# Meta-population evidence of oriented chain migration in northern gannets (*Morus bassanus*)

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**Although oriented migrations have been identified in many terrestrial bird species, the post-breeding-season movements of seabirds are generally regarded as dispersive. We used geolocator tags to reveal post-breeding movements and winter distribution of northern gannets (*Morus bassanus*) at a meta-population scale. By focusing on five breeding colonies of European gannets, we show that their breeding and wintering grounds are connected by a major flyway running along the coasts of Western Europe and Africa. Moreover, maximum winter distance to colony was similar across colonies despite their wide latitudinal range. In contrast with the general opinion that large pelagic birds such as gannets have unlimited ranges beyond the breeding season, our findings strongly suggest oriented chain migration in northern gannets (a pattern in which populations move uniformly southward) and highlight the benefit of meta-population approaches for studying seabird movements. We argue that the inclusion of such processes in ocean management plans is essential to improve efforts in marine biodiversity conservation.**

*Front Ecol Environ* 2012; 10(5): 237–242, doi:10.1890/110194

Defining animal movements and distribution in space and time is crucial for the management and conservation of organisms facing threats from climate change and habitat degradation (Nathan *et al.* 2008). For instance, determining bird migration routes, and their main wintering grounds, is necessary to identify Important Bird Areas (ie critical areas for bird conservation; www.birdlife.org) during different periods of their annual cycle. Following analysis of ring recoveries performed in recent decades, seabird post-breeding movements have generally been considered as dispersive (Wernham *et al.* 2002; Newton 2008) – a conclusion reinforced by seabirds' ability to travel thousands of kilometers over very large areas of apparently suitable feeding habitat. This concept has recently been challenged by the results of studies with miniaturized electronic devices that allow the tracking of seabird migratory movements at different spatiotemporal scales (Ropert-Coudert and Wilson 2005). These biotelemetry studies suggested that migration corridors might occur, even in highly pelagic species (eg Shaffer *et al.* 2006; Egevang *et al.* 2010; Stenhouse *et al.* 2011). This is of conservation relevance because it suggests that seabird hotspots are important not only during their breeding period but throughout their entire annual cycle. Nonetheless, most of these investigations were based on relatively small sample sizes and/or on single colonies (but see Phillips *et al.* 2005; González-Solís *et al.* 2007; Montevecchi *et al.* 2011). Given that different populations are expected to have contrasting migratory behaviors (Newton 2008), it is essential to test for oriented seabird migration at a meta-population level in order to identify, at large spatial scales, those sensitive marine areas that might require particular attention and protection.

Here, we focus on the northern gannet (*Morus bassanus*, hereafter "gannet"), a species that is widely distributed in the North Atlantic. The biology and foraging distribution of gannets during the breeding season are relatively well understood (Nelson 2002; Pettex *et al.* 2010; Votier *et al.* 2010). However, knowledge of their migratory patterns and wintering areas, particularly in the eastern North Atlantic, remains limited (Montevecchi *et al.* 2011). Extensive ringing and at-sea surveys helped to identify some staging areas for gannets during the non-breeding period (Barrett 1988; Nelson 2002), although these are limited in scope owing to temporal and spatial biases associated with ring-recovery data. Similarly, ship-based monitoring only allows community-level observations, with no information on the origin of individual birds (Tremblay *et al.* 2009a). Kubetzki *et al.* (2009) used geolocators to investigate the migration and wintering areas of individual gannets from a single colony in Scotland, illustrating that individuals used different, and rather small, wintering areas, which is consistent with ring-recovery findings (Nelson 2002).

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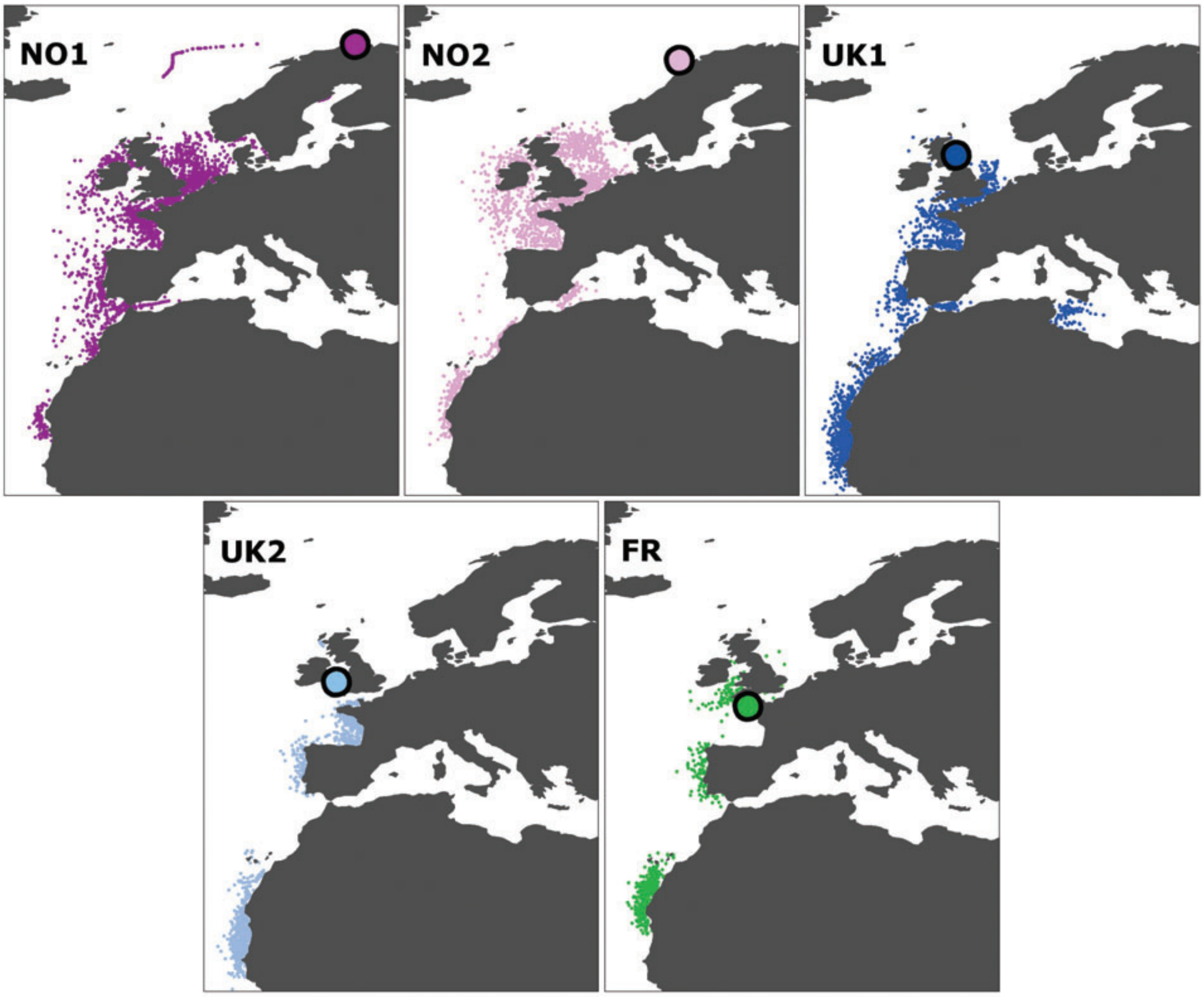

***Figure 1.** Estimated winter (December) positions for all tracked individual northern gannets (*Morus bassanus*). On each map, the large, black-outlined, solid-colored dot represents the location of the breeding colony.*

Our study therefore aims to (1) identify hotspots for different gannet populations during the non-breeding period and (2) test the hypothesis of oriented post-breeding migration in gannets at the meta-population scale.

## Methods

### *Study sites and data collection*

We studied the non-breeding distribution of a subset of gannets from five European colonies over several years (Figure 1; WebTable 1; see Kubetzki *et al.* [2009] for details regarding "UK1" data):

- NO1: Storstappen, Norway
  71°14'N, 25°30'E 2008/2009–2009/2010;
- NO2: Store Ulvøyholmen, Norway
  68°51'N, 14°51'E 2008/2009–2009/2010;
- UK1: Bass Rock, Scotland, UK
  56°04'N, 2°38'W 2002/2003–2003/2004;
- UK2: Grassholm, Wales, UK
  51°43'N, 5°28'W 2007/2008;
- FR: Rouzic, France
  48°54'N, 3°26'W 2006/2007.

These colonies are distributed along a gradient spanning ~23° of latitude, with Storstappen and Rouzic being the northernmost and southernmost sites, respectively. At each colony, selected breeding gannets were fitted with a miniaturized Global Location Sensor (GLS) geolocator tag (see WebTable 1 for details), which recorded time, light levels, and temperature throughout the non-breeding period. GLS technology allowed us to measure non-breeding movements for 86 gannets, each of which belonged to one of the five colonies. For three of the colonies, monitored birds were equipped over two successive non-breeding periods, revealing high consistency in colony-specific migration patterns (WebFigure 1). Colony-specific data were therefore pooled across years for analyses.

### *Data analyses*

Light-level data were extracted from GLS units and converted into geographic coordinates through two programs: MultiTrace Geolocation (Jensen Software System) for UK1, UK2, and FR data, and LAT Viewer Studio (Lotek Wireless) for NO1 and NO2 data. Raw spatial positions obtained from these extractions may contain substantial errors (Phillips *et al.* 2004) related to (1) latitude (higher latitudes have constant daylight during summer and constant darkness during winter), (2) the period considered (equal day and night duration during equinoxes), or (3) animal behavior that might occasionally alter the quality of the light readings. To compensate for these errors, we processed all raw positions using Tremblay *et al.*'s (2009b) method (see also WebPanel 1). The maximum distance to the colony of origin was calculated from the estimated non-breeding positions for the entire period and for each individual. Distances were computed on the Earth spheroid, thus accounting for the Earth's curvature but not land avoidance. These estimates were assumed to represent the distance for each bird between the breeding colony and wintering ground. Values are reported as means ± standard deviation.

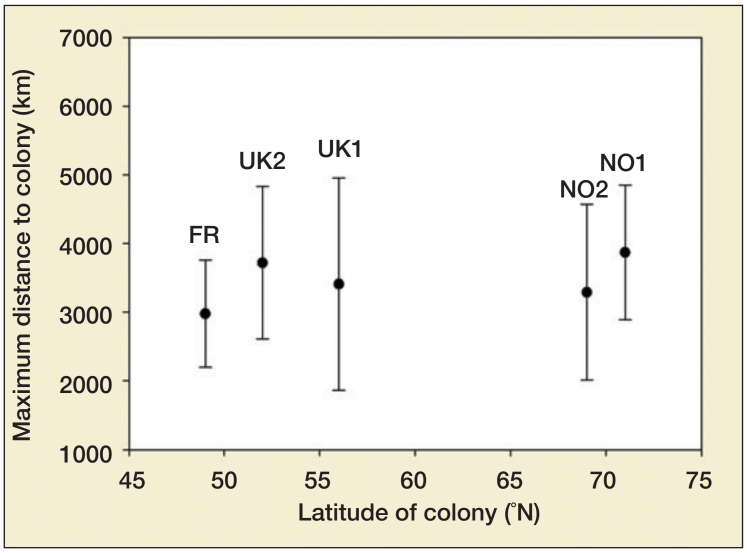

***Figure 2.*** *Maximum distance (mean ± standard deviation, in kilometers) between breeding and wintering grounds of tracked gannets from each of the five study colonies.*

We performed kernel analyses in Matlab R2010b (MathWorks) using 50-km × 50-km grid cells to determine the areas preferentially occupied by gannet populations during the non-breeding period, also defined as hotspots. Estimation of the kernel bandwidth parameter followed that of Sheather and Jones (1991). Only cells used by two individuals or more were considered, to avoid assigning importance to areas used by only one individual. Furthermore, the number of locations within one cell was multiplied by the total number of birds contributing to these locations. This transformation favors areas used by many individuals over areas used for a long time by only a few individuals. We delimited gannet hotspots using 25% kernel density contours, which we considered to be the best representation of core areas occupied. Kernel analyses were performed during three distinct periods, defined as (1) *pre-winter period* (1–31 October; when birds were assumed to migrate to their wintering area), (2) *winter period* (1–31 December; when birds were observed to stay in a restricted area without any large-scale movements), and (3) *post-winter period* (1–28 February; when birds were assumed to migrate back to their breeding site).

## ■ Results

### *Ocean-basin-scale movements*

After their breeding season, almost all monitored gannets moved to the south. The birds exhibited considerable inter-individual variability in spatial movement, using an elongated area ranging from the northern North Sea to northwest Africa. Yet analyses also revealed colony-specific strategies (Figure 1): during winter, gannets breeding at NO1 were distributed continuously between the North Sea and the northern part of northwest Africa, with one individual reaching the coast of Mauritania. Birds from NO2 presented a more restricted and bimodal distribution, with most birds remaining in European waters (North Sea, English Channel, and Bay of Biscay); three other individuals were detected much farther south in northwest African waters and in the western Mediterranean. Birds from UK1 showed a wide distribution between the North Sea and the Senegal coast in northwest Africa. One UK1 bird also wintered in the Mediterranean Sea, between Tunisia and Sicily. Similarly to UK1 birds, individuals from UK2 were widely distributed between European seas and northwest Africa. Nevertheless, they generally remained in the Bay of Biscay, off Portugal's west coast, and off northwest Africa. The winter distribution of gannets breeding at FR was also restricted, with almost all birds reaching the northwest African coast; one bird wintered in the Irish Sea, while another stayed off the Portuguese coast (Figure 1). Interestingly, analysis of individual maximum winter ranges (ie maximum distance to colony) showed that birds from the different colonies wintered, on average, at similar distances to their colony of origin (NO1 = 3872 ± 980 km; NO2 = 3290 ± 1282 km; UK1 = 3411 ± 1546 km; UK2 = 3721 ± 1114 km; FR = 2979 ± 781 km; analysis of variance, $F_{4,80} = 1.30$, $P = 0.278$; Figure 2).

### *Non-breeding hotspots*

#### *Pre-winter period*

In October, kernel analyses (25% kernels) revealed gannet hotspots around the UK, with large overlaps among the five study populations (Figure 3a). However, despite

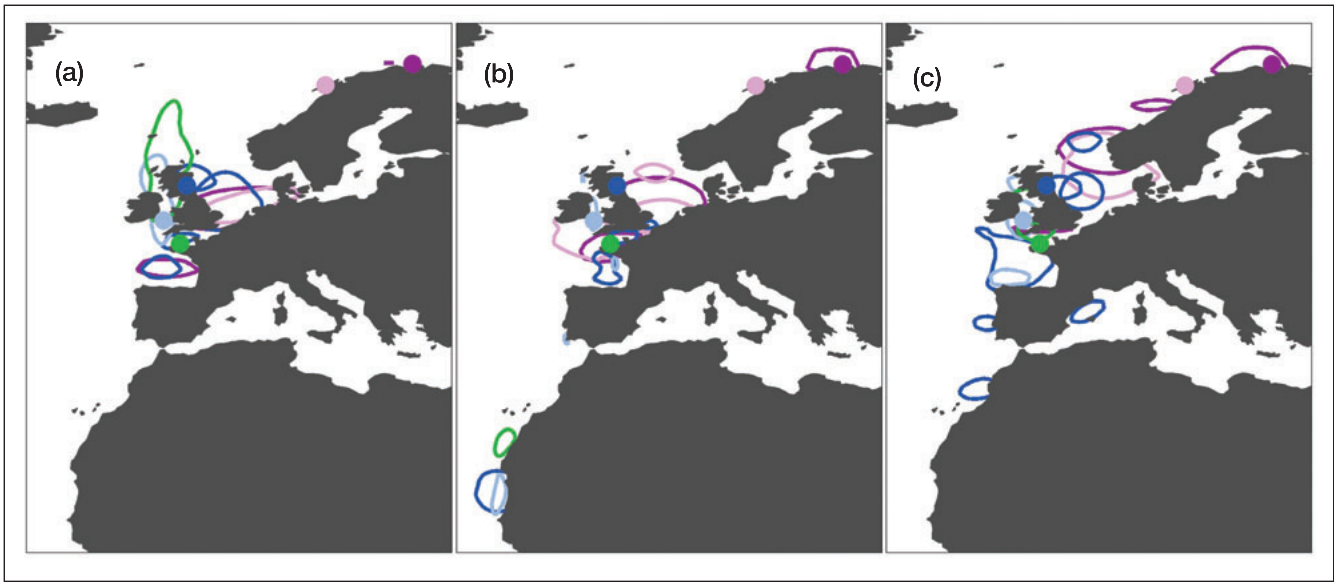

***Figure 3.*** *Main areas occupied by tracked gannets during the non-breeding period, represented by 25% kernel density contours: (a) pre-winter (October) distribution, (b) winter (December) distribution, (c) post-winter (February) distribution. On each map, solid-colored dots represent the different breeding colonies (see Figure 1), with the same colony-specific color associated with the kernel density contours.*

this overall common distribution, different pre-winter strategies were observed among colonies. Birds from UK2 and FR adopted a similar pre-winter strategy, with birds mainly distributed in the Irish Sea. Conversely, the main distribution of birds from NO2 was located in the southern part of the North Sea. Gannets breeding at UK1 and NO1 adopted very similar distributions with, in each case, a distribution divided in two main areas: one located in the North Sea overlapping the NO2 distribution, and one located in the Bay of Biscay. Surprisingly, while FR birds wintered well to the south (see below), our analysis showed that they initially moved northward after the breeding season (Figure 3a).

### *Winter period*

Gannets clearly adopted two distinct and contrasting winter strategies, split in two main distribution areas: one located in northern Europe and one off the coast of northwest Africa (Figure 3b). Overall, there were again large overlaps among the main wintering areas occupied by birds from the five colonies. Nevertheless, smaller spatial-scale segregations also appeared among colonies. Norwegian birds (NO1 and NO2) were mainly distributed in the North Sea and the English Channel, with a very similar spatial distribution between these two colonies. Unlike autumn, during winter birds from these colonies were the only ones in the North Sea. French birds (FR) also had a single major distribution during winter, located in northwest Africa. Conversely, the main distribution of birds from UK colonies was divided between two areas, some birds spending the winter in northern Europe (Irish Sea, English Channel, and Bay of Biscay) while the others wintered in northwest Africa. Interestingly, in northwest African waters, there was a spatial segregation between birds from France and from the UK (UK1 and UK2). Indeed, the main wintering area of French gannets was located off Morocco, whereas birds from UK colonies wintered farther south, off the coasts of Mauritania and Senegal (Figure 3b).

### *Post-winter period*

The kernel analyses displayed a strong heterogeneity in gannet at-sea distributions (25% kernels) in February among colonies. There was an important segregation between Norwegian birds and those from France and UK, with the former group generally remaining farther north (Figure 3c). Divergent distributions were also observed in western European waters, with FR birds mainly distributed in the English Channel, UK2 birds restricted to the Irish Sea and to an area along the north coast of Spain, and UK1 birds distributed more widely, mainly in the Bay of Biscay, along the Portuguese coast, in the Mediterranean, and off northwest Africa (Figure 3c).

## ■ Discussion

By focusing on five European breeding gannet colonies distributed along a latitudinal gradient of approximately 2500 km, including the species' southernmost and northernmost breeding sites in the eastern Atlantic, this study is one of the first to investigate the non-breeding movements and winter distribution of a seabird species at a meta-population scale (but see Frederiksen *et al.* 2011; Montevecchi *et al.* 2011). As hypothesized, our findings suggest that gannet post-breeding movements should not be attributed to dispersive migration or vagrancy, but are instead oriented along a major flyway following the coasts of Western Europe and Africa, from the North Sea to Senegal. These findings confirm recent GLS studies suggesting that seabirds, similar to their terrestrial relatives, can follow migration corridors when moving between their breeding and wintering grounds (Egevang *et al.* 2010; Stenhouse *et al.* 2011). The GLS method (sensu Wilson *et al.* 1992) – based on light-level recordings – has been effective for tracking small- to medium-sized animals over extended time scales but entails a large error of 100–200 km, which restricts its use to the study of wide-scale movements (Phillips *et al.* 2004). Although we used a refined model accounting for the method's potential biases and including sea-surface temperatures to predict individual positions more accurately (WebPanel 1; Tremblay *et al.* 2009b), we emphasize that small-scale results should be interpreted with caution.

Our results support previous descriptions of gannet non-breeding areas from ring recoveries and GLS data (eg Barrett 1988; Nelson 2002). We observed high variability in winter distribution at both the individual and colony levels. Individual seabirds from a single colony can segregate during winter and use different wintering areas (Shaffer *et al.* 2006; González-Solís *et al.* 2007). In the case of gannets (Kubetzki *et al.* 2009), such segregation also exists at a meta-population scale, with two distinct wintering areas occupied in northern European seas and off the northwest African coast. The latter area is important for several other wintering seabirds (Wernham *et al.* 2002; Camphuysen and van der Meer 2005; González-Solís *et al.* 2007). This zone off northwest Africa features one of the four major oceanic upwelling systems of the world. Extending between 10°N and 22°N during winter, it holds substantial biomass of pelagic fish available to gannets and other marine predators. Local fisheries also discard large volumes of fishery wastes, which are an important food source for some gannets (Camphuysen and van der Meer 2005; Votier *et al.* 2010). Our findings also confirm that seabirds from various colonies can target and aggregate in a few highly profitable wintering areas (González-Solís *et al.* 2007; Block *et al.* 2011). Several tracked individuals adopted alternative strategies and instead wintered along the coasts of Portugal, south of Spain, and Tunisia. Although these strategies are likely to be marginal, our sample sizes (notably at UK2 and FR; see WebTable 1) are small, and further studies are required to understand the importance of these alternative grounds for wintering gannets.

Beyond the overall bimodal distribution adopted by the European gannet meta-population, differences arose between colonies at smaller spatial scales in the main wintering areas (estimated from 25% kernel analysis). These differences are mainly linked to the respective latitude of each colony and strongly suggest chain migration (a pattern in which populations move uniformly southward, with more northern birds wintering in northernmost grounds; Salomonsen 1955; Newton 2008). Indeed, Norwegian birds breeding at higher latitudes mainly wintered in northern Europe, birds breeding at intermediate latitudes (UK birds) showed a bimodal winter distribution between northern Europe and northwest Africa, and French birds breeding at lower latitudes mainly wintered off northwest Africa. This pattern differs from that of leapfrog migration, in which birds that breed at the highest latitudes winter at the lowest latitudes, a behavior observed in many terrestrial and waterbird species (Newton 2008). Seabirds can travel impressive distances to reach their wintering grounds (eg Egevang *et al.* 2010), and this is also the case for northern gannets, which are capable of traveling up to 7000 km from their colony after breeding. Nevertheless, the similarity observed between colonies in average maximum winter range (Figure 2) suggests that an upper limit to gannet traveling may exist. This is surprising because, in contrast to passerines migrating over water, gannets can presumably rest and feed en route.

Although chain migrations have been observed in several terrestrial bird species (see examples in Newton 2008), this is, to our knowledge, the first direct evidence of an oriented chain migration in a seabird species. Evidence of such migratory processes has important implications for seabird conservation and related studies, including those aiming to define Important Bird Areas at sea. First, our findings confirm recent investigations suggesting that seabird hotspots exist – and should be considered – during the non-breeding period, along migration corridors, and at their wintering grounds (Egevang *et al.* 2010; Block *et al.* 2011). Moreover, we show that the location of these winter hotspots could be dictated by the origin of birds, suggesting genetic control and reduced short-term individual adaptation to local habitat degradation (Newton 2008), crucial information in a context where marine ecosystems are highly threatened by climate change and human activities (Halpern *et al.* 2008). Second, our results validate the importance of studies conducted at meta-population scales, and call for similar investigations to be performed on various other species to gain a more comprehensive understanding of sensitive marine areas that might require protection. Third, because gannet hotspots vary in space along migration routes and may extend into international waters, future conservation of marine avian biodiversity might largely depend on an adaptive design for protected area boundaries in pelagic waters and on the capacity of countries to adopt collaborative management plans. Finally, the bimodal strategy exhibited by UK birds merits further investigation. For instance, the breeding performance of black-legged kittiwakes (*Rissa tridactyla*) can affect the species' winter distribution, with individuals experiencing a breeding failure wintering in different (farther) places from successful breeders (Bogdanova *et al.* 2011). Such mechanisms might also condition the important inter-individual variability observed in the migratory behavior of gannets from UK colonies. Identifying carry-over effects (ie processes occurring during one season and affecting individuals during a subsequent season; Harrison *et al.* 2011) in seabird behavior during the non-breeding period, and identifying their impact on population dynamics, should be a major goal of forthcoming studies.

## Acknowledgements

We thank G Morgan, L Morgan, M Witt, N El Ksaby, and M Le Nuz for field assistance, RA Phillips for having provided and analyzed data from two GLS units from the British Antarctic Survey, and L Pichegru for comments on an earlier version of the paper. Permission to enter the Norwegian colonies was issued by the County Governors of Nordland and Finmark; permission to handle the birds was given by the Norwegian Directorate for Nature Management and the Norwegian Animal Research Authority. Fieldwork at Rouzic was performed by permission of the Ministère Français de l'Alimentation, de l'Agriculture et de la Pêche (permit 34369). H Hamilton-Dalrymple allowed us to work on Bass Rock, where fieldwork was permitted by Scottish Natural Heritage and the British Trust for Ornithology (permit A2282), and funded by European Union project "DISCBIRD" (contract Q5RS-2001-00839). Fieldwork on Grassholm Island was performed by permission of the Royal Society for the Protection of Birds and the Countryside Council for Wales. The Norwegian part of the study was financed by the Directorate for Nature Management and SEAPOP (www.seapop.no). JF is supported by a Marie Curie Intra-European Fellowship within the 7th Framework Programme.

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