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Northern gannets anticipate the spatio–temporal occurrence of their prey

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SUMMARY

Seabirds, as other marine top predators, are often assumed to forage in an unpredictable environment. We challenge this concept and test the hypothesis that breeding Northern gannets (*Morus bassanus*) anticipate the spatio–temporal occurrence of their prey in the English Channel. We analyzed 23 foraging tracks of Northern gannets breeding on Rouzic Island (Brittany) that were recorded using GPS loggers during 2 consecutive years. All birds commuted between the breeding colony and foraging areas located at a mean distance of 85km and 72km (in 2005 and 2006, respectively) from the colony. Mean linearity indices of the outbound and inbound trips were between 0.83 and 0.87, approaching a beeline path to and from the foraging area. Additional parameters (flight speed, and number and duration of stopovers at sea) for the outbound and inbound trip were not statistically different, indicating that birds are capable of locating these feeding areas in the absence of visual clues, and to pin-point their breeding site when returning from the sea. Our bearing choice analysis also revealed that gannets anticipate the general direction of their foraging area during the first 30min and the first 10km of the trip. These results strongly suggest that birds anticipate prey location, rather than head into a random direction until encountering a profitable area. Further investigations are necessary to identify the mechanisms involved in seabird resource localization, such as sensorial abilities, memory effects, public information or a combination of these factors.

Key words: seabirds, *Morus bassanus*, GPS-tracking, orientation, optimal foraging.

INTRODUCTION

Spatio–temporal heterogeneity in the distribution of food resources is a major environmental constraint upon animals, which need to find resources to acquire energy. Time dedicated to foraging might change over the annual cycle, depending on the seasonal rhythm and the reproductive status of the animal (Rydell, 1993; McCafferty et al., 1998). For individuals commuting between feeding areas and breeding/shelter sites (called central places foragers), the energy needed is augmented by the energetic costs associated with commuting. During the reproductive period, energy and food requirements rise substantially, and foraging effort reaches a maximum, as adults collect food to fulfil their own requirements, as well as those of their offspring. Then, central place foragers experience increased constraints as their progeny requires feeding at regular intervals in order to avoid starvation and/or because the mate may abandon the young if its survival is threatened by starvation. For example, if not relieved by their partner, blue petrels (*Halobena caerulea*) leave the nest when their body mass reaches a minimum threshold (Chaurand and Weimerskirch, 1994).

Optimal foraging largely depends upon the animal's ability to find food within the accessible range (Bell, 1991). Individuals that successfully anticipate the spatio–temporal occurrence of profitable prey patches are most likely to optimize their foraging efficiency and their reproductive success, thereby increasing their fitness (Krebs and Davies, 1978). Locating profitable feeding areas may be a highly challenging task in an apparently poor or featureless environment, such as open seas exploited by foraging seabirds. The marine environment has long been considered as unpredictable, with a highly scattered, patchy distribution of resources (Ashmole, 1971). However, recent tracking results from biotelemetry studies clearly demonstrate that marine top predators do not search for prey randomly (Staniland et al., 2004; Weimerskirch, 2007). Physical features of ocean basins influence marine productivity. Upwelling areas, frontal zones and shelf edges are highly profitable areas that attract large number of marine predators (Hunt et al., 1999; Bost et al., 2009). These areas may provide clues exploited by marine predators to locate them. For example, several Procellariiform species are attracted by dimethyl sulphide (DMS), the concentration of which is particularly high in areas where primary productivity is enhanced (Nevitt and Bonadonna, 2005; Nevitt, 2008).

Beyond sensory abilities, individual experience, cognitive processes and information exchange between individuals (Ward and Zahavi, 1973) might help seabirds to find profitable areas and improve their foraging efficiency across successive foraging trips. The key role of experience and memory is supported by studies showing significant levels of foraging site fidelity in seabird species such as great cormorants *Phalacrocorax carbo* (Grémillet et al., 1999), black-browed albatrosses *Diomedea melanophris* (Weimerskirch, 2007) and Northern gannets *Morus bassanus* (Hamer et al., 2007).

Northern gannets are large seabirds that forage for pelagic fish in the North Atlantic, travelling tens to hundreds of kilometers away from their breeding sites (Hamer et al., 2000). Their reproductive success, therefore, largely relies upon their ability to identify profitable areas within a vast foraging range.

In this paper, by analyzing GPS-logged foraging tracks, we test the hypothesis that gannets anticipate the position of their first feeding patch and determine the bearing of their foraging location soon after leaving their nest sites.

MATERIALS AND METHODS

GPS deployments

Field work took place on Rouzic Island, Sept-Iles archipelago, Brittany (48°54′0″N, 3°26′11″W) under permits from the Réserve Naturelle des Sept Iles. Fourteen adults raising a chick and nine incubating adults were equipped with a GPS logger in July 2005 and June 2006, respectively. Birds were caught on the nest with a telescopic pole fitted with a noose, when both parents were present. We took great care to minimize the impact of our study and caught birds mainly at dawn to avoid heat stress (Hochscheid et al., 2002). Immediately after the changeover, the bird which was about to initiate a foraging trip was caught and equipped with a data logger, while its mate remained at the nest site attending the egg or chick. Handling lasted less than 10 min in all cases, during which time the bird's head was covered to reduce stress. Birds were only equipped for a single foraging trip not exceeding 38 h.

We used white Tesa (Hamburg, Germany) tape to attach the devices to the lower back of the birds. The tape, matching plumage colour, guaranteed a safe attachment during the whole trip at sea and a minimal damage to feathers upon removal (Wilson et al., 1997). A previous study at the same field site used these methods without noticeable impact on the birds (Grémillet et al., 2006).

