individuals in a small number of sub-colonies are assumed to be representative of those from the colony as a whole. Here, we use GPS loggers and stable isotope analysis of red blood cells to test for differences in foraging behaviour among 7 sub-colonies of a large northern gannet *Morus bassanus* colony over 3 yr. We found no instances of statistically significant differences in foraging behaviour among sub-colonies. Although complimentary *in situ* observations found similarities among neighbours' departure directions, these results may be attributable to wind vectors. We therefore conclude that sub-colony foraging asymmetries are either limited or absent in northern gannets. However, given the current lack of knowledge across seabird species, we urge similar studies elsewhere.

KEY WORDS: *Morus bassanus* · Foraging ecology · Social information · GPS tracking · Stable isotope analysis · Colonial living

INTRODUCTION

Around 96% of seabird species form densely populated colonies (Coulson 2002). While the processes that ultimately led to the evolution of coloniality are unknown (Danchin & Wagner 1997), it is clear that intraspecific interactions among colony members play an important role in seabird ecology during the breeding season. Studying interactions among colony members has implications for both our under- standing of the ecological processes associated with colonial living (Wakefield et al. 2013) and conservation biology (Votier et al. 2007, Weimerskirch et al. 2010).

Intra-colony differences in individual foraging behaviour may be driven in part by intense intraspecific competition for prey around colonies. Foraging differences may arise because of age (Daunt et al. 2007, Votier et al. 2011) and sex (Wearmouth & Sims 2008), while individual-level specialisations independent of these factors are also increasingly apparent (Araújo et al. 2011). In addition, there may also be differences in foraging behaviour that arise because of spatial structuring of individuals within the colony, but these have been less well studied. For instance, colonies can often be divided into several discrete and isolated sub-colonies. An exchange of social information among neighbours at the nest site regarding the location of foraging opportunities (Ward & Zahavi 1973) could lead to at-sea segregation among sub- colonies. Alternatively, if colony members grouped themselves by age or intrinsic qualities (Velando & Freire 2001), then sub-colonies containing mainly older or more dominant individuals may forage closer to the colony or spend less time at sea (Catry & Furness 1999, Daunt et al. 2007, Votier et al. 2011). Therefore, sub-colony foraging asymmetries could offer useful insights into the ecological processes associated with colonial living, but such studies are scarce (Hipfner et al. 2007).

The presence of sub-colony foraging asymmetries could also have important methodological consequences. In recent years, there has been a rapid in- crease in the use of GPS loggers (Ropert-Coudert & Wilson 2005) and stable isotope analysis (SIA; Inger & Bearhop 2008) to study the foraging behaviour of colonial seabirds during the breeding season. Much of this work requires individuals to be captured at the nest site. However, because of problems of accessibility, individuals are rarely captured randomly throughout the colony. Instead, many are captured from a few easily accessible sub-colonies. In most cases, the foraging behaviours recorded from these individuals are then assumed to be representative of those from the colony as a whole (Soanes et al. 2013b). In the presence of sub-colony foraging asymmetries, these assumptions may be incorrect. This could have important implications in studies estimating colony-level impacts from marine renewable energy installations (Soanes et al. 2013a), commercial fisheries (Votier et al. 2010, 2013), marine pollution (Montevecchi et al. 2012) and climate change (Weimerskirch et al. 2012).

Here, we test for differences in foraging behaviour among 7 sub-colonies of a large northern gannet *Morus bassanus* (hereafter gannet) colony over 3 yr, during the chick-rearing stages. We used a combination of GPS loggers and SIA to quantify and then compare a range of individual foraging behaviours among sub-colonies. We also tested for similarities in neighbours' (individuals from the same sub-colony) initial flight directions at the start of their foraging trips by performing *in situ* observations in 1 sub-colony in 1 yr. Our overall aim was to determine the extent to which sub-colonies explained the variation in individual foraging behaviours within the colony. We then considered these results with regards to spatial structuring of individuals within colonies as well as the sampling design of GPS logger and SIA studies aiming to quantify the foraging behaviours of the colony as a whole.

MATERIALS AND METHODS

Study site and sampling

Fieldwork was conducted on Grassholm, Wales, UK (51° 43' N, 05° 28' W; Fig. 1a), in June and July 2006, 2010 and 2011. Approximately 40 000 pairs of gannets breed on Grassholm between April and October. We were able to access 7 sub-colonies without causing detrimental levels of disturbance to breeding birds (Fig. 1b). As northern and western sub-colonies were inaccessible, our sampling efforts were biased towards southern and eastern sub- colonies. However, in all cases, sub-colonies represented groups of neighbours that were isolated from the rest of the colony by topographic features such as valleys and rocky outcrops. Therefore, birds from one sub-colony were unable to see those from another sub-colony while at their nest site.

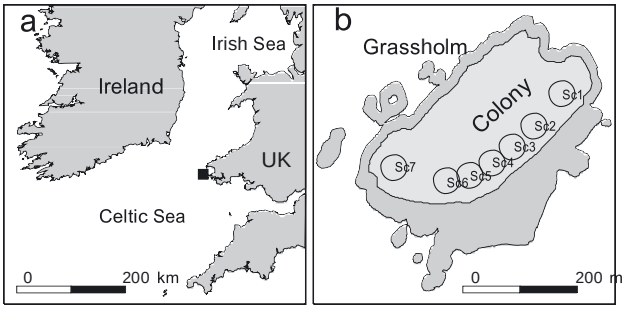

Fig. 1. *Morus bassanus*. Study sites. (a) Fieldwork was con- ducted on the large (~40 000 breeding pairs) northern gannet colony on Grassholm, Wales, UK, indicated by a black square. (b) We focused on 7 sub-colonies (Sc1 to Sc7) that were situated around the periphery of the colony. Sub- colonies were separated from one another by topographic features such as rocky outcrops and valleys. Therefore, birds from one sub-colony were unable to see those from another sub-colony while at their nest site

We caught 72 chick-rearing gannets at their nest sites using a brass noose or hook on a carbon-fibre pole, under licence from the Countryside Council for Wales. All birds were equipped with a GPS loggerwith permission from the British Trust for Ornithology (see 'GPS tracking', below), and blood was sampled (see 'SIA', below) under licence from the UKHome Office. Blood samples were also used for sub- sequent sexing using molecular techniques (Stauss et al. 2012). Following release, all birds flew off strongly with no obvious ill effects. Our sample sizes and dates are summarised in Table 1.

GPS tracking

We equipped all 72 birds with GPS loggers. In 2006, we used 65 g GPSlog loggers (earth&OCEANTechnologies), whereas in 2010 to 2011, we used 35 g i-gotu GPS loggers (Mobile Action Technology).These were attached to the base of the tail or lower back using Tesa® tape. Devices recorded GPS fixesat 3 and 1 min intervals in 2006 and 2010 to 2011, respectively. In many cases, devices recorded multiple foraging trips from a single bird. However, because gannets on Grassholm have consistent foraging behaviours within breeding seasons (Patrick et al. 2014), we only analysed the first foraging trip to prevent issues of pseudoreplication.

We calculated each bird's departure direction (°), distal direction (°), trip duration (decimal days), trip length (total distance covered, km) and range (maximum distance from the colony, km). Departure directions were calculated between Grassholm and their first location

Table 1. *Morus bassanus*. Sample sizes divided into sex, sub-colonies and years on Grassholm, UK. Also shown are sampling dates within each sub-colony (Sc1 to Sc7) by year. All birds were equipped with GPS loggers, and blood was sampled for stable isotope analysis

Year	Sampling date	Sub-colony	No. of males	No. of females
2006	12–14 July	Sc5	5	2
	12–14 July	Sc6	2	5
	17 June–14 July	Sc7	2	7
2010	6–11 July	Sc1	1	4
	5–11 July	Sc2	1	3
	5–11 July	Sc4	1	4
	6–12 July	Sc7	1	2
2011	23 June–13 July	Sc1	3	4
	10–22 July	Sc2	2	4
	10–22 July	Sc3	1	2
	27 June–23 July	Sc4	1	5
	27 June–23 July	Sc7	6	4

at 10 km distance from the colony, to exclude any rafting behaviour (resting on the sea surface) near the coastline. Distal directions were calculated between Grassholm and their most distant location from the colony. In addition to these 5 measurements, we also estimated each bird's core foraging areas using fixed kernel density estimation (KDE) with a smoothing parameter (h) of 10 km and a cell size of 1 km^2. This smoothing parameter was chosen because of the mean scale of area-restricted search (ARS) behaviour (sinuous and slow movements associated with foraging activities) in gannets (9.1 ± 1.9 km; Hamer et al. 2009). In many cases, 50% density contours are used to identify a bird's core foraging area (Hamer et al. 2007). Here, comparisons be- tween KDE analysis and GPS fixes showed that 50% contours often included commuting flights between foraging locations and the colony. However, for the most part, 25% contours only identified areas where birds intensified their ARS behaviours (Hamer et al. 2009). Therefore, we used 25% contours to identify and quantify core foraging areas, taking the centroid of their easting and northing values (km) using the Universal Transverse Mercator zone 30N coordinate system. KDE was performed using the 'adehabitat HR' package (Calenge 2006) in R (version 2.13.0, R Development Core Team 2010).

SIA

We analysed stable carbon ($^{13}C/^{12}C$, $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$, $\delta^{15}N$) isotope ratios of red blood cells (RBCs) in all 72 birds. This provides integrated foraging information from the previous 3 to 4 wk. This approach relies on the fact that stable isotope ratios in consumer tissues reflect those in their prey in a predictable manner. $\delta^{13}C$ exhibits a slight stepwise trophic enrichment (~1%) but varies mainly because of geographical differences in photosynthetic biochemistry within and among marine primary producer communities. In marine environments, $\delta^{13}C$ also varies because of differences in latitude, depth and distance to land masses (Farquhar et al. 1989, Robinson 2001). $\delta^{15}N$ becomes enriched by 3 to 5‰ with each trophic level (Deniro & Epstein 1981, Hob- son & Clark 1992, Bearhop et al. 2002) and reflects differences in the trophic level of prey or differencesin food chain length. Therefore, combining $\delta^{15}N$ and $\delta^{13}C$ values into an isotopic signature can provide a useful proxy for foraging locations by quantifying both their geographical properties and prey composition. If there are consistent differences in foraging locations among sub-colonies, this should be reflected

in the respective isotopic signatures of birds sampled there.

Approximately 0.2 ml of blood was taken from the tarsal vein using a 23 gauge needle under license from the UK Home Office. Within 2 to 3 h, RBCs were separated from plasma using a centrifuge before being stored on ice. Prior to elemental analysis, samples were freeze dried and homogenised, and approximately 0.7 mg was weighed into tin capsules. Isotope analysis was conducted at the East Kilbride node of the Natural Environment Research Council (NERC) Life Sciences Mass Spectrometry Facility (LSMSF) via continuous flow isotope ratio mass spectrometry using a Costech ECS 4010 elemental analyser interfaced with a Thermo Electron deltaXP mass spectrometer. Isotope ratios (R) of $^{15}N/^{14}N$ and $^{13}C/^{12}C$ are expressed in delta (δ) units, as parts per thousand (‰), where $\delta^{13}C$ or $\delta^{15}N = [(R \text{ sample}/R \text{ standard}) - 1] \times 1000$. The international standards (= 0 ‰) for SIA are atmospheric N^2 for nitrogen and Pee Dee Belemnite for carbon.

In situ observations

Previous studies using GPS loggers found that the initial flight directions of most gannets at around 1 km from the nest site differed only slightly (<40°) from their subsequent departure directions at 10 km from the nest site (Pettex et al. 2010). Therefore, recording a bird's initial flight direction at the start of a foraging trip may be a useful proxy of its subsequent departure direction. To record departure directions from a larger number of birds than we could from our GPS loggers, we performed *in situ* observations within 1 sub-colony (Sc6; Fig. 1b) on 6, 12 and 13 July 2010. Observations were performed be- tween 06:00 and 11:00 h GMT to coincide with the time period when most birds start their foraging trips. Observation periods avoided times of poor visibility. We recorded departure directions for each bird starting a foraging trip during observation periods. Departure directions were recorded as the bearing between Sc6 and the location where they were no longer visible with the naked eye. As visibility was good during observation periods, this was usually around 1 km from their nest site. All birds departed individually (i.e. birds did not depart in flocks), and each recording represented an independent sample. Because of the topography around the observation point, our field of view was restricted to between 140 and 280°. However, only 7 of 305 birds starting a foraging trip during observations periods took bearings of <140° and 280°. Despite our restricted field of view, we expected that neighbours commuting towards the same foraging location would have similar departure directions within this range of values (140 to 280°).

Analysis

Because combinations of sub-colonies were not the same in all years (Table 1), we statistically tested for differences in foraging behaviours among sub-colonies in 2006, 2010 and 2011 separately. This removed the possibility of Type I errors, i.e. interpreting differences between years as differences between sub-colonies. In all statistical tests, we included both sub-colony and sex as explanatory variables to account for differences in foraging behaviours between sexes (Stauss et al. 2012).

We tested for sub-colony differences in trip duration, trip length and range using ANOVA tests, with one of these 3 foraging behaviours as the response variable and sub-colony and sex as explanatory factors. We log transformed trip duration, trip length and range to correct for a small number of very long foraging trips. As isotopic signatures ($\delta^{15}N$ and $\delta^{13}C$) and core foraging areas (eastings and northings, km) both had 2 response variables, we tested for sub-colony differences using multivariate analysis of variance (MANOVA; Pillai's trace, V). These models had either $\delta^{15}N$ and $\delta^{13}C$ or eastings and northings as response variables and sub-colony and sex as explanatory variables. For directional tracking data (departure directions, distal directions), we calculated the northerly and easterly components using their cosine and sine values, respectively. By using cosine and sine values, we were able to use conventional rather than circular statistics. We then tested for sub-colony differences using MANOVA tests, with cosine and sine values as response variables and sub-colony and sex as explanatory variables.

In all ANOVA and MANOVA tests, residuals were normally distributed (following log transformation of trip duration, trip length and range), with no clear outliers or high leverage points. For all tests, we included 2 additional analyses. First, we calculated an estimate of statistical power (based on an alpha of 0.05) to quantify the probability of committing Type II errors. When using MANOVA tests, we chose the response variable with the least leverage as a conservative measure of power (Murphy et al. 2012). Second, we calculated the intra-class correlation coefficient (Nakagawa & Schielzeth 2010) to compare the variance in foraging behaviours within sub-colonies to the variance among sub-colonies. This provides a repeatability index between 0 and 1, where an index of 0 would indicate low similarities among neighbours and an index of 1 would indicate high similarities among neighbours. Here, we interpret high repeatability indices as consistent with the emergence of sub-colony foraging asymmetries (i.e. that the variance in foraging behaviours within sub-colonies was greater than the variance among sub-colonies).

For our *in situ* observations, we tested for similarities among neighbours' departure directions in Sc6 using 2 approaches. First, we calculated the variance (σ^2) to mean (μ) ratio (VMR) among departure directions for each day. This provided a dispersion index between 0 and 10, where an index of 0 would indicate maximum similarities, with all neighbours' departure directions being identical, and an index of ~10 would indicate maximum dissimilarities, with neighbours' departure directions being equally distributed between 140 and 280°. Second, we tested for differences in departure directions among days using an ANOVA test. In this test, we used departure directions as response variables and the day as the explanatory variable. From the results of this ANOVA, we were able to calculate the intra-class correlation coefficient (see above) to provide an indication of thevariance in departure directions within each day compared to the variance among days. VMR and repeatability indices were then used in conjunction with a visual inspection of histograms to determine whether neighbours had similar departure directions and may have been commuting towards the same foraging locations.

All statistical analysis was performed in R (version 2.13.0, R Development Core Team 2010). For power analysis we used the 'pwr' package (Champely 2009), and for repeatability analysis we used the 'rptR' package (Nakagawa & Schielzeth 2010). Means are usually shown with standard deviations. However, in the case of the directional data that were recorded from GPS loggers (departure and distal directions), means are shown with estimations of circular variance. This is a dispersion index between 0 and 1, where values of 0 indicate that all directions are equal and values of 1 indicate that directions were equally distributed across 360° (Zar 2010). This approach was taken because the use of standard deviations is inappropriate on directional data with a potential range of values greater than 180° (Zar 2010).

RESULTS

GPS tracking

Mean foraging behaviours by sub-colony and year are shown in Table 2. At-sea movements and core foraging areas by sub-colony and year are shown in Figs. 2 & 3, respectively. Visual inspection of at-sea movements and core foraging areas revealed no clear qualitative differences among sub-colonies in any year. We also found no statistically significant differences in foraging behaviours among sub-colonies in any year. Repeatability within sub-colonies was also generally low (Table 3). However, there was a statistically significant influence of sex on distal directions and core foraging areas in 2006 (Table 3).

