

Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint

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ABSTRACT: Many seabirds nesting in areas bordering the North Sea have recently experienced large annual variation in breeding success, including reproductive failures in some cases. In contrast, the breeding success of northern gannets *Morus bassanus* has remained remarkably stable. The present study examines data from the large gannet colony at the Bass Rock (southeast Scotland) across 3 years, to assess the extent to which such stability may reflect both flexibility and consistency in diets and foraging behaviour. Adults exhibited great flexibility both in the species and sizes of prey consumed and in foraging trip durations, ranges and total distances travelled. They also showed a high degree of consistency in bearings of foraging trips and in behaviour at sea; the sinuosity of foraging tracks and average speed of travel was very similar each year and birds in all years spent about half their time at sea in flight. Adults returned to the nest at higher speeds from more distant foraging locations up to ca. 300 km from the colony, but speeds decreased for the farthest destinations (>ca. 400 km). Moreover, the relationship between trip duration and distances travelled at sea was asymptotic beyond ca. 60 h. These non-linear relationships probably reflected constraints on energy expenditure during flight. As a result, nest attendance was low in years with long average trip durations and chicks were left unattended and vulnerable to attack by conspecifics. These data suggest that while adults have so far been able to maintain high reproductive success in years of low prey availability, they may not be able to do so in future years if providing sufficient food for chicks entails any further increases in trip duration or foraging effort.

KEY WORDS: *Morus bassanus* · Wildlife telemetry · Geolocation · Home range · Optimal foraging

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INTRODUCTION

Foraging behaviour is a major component of the daily routine of many species and during the breeding season forms an essential link between prey availability and predator reproductive success. Flexibility in diet and foraging behaviour may be particularly important when the distribution and abundance of dif-

ferent prey species is highly variable. One central issue in this context is how foraging behaviour varies in trips of different duration, especially when parents need to travel long distances to obtain prey (Ropert-Coudert et al. 2004, Wilson et al. 2005).

Pelagic seabirds routinely travel long distances from the nest, making foraging trips of several hours to several days duration and travelling tens to hundreds

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of kilometres from the breeding site on a single trip (Awkerman et al. 2005, Head & Gales 2005). Advances in remote-sensing technology have provided increasingly detailed information on the foraging locations and behaviour of pelagic seabirds (Lewis et al. 2004a, 2005, Weimerskirch et al. 2006), but there is still relatively little information on how distances travelled and behaviour during foraging trips vary in relation to trip duration under different environmental conditions (Litzow & Piatt 2003, Grémillet et al. 2004). Whilst strong evidence exists from a number of species of seabirds that adults are able markedly to increase trip durations in response to low prey availability (e.g. Hamer et al. 1993, Croxall et al. 1999), there is relatively little information to assess how adults adjust their foraging behaviour to compensate for such changes in travel time (Monaghan et al. 1994).

The North Sea is one of the most heavily fished areas in the world and has been affected in recent years by rapid climate-driven changes at multiple trophic levels (Frederiksen et al. 2006). As a result, many species of seabird at colonies bordering the North Sea have recently experienced large annual variation in breeding success, including reproductive failures in some cases (Mavor et al. 2005). In contrast, the breeding success of northern gannets *Morus bassanus* has remained remarkably stable, varying only between about 0.65 and 0.8 chicks fledged per nest (i.e. 65 to 80% of the maximum possible) across multiple years at established colonies throughout the region (e.g. see Table 3.6.1 in Mavor et al. 2005). One possible reason for this stability is that gannets appear to have very flexible diets and time/activity budgets during the breeding season. For instance, at one of the largest colonies (>40 000 breeding pairs) of gannets in the UK (Bass Rock, southeast Scotland; 56° 6' N, 2° 36' W) where breeding success is consistently high at around 0.75 chicks fledged per nest (Nelson 2006), the diet in a single year included a wide range of species and sizes of prey while foraging trips lasted from <2 to >84 h and extended >500 km from the nest on some occasions (Hamer et al. 2000). Such flexibility could provide a buffer against the effects of annual variation in prey abundance and distribution and Hamer et al. (2006) found marked annual variation in mean trip durations of chick-rearing adults at the Bass Rock, with particularly long trips in 2002 and short trips in 2003. However, it was not known how much annual variation there was in species and sizes of prey or in foraging locations and movements of adults at sea.

In addition to benefiting from flexibility in diets and foraging behaviour, parents might also benefit in some circumstances from consistency. For instance, they can increase their foraging efficiency by learning the

whereabouts of spatially and temporally predictable sources of prey and returning repeatedly to such locations. Gannets at the Bass Rock were shown to display a high degree of such foraging area fidelity in one year (Hamer et al. 2001), but it was not known how this pattern varied between years with different average trip durations.

Gannets feed throughout their foraging trips and Lewis et al. (2004a) found no variation in average feeding rate in relation to trip duration. However, it was not known how the movements of birds at sea or the allocation of time between foraging and nest attendance varied with trip duration. Gannet chicks are normally attended by one parent whilst the other parent is foraging, but prolonged periods of attendance can result in both parents foraging simultaneously, leaving the chick unattended and at risk of attack (Lewis et al. 2004b). It might, thus, be important for birds to return quickly from long trips to relieve their partner at the nest, but no previous data exist to assess the extent to which parents are able to do this. Gannets have an energetically expensive mode of flight that results in high mass-specific energy expenditure during foraging trips (Enstipp et al. 2006). A metabolic ceiling on energy expenditure might, thus, constrain the ability of parents to return quickly from distant foraging sites, but this possibility has not previously been investigated.

This paper provides quantitative information on the diets of gannets at the Bass Rock in different years and uses satellite telemetry to examine annual variation in the foraging locations, distances travelled and at-sea behaviour of chick-rearing adults. We assess how both the consistency in foraging locations exploited by adults and the movements and behaviour of birds during foraging trips differed among 3 years (1998, 2002 and 2003) with marked differences in average trip duration.

MATERIALS AND METHODS

Diet. Fieldwork on the Bass Rock (southeast Scotland) took place between 14 June and 28 August each year (1998, 2002 and 2003). Diet was assessed from regurgitates from adults, and to minimize disturbance most samples were collected from birds at the periphery of the colony, the majority of which were likely to be non-breeders. Comparisons of the frequency of occurrence and sizes of the main prey items in these samples with 20 or more samples known to have come from adults with chicks in the same year showed no evidence of any significant differences in diet between the 2 groups (i.e. these breeders and likely non-breeders) (all χ^2 and F -tests, $p > 0.05$).

Regurgitates were collected over a period of 2 to 3 d on 4 to 6 occasions spanning the majority of the chick-rearing period before chicks attained peak mass (2 to 3 wk before fledging) each year. Each regurgitate was stored separately in a sealed polythene bag and transported to the laboratory where it was weighed (nearest 1 g) and the prey were identified either visually or from sagittal otoliths and vertebrae extracted from the sample (Härkönen 1986, Watt et al. 1997, authors' unpubl. data). Body length of prey was measured to the nearest 1 cm (1 mm for sandeels *Ammodytes marinus*) or, where this was not possible, estimated using species-specific body length/otolith or vertebra length relationships (Härkönen 1986, Watt et al. 1997, authors' unpubl. data). In addition, sandeels were aged by the absence (0-group) or presence (older age groups) of annual growth rings in the otoliths (Anonymous 1995). Dietary data are presented in terms of both frequency of occurrence and the proportions of the total biomass comprised of the different species each year.

Satellite telemetry. One chick-rearing adult from each of 53 nests with hatching dates ± 2 wk from the annual mode ($n = 17$ birds in 1998, 14 in 2002, 22 in 2003) was captured at the nest using a roach pole with a brass noose. In 1998 and 2002, a platform terminal transmitter (PTT; Microwave Telemetry) weighing 30 g (ca. 1% of adult mass) and with a duty cycle of continuous transmission was then attached with self-amalgamating tape (RS Components) to the underside of the 4 central tail feathers of each bird, close to the base of the tail with the aerial pointing upwards through the feathers. This arrangement minimized drag during flight and prevented tags being displaced during plunge diving. In 2003, a PTT was attached to 9 birds as above and a GPS logger (Earth & Ocean Technologies) weighing 70 g (<3% of adult mass) was attached to the feathers on the back of 13 birds using Tesa tape, such that the wings of the bird protected the device during plunge diving. Attachment of all tags took <15 min, and after release every bird returned to the nest almost immediately.

After release, birds were tracked for 5 to 21 d each (mean = 12 d) for birds wearing PTTs and for 1 to 4 d each (mean = 3 d) for birds wearing GPS loggers, during a period of 2 mo (24 June to 25 August) excluding late chick rearing, after which time the bird was recaptured and the tag removed. A recent review of effects of satellite transmitters indicated negligible adverse effects for tags weighing up to 3% of adult body mass (Phillips et al. 2003) and in our study, PTTs had no discernible effects on trip durations or body masses of birds in comparison with untagged controls (Hamer et al. 2000). In addition, there was no difference between birds carrying PTTs and those carrying GPS loggers in trip durations (mean \pm SD, 27.3 \pm 10.2 h, $n = 43$ and

21.5 \pm 6.7 h, $n = 15$, respectively, $t_{56} = 2.0$, $p = 0.1$) or maximum distances travelled from the colony (see below for method of calculation; mean = 105.7 \pm 102.4 km, $n = 43$ and 155.2 km \pm 65.3, $n = 15$, respectively; $t_{56} = 0.7$, $p = 0.5$) in 2003.

Data provided by PTTs were processed using the Advanced Research and Global Observation Satellite (ARGOS) facility in France (Centre National d'Etudes Spatiales [CNES]). Following Hamer et al. (2000), we used only data of Class A or better to examine foraging locations at sea, giving us a maximum SD on each location of 7 km, which was small in comparison with distances travelled by birds (see below). GPS loggers provided data at intervals of 3 min, which were then sampled at 30 min intervals to maintain comparability with the PTT data. Trials indicated that the accuracy of this system was within 20 m for 90% of all fixes. Locations of birds at sea were examined in Arc-View GIS and the scale of movements each year was compared using fixed kernel density (FKD) estimates (Beisiegel & Mantovani 2006). As described by others (e.g. Iversen & Esler 2006) we considered the 95 and 50% FKD estimates to represent the area of active use and the core area of foraging activity, respectively.

To examine individual foraging trips in more detail, we used trips with locations at average intervals of ≤ 3 h to assess the routes taken by birds. We used the farthest recorded location from the colony during each of these trips to provide information on trip destinations and we calculated trip durations from the time of the first location after the bird had left the colony until the time of the first location after it had returned, as described by Hamer et al. (2000). We also calculated total distance travelled as the sum of distances between consecutive locations at sea. To assess whether there were constraints on foraging ranges we examined both linear and asymptotic relationships between trip durations and distances travelled at sea. Using an information-theoretic approach to model selection, we calculated Akaike's Information Criterion (AIC; Burnham & Anderson 1998) for each model and used F -tests to determine whether differences between models were significant. We then calculated the proportion of time that each bird spent foraging as:

$$\frac{\text{Mean trip duration}}{\text{Mean trip duration} + \text{Mean time at colony between trips}} \quad (1)$$

This made the most efficient use of the data whilst ensuring that periods of foraging and attendance at the nest were equally represented. To reduce sampling error, this analysis was restricted to birds with 3 or more consecutive foraging trips and hence 2 or more consecutive periods at the nest between trips.

To examine whether or not there was consistent variation in the foraging locations of individual birds, we used data recorded at average intervals of 3 h or less over a minimum of 3 consecutive foraging trips. Following Hamer et al. (2001), we calculated mean bearings of destinations from the colony for each bird and used angular deviation to measure how consistent birds were in their bearings on successive trips (angular deviation is equivalent to SD in linear data and ranges from a minimum of zero to a maximum of 81.0°).

To examine movements over shorter intervals within the total foraging ranges of birds, we estimated travel speeds during short sections of each trip as the distance between consecutive pairs of locations divided by the time elapsed between them. In view of the maximum SDs on locations (see above), very short intervals between locations could produce erroneous estimates of speed. To avoid this problem, we used only pairs of locations at sea separated by at least 1 h for PTTs or by 30 min for GPS loggers.

In many cases we recorded more than 1 trip per bird. To examine annual and individual variation in foraging behaviour and to take account of potential pseudoreplication of data, we used generalized linear models (GLMs) with year included as a fixed effect, and bird identity included as a random effect nested within year.

RESULTS

Diet

We obtained a total of 472 regurgitates (biomass = 51.1 kg), all of which either contained 1 species of prey or 2 species occupying different portions of the sample and so probably ingested separately. The diet included a wide range of species, but the main prey in terms of frequency of occurrence and proportion of biomass were sandeels (mainly 0-group), mackerel *Scomber scombrus*, herring *Clupea harengus*, sprat *Sprattus sprattus* and Gadidae (Table 1). There was marked variation in diet between years (χ^2 -test of frequency data with 0-group and older sandeels combined; $\chi^2_{10} = 67.4$, $p < 0.0001$). In particular, sandeels were 2 to 3 times more abundant in the diet in 2002 and 2003 than in 1998, whereas the abundance of herring and sprat in 2002 was about one-quarter to one-third of that in

Table 1. *Morus bassanus*. Frequency (% of regurgitates containing each species) and biomass (% of total estimated biomass comprising each species) of various fish in the diet of gannets at Bass Rock, southeast Scotland, in the 3 years studied. Based on a biomass of 27.3 kg from 266 regurgitates in 1998, 13.6 kg from 114 regurgitates in 2002, 10.2 kg from 92 regurgitates in 2003

Species	1998		2002		2003	
	Frequency	Biomass	Frequency	Biomass	Frequency	Biomass
Mackerel	31.6	30.8	21.9	23.6	17.2	14.6
Herring	21.5	20.3	7.7	5.4	22.2	12.2
Sprat	23.0	12.6	6.7	2.3	19.0	6.6
Sandeels ^a	29.3	17.9	69.3	55.1	73.9	51.5
0-group	27.0	12.5	68.4	55.0	68.5	51.4
Older	2.3	5.4	0.9	0.1	5.4	0.1
Gadidae ^b	15.0	16.4	15.6	10.7	11.9	10.4
Others ^c	3.7	2.1	4.5	2.9	6.5	4.8

^aAll lesser sandeel *Ammodytes marinus* except for 3 greater sandeel *Hyperoplus lanceolatus* (all older than 0-group) in 2003

^bMainly haddock *Melanogrammus aeglefinus*, whiting *Merlangius merlangus* and cod *Gadus morhua*

^cPlaice *Pleuronectes platessa*, Atlantic salmon *Salmo salar*, sea trout *S. trutta*, grey gurnard *Eutrigla gurnadus*, red gurnard *Aspitrigla cuculus*, garfish *Belone belone*, common dragonet *Callionymus lyra*, scad *Trachurus trachurus* and greater forkbeard *Phycis blenoides*

other years. Estimates of the sizes of prey taken indicated that these also varied markedly in all 3 years, with a total range from 5 cm (0-group sandeels) to 40 cm (mackerel and haddock *Melanogrammus aeglefinus*; Table 2). However, there was little difference between years in the range of prey sizes (5 to 37 cm in 1998, 5 to 40 cm in 2002, 5 to 38 cm in 2003; Table 2).

Foraging trip durations and time spent foraging

We obtained 5716 high-quality locations at sea (SD \pm 7 km; see 'Materials and methods') during foraging trips made by 53 birds (17 birds in 1998, 14 birds in 2002, 22 birds in 2003 of which 13 were carrying GPS-loggers). From these, there were 170 foraging trips from 48 birds with locations at average intervals of \leq 3 h, allowing reasonably accurate assessment of trip durations and routes taken by adults. Trips lasted up to 75 h in 1998, 93 h in 2002 and 54 h in 2003. Mean trip duration in 2002 was about 60% longer than in 2003 and 30% longer than in 1998 (Table 3; GLM; $F_{2,122} = 16.6$, $p < 0.001$). There were, however, no significant differences in trip durations of individual birds within each year ($F_{45,122} = 0.8$, $p = 0.8$).

Adults each spent slightly more than half of their time at sea on average (Table 3), so that chicks were sometimes left unattended in all 3 years (authors' pers. obs. at colony). Coinciding with the shortest trip durations in 2003, the proportion of time that each

Table 2. *Morus bassanus*. Lengths (cm) of fish eaten at Bass Rock in the 3 years studied

Species	1998				2002				2003			
	n	Mean	SD	Range	n	Mean	SD	Range	n	Mean	SD	Range
Lesser sandeel ^a												
0-group	2016	7.8	0.90	5–10	7477	8.2	0.86	5–9	5177	7.7	0.72	5–10
Older	432	11.6	1.45	9–17	2	11.0	0.98	11–11	77	9.7	0.53	9–11
Sprat ^a	375	9.8	1.55	5–15	21	8.8	3.07	6–15	35	10.6	1.60	8–16
Herring	53	20.7	4.00	10–30	21	24.4	6.87	10–31	41	17.6	7.17	8–25
Mackerel	42	24.9	4.41	15–33	28	32.0	4.39	23–40	18	30.5	3.78	21–36
Haddock	15	29.1	6.24	18–37	5	35.6	3.15	31–40	7	32.7	5.16	22–38
Whiting	12	26.9	5.33	18–34	19	20.9	5.19	12–32	2	27.8	3.05	24–30
Cod	4	26.2	6.58	20–30	2	32.3	9.23	26–39	–	–	–	–
Grey gurnard	3	13.0	1.73	11–16	–	–	–	–	–	–	–	–
Salmon	2	26.0	0	26–26	–	–	–	–	–	–	–	–
Trout	1	34.0	–	–	–	–	–	–	–	–	–	–
Greater forkbeard	1	25.0	–	–	–	–	–	–	–	–	–	–
Dragonet	–	–	–	–	1	22.9	–	–	–	–	–	–
Greater sandeel	–	–	–	–	–	–	–	–	3	16.2	0.66	16–17
Garfish	–	–	–	–	–	–	–	–	1	36.0	–	–
Scad	–	–	–	–	–	–	–	–	1	38.3	–	–

^aBased on all otoliths extracted from samples

Table 3. *Morus bassanus*. Characteristics of foraging trips made by adults rearing chicks at Bass Rock in the 3 years studied. Based on 70 trips (21 to north of colony; 49 to south) from 14 birds in 1998, 42 trips (24 to north; 18 to south) from 13 birds in 2002, 58 trips (36 to north; 22 to south) from 21 birds in 2003. FKD: fixed kernel density estimate

	1998		2002		2003	
	Mean	SD	Mean	SD	Mean	SD
Proportion of time foraging (%) ^a	60.3	5.5	57.4	4.0	52.5	7.5
Trip duration (h)	31.5	13.0	40.0	17.6	25.9	9.6
95 % FKD (km ²)	96 290		211 120		45 890	
50 % FKD (km ²)	10 822		30 555		4 202	
Max. distance (km)	224.3	96.8	319.7	132.9	170.5	94.2
Total distance (km)	588.2	245.5	786.0	344.3	417.6	231.3
Trips to north of colony						
Max. distance (km)	203.0	85.2	363.7	93.9	181.7	93.9
Total distance (km)	546.8	216.1	902.9	331.0	444.4	230.0
Trips to south of colony						
Max. distance (km)	233.4	100.8	261.0	112.0	152.2	93.8
Total distance (km)	606.0	257.0	630.2	304.5	373.7	231.8
Speed ^b (km h ⁻¹)	14.4	3.2	16.3	3.7	14.1	3.9
Speed ^c (km h ⁻¹)	18.9	3.8	19.5	4.3	18.3	4.2

^aData for a subset of 25 birds (see Table 2) with data for 3 or more consecutive foraging trips
^bCalculated using maximum distance from the colony for trips <62 h
^cCalculated using total distance travelled for trips <64 h

adult spent foraging was also lowest in 2003 (Table 3), although there was no significant difference between 1998 and 2002 in this respect (1-way ANOVA using arcsine-transformed data with a single value for each bird, followed by post-hoc Tukey tests; $F_{2,22} = 4.0$, $p = 0.03$).

Locations of adults at sea

Locations of birds during trips covered a wide area of the North Sea (>200 000 km²; Fig. 1), extending as far as Bergen/Viking Bank (southwest Norway) in the north and the Frisian Islands (northwest Netherlands) in the south. Fixed kernel density estimates indicated that the area used for foraging (95 % FKD) was largest in 2002; 2.2 times larger than that in 1998 and 4.6 times larger than that in 2003 (Table 3), with the foraging areas in 1998 and 2003 almost entirely nested within the larger area used in 2002 (Fig. 2). The core foraging area (50 % FKD) was also largest in 2002; 2.8 times larger than that in 1998 and 7.3 times larger than that in 2003 (Table 3). Despite these differences between years in distances travelled by birds, the core foraging area was a similar proportion of the total area used for foraging each year (11.2 % in 1998, 14.5 % in 2002, 9.2 % in 2003; calculated from data in Table 3).

Individual foraging trips showed approximately 10-fold variation each year in terms of both total distance travelled (146–1291 km in 1998, 156–1547 km in 2002, 68–1175 km in 2003) and maximum distance attained from the colony (39–545 km, 67–590 km and 24–430 km, respectively). Destinations of trips had a highly non-random distribution (propor-

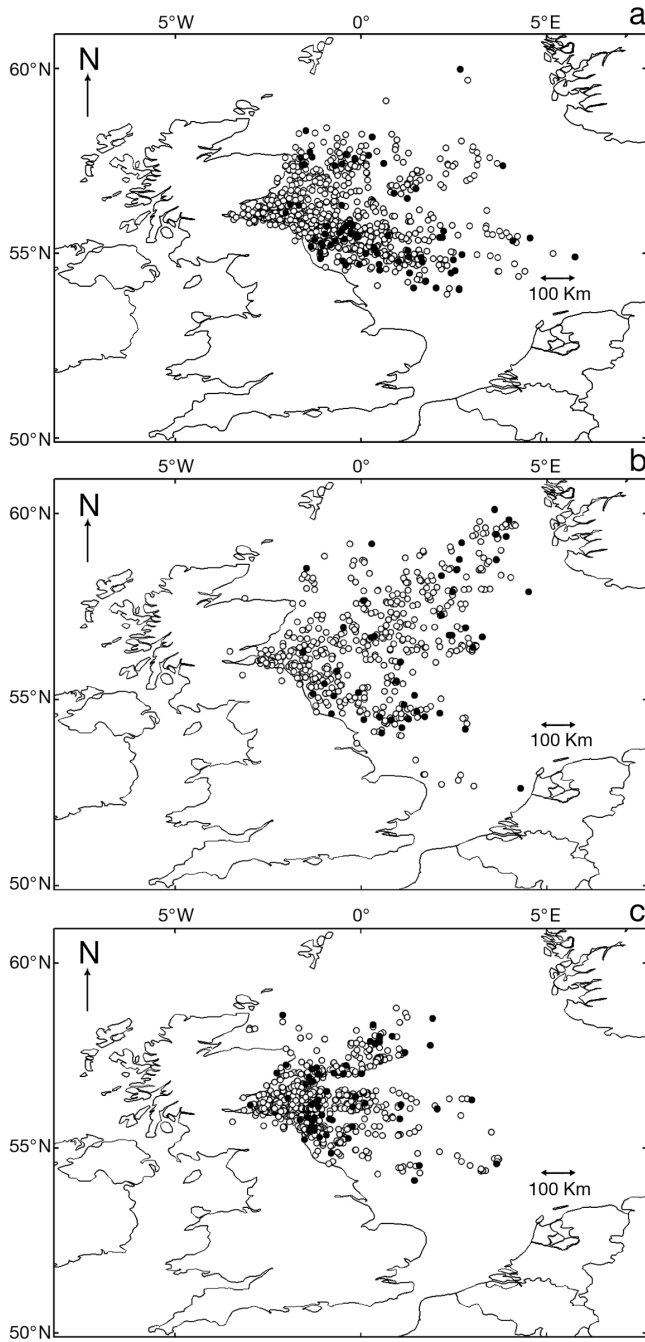


Fig. 1. *Morus bassanus*. Foraging ranges and destinations of foraging trips from Bass Rock, southeast Scotland in (a) 1998, (b) 2002, (c) 2003. ○: locations of adults at sea; ●: destinations of foraging trips