We could not sex birds reliably during this study but assumed that random bird capture ensured a balanced sex ratio of our sample [validated in Lewis et al. (Lewis et al., 2002)]. In an expanding gannetry, the colony fringe consists almost entirely of young breeders (Nelson, 2002). To avoid any biases resulting from a site–age effect and to ensure a normal age distribution among the equipped birds, nests were selected randomly from the periphery to 10 m within the colony (i.e. the maximum length of the catching pole).

Data logger specifications and analysis of electronic data sets

We deployed GPS data loggers from Technosmart, Rome, Italy (95 mm×48 mm×24 mm; 65 g, i.e. 2.1% of the body mass of the birds) recording latitude, longitude and speed every 10 s. The GPS data loggers were removed from birds after a single foraging trip (Fig. 1). From GPS positions and speed values recorded off the colony, we calculated path lengths between two fixes, distances to the nest and the time spent flying – birds were assumed to fly when GPS speed exceeded 10 km h^{-1} (for details see Grémillet et al., 2004). In order to identify feeding areas for each bird, we used a path sinuosity index, defined as the ratio of the actual flight speed given by the GPS receiver to the velocity calculated from the distance travelled between every third fix (i.e. total displacement every 30 s). A bird circling around in a restricted area will have a lower calculated speed than the actual GPS speed, resulting in a higher sinuosity index. Such positions of high sinuosity have been shown to be associated with active feeding behaviour in gannets [for validation, see Grémillet et al. (Grémillet et al., 2006)]. Plotting all feeding locations as individual data points does not reveal the locations of the most intensively exploited areas within a home range. Following Wood et al. (Wood et al., 2000), we used kernel analysis to transform point distributions into density estimates of feeding positions. Analyses were conducted with the Kernel Density Estimate tool (Arcview GIS 3.2). The smoothing factor was chosen according to the Least Square Cross Validation method (Girard et al., 2002). This approach allows statistical analysis of distribution patterns and therefore highlights feeding hotspots.

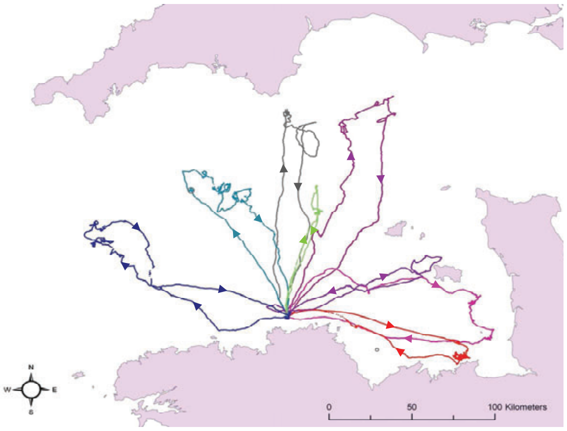

Fig. 1. *Morus bassanus.* Examples of GPS tracks recorded during the foraging trips of eight Northern gannets from the Sept-Iles in the western English Channel (2005 and 2006). Different colours show tracks from different birds, arrows show the outbound and inbound parts.

Comparison of outbound and inbound trip features

When gannets start a foraging trip at sea, different strategies may lead them to a profitable area, from a purely 'random walk' type path to an orientated path. There are three scenarios.

(1) Food is heterogeneously distributed and no information is available to the birds about the location of potential resource patches: a sinuous walk is then predicted to maximize chances to come across food (reviewed in Hawkes, 2009).

(2) Food is homogeneously distributed around the colony (with an extreme case whereby food is distributed along a 'ring' around the breeding site) and no information about the location of potential resource patches is available: the animal takes and keeps a random bearing and follows it in a beeline to reduce flight costs. It is important to note that this 'linear and random' strategy is entirely theoretical, and has never been observed in nature (Hawkes, 2009).

(3) Information about food distribution is available to the birds (e.g. from previous experience, public information or sensory cues), and a linear, goal-oriented trip towards the target is therefore expected (Hawkes, 2009). Animals then tend to follow a beeline, but potential errors in the orientation mechanisms induce deflections from this beeline and adjustments, that reduce path linearity.

Thus, if recorded paths show high linearity levels, we will have to determine whether gannets follow an anticipatory strategy or a 'linear and random' strategy during their foraging trips. We therefore hypothesised that the theoretical 'linear and random' trip will follow a perfect beeline, and that the characteristics of a goal-oriented trip are given by the inbound trip. Indeed, the location of the breeding site is known to the birds. We thus compared the outbound trip (between the colony and the main feeding area) to the inbound trip (return from offshore to the island). The end of the outbound trip, i.e. the area where birds foraged most intensively, was defined using a combination of three criteria: a high sinuosity index, an occurrence of drastic changes in the recorded flight speed (each dive induces a speed drop for a few seconds), and a visual assessment of the tracks using Arcgis 9.2 (Environmental Systems Research Institute). As our analyses confirmed that birds usually focused their foraging effort on one major foraging area, we assumed that it was the goal of their foraging trip.

To locate the start of the inbound journey, we analyzed the foraging track backwards, starting from the nest site towards the last intense foraging activity and/or overnight rest at sea [northern gannets spend nearly half of their time at sea resting at the water surface (Grémillet et al., 2006)]. For both trips, we calculated linearity index (i.e. the sum of the distances between each fix divided by the beeline distance between the breeding site and the foraging area), average flight speed, and the number and duration of stops at the sea surface along the track segment.

The colony is a predictable location that the gannets are able to anticipate. If gannets also anticipate the location of their foraging site, outbound and inbound journeys should show similar patterns. We therefore compared these indices for outbound and inbound sections of the foraging track using a paired-wise Wilcoxon test.

Data recorded in 2005 and 2006 were compared using non-parametric Mann–Whitney tests for each parameter. Values are presented as means ± s.d.

Bearing choice

After defining a main foraging area for each equipped bird (i.e. the area where birds foraged most intensively), we selected the position of the first diving event in the main foraging area (i.e. at the end of the outbound trip) and recorded it as 'B': the assumed goal of the bird. Using the geographical coordinates of the nest 'A' and the first foraging event 'B', we then calculated $\alpha(f)$, the theoretical bearing that birds should follow to reach the foraging area in a beeline (between 0 and 360°). Secondly, we calculated $\alpha(t)$, the angle between 'A' and each positional fix of the outbound trip. Finally, we calculated the angle Φ, which is the difference between $\alpha(f)$ and $\alpha(t)$ along the outbound trip, using the following equation (Fig. 2):

$$\Phi = \alpha(f) - \alpha(t)\,. \tag{1}$$

The value of Φ in relation to flight duration and distance to the nest indicate the moment when gannets orientate their flight towards the foraging area. We assumed that birds headed towards the foraging area when Φ reached the asymptote.

RESULTS

All equipped birds bred normally after device deployment. In 2005, gannets encountered their first major fishing area within an average distance of 85±31 km (range: 35–133 km). They started their return journey to the breeding site from an average distance of 94±33 km (range: 36–145 km). Similarly in 2006, gannets foraged mainly within 72±25 km (range: 32–107 km) of the colony and travelled 71±26 km (range: 36–102 km) to get back to their nest.

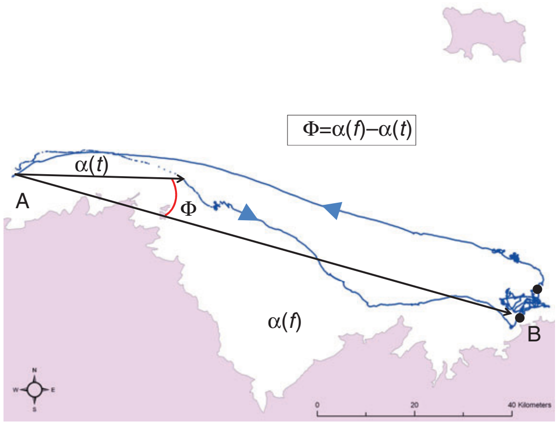

Fig. 2. *Morus bassanus*. GPS track recorded during the foraging trip of a Northern gannet from Rouzic Island. $\alpha(f)$ is the bearing between the nest site (A) and the foraging area (B). $\alpha(t)$ is the bearing between the nest site and each fix recorded at 10-second intervals along the outbound trip. Φ is the difference between $\alpha(f)$ and $\alpha(t)$. Arrows show the outbound and inbound parts, black dots show the end of outbound trip and the start of the inbound trip.

Birds spent the major part of their trip within a specific foraging area, either fishing or resting at sea. In fact, although total trip duration was 19.2±8.5 h in 2005 and 19.8±9.9 h in 2006, the duration of the outbound journey (2.7±2.3 h and 2.8±1.3 h in 2005 and 2006, respectively) and the homeward journey (2.4±0.8 h in 2005 and 1.8±0.6 h in 2006) accounted only for a small proportion of total trip duration: the sum of the outbound and return journey made up 26% and 23% of total foraging trip duration in 2005 and 2006, respectively. Summary statistics of foraging trip characteristics are given in the Table 1.

Density Kernel analyses of the foraging locations revealed that gannets were exclusively foraging in the Western English Channel (WEC) in both years (Fig. 3A,B). In 2005, gannets preferentially exploited the tidal front area situated in the central WEC, northwest of Guernsey, and coastal areas on both sides of the English Channel (Grémillet et al., 2006). In 2006, gannets mainly exploited the frontal zone of the WEC, north of the colony, as well as the French coastal area.

Comparison of the outbound and inbound trip features

Median linearity indexes in 2005 and in 2006 were between 0.83 and 0.87 (Fig. 4A), with the maximum value of 1 corresponding to a beeline trip. A Wilcoxon signed-rank test showed no significant differences between the linearity of the outbound and the inbound sections of the foraging path in both years (W=48, *P*=0.77 in 2005; W=14, *P*=0.31 in 2006).

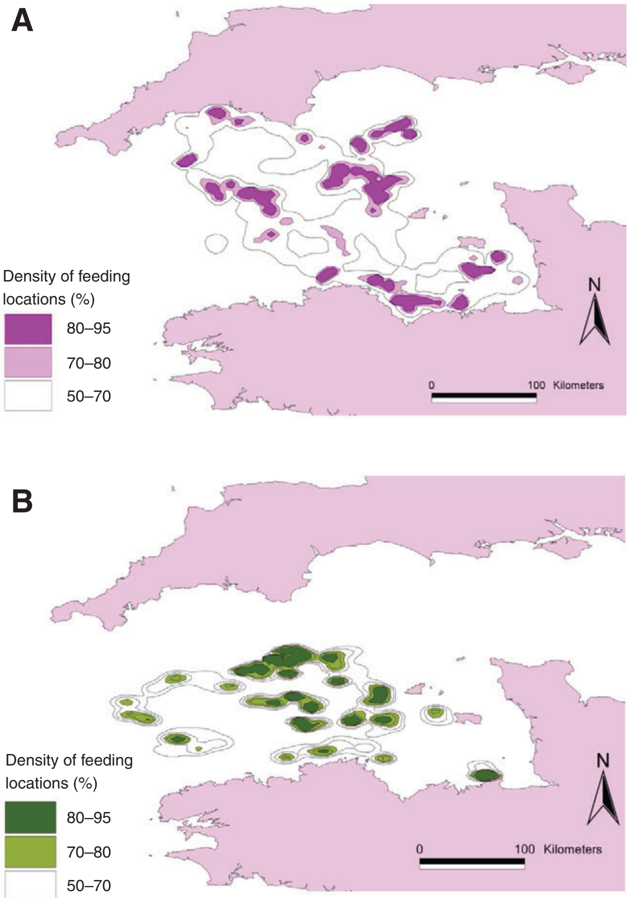

Fig. 3. *Morus bassanus.* Relative density of feeding locations in the Channel (from Kernel Density Estimate analysis, 50–70, 70–80, 80–95%): (A) in 2005 (*N*=20); (B) in 2006 (*N*=20).

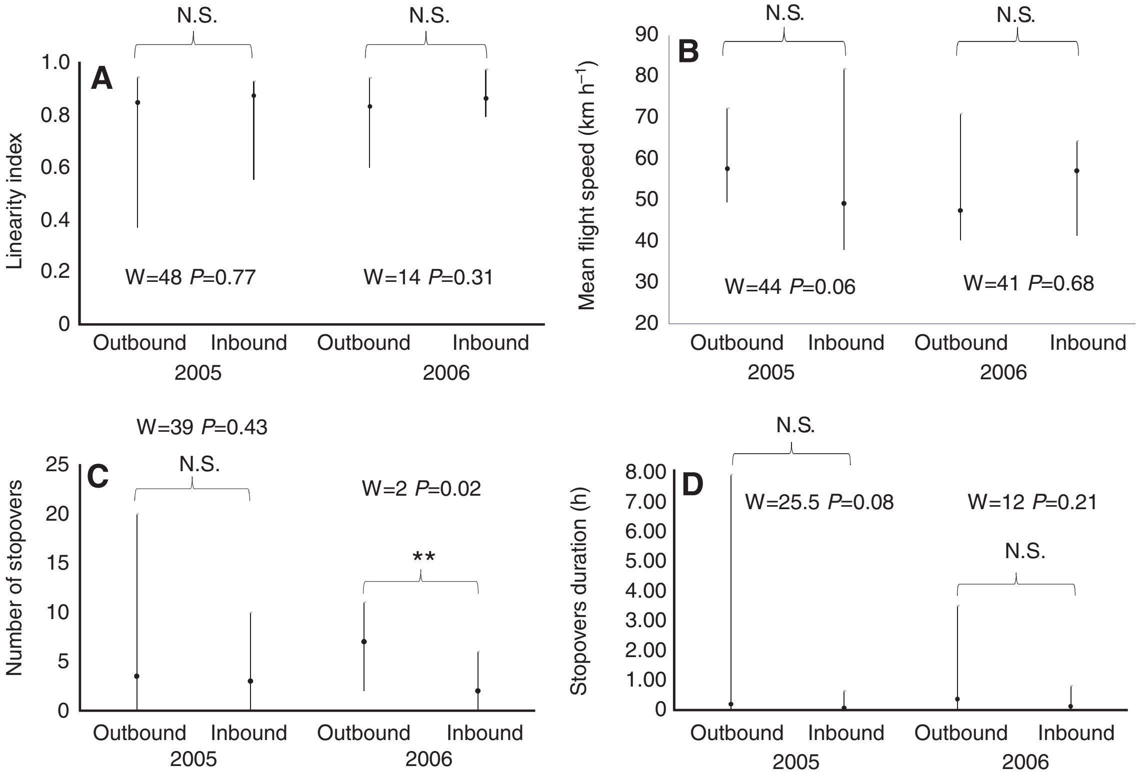

Fig. 4. *Morus bassanus*. Comparison of the outbound and the inbound section of foraging trips by breeding adults in 2005 (N=14) and 2006 (N=9) using a Wilcoxon signed-rank test (mean and range). (A) Linearity index. (B) Mean flight speed (km h^{-1}). (C) Number of stopovers at sea. (D) Stopover duration (hours).

When flying between nesting and foraging site, median speeds in 2005 and 2006 were between 47.4 km h^{-1} and 57.1 km h^{-1} (Fig. 4B). There was no significant difference between the outbound and return flight speeds in 2005 or in 2006 (Wilcoxon signed-rank test: W=44, P=0.06; W=41, P=0.68, respectively).

Birds showed a similar number of stop events during the outbound and the return trip in 2005 (Wilcoxon signed-rank test: W=39, P=0.43, see Fig. 4C). However, in 2006, birds stopped more frequently during the outbound section than during the return section (Wilcoxon signed-rank test: W=2, P=0.02, see Fig. 4C). There were no significant differences between the median duration of these stops for the outbound and inbound sections of foraging trips in either 2005 or 2006 (Wilcoxon signed-rank test W=25.5, P=0.08 in 2005; W=12, P=0.21 in 2006, see Fig. 4D).

Although, generally, all of these tests showed no significant differences between years, we nonetheless decided to analyze the 2 years separately, as birds were equipped at different stages of their reproductive cycle, during which they might potentially pursue different foraging strategies.

Bearing choice

Relationships between Φ and flight durations in 2005 and 2006 are shown in Fig. 5A,B. These relationships are best described by a logarithmic function, where the value of Φ drops rapidly after departure from the nest site and subsequently decreases more gradually towards zero as birds approach the foraging site. Crucially, the bearing followed by gannets after 15 and 9 min of flight (in 2005 and 2006, respectively) differed only by 20° from $\alpha(f)$, the ideal bearing to reach the foraging area in a beeline. The value of Φ decreased further to 14° and 13° after 30 min of flight (in 2005 and 2006, respectively).

Relationships between Φ and distance to the nest in 2005 and 2006 are shown in Fig. 5C,D. They are of similar shape as those between Φ and flight duration. In 2005, Φ dropped below 20° at a distance of 10 km from the nest site and reached 14.7° at a distance of 20 km from the nest (for a mean distance of 85 km between the nest site and the foraging area). In 2006, Φ dropped below 20° at a distance of 3 km from the nest site and reached 10.5° at a distance of 20 km from the nest (for a mean distance of 72 km between the nest site and the foraging area).

DISCUSSION

Movement patterns of foraging animals have been studied for decades in a broad range of species, from social insects such as bumble bees (Dukas and Real, 1993) and ants (Bovet et al., 1989; Müller and Wehner, 1988; Schmid-Hempel, 1984) to mammals (Loureiro et al., 2007). Weimerskirch (Weimerskirch, 2007) showed that marine predators do not forage randomly in an unpredictable environment at large and mesoscales, and numerous studies in seabirds focused on the identification of sinuous sections of the foraging trip, potentially associated with feeding activity (Area Restricted Search) (see Pinaud and Weimerskirch, 2007). However, recent work indicated that the ecological relevance of linear foraging tracks followed by seabirds has not been sufficiently explored (Trathan et al., 2008).

Our analysis of outbound and inbound paths from gannets foraging off Brittany revealed that birds followed equally straight paths on their way to the foraging area and when returning to their breeding site. All tracks showed similar patterns (see Fig. 1): (1) a

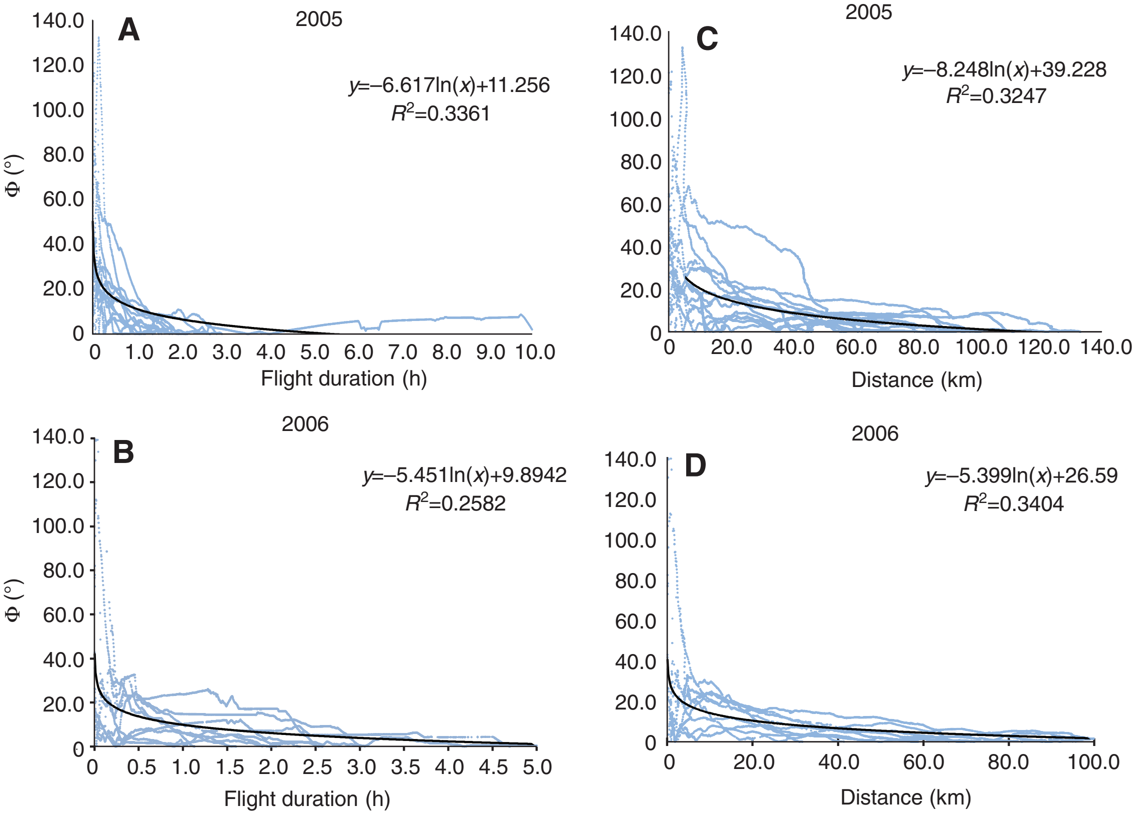

Fig. 5. *Morus bassanus*. Relationship between Φ (in degrees) and flight duration (in hours) during the outbound trip: (A) in 2005 (N=14); (B) in 2006 (N=9). Relationship between Φ (in degrees) and the distance to the nest site (in kilometers) during the outbound trip: (C) in 2005 (N=14); (D) in 2006 (N=9). Φ represents the difference between α(f), the bearing to the foraging area, and α(t), the bearing followed by the gannets at each fix (see Fig. 3). The solid black line represents the regression.

linear trajectory between the colony and the first foraging area (Fig. 4A); (2) a highly sinuous path in association with fishing activity, punctuated by resting periods at the sea surface; (3) a linear return trajectory to the nest (Fig. 4A). Travel time represented only a quarter of the total trip duration, with the remaining time being dedicated to fishing activity and resting at the sea surface within the foraging area (Table 1).

Gannets from Rouzic Island can therefore be defined as commuting foragers (*sensu* Nevitt, 2008), which travel rapidly towards a profitable area using navigation mechanisms yet to be investigated, and, once on site, engage in area-restricted search (ARS) (*sensu* Kareiva and Odell, 1987). They then rest and digest at the water surface (Ropert-Coudert et al., 2004) before flying straight back to their breeding site.

To compare outbound and inbound trips, we tested three additional parameters (Fig. 4B–D), which may reveal differential strategies adopted by gannets during these two phases. Median flight speed and stopover duration were not significantly different, supporting the anticipatory hypothesis. However, in 2006, the number of stopovers was higher during the outbound trip than during the return trip. As stopover numbers during outward and inward trip phases were not different in 2005, we think that the breeding status of the birds (chick rearing in 2005 and incubating in 2006) might explain this difference.

Table 1. Characteristics of foraging trips made by adult *Morus bassanus*

		Foraging trip duration (h)	Outbound distance (km)	Inbound distance (km)	Outbound flight duration (h)	Inbound flight duration (h)	Total path length (km)	Outbound path length (km)	Inbound path length (km)
2005 (N=14)	Mean	19.2	85	94	2.7	2.4	450	108	136
	s.d.	8.5	31	33	2.3	0.8	224	40	106
	Min.	3.2	35	36	0.9	0.9	122	39	51
	Max.	28.2	133	145	10.1	3.9	856	166	487
2006 (N=9)	Mean	19.8	72	71	2.8	1.8	310	88	81
	s.d.	9.9	25	26	1.3	0.6	116	33	29
	Min.	7.3	32	36	1.1	0.8	125	45	42
	Max.	36.7	107	102	5.2	2.8	509	136	120

Measurements were made during the incubation phase (N=9; 2006) and chick-rearing phase (N=14; 2005) on Rouzic Island, Réserve des Sept-Iles. Information derived from GPS data loggers.

However, the linearity index was not significantly different between incubating and chick-rearing gannets, suggesting that anticipation of the foraging site might occurs regardless of the stage of the reproductive cycle (Fig. 4A).

The fact that gannets foraged in one restricted area does not automatically induce an early anticipation of its location. We saw that the linearity index was high (LI=0.87 and LI=0.86 in 2005 and 2006, respectively) for the outbound trip, so that birds nearly followed a beeline trajectory towards the foraging site. Nevertheless, we have seen that two opposite and mutually exclusive strategies could generate this high path linearity.

(1) Birds randomly choose a bearing and keep flying in the same direction until they encounter a resource patch with a high degree of uncertainty. As alluded to earlier, it is important to note that this possibility has been largely excluded by theoretical work, and that it has so far never been observed in nature (Hawkes, 2009).

(2) Birds are anticipating the location of a profitable area when they start the foraging trip either by using sensory cues, public information (Ward and Zahavi, 1973) or their own experience gained during previous successful trips (Hamer et al., 2007). The latter strategy is the one expected for the inbound trip, from the feeding area towards the colony, the invariable position of which is obviously known to breeders from past experience.

Two further points support the idea that northern gannets foraging in the English Channel possess information about the position of the targeted prey patch.

(1) We compared the characteristics of outward *versus* homeward sections of the foraging trip. If a bird chooses a direction at random and follows it until encountering a prey patch, we would expect the path to be more linear than it would be for a bird that flies towards a known foraging area, gradually adjusting its bearing. In this case, if the gannets were following a 'linear and random' strategy, outbound trips would have been more linear than inbound trips, independent of distance, visibility and weather conditions, which occur randomly during the foraging trip. By contrast, our results show that the outbound and inbound linearity indexes are similar and the values (between 0.83 and 0.87) strongly support the theory that gannets succeed in orientating their flight to the foraging area and to their colony in an apparently featureless oceanic environment.

(2) Moreover, kernel analysis of the GPS positions of foraging gannets revealed that they exploited specific areas of the Western English Channel in both years, preferentially the area located to the north of the colony, which features a marked tidal front (Fig. 3A,B). This tidal front corresponds to a boundary layer between stratified Atlantic surface waters in the west and highly mixed surface Channel waters in the east (Southward et al., 2005). High productivity at this front favours aggregations of marine top predators (Sims et al., 2005), including northern gannets (Pingree et al., 1974; Siorat and Rocamora, 1992).

Clustered gannet foraging locations support the idea that prey distribution is not homogeneous in the vicinity of the colony and that it is advantageous for gannets to setup their own mental map of the profitable patches.

Our findings are in accordance with the conclusions of previous studies conducted in a wide range of foraging animals. For example, Bovet et al. (Bovet et al., 1989) analyzed movements in Serrastruma lujae ants and showed that the outbound trip was erratic and very sinuous, whereas the path towards the colony, of known location, was linear and directional.

These results could be further substantiated by recording a series of successive foraging trips for the same individuals. If single birds return time and again straight to the same feeding location, this will certainly be a clear sign that they anticipate its position. However, they might also use long-term experience for daily updates of the likely position of spatio–temporally labile food patches. In this case, an orientated trip of varying bearing will take them to a different feeding patch during each trip. Preliminary analysis of successive foraging trips conducted by northern gannets foraging off Norway supports this latter option (E.P., unpublished).

Bearing choice analysis supports the idea that gannets anticipate the direction towards the foraging area rapidly after starting the foraging trip (Fig. 5A–D). Indeed, the difference between the ideal bearing to the foraging area and the one actually followed by the gannets decreased dramatically during the first 30 min of the trip, and within the first 10 km from the nest site. At this point, gannets are not able to see the foraging area that they intend to visit, as the mean distance to the feeding site was >70 km in both years. For a seabird flying at 30 meters above the sea level, linear distance to the horizon does not exceed 20 km, independent of its visual capabilities. In this case, gannets that fly rather low when compared with other seabirds (Nelson, 2002), may rely upon further cues such as olfaction, public information and their own knowledge of the foraging grounds (the western English Channel in this case) to decide on a general orientation. They might later refine their navigation as additional information from the environment becomes available.

Previous studies investigating the foraging strategies of gannets have shown that changes in prey distribution might occur from one year to another and force birds to adapt their foraging behaviour (Hamer et al., 2007; Pichegru et al., 2007). In this context, three mechanisms can be envisaged.

(1) Main prey distribution does not vary significantly over time and gannets that return to a specific breeding area may use past experience to exploit these areas effectively from the start of the breeding season. Recurrent high productivity areas such as the mid-channel tidal front (see Grémillet et al., 2006) are typical examples of oceanic features that facilitate efficient seabird foraging in the long term.

(2) Main prey distribution changes significantly across breeding seasons: in this case gannets may engage in some form of random search early in the season while nest building and incubating. This will allow them to draw or update their own prey distribution map, to be efficiently exploited during the most demanding times of chick rearing.

(3) Finally, gannets may complement the first two strategies by fine-tuning their local knowledge of the most profitable foraging areas as they accumulate experience during the many foraging trips conducted during their extended breeding season (approximately 60 foraging trips over 4 months).

Such mechanisms are potentially applicable to a wide range of foraging animals. In the case of marine top predators, novel technologies now allow tracking the movements of individuals at a very fine spatial and temporal resolution, while assessing the biotic and abiotic parameters affecting their senses (Nevitt, 2008, Nevitt et al., 2008). These investigations will trigger a leap in our understanding of the cognitive abilities of marine animals and will most certainly demonstrate that these animals are very far from roaming in a featureless environment.

LIST OF SYMBOLS AND ABBREVIATIONS

GPS	global positioning system
s.d.	standard deviation
$\alpha(f)$	bearing between the nest 'A' and the foraging area 'B'
$\alpha(t)$	bearing between the nest 'A' and each positional fix of the outbound trip
Φ	measured difference between $\alpha(f)$ and $\alpha(t)$

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REFERENCES

Ashmole, N. P. (1971). Seabird ecology and the marine environment. *Avian Biol.* **1**, 223-286.

Bell, W. J. (1991). *Searching Behaviour: the Behavioural Ecology of Finding Resources.* New York: Chapman and Hall.

Bost, C. A., Cotte, C., Bailleul, F., Cherel, Y., Charrassin, J. B., Guinet, C., Ainley, D. G. and Weimerskirch, H. (2009). The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *J. Mar. Syst.* **78**, 363-376.

Bovet, P., Dejean, A. and Granjon, M. (1989). Trajets d'approvisionnement à partir d'un nid central chez la fourmi *Serrastruma lu]ae* (Formicidae: Myrmicinae). *Insectes Sociaux* **36**, 51-61.

Chaurand, T. and Weimerskirch, H. (1994). Incubation routine, body-mass regulation and egg neglect in the blue petrel *Halobaena caerulea*. *Ibis* **136**, 285-290.

Dukas, R. and Real, L. A. (1993). Effects of recent experience on foraging decisions by bumble bees. *Oecologia* **94**, 244-246.

Girard, I., Ouellet, J. P., Courtois, R., Dussault, C. and Breton, L. (2002). Effects of sampling effort based on GPS telemetry on home range size estimations. *J. Wildl. Manage.* **66**, 1290-1300.

Grémillet, D., Wilson, R. P., Storch, S. and Gary, Y. (1999). Three-dimensional space utilization by a marine predator. *Mar. Ecol. Prog. Ser.* **183**, 263-273.

Grémillet, D., Dell'Omo, G., Ryan, P. G., Peters, G., Ropert-Coudert, Y. and Weeks, S. J. (2004). Offshore diplomacy, or how seabirds mitigate intra-specific competition: a case study based on GPS tracking of Cape gannets from neighbouring colonies. *Mar. Ecol. Prog. Ser.* **268**, 265-279.

Grémillet, D., Pichegru, L., Siorat, F. and Georges, J. Y. (2006). Conservation implications of the apparent mismatch between population dynamics and foraging effort in French northern gannets from the English Channel. *Mar. Ecol. Prog. Ser.* **319**, 15-25.

Hamer, K. C., Phillips, R. A., Wanless, S., Harris, M. P. and Wood, A. G. (2000). Foraging ranges, diets and feeding locations of gannets in the North Sea: evidence from satellite telemetry. *Mar. Ecol. Prog. Ser.* **200**, 257-264.

Hamer, K. C., Humphreys, E. M., Garthe, S., Hennicke, J., Peters, G., Grémillet, D., Phillips, R. A., Harris, M. P. and Wanless, S. (2007). Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint. *Mar. Ecol. Prog. Ser.* **338**, 295-305.

Hawkes, C. (2009). Linking movement behaviour, dispersal and population processes: is individual variation a key? *J. Anim. Ecol.* **78**, 894-906.

Hochscheid, S., Grémillet, D., Wanless, S. and du Plessis, M. A. (2002). Black and white under the South African sun: are juvenile Cape gannets heat stressed? *J. Therm. Biol.* **27**, 325-332.

Hunt, G. L., Melhum, F., Russel, R. W., Irons, D., Decker, M. B. and Becker, P. H. (1999). Physical processes, prey abundance, and the foraging ecology of seabirds. In *Proceedings from the 22nd International Ornithology Congress, Durban* (ed. N. J. Adams and R. H. Slotow), pp. 2040-2056. Johannesburg: BirdLife South Africa.

Kareiva, P. and Odell, G. (1987). Swarms of predators exhibit preytaxis if individual predators use area-restricted search. *Am. Nat.* **130**, 233-270.

Krebs, J. R. and Davies, N. B. (1978). *Behavioural Ecology, an Evolutionnary Approach.* Oxford: Blackwell.

Lewis, S., Benvenuti, S., Dall'Antonia, L., Griffiths, R., Money, L., Sherratt, T. N., Wanless, S. and Hamer, K. C. (2002). Sex-specific foraging behaviour in a monomorphic seabird. *Proc. R. Soc. Lond. B. Biol. Sci.* **269**, 1687-1693.

Loureiro, F., Rosalino, L. M., Macdonald, D. W. and Santos-Reis, M. (2007). Path tortuosity of Eurasian badgers (*Meles meles*) in a heterogeneous Mediterranean landscape. *Ecol. Res.* **22**, 837-844.

McCafferty, D. J., Boyd, I. L., Walker, T. R. and Taylor, R. I. (1998). Foraging responses of Antarctic fur seals to changes in the marine environment. *Mar. Ecol. Prog. Ser.* **166**, 285-299.

Müller, M. and Wehner, R. (1988). Path integration in desert ants, *Cataglyphis fortis*. *Proc. Natl. Acad. Sci. USA* **85**, 5287-5290.

Nelson, J. B. (2002). *The Atlantic Gannet*. Norfolk: Fenix Books.

Nevitt, G. A. (2008). Sensory ecology on the high seas: the odor world of the procellariiform seabirds. *J. Exp. Biol.* **211**, 1706-1713.

Nevitt, G. A. and Bonadonna, F. (2005). Sensitivity to dimethyl sulphide suggests a mechanism for olfactory navigation by seabirds. *Biol. Lett.* **1**, 303-305.

Nevitt, G. A., Losekoot, M. and Weimerskirch, H. (2008). Evidence for olfactory search in wandering albatross, Diomedea exulans. *Proc. Natl. Acad. Sci. USA* **105**, 4576-4581.

Pichegru, L., Ryan, P. G., van der Lingen, C. D., Coetzee, J., Ropert-Coudert, Y. and Grémillet, D. (2007). Foraging behaviour and energetics of Cape gannets Morus capensis feeding on live prey and fishery discards in the Benguela upwelling system. *Mar. Ecol. Prog. Ser.* **350**, 127-136.

Pinaud, D. and Weimerskirch, H. (2007). At-sea distribution and scale-dependent foraging behaviour of petrels and albatrosses: a comparative study. *J. Anim. Ecol.* **76**, 9-19.

Pingree, R. D., Forster, G. R. and Morrison, G. K. (1974). Turbulent convergent tidal fronts. *J. Mar. Biol. Assoc. UK* **54**, 469-479.

Ropert-Coudert, Y., Grémillet, D., Kato, A., Ryan, P. G., Naito, Y. and Le Maho, Y. (2004). A fine-scale time budget of Cape gannets provides insights into the foraging strategies of coastal seabirds. *Anim. Behav.* **67**, 985-992.

Rydell, J. (1993). Variation in foraging activity of an aerial insectivorous bat during reproduction. *J. Mammal.* **74**, 503-509.

Schmid-Hempel, P. (1984). Individually different foraging methods in the desert ant *Cataglyphis bicolor* (Hymenoptera, Formicidae). *Behav. Ecol. Sociobiol.* **14**, 263-271.

Sims, D. W., Southall, E. J., Tarling, G. A. and Metcalfe, J. D. (2005). Habitat specific normal and reverse diel vertical migration in the plankton-feeding basking shark. *J. Anim. Ecol.* **74**, 755-761.

Siorat, F. and Rocamora, G. (1992). Evolution comparée des effectifs de Fou de Bassan, Macareux moine et Puffin des Anglais sur l'archipel des Sept-Iles (Bretagne). Rapport Ministère de l'Environnement – Ligue pour la Protection des Oiseaux. 45 pp.

Southward, A. J., Langmead, O., Hardman-Mountford, N. J., Aiken, J., Boalch, G. T., Dando, P. R., Genner, M. J., Joint, I., Kendall, M. A., Halliday, N. C. et al. (2005). Long-term oceanographic and ecological research in the western English Channel. *Adv. Mar. Biol.* **47**, 1-105.

Staniland, I. J., Reid, K. and Boyd, I. L. (2004). Comparing individual and spatial influences on foraging behaviour in Antarctic fur seals *Arctocephalus gazella*. *Mar. Ecol. Prog. Ser.* **275**, 263-274.

Trathan, P. N., Bishop, C., Maclean, G., Brown, P., Fleming, A. and Collins, M. A. (2008). Linear tracks and restricted temperature ranges characterise penguin foraging pathways. *Mar. Ecol. Prog. Ser.* **370**, 285-294.

Ward, P. and Zahavi, A. (1973). Importance of certain assemblages of birds as information-centers for food-finding. *Ibis* **115**, 517-534.

Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources? *Deep Sea Res. II Top. Stud. Oceanogr.* **54**, 211-223.

Wilson, R. P., Pütz, K., Peters, G., Culik, B. M., Scolaro, J. A., Charassin, J. B. and Ropert-Coudert, Y. (1997). Long-term attachment of transmitting and recording devices to penguins and others seabirds. *Wildl. Soc. Bull.* **25**, 101-106.

Wood, A. G., Naef-Daenzer, B., Prince, P. A. and Croxall, J. P. (2000). Quantifying habitat use in satellite-tracked pelagic seabirds: application of kernel estimation to albatross locations. *J. Avian Biol.* **31**, 278-286.