SIA

Mean $\delta^{13}C$ and $\delta^{15}N$ RBC values by sub-colony and year are shown in Table 2 and Fig. 4. We found no statistically significant differences in mean isotopic signatures among sub-colonies. Repeatability within sub-colonies was also generally low (Table 3). However, there was a statistically significant influence of sex on isotopic signatures in 2006 (Table 3).

In situ observations

Our *in situ* observations are summarised in Table 4 and Fig. 5. In total, we recorded departure directions from 305 birds in Sc6. Counts ranged from 87 to 113 birds per day. The daily VMR varied between 2.12 and5.62, and the overall repeatability index was 0.267. Taken together with visual inspections of histograms (Fig. 5), these results suggested some similarities in neighbours' departure directions. Significant differences in departure direction were seen among days (ANOVA; $F_{2,303} = 37.735$, $p < 0.01$), with a shift towards more westerly bearings seen on 13 July. This shift to- wards more westerly bearings coincided with stronger easterly winds during the observation period (6 July: speed = 2.49 m s^{-1}, direction = 133°; 12 July: speed = 2.49 m s^{-1}, direction = 119°; 13 July: speed = 6.75 m s^{-1}, direction = 148°; Skomer Reserve Marine Team).

DISCUSSION

Here, we investigate whether foraging behaviours differed among 7 sub-colonies of a large gannet colony using a combination of GPS loggers and SIA. Even when sampling 72 individuals from 7 sub-colonies across 3 yr, we found no clear evidence of any sub-colony foraging asymmetries. Repeatability indices also suggested low similarities in neighbours' foraging behaviours (Table 3).

Despite our highly variable statistical power (Table 3), there is no clear indication that this lack of a statistically significant difference is a Type II error. Although complimentary *in situ* observations suggested similarities among neighbours' departure directions in 1 sub-colony (Fig. 5), this may be attributable to a strong influence of wind vectors on individuals' initial flight directions at the start of a foraging trip. Below, we discuss our results from GPS loggers, SIA and *in situ* observations separately before considering the ecological and methodological implications of this research.

Table 2. *Morus bassanus*. Summary of foraging behaviours recorded from 72 chick-rearing gannets on Grassholm, UK, showing mean values by sub-colony (Sc1 to Sc7) and year (2006, 2010 and 2011). Sample sizes are shown (n). Values are presented as means ± SD with the exception of mean departure and distal directions, where means are presented with circular variances. This is a dispersion index between 0 and 1, where values of 0 indicate that directions were equal and values of 1 indicate that directions were equally distributed over a 360° range. Foraging behaviours were recorded using GPS loggers (range, distance, duration, departure directions, distal direction, core foraging areas) and stable isotope analysis of red blood cells (RBCs, $\delta^{13}C$ and $\delta^{15}N$)

Year	Sub-colony (n)	At-sea movement			Direction		Isotopic signature in RBCs		Core foraging area	
		Range (km)	Distance (km)	Duration (d)	Departure (°)	Distal (°)	$\delta^{15}N$	$\delta^{13}C$	Eastings (km)	Northings (km)
2006	Sc5 (7)	144.71 ± 89.17	467.43 ± 251.07	1.01 ± 0.43	311.80 ± 0.41	331.10 ± 0.40	15.10 ± 0.71	17.28 ± 0.95	295.34 ± 110.16	5659.06 ± 44.20
	Sc6 (7)	112.71 ± 76.76	333.86 ± 217.24	0.86 ± 0.39	69.06 ± 0.35	32.13 ± 0.44	15.33 ± 0.61	17.31 ± 0.58	291.97 ± 92.69	5693.20 ± 25.24
	Sc7 (9)	104.33 ± 54.28	314.44 ± 169.80	1.06 ± 0.78	144.67 ± 0.23	109.54 ± 0.21	15.31 ± 0.62	17.25 ± 0.53	266.69 ± 58.87	5700.99 ± 35.63
2010	Sc1 (5)	149.2 ± 77.15	435.8 ± 176.84	0.65 ± 0.26	283.02 ± 0.36	348.44 ± 0.42	14.29 ± 0.48	17.84 ± 0.41	323.28 ± 36.09	5663.33 ± 93.98
	Sc2 (4)	162.5 ± 91.60	435 ± 269.77	1.03 ± 0.68	48.77 ± 0.19	19.82 ± 0.28	14.02 ± 0.48	17.64 ± 0.23	309.94 ± 38.35	5593.42 ± 91.34
	Sc4 (5)	135.4 ± 28.02	518.6 ± 138.64	1.20 ± 0.65	311.29 ± 0.54	324.19 ± 0.61	14.14 ± 0.75	17.61 ± 0.41	342.48 ± 59.48	5677.36 ± 85.21
	Sc7 (3)	116.33 ± 83.34	314.33 ± 205.90	0.62 ± 0.25	123.19 ± 0.11	83.93 ± 0.12	14.96 ± 0.92	17.30 ± 0.59	266.80 ± 73.35	5660.70 ± 42.70
2011	Sc1 (7)	100 ± 38.06	335.43 ± 132.84	0.66 ± 0.23	11.62 ± 0.49	326.38 ± 0.43	14.85 ± 0.51	17.64 ± 0.48	333.53 ± 41.21	5681.55 ± 64.00
	Sc2 (6)	174.83 ± 140.68	688.83 ± 552.30	1.94 ± 1.61	81.75 ± 0.25	103.31 ± 0.16	15.27 ± 0.70	17.14 ± 0.55	252.26 ± 49.71	5680.17 ± 61.42
	Sc3 (3)	87 ± 58.03	296.67 ± 254.30	0.80 ± 0.92	307.38 ± 0.55	276.16 ± 0.45	14.81 ± 0.33	17.56 ± 0.51	356.17 ± 38.90	5741.60 ± 76.85
	Sc4 (6)	139.83 ± 57.40	433.83 ± 171.92	0.83 ± 0.39	59.14 ± 0.70	3.83 ± 0.78	14.94 ± 0.47	17.29 ± 0.49	310.29 ± 81.50	5685.06 ± 91.45
	Sc7 (10)	145 ± 127.57	402.2 ± 324.28	0.90 ± 0.68	130.23 ± 0.11	127.65 ± 0.15	14.86 ± 0.59	17.40 ± 0.47	229.27 ± 109.58	5671.14 ± 68.85

GPS loggers

While we found no clear differences among 7 sub-colonies in 6 different measures of foraging behaviour derived from GPS loggers, we need to discuss the possibility of falsely accepting our null hypothesis. Within each year, the foraging trips used in our analysis were spread over several weeks (Table 1). This could render it difficult to detect sub-colony foraging asymmetries because of the temporal variations in foraging behaviour associated with, for example, changes in prey availability and distribution (Wanless et al. 1998) or reproductive duties (Ito et al. 2010) within breeding seasons. However, we think this is unlikely. Previous studies show that gannets on Grassholm are consistent in their departure directions, their most distant locations and also their dive locations within breeding seasons (Patrick et al. 2014). This indicates that gannets are probably exploiting temporally predictable foraging locations, something which would reduce these potentially confounding effects. We did find much variation in our 5 measurements of foraging behaviours (Table 2), and this led to greatly varying levels of statistical power (Table 3). However, at least for some measurements of foraging behaviours (distance, departure direction and core foraging area, depending on the year), there was good statistical power (Table 3), suggesting that we were correct to accept the null hypothesis of no differences in foraging behaviour among sub-colonies.

SIA

Previous work demonstrated clear differences in the isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) of tufted puffin *Fratercula cirrhata* eggs and chick blood cells between 2 sub-colonies on Triangle Island in British Columbia, Canada (Hipfner et al. 2007). These results suggested differences in foraging locations between sub-colonies. Here, we interpret similar isotopic signatures among sub-colonies as evidence of no differences in foraging location among sub-colonies. Although it is possible that individuals captured different prey from the same foraging location, this would typically lead to differences in $\delta^{15}N$ only. For example, individuals taking discards from demersal fishing vessels will have much higher $\delta^{15}N$ values than those taking pelagic fish (Votier et al. 2010). However, individuals exploiting the same foraging location will have broadly similar $\delta^{13}C$ values regardless of their prey choice (Farquhar et al. 1989, Robinson 2001). Therefore, when considering the relatively high statistical power in some cases (Table 3), the lack of significant differences represents good evidence that foraging locations did not differ among sub-colonies. Furthermore, by analysing RBCs, there is also a low likelihood of any temporal variations in foraging behaviour (see above) influencing our results, because they represent an integrated signature over the 3 to 4 wk prior to sampling.

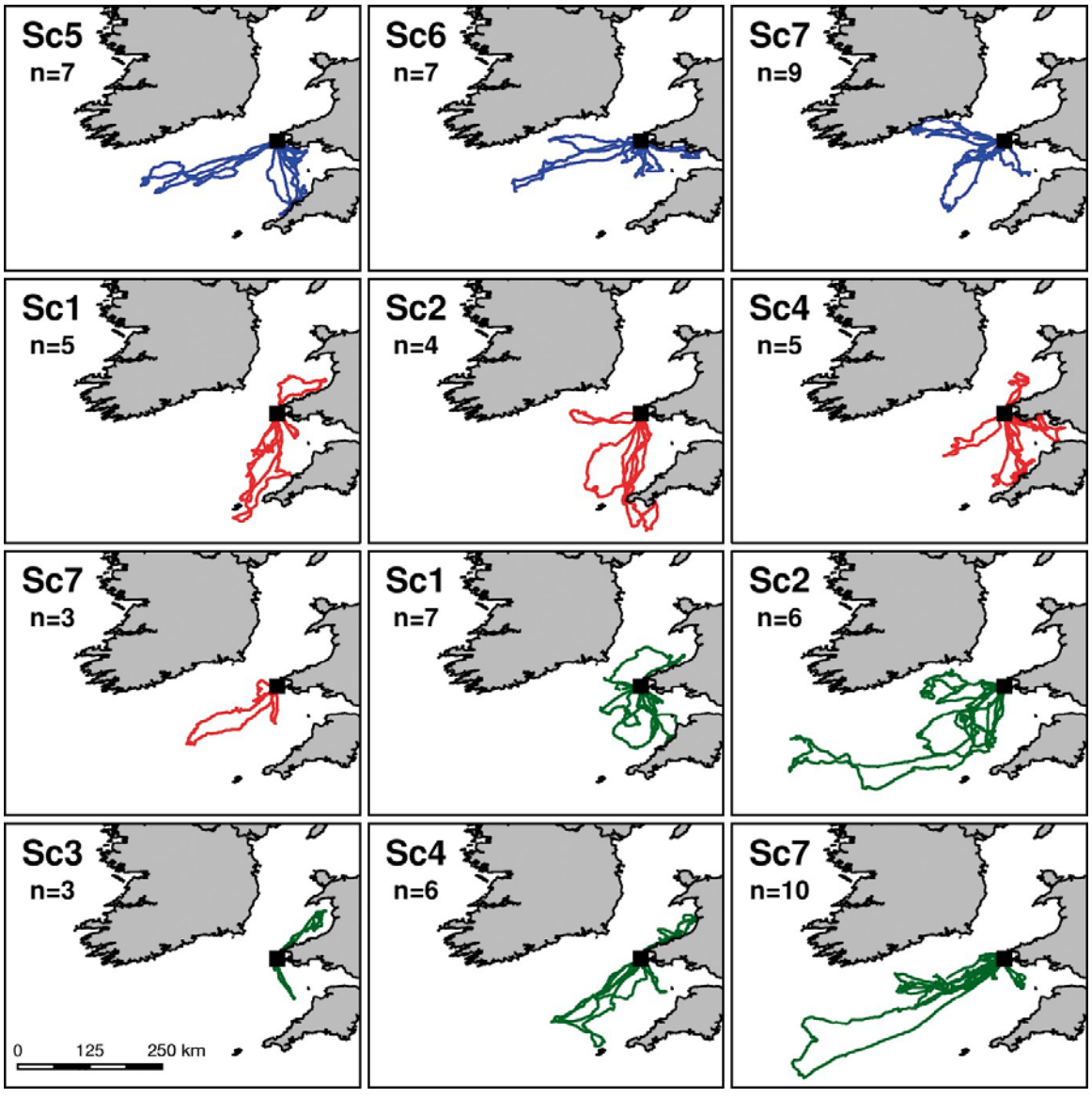

Fig. 2. *Morus bassanus*. Foraging movements of chick-rearing northern gannets on Grassholm, UK, recorded from GPS loggers. Foraging movements are divided into sub-colonies (Sc1 to Sc7) and years (2006 = blue, 2010 = red, 2011 = green). The location of Grassholm is indicated by the black square.

Sample sizes are also shown (n)

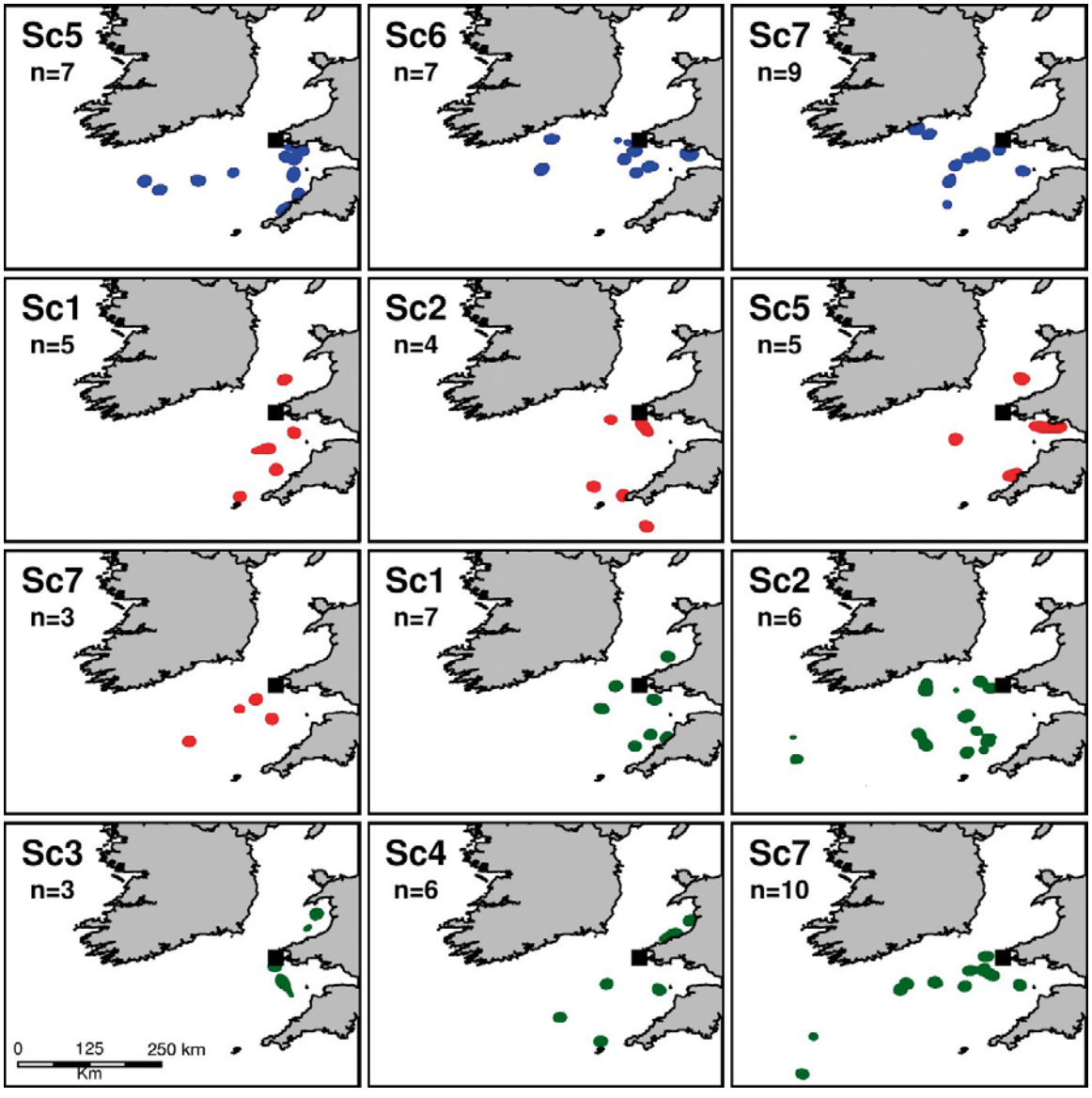

Fig. 3. *Morus bassanus*. Twenty-five percent kernel density (KD) contours from chick-rearing northern gannets on Grassholm, UK, calculated from GPS logger data (Fig. 2). KD contours are divided into sub-colonies (Sc1 to Sc7) and years (2006 = blue, 2010 = red, 2011 = green). The location of Grassholm is indicated by the black square. Sample sizes are also shown (n). Kernel smoothing parameter = 10 km, cell size = 1 km

