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RESEARCH ARTICLE

Oceanic navigation in Cory's shearwaters: evidence for a crucial role of olfactory cues for homing after displacement

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SUMMARY

Pelagic birds, which wander in the open sea most of the year and often nest on small remote oceanic islands, are able to pinpoint their breeding colony even within an apparently featureless environment, such as the open ocean. The mechanisms underlying their surprising navigational performance are still unknown. In order to investigate the nature of the cues exploited for oceanic navigