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Individual variability in the migratory path and stopovers of a long-distance pelagic migrant



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The analysis of repeated journeys of the same individuals is becoming an important tool in the study of animal migration. This approach has been used to analyse the migratory consistency (in schedules, routes and stopovers) of various species, with implications for the understanding of navigation mechanisms, travel strategies and conservation. However, few studies have addressed the individual consistency in pelagic long-distance migrations, in particular in the routes followed in different years. By analysing 100 journeys from 35 individual Cory's shearwaters, *Calonectris diomedea*, that repeatedly migrated to the South African region we examined the fidelity to migratory paths and stopovers of a transequatorial seabird migrant. Cory's shearwaters showed an overall trend to be faithful to their routes in different years, which was particularly obvious in the first (southbound) part of the outward migration. Nevertheless, we did not detect any individual consistency in the final part of the outward migration, in the return migration or in the location of the stopovers. The fact that Cory's shearwaters can be either consistent or inconsistent in different parts of their routes is possibly related to the variability of the external factors (such as wind conditions and location of good foraging areas) found along the way. © 2013 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Individuality in behavioural traits is increasingly becoming the focus of studies of animal ecology (Dall et al. 2004), including those related to migratory movements (Alerstam 2006; Vardanis et al. 2011; Brodersen et al. 2012). This individual-based approach has been made possible by technological advances in tracking systems, which have allowed researchers to discover the previously unknown migratory routes of several species (e.g. Green et al. 2002; Alonso et al. 2008; Bairlein et al. 2012), and to analyse in detail intraindividual variation in migratory patterns, such as year to year consistency in time and space (Dias et al. 2011; Guilford et al. 2011; Vardanis et al. 2011; Stanley et al. 2012). Repeated measures of single individuals can also provide fundamental cues to understanding the causes of variability in migratory behaviour (for example, the relative role of genetic background versus environmental conditions; van Noordwijk et al. 2006), and also to unveil the mechanisms underlying long-distance navigation (Alerstam 2006; Guilford et al. 2011). By repeatedly tracking individual birds it was possible, for example, to show that (at least some) terrestrial long-distance migrants do not rely on learned visual

maps of landscape features for most of the journeys to and from the wintering areas (Vardanis et al. 2011).

Various degrees of behavioural consistency can be found among migrants (Sutherland 1998; Alerstam 2006). Some species are clearly more faithful than others to their wintering sites, routes, stopovers and timings (Sutherland 1998; Catry et al. 2004). Most studies carried out so far on fidelity to migratory paths and stopovers have focused on species that migrate mostly over land, such as passerines, storks, geese and raptors (Fox et al. 2002; Berthold et al. 2004; Catry et al. 2004; Alerstam et al. 2006; Vardanis et al. 2011; Stanley et al. 2012). While some studies have analysed spatial consistency during migration in pelagic travellers (Hunter et al. 2003; Phillips et al. 2005; Broderick et al. 2007; Guilford et al. 2011), none have attempted to disentangle the fidelity to routes or paths from individual consistency in winter destinations. By controlling for the effect of winter destination we can understand whether the route consistency revealed by species that use several geographically isolated wintering areas is a consequence of their fidelity to wintering sites or whether it is an individual choice for a specific path in subsequent years.

Several studies have revealed the exceptional migratory performances of many seabirds (Croxall et al. 2005; Phillips et al. 2005; Egevang et al. 2010; Kopp et al. 2011), in particular of shearwater species (e.g. Shaffer et al. 2006; González-Solís et al. 2007; Guilford

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et al. 2009; Dias et al. 2012a). Like other pelagic migrants, shearwaters are often faithful to their wintering sites in successive years (Dias et al. 2011; Raine et al. 2013), but so far no studies have addressed their year-to-year fidelity in routes and stopovers. Besides the relevance of this knowledge for the above-mentioned research topics, the study of the consistency in migratory behaviour of long-distance pelagic migrants also has obvious implications for their conservation, in particular for their capacity to deal with global changes in the marine environment (Grémillet & Boulinier 2009; Knudsen et al. 2011; Costa et al. 2012).

Wind conditions are believed to play a central role in determining the migratory routes (and possibly also the location and duration of stopovers) for seabirds that fly mainly by dynamic soaring, such as albatrosses and shearwaters (González-Solís et al. 2009; Guilford et al. 2009). Spatiotemporal variation in wind strength and direction can shape not only the routes followed by birds, resulting in the well-known ‘figure-of-eight’ path of some transequatorial migrants (e.g. Shaffer et al. 2006; González-Solís et al. 2007), but also the timings of migration (Felicísimo et al. 2008). This dependence on wind conditions is closely related to the type of flight adopted. Large shearwaters and albatrosses often fly by dynamic soaring, a technique that entails very low energetic costs but that is highly dependent on wind (Furness & Bryant 1996; Pennycuik 2002). Other environmental factors, such as the existence of profitable foraging patches, may also influence the routes and stopovers chosen by seabirds, especially those that migrate using a ‘fly-and-forage’ strategy, as do some shearwaters (Dias et al. 2012a). The location of these foraging patches is probably variable from year to year, at least in more oceanic areas and in short to medium timescales (Weimerskirch 2007). In light of this, we could expect that long-distance seabird migrants, particularly those that rely mainly on variable environmental conditions to travel, would present a low year-to-year fidelity to their migratory routes and stopovers.

We addressed these questions using the Cory’s shearwater, *Calonectris diomedea borealis*, as a model species, potentially representative of the large group of pelagic birds that use dynamic soaring for travel. This long-distance pelagic migrant breeds in the Northeast Atlantic and winters in six different zones spread throughout the North and South Atlantic (Catry et al. 2011; Dias et al. 2011). The majority of individuals migrate to/from the South African coast (Dias et al. 2012a). Using a data set of birds that wintered in this area in different years (ranging from two to six migratory journeys per individual) we examined the consistency in migratory routes and stopovers of this species. Cory’s shearwaters are highly consistent in their migratory schedules (Dias et al. 2011), like many other long-distance migrants (Battley 2006; Lourenço et al. 2011; Vardanis et al. 2011; Stanley et al. 2012). Individual birds tend to depart repeatedly earlier (late October) or later (early December) from their breeding grounds in different years. This consistency in their timings can promote fidelity to routes if birds departing at the same time are subject to similar wind conditions, and if the location of the wind corridors varies in a consistent way in different years. In this study we also accounted for this possible effect by comparing the routes of birds departing at different dates.

METHODS

Bird Tracking

We tracked the migration of 51 individual adult Cory’s shearwaters between 2006 and 2012 using leg-mounted geolocators, and obtained a total data set of 155 trips. Since we intended to analyse year-to-year fidelity to the migratory routes, we had to control for the effect of the location of winter grounds. Therefore,

we selected the routes of birds that wintered around the South African coast in more than 1 year (including the Benguela and Agulhas currents; Fig. 1). These two areas are the destination of ca. 72% of the individuals each year (Dias et al. 2011, 2012a). This resulted in a final data set of 35 individuals (17 males, 18 females) and 100 journeys (16 individuals were tracked twice, 12 were tracked three times, four were tracked four times, two were tracked five times and one was tracked six times).

All Cory’s shearwaters tracked were adults breeding in the Selvagem Grande colony (Portugal; 30°02’N; 15°52’W). The geolocators (mk7 and mk19 models, produced by the British Antarctic Survey, Cambridge, U.K.) were deployed at the end of each breeding season (August/September), and recovered at the beginning of the subsequent year (April–June). Detailed procedures related to the deployment of the devices and subsequent analyses of geolocation data are provided in Dias et al. (2011, 2012a). In short, the analysis of light data provided by the geolocators delivered (a maximum of) two positions per day for the whole migratory period. The tracks were double-filtered (following Phillips et al. 2004) to remove any outlying positions, resulting in an estimated locational error of 186 ± 114 km (Phillips et al. 2004).

Data Analysis

We calculated the individual repeatability of migratory route choice following the approach used by Vardanis et al. (2011). For each journey we estimated the position of birds at which several ‘landmarks’ were crossed. We estimated the longitudes at the 10th north and 20th south parallel and the latitude at the prime meridian during the outward migration, and the longitudes at the 10th south and 10th north parallels during the return migration (Fig. 1 and Supplementary material). We only considered landmarks located in the first part of the return migration because for

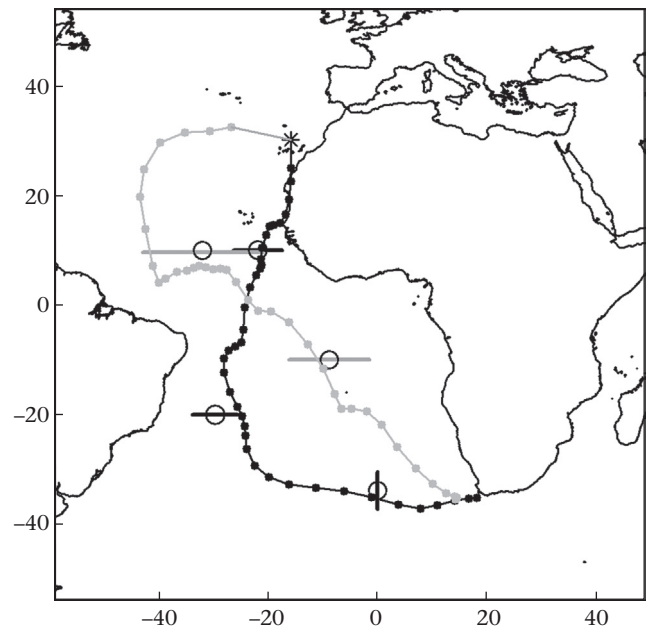


Figure 1. Example of a route taken by an individual Cory’s shearwater during the outward (black) and return (grey) migrations to the South African coast (dots represent the positions, twice each day, estimated from the geolocator data). The landmarks considered during both migrations are also shown (thick black and grey line segments). The lengths of the segments represent the means \pm SD of the positions recorded for the study individuals (see Methods). Black circles indicate the mean error of the positions provided by the geolocators (186 km; following Phillips et al. 2004). The star indicates the location of the colony (Selvagem Grande).

many Cory's shearwaters the final part of the journey coincides with the spring equinox, when latitude estimation is not possible. Geolocators provide position estimates with a large error (see above). The magnitude of this error is far lower than the variability found in the longitudinal and latitudinal positions at the landmarks used in our study to calculate the repeatabilities (SD values of longitudes varied between 434 km and 491 km in the outward migration and between 780 km and 1197 km in the return migration; SD value of latitude estimates was 388 km; see Fig. 1).

The existence and location of stopovers during the outward journey were evaluated using first-passage time analysis (Fauchald & Tveraa 2003), following the procedures described in Dias et al. (2011). We excluded the return migrations from the analyses of stopovers because of the lack of good-quality data for the entire journeys in several cases; nevertheless, previous studies have shown that Cory's shearwaters only make stopovers during the outward migration (Dias et al. 2012a). Some individuals go to the Northwest Atlantic before heading south (Catry et al. 2011). We did not consider detours through this area in the analyses of fidelity, given that they are not 'typical' stopovers (i.e. pauses on the way to/from the wintering area), but rather a 'diversion' of an additional ca. 5000 km towards a specific destination (Catry et al. 2011; Dias et al. 2012a). Also, given that these detours may influence the positions at which the landmarks are crossed during the outward migration (and consequently may increase the repeatability values, if individual birds tend to be consistent in making detours), we also calculated the repeatabilities considering only repeated trips of birds that did not detour to the North Atlantic. We also checked for the possible influence of the wintering destination (Benguela or Agulhas) and of the year of tracking on the positions at the landmarks, using ANOVA models that included the identity of the birds as a random factor.

As an additional measure of route consistency, we also calculated the mean distance between the outward route of each individual in the first year and (1) its own route(s) in the second (and/or subsequent) year(s), and (2) the route(s) from other individuals, randomly chosen from the set of birds tracked in the second (and/or subsequent) year(s) (see Guilford et al. 2011 for a similar approach). The distance between routes was calculated as the mean distance between each position on one route and the nearest position on another route. The mean distances between paired routes were then compared using a linear mixed model that included the individual (same versus other) as a random term and assuming a Gaussian error distribution. Positions during stopovers were removed from this analysis to avoid their overrepresentation within each route.

Individual Cory's shearwaters tend to be consistent in the departure date between years (Dias et al. 2011). This results in inter-individual differences in the timings of crossing several landmarks (for example, the dates at which the landmark 10°N is crossed varies between 2 November and 17 December; mean \pm SD = 17 November \pm 10 days). To consider the possible effect of this temporal consistency on route fidelity we analysed whether individuals that crossed the landmarks at similar timings in different years (i.e. with a lower time lag) also showed more similar (i.e. closer) routes. We randomly chose one route per individual, and compared it with all the routes of all other individuals in different years. This comparison was made by calculating (1) the absolute difference in relative dates (time lag, in days) and (2) the absolute difference in the positions (in degrees) at which the landmarks were crossed. Thus, for each individual (relative to all others) we obtained several values of time lags (some of which were repeated), each associated with a difference in the positions. We then calculated the mean difference in the positions per time lag (for example, we averaged all

the differences in the positions for birds that crossed within a time lag of 1 day, 2 days and so on) and per individual. The influence of the time lag on the differences in the positions was finally tested using linear regression models. This analysis was only carried out for the landmarks for which a significant repeatability was found.

Analyses were carried out using R software (R Development Core Team 2010) including the packages *maptools*, *proj4*, *rptR* and *adehabitat*. Sample sizes differed between the analyses performed, essentially because of the removal of low-quality data from some samples (see above). Values are presented as means \pm SE.

Ethical Note

The deployment of geolocators did not take more than 10 min and on no occasion had visible deleterious effects on study animals. All birds were caught directly at the nest during the chick-rearing period (to deploy the geolocators) and soon after colony arrival/during incubation (to recover them). The geolocators weighed 3.6 g (mk7) and 2.5 g (mk19) (less than 0.5% of the weight of the birds; minimum bird weight = 754 g), and were mounted on a metal ring placed on the leg of the birds. Previous studies have shown that these devices do not negatively influence the breeding success of Cory's shearwaters (in a comparison of the previous and following breeding events; Igual et al. 2005). The probability of returning to breed in the year following a deployment is also similar between birds with and without geolocators (the results of a detailed analysis with part of the sample presented here are available as supplementary material [Methods S1] in Dias et al. 2012a). All work was approved by the relevant authorities (Instituto da Conservação da Natureza e da Biodiversidade and Serviço do Parque Natural da Madeira; research and ringing permits 107/2006, 116/2007, 107/2010/CAPT).

RESULTS

Consistency in Individual Positions

Individual Cory's shearwaters showed a significant route consistency at the landmarks located in the first part of the outward journey (10°N and 20°S), but not in the remaining outward journey or in the return migration (Table 1). The results remained significant even when considering only the birds that did not detour to the Northwest Atlantic before heading south (10°N: repeatability test: $r = 0.30$, $P = 0.006$; 20°S: repeatability test: $r = 0.30$, $P = 0.001$; both $N = 84$ trips from 31 individuals; Fig. 2). The wintering destination and the year did not influence the positions at each landmark in any case (ANOVA tests: all $P > 0.15$).

The mean distance between the outward routes of an individual in successive years (362 ± 25 km, $N = 35$) was significantly shorter than the mean distance between the routes of different individuals (406 ± 27 km; GLMM₁₇₈: same versus other: = 56.17 ± 23.38 km; $P = 0.017$).

Table 1

Repeatability (r) in the positions at which specific landmarks were crossed by individual Cory's shearwaters during successive years

Migration	Position	Repeatability
Outward	Longitude at 10°N	$r = 0.32$, $P = 0.002$ ($N = 99/35$)
	Longitude at 20°S	$r = 0.43$, $P < 0.001$ ($N = 99/35$)
	Latitude at 0°	$r = 0.08$, $P = 0.394$ ($N = 99/35$)
Return	Longitude at 10°S	$r = 0.02$, $P = 0.451$ ($N = 49/20$)
	Longitude at 10°N	$r = 0.14$, $P = 0.283$ ($N = 24/10$)

N: (total number of trips/number of individuals). Significant P values are shown in bold.

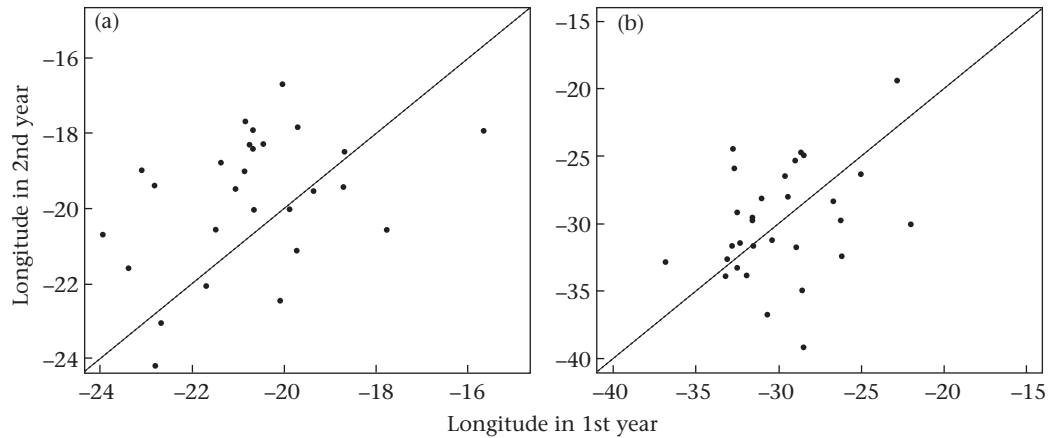


Figure 2. Relationship between the positions at which the same individuals crossed the landmarks (a) 10°N and (b) 20°S in the 1st and 2nd (or other subsequent) years of tracking (considering only the birds that did not detour to Northwest Atlantic; see *Methods*). Dashed lines represents $x = y$.

Fidelity to Stopover Sites

Stopovers were made by 21 different individuals ($N = 35$ individuals tracked more than once). Only seven birds made stopovers in more than 1 year and, from these, only two stopped in the same area in different years (in both cases in the Canary current, thus soon after leaving the colony).

Influence of Migratory Schedules on Spatial Consistency

The difference in the dates at which the landmarks were crossed in different years did not influence the difference in the positions at the same landmarks (effect of the time lag on the difference in the longitude at 10°N: linear regression: $F_{1,19} = 0.15$, $P = 0.701$; and on the difference in the longitude at 20°S: linear regression: $F_{1,19} = 0.00$, $P = 0.999$; *Fig. 3*).

DISCUSSION

In this study we found individual consistency in the migratory routes followed by Cory's shearwaters in different years, but only to a limited extent. In fact, this spatial consistency did not occur along the entire route and was also not noticeable in the location of the stopovers.

Overall, the paths followed by the same individual when migrating from the nesting area to the South African coast in different years were closer to each other than those followed by different individuals. We found significant repeatabilities in longitudes used by individuals when crossing 10°N and at 20°S. This was not an effect of breeding location (all individuals belong to the same colony), or of the detour that some individuals made to the North Atlantic (results remained significant even after removing these birds from the analyses). Also, this spatial repeatability was not a by-product of consistency in migratory schedules. The differences in routes taken by the birds were not affected by the proximity in dates on which the landmarks were crossed. These results suggest that the repeatability found is related to individual choices. This means that Cory's shearwaters tended to be faithful to their own migratory paths in different years, at least in some parts of their journeys, and despite their high dependence on the wind circulation patterns (Felicísimo et al. 2008; González-Solís et al. 2009). Possibly, the wind affects their route patterns at a broad scale, that is, it defines a possible 'wind corridor' (Felicísimo et al. 2008), within which there is still enough room to allow for an individual preferred path.

Despite the repeatability we observed in Cory's shearwaters' routes, movement paths were found to differ in the final part of their outward journey, and also in the pre-migratory journey. We

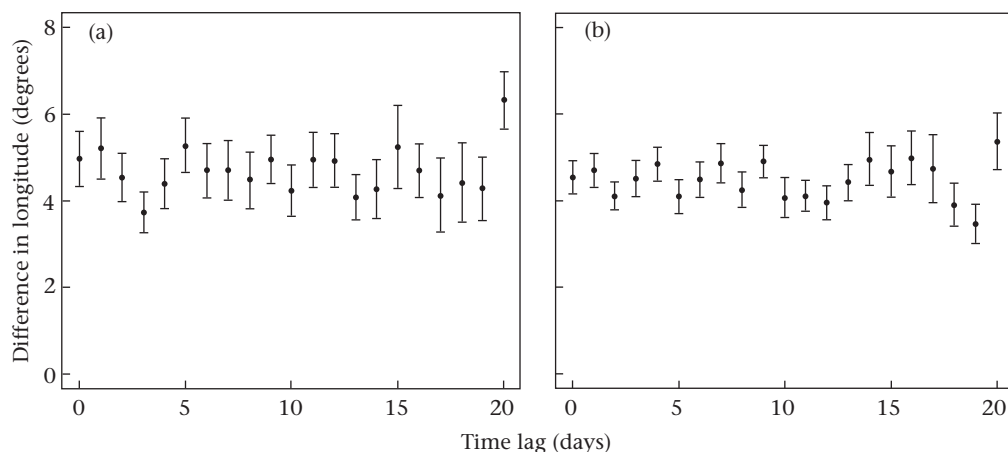


Figure 3. Relationship between the difference in days (time lag) and the difference in the longitude (in degrees) at which the landmarks (a) 10°N and (b) 20°S were crossed in different years (means \pm SE).

cannot completely rule out a potential effect of the lack of accuracy of geolocator position estimates on this lack of consistency, especially where migrations occur close to the equinox period (during February–March). However, the variance in longitude and latitude values between routes was considerably larger than the error typically associated with this method, and so this is unlikely to be a major factor driving the patterns we found. Cory's shearwaters were also not faithful to their stopover sites. The stopovers made by Cory's shearwaters during the outward migration apparently have a refuelling function (Dias et al. 2011, 2012a). Nevertheless, Cory's shearwaters also forage when actively travelling (adopting a 'fly-and-forage' strategy; Strandberg & Alerstam 2007), particularly when not crossing ecological barriers, such as the low-productivity waters around the equator during autumn (Dias et al. 2012a). Thus, the lack of consistency (found both in the southern part of the outward route, in the return route and in the location of stopovers) may be related to the mobile nature of potential profitable areas in the oceanic environment, at least at a large temporal (year-to-year) scale (Weimerskirch 2007; Guilford et al. 2009). Seabirds are known to recognize potential productive areas by detecting changes in olfactory landscapes at very large spatial scales (thousands of square km; e.g. Nevitt & Bonadonna 2005). Therefore, they may potentially follow paths located several kilometres apart in different years, driven by the variable foraging conditions found during the journey. Interannual variations in local conditions found on the route (both in the wind and in the availability of foraging areas) has also recently been pointed out as the likely factor underlying the low route fidelity of some long-distance terrestrial migrants (Stanley et al. 2012).

The 'fly-and-forage' strategy of Cory's shearwaters can also explain the relatively low proportion of journeys with stopovers (Dias et al. 2012a), as well as the lack of consistency in their location. The decision to stop in a particular site is probably dependent on the foraging conditions found during the previous steps (which would determine the body reserves; e.g. Fusani et al. 2009), in addition to local wind circumstances (Guilford et al. 2009). In fact, other long-distance migrants that are also very dependent on wind conditions, such as some small passerines, raptors and storks, can also present low levels of stopover fidelity (Berthold et al. 2004; Catry et al. 2004; Shiu et al. 2006; Chevallier et al. 2011).

The main causes for the variation in consistency throughout the migratory routes of Cory's shearwaters remain unknown. A similar pattern was recently described in a terrestrial long-distance migrant, the marsh harrier, *Circus aeruginosus* (Vardanis et al. 2011). In both cases, higher route fidelity seems to be associated with the existence of an ecological barrier (the equatorial waters, in our case, and the Mediterranean Sea for the marsh harriers), suggesting that routes might be more consistent when crossing environmentally challenging areas. Migrants possibly develop individual strategies to cope with particularly harsh conditions found along the route, which may be modulated by individual learning. This process may develop through successive refinements following a set of exploratory movements carried out during the first years of migration (Guilford et al. 2011), which are typical of many seabird species (Baker 1980; Åkesson & Weimerskirch 2005; Dias et al. 2011). This mechanism would be particularly relevant in species without cultural inheritance of migratory behaviour; juvenile shearwaters, probably like most procellariiformes, migrate on their own (Åkesson & Weimerskirch 2005).

The existence of a variable individual consistency along the migratory routes of seabirds has important conservation implications. In fact, their behavioural flexibility (also expressed in other traits of the migratory behaviour; Dias et al. 2011, 2012b) can be regarded as an adaptive advantage in the context of human-induced changes in marine ecosystems (Grémillet & Boulinier

2009). However, the variability in the location of their stopovers and paths, at least in some parts of the routes and at a medium scale (tens to a few hundreds of kilometres), poses relevant challenges in the definitions of marine protected areas or of conservation corridors for marine migrants (Block et al. 2011; Camphuysen et al. 2012). Even in the northern parts of the outward routes, where birds tend to be consistent, paths can be located several kilometres apart (see Supplementary material Fig. S1). For seabird species that use a 'fly-and-forage' strategy during migration (Dias et al. 2012a), i.e. that are more dependent on the feeding conditions found along the route, the definition of dynamic marine protected areas based on foraging habitat requirements may be considered (Hyrenbach et al. 2000; Grantham et al. 2011). Nevertheless, and despite the growing knowledge regarding seabird migration, the migratory ecology of most pelagic avian species remains largely unknown, which currently limits conservation approaches based on habitat modelling (Louzao et al. 2006; Hooker et al. 2011).

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2013.05.026>.

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