tion of trips with farthest locations in each of 5 consecutive sectors, each subtending an angle of 30° at the colony; $\chi^2_4 = 17.6$, $p = 0.001$) with more trips northeast and southeast and fewer trips east of the colony than would be expected by chance (Fig. 1). Both for trips north of the colony (bearing $\leq 90^\circ$) and for trips south of the colony (bearing $> 90^\circ$), individual birds in all

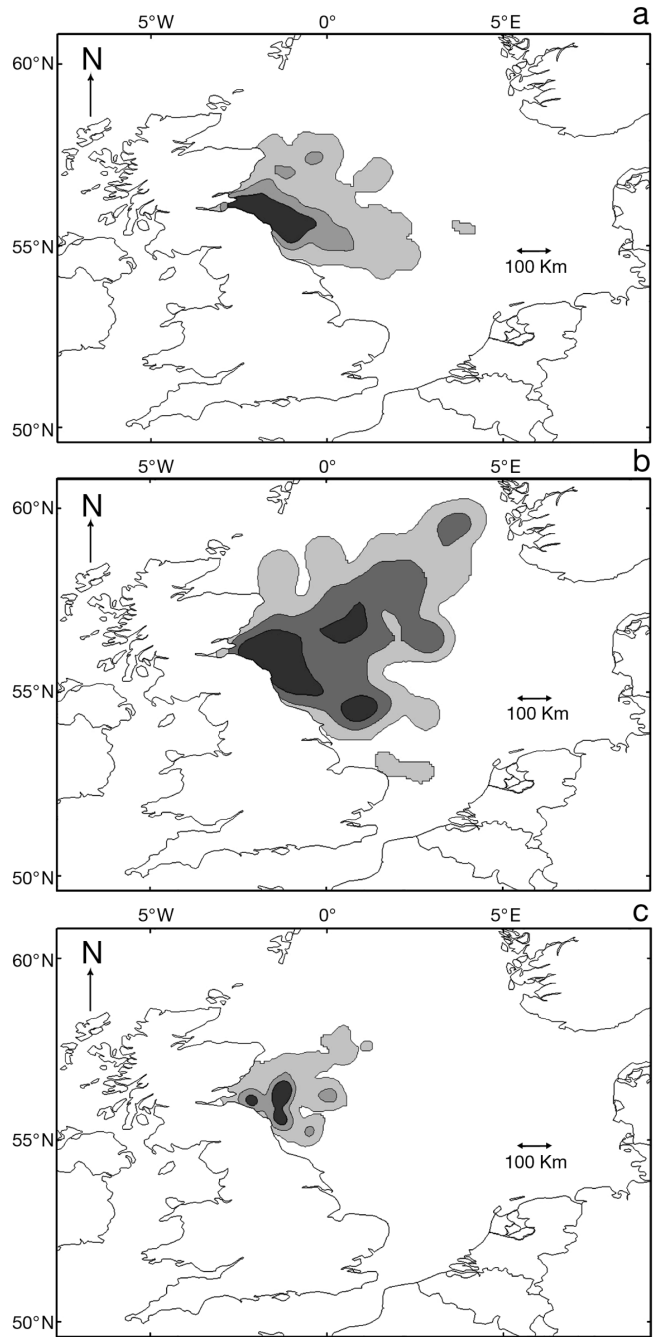


Fig. 2. *Morus bassanus*. Kernels encompassing 50% (dark grey), 75% (medium grey) and 95% (light grey) of foraging locations from the Bass Rock in (a) 1998, (b) 2002 and (c) 2003

3 years tended to make successive trips on similar bearings with little angular deviation from one trip to the next (Table 4). Accordingly, bearings of destinations varied significantly among birds both for trips to the north of the colony (GLM with bird identity nested within year; $F_{30,48} = 3.0$, $p < 0.001$) and for trips to the south of the colony ($F_{24,62} = 5.5$, $p < 0.001$). There was,

Table 4. *Morus bassanus*. Mean bearings and angular deviations for foraging trips from Bass Rock. n: number of foraging trips in each direction for each bird

	Bird	n	Trips SE		n	Trips NE	
			Mean bearing (°)	Angular deviation		Mean bearing (°)	Angular deviation
1998	1	5	137.4	5.7	3	45.6	7.8
	2	4	130.2	5.8	3	74.6	0.2
	3	4	118.2	5.8	2	21.8	1.0
	4	6	111.7	8.3	1	38.1	–
	5	1	119.4	–	7	37.8	12.6
	6	1	100.9	–	3	50.9	24.3
	7	8	110.5	7.6	0	–	–
	8	8	124.5	9.8	0	–	–
	9	6	122.3	5.1	0	–	–
	10	6	111.2	7.4	0	–	–
2002	11	3	132.0	3.2	6	61.9	22.8
	12	4	128.4	7.1	0	–	–
	13	3	103.4	9.3	0	–	–
	14	3	133.2	5.1	0	–	–
	15	3	117.0	8.1	0	–	–
	16	0	–	–	6	53.1	8.2
	17	0	–	–	5	65.6	11.2
	18	0	–	–	3	42.0	3.1
2003	19	2	139.7	3.5	4	42.6	28.3
	20	9	121.4	11.6	1	59.4	–
	21	2	101.9	4.1	1	86.2	–
	22	6	121.6	8.1	0	–	–
	23	0	–	–	8	41.3	6.4
	24	0	–	–	5	35.5	3.4
	25	0	–	–	3	15.8	12.9

however, no difference between years in bearings of trips in either case ($F_{2,48} = 1.9, p = 0.2$ and $F_{2,62} = 2.0, p = 0.2$, respectively).