In situ observations

Based on previous studies, we believed that re- cording gannets' initial flight directions at the start of a foraging trip should provide reasonably accurate (e.g. <40°) proxies of their subsequent departure direction (Pettex et al. 2010). However, wind vectors seemed to influence gannets' initial flight directions at the start of foraging trips, as an almost 3-fold increase in the strength of easterly winds on 13 July resulted in much more westerly departure directions being recorded on this day. Because of this doubt, we cannot interpret the similarities seen among neighbours' departure directions as evidence that they may have been commuting towards similar foraging locations.

Table 3. *Morus bassanus*. Summary of ANOVA and MANOVA tests for differences in the foraging behaviour of chick-rearing gannets among sub-colonies and sexes on Grassholm, UK, in 2006, 2010 and 2011. Also displayed are estimates of statistical power and calculations of repeatability within sub-colonies. V = Pillai's trace test, EW = easterly component, NS = northerly component. Significant differences shown in **bold**

Year	Foraging behaviour	Sex				Sub-colony				Repeatability	Power (%)
		V	*F*	df	p	V	*F*	df	p		
2006	Range (km)		2.925	1,22	0.103		0.499	2,21	0.615	−0.05	55
	Distance (km)		3.987	1,22	0.060		1.329	2,21	0.290	0.02	79
	Duration (d)		0.558	1,22	0.464		0.158	2,21	0.855	−0.11	15
	Departure direction (EW, NS)	0.247	2.965	2,21	0.070	0.396	2.347	4,19	0.072	EW = 0.11, NS = 0.27	85
	Distal direction (EW, NS)	**0.295**	**3.772**	**2,21**	**0.042**	0.232	1.245	4,19	0.308	EW = −0.11, NS = 0.17	23
	Isotope signature ($\delta^{15}N$, $\delta^{13}C$)	**0.531**	**10.213**	**2, 21**	**0.001**	0.180	0.960	4,19	0.440	$\delta^{13}C$ = −0.15, $\delta^{15}N$ = −0.11	99
	Core foraging area (Lat., Lon.)	**0.401**	**6.038**	**2,21**	**0.009**	0.295	1.645	4,19	0.183	Lat. = 0.2, Lon. = −0.11	76
2010	Range (km)		1.274	1,16	0.281		0.281	3,14	0.838	−0.13	24
	Distance (km)		4.122	1,16	0.065		1.001	3,14	0.426	−0.10	69
	Duration (d)		0.424	1,16	0.527		0.482	3,14	0.701	−0.01	22
	Departure direction (EW, NS)	0.084	0.507	2,15	0.615	0.598	1.669	6,11	0.172	EW = −0.11, NS = 0.53	17
	Distal direction (EW, NS)	0.011	0.063	2,15	0.939	0.207	0.562	6,11	0.829	EW = 0.03, NS = 0	11
	Isotope signature ($\delta^{15}N$, $\delta^{13}C$)	0.586	0.668	2,15	0.532	0.580	1.660	6,11	0.170	$\delta^{13}C$ = −0.06, $\delta^{15}N$ = −0.06	45
	Core foraging area (Lat., Lon.)	0.909	0.407	2,15	0.675	0.417	1.055	6,11	0.416	Lat. = −0.04, Lon. = 0.09	90
2011	Range (km)		0.789	1,31	0.382		0.636	4,28	0.641	−0.06	28
	Distance (km)		1.434	1,31	0.242		0.718	4,28	0.587	0.04	36
	Duration (d)		1.633	1,31	0.213		0.567	4,28	0.688	0.16	32
	Departure direction (EW, NS)	0.019	0.240	2,30	0.782	0.360	1.428	8,24	0.207	EW = −0.13, NS = 0.25	17
	Distal direction (EW, NS)	0.021	0.270	2,30	0.765	0.441	1.838	8,24	0.091	EW = −0.1, NS = 0.32	11
	Isotope signature ($\delta^{15}N$, $\delta^{13}C$)	0.164	2.461	2,30	0.106	0.320	1.250	8,24	0.280	$\delta^{13}C$ = −0.01, $\delta^{15}N$ = −0.06	53
	Core foraging area (Lat., Lon.)	0.013	0.185	2,30	0.832	0.412	1.817	8,24	0.093	Lat. = −0.07, Lon. = 0.25	42

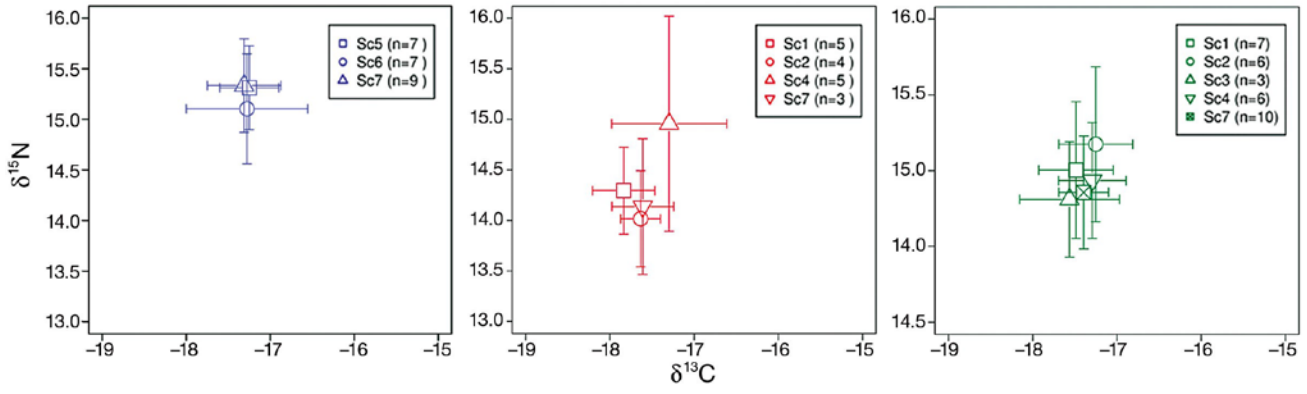

Fig. 4. *Morus bassanus*. Mean (± SE) $\delta^{13}C$ and $\delta^{15}N$ values in red blood cells of chick-rearing northern gannets on Grassholm, UK. Mean $\delta^{13}C$ and $\delta^{15}N$ values are divided into sub-colonies (Sc1 to Sc7) and years (2006 = blue, 2010 = red, 2011 = green). Sample sizes are also shown (n)

Table 4. *Morus bassanus*. Mean ± SD departure directions of gannets nesting in sub-colony 6 (Sc6) on Grassholm, UK, that were seen starting foraging trips between 06:00 and 11:00 h GMT on 3 d in July 2010. Sample sizes are shown (n). Also shown are the variance to mean ratios (VMR)

Date	n	Departure direction (°)
6 July 2010	87	215 ± 35
12 July 2010	113	205 ± 21
13 July 2010	105	236 ± 24

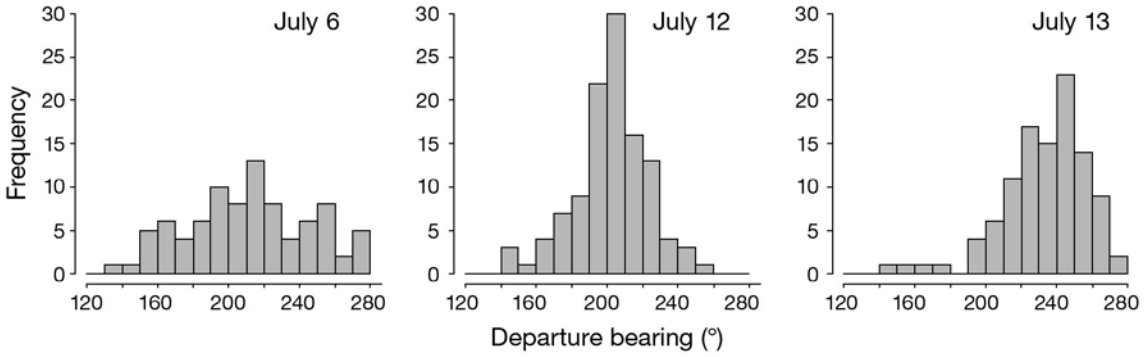

Fig. 5. *Morus bassanus*. Departure directions of breeding northern gannets in sub-colony 6 (Sc6) on Grassholm, UK, on 3 d in July 2010

Ecological implications

Although the precise mechanisms remain un- known, there is growing evidence suggesting that gannets use social information to inform foraging decisions (Gremillet et al. 2004, Wakefield et al. 2013). Theoretical models suggest that both local enhancement and the exchange of social information within the colony could influence the at-sea distributions of gannets (Wakefield et al. 2013). If social information was primarily exchanged at the nest site, where individuals can observe their neighbours' chick-provisioning duties and flight directions, then we might expect at-sea segregation among sub-colonies. This is not the case here. Although we cannot completely dismiss an exchange at the nest site, it seems possible that most exchanges of social information in the colony could occur elsewhere, such as when individuals raft on the water surface before starting a foraging trip (Weimerskirch et al. 2010).

The tendency for older or more dominant individuals to occupy preferential nest sites (Velando & Freire 2001) could lead to colony members grouping themselves by age or intrinsic quality. If it is assumed that older or more dominant individuals are competitively superior or more efficient foragers, then sub-colonies containing mainly older or dominant individuals would tend to forage closer to the colony or spend less time at sea (Catry & Furness 1999, Daunt et al. 2007, Votier et al. 2011). Results here suggest that colony members are probably not grouping themselves by age or intrinsic qualities. This could indicate that there is low variation in the quality of nest sites and/or that the locations of preferential nest sites are not spatially aggregated.

Methodological implications

Our results suggest that sampling several different sub-colonies of gannets may not be necessary when quantifying the foraging behaviours of the colony as a whole. However, we cannot yet draw robust conclusions for seabirds in general. For instance, there are likely to be variations in the accuracy and exploitability, and therefore the use, of social information at the nest site among different species (King & Cowlishaw 2007). Grouping by age or intrinsic qualities may also be more likely in species where there is high variation in the quality of nest sites and the locations of preferential nest sites are spatially aggregated (Velando & Freire 2001). Given our current lack of knowledge across seabird species, we urge further tests of this hypothesis elsewhere. By understanding when and why sub-colony foraging asymmetries occur, appropriate sampling designs can be developed to ensure that the foraging behaviours recorded from both GPS loggers and SIA are representative of the colony as a whole. By increasing our confidence in the accuracy of studies aiming to record and monitor individual foraging behaviours within colonies, we can start to improve our understanding of how changes to the environment brought about by marine renewable energies, commercial fisheries, marine pollution or climate change could affect seabird populations.

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