Despite the large variation in distances travelled during foraging trips each year, there was a highly significant difference between years in distances to destinations of trips (Table 3; GLM including direction [to north or south of colony] as a fixed effect; $F_{2,119} = 14.5, p < 0.001$). Trips were longest in 2002 and shortest in 2003, with distances in 1998 intermediate. Total distances travelled during trips followed a similar pattern (Table 3; $F_{2,119} = 13.8, p < 0.001$). Neither total distance travelled nor maximum distance from the colony differed significantly among birds within each year ($F_{45,119} = 0.9, p = 0.7$ and $F_{45,119} = 1.1, p = 0.3$, respectively) or between trips to the north and south of the colony ($F_{1,119} = 0.04, p = 0.8$ and $F_{1,119} = 0.04, p = 0.8$, respectively; there were no significant interactions between direction and year). Total distance travelled was on average 2.47 (SE \pm 0.03) times the maximum distance from the colony and there was no difference in the slope of this relationship between years (GLM excluding intercept; $F_{2,119} = 2.5, p = 0.1$) or between birds within each year ($F_{45,119} = 1.3, p = 0.1$).

Average speeds of travel over complete trips

Despite the large differences between years in trip durations and distances travelled, there was a highly significant relationship between trip duration and both maximum distance (Fig. 3) from the colony ($F_{1,169} = 1691.04, p < 0.001, R^2 = 0.91$) and total distance travelled (Fig. 4; $F_{1,169} = 1944.5, p < 0.001, R^2 = 0.92$). The most appropriate model, as determined from AIC, was a linear relationship up to an asymptote of 440 km for trips longer than 62 h in the case of

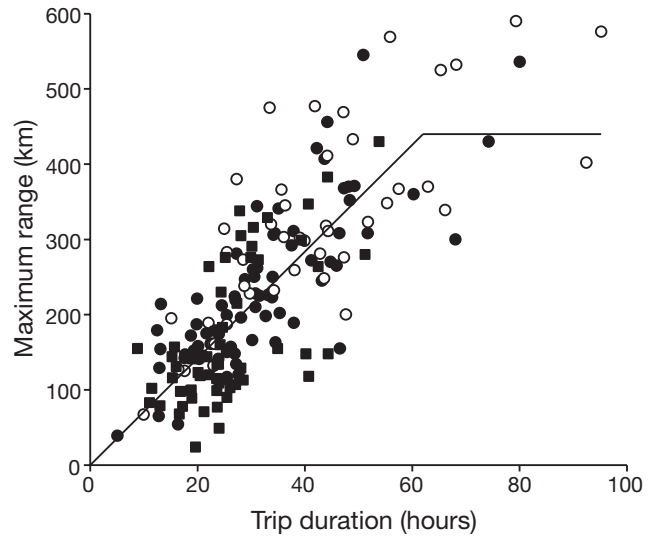


Fig. 3. *Morus bassanus*. Relationship between distance to destination and foraging trip duration in 1998 (●), 2002 (○) and 2003 (■)

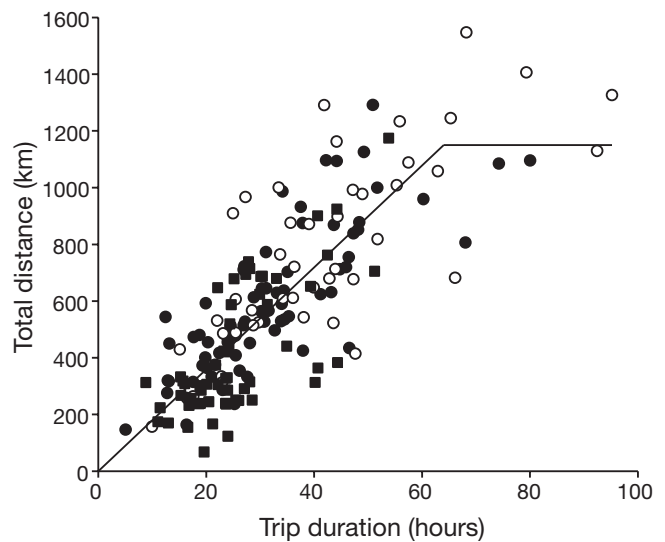


Fig. 4. *Morus bassanus*. Relationship between total distance travelled and foraging trip duration in 1998 (●), 2002 (○) and 2003 (■)

maximum distance and 1150 km for trips longer than 64 h in the case of total distance travelled (Fig. 4; F -test for improvement over linear model; $F_{1,168} = 9.3$, $p < 0.01$ and $F_{1,168} = 7.2$, $p < 0.01$ respectively). For trips below these asymptotes, linear relationships were according to the following equations:

$$\begin{aligned} \text{Maximum distance (km)} = \\ 7.4 (\text{SE} \pm 0.18) \times \text{trip duration (h)} \end{aligned} \quad (2)$$

$$\begin{aligned} \text{Total distance (km)} = \\ 18.5 (\text{SE} \pm 0.41) \times \text{trip duration (h)} \end{aligned} \quad (3)$$

Average speed during these trips was, thus, estimated as $14.8 (\text{SE} \pm 0.4) \text{ km h}^{-1}$ (twice the slope of Eq. 2) using maximum distance from the colony and as $18.5 (\text{SE} \pm 0.4) \text{ km h}^{-1}$ (the slope of Eq. 3) using total distance travelled. GLM indicated no difference between years in the slopes of these relationships ($F_{2,112} = 1.4$, $p = 0.3$ and $F_{2,112} = 0.6$, $p = 0.5$, respectively) and this was confirmed by comparison among years of the mean travel speeds for individual birds (Table 3; 1-way ANOVA with a single value for each bird; from maximum distance from the colony, $F_{2,44} = 1.5$, $p = 0.2$; from total distance travelled, $F_{2,44} = 1.0$, $p = 0.4$). Average travel speeds on trips longer than 60 h were significantly slower (from maximum distance from the colony, mean = $12.2 (\text{SE} \pm 0.51) \text{ km h}^{-1}$, $t_{168} = 5.7$, $p < 0.001$; from total distance travelled, mean = $15.5 (\text{SE} \pm 1.9) \text{ km h}^{-1}$, $t_{168} = 2.3$, $p = 0.02$).

Variation in travel speeds during trips

Speeds of travel over short intervals within trips were calculated using consecutive pairs of locations with ≥ 30 min between them (see 'Materials and methods'). Gannets do not travel at night (Hamer et al. 2000) and in this study, speed of travel during daylight hours was highly dependent on the interval between locations (GLM; $F_{1,1162} = 72.5$, $p < 0.001$), according to the following equation:

$$\begin{aligned} \text{Travel speed (km h}^{-1}\text{)} = 31.8 (\text{SE} \pm 1.1) \\ - 3.2 (\text{SE} \pm 0.4) \text{ interval (h)} \end{aligned} \quad (4)$$

There was no difference between years in either the slope or the elevation of this relationship ($F_{2,1162} = 0.7$, $p = 0.5$ and $F_{2,1162} = 2.5$, $p = 0.1$, respectively), but there was significant variation among birds within each year ($F_{45,1162} = 2.2$, $p < 0.001$). Travel speed over the shortest intervals (32 km h^{-1} , from Eq. 4) was about half average flight speed (55 km h^{-1} ; Grémillet et al. 2004).

Birds travelled out from the colony and returned at similar speeds (mean \pm SD; $20.1 \pm 13.8 \text{ km h}^{-1}$, $n = 170$ and $17.0 \pm 11.6 \text{ km h}^{-1}$, $n = 170$, respectively). Travel speed during the outward leg of the journey was independent of distance to destination, but speed during

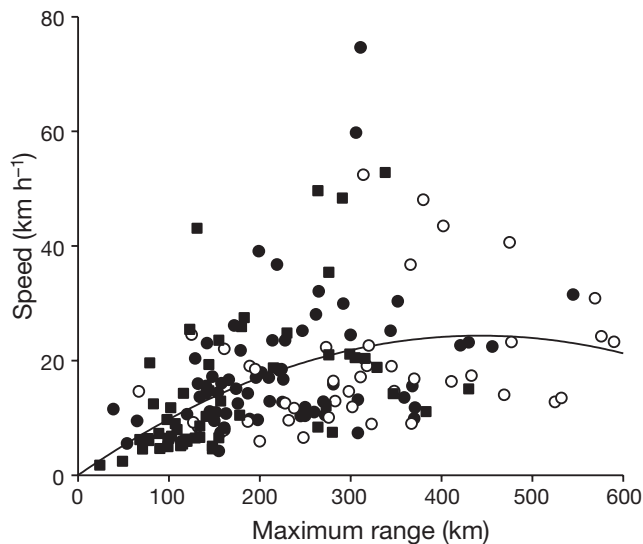


Fig. 5. *Morus bassanus*. Relationship between distance to destination and return travel speed in 1998 (●), 2002 (○) and 2003 (■)

the return leg was significantly related to distance (Fig. 5; stepwise multiple regression; $F_{2,168} = 248.8$, $p < 0.001$, $R^2 = 0.75$) according to the following quadratic equation:

$$\begin{aligned} \text{Travel speed (km h}^{-1}\text{)} = 0.11 (\text{SE} \pm 0.01) \text{ distance} \\ - 1.24 \times 10^{-4} (\text{SE} \pm 0.01 \times 10^{-4}) \text{ distance}^2 \end{aligned} \quad (5)$$

A GLM confirmed that return travel speed was significantly related to both distance ($F_{1,120} = 12.1$, $p = 0.001$) and distance² ($F_{1,120} = 5.5$, $p = 0.02$) with no difference in this relationship between years ($F_{2,120} = 1.5$, $p = 0.2$) or between birds within each year ($F_{45,119} = 0.8$, $p = 0.7$). Calculation of AIC further indicated that Eq. (5) described the data significantly better than a simple linear relationship (F -test for improvement in AIC; $F_{1,169} = 27.4$, $p < 0.01$). Birds returned at a faster rate from more distant locations up to 300–400 km from the nest, beyond which there was a significant reduction in speed (Fig. 5).

DISCUSSION

Flexibility in diet and foraging ranges

Many seabirds along North Sea coasts as far north as Shetland experienced very low reproductive success in 1998, which was linked to low availability of sandeels in late June and July (Thompson et al. 1999). In addition, several species at colonies in southeast Scotland and northeast England experienced below average success in 2002 whilst, with the exception of colonies in Shetland, breeding success was generally high in 2003 (Mavor et al. 2004). In contrast, gannets experienced

very little variation in reproductive success over this period, and this stability largely reflects the high degree of flexibility that they exhibited in their diets and foraging ranges. Not only were adults able to exploit a wide range of species and sizes of prey, obtained using several distinct capture techniques (vertical plunge-diving, underwater pursuit, scooping from the surface and scavenging discards from fishing vessels; Garthe et al. 2000, Lewis et al. 2002), but also the proportions of the different species caught varied markedly between years, with only 0-group sandeels being an important component (>25%) of the diet every year (Table 1). In addition, adults were not only able to exploit prey resources over a very large foraging area (Figs. 1 & 2), but also exhibited marked annual variation in trip durations, foraging ranges and total distances travelled at sea (Table 3). Trips were longest in 2002, when the abundance of 0-group sandeels over the majority of the North Sea was an order of magnitude lower than in the other 2 years studied and only 13% of the long-term (1983 to 2005) average (Table 1.4.24.4. in ICES 2005).

In all years studied, gannets at the Bass Rock made more trips to the northeast and southeast and fewer trips due east of the colony than would be expected by chance (Fig. 1). There was no difference in distances travelled by birds in these directions but the proportion of trips to the north of the colony increased from 30% in 1998 to 62% in 2003 (Table 3). This change may have reflected a decrease in the quality of prey at lower latitudes in recent years in terms of both size and lipid content (Wanless et al. 2004, 2005), but further data are needed to examine latitudinal variation in the sizes and caloric densities of prey species within the North Sea.

Consistency of foraging behaviour

Despite marked differences between years in trip durations, foraging ranges and total distances travelled, the behaviour of birds during foraging trips was very similar each year. This agrees with previous findings from another study comparing 2 different gannet colonies (Hamer et al. 2001). In the present study, the average speed of travel over complete foraging trips was almost identical in all 3 years (Table 3) and the relationship between distance to destination and total distance travelled was also similar each year, as was the proportion of the total foraging area (95% FKD) that comprised the core foraging area (Fig. 2). These data suggest that gannets did not alter their overall search strategy or sinuosity of foraging paths (i.e. the extent of deviation from a straight-line course) between years in relation to trip duration or foraging range.

In all 3 years studied, travel speed during daylight hours decreased significantly with increasing time intervals between locations (Eq. 4), presumably because travel speeds over longer intervals were more affected by deviations from a straight line course and by time that birds spent feeding and resting on the water (Ryan et al. 2004). Over the shortest intervals, where estimates were least affected by deviations from a straight line course, the mean travel speed was 32 km h⁻¹ (from Eq. 4). This value is close to half the normal flight speed of gannets (55 km h⁻¹; Grémillet et al. 2004), indicating that birds in all years spent roughly half their time at sea in flight. Garthe et al. (1999) and Lewis et al. (2004a) also found from external temperature loggers and activity loggers, respectively, that birds spent about half their time away from the colony in flight and the other half on the sea surface.

Hamer et al. (2001) recorded that gannets breeding at the Bass Rock foraged repeatedly over a narrow range of bearings before switching to a separate range of bearings in a markedly different direction from the colony, providing strong evidence that individuals learned and remembered the directions to feeding sites and used that knowledge on subsequent foraging trips. In contrast, birds at a much smaller colony (Great Saltee) in the Celtic Sea did not show this pattern (Hamer et al. 2001). This difference between colonies could have reflected differences in the spatial and temporal predictability of prey resources in the North Sea and Celtic Sea or differences in the costs and benefits of different foraging strategies in relation to travel time. Data from the present study indicate that birds at the Bass Rock foraged repeatedly over a narrow range of bearings in all 3 years despite marked annual variation in trip durations and foraging ranges (Table 2), supporting the notion that differences between colonies in the consistency of foraging locations are related mainly to differences in the spatial and temporal predictability of prey. Despite marked individual variation in the bearings of successive foraging trips, there was no variation among individuals in the durations or ranges of foraging trips, consistent with the notion that birds employed a form of network foraging (Clode 1993, Jaquemet et al. 2005) in which they set out on a bearing to a known feeding site and continued until they either located prey for themselves or encountered other birds flying towards a feeding flock (Hamer et al. 2001).

Constraints on foraging range

In several species of seabirds, parents spend less time together at the nest between foraging trips in years with longer average trip durations (e.g. Mon-

aghan et al. 1994, Litzow & Piatt 2003). Gannets at the Bass Rock normally spend little time with their partners during chick rearing, and so long foraging trips can result in chicks being left unattended whilst both parents forage simultaneously (Lewis et al. 2004b). In this study, each adult was at the nest for about half the time in 2003 but for significantly less than that in the 2 years with longer average trip durations (Table 3), which strongly suggests that longer trips resulted in chicks being left unattended more often, as has also been observed in other species (e.g. great skuas *Catharacta skua*, Hamer et al. 1991; common guillemots *Uria aalge*, Wanless et al. 2005).

Unattended gannet chicks are frequently attacked and sometimes killed by conspecifics (Lewis et al. 2004b), which is likely to result in a selective advantage to adults that return to the nest more quickly from distant foraging locations. In support of this notion, adults that attained greater distances from the colony returned significantly faster over distances up to ca. 300 km (Fig. 5), presumably returning by a more direct route and/or spending more time in flight and less time on the water resting and digesting prey. However the relationship contained a negative quadratic term, indicating that adults returned at slower average speeds from the furthest destinations (beyond ca. 400 km from the colony; Fig. 5). Moreover both maximum range and total distanced travelled at sea had an asymptotic relationship with trip duration, as also found for flight durations of black-legged kittiwakes *Rissa tridactyla* (Daunt et al. 2002), and these data provide further evidence of a constraint on the foraging ranges of gannets for trips longer than ca. 60 h (Figs. 3 & 4). Gannets employ an energetically expensive mode of flight, and bioenergetics modelling indicated that whilst gannets at the Bass Rock had the capacity within their time/activity budgets to increase the proportion of time spent in flight during foraging trips, any such increase would probably exceed their maximal energetic capacity (Enstipp et al. 2006). The non-linear relationships observed in the present study, thus, probably reflected a constraint on the time that adults could spend in continuous flight back to the colony from distant foraging locations before exceeding their metabolic ceiling, and this constraint probably explains why there was no systematic increase in the proportion of time that birds spent in flight each year in relation to average trip duration.

Chicks were invariably fed at the end of foraging trips, and the results of this study indicate marked annual variation in feeding frequency. This may have been compensated for to some extent by variation in the sizes or caloric densities of meals delivered to chicks (as found by Lewis et al. 2003 in a comparison between gannet colonies). Thus, longer foraging trips

need not necessarily have led to poor chick growth. However, long trips resulted in chicks being left unattended and vulnerable to attack, and adults were apparently constrained in their ability to reduce trip duration by returning more quickly from distant foraging locations. These data suggest that whilst adults have so far been able to maintain high reproductive success in years of low prey availability, they may not be able to do so in future years if providing sufficient food for chicks entails any further increases in trip duration or foraging effort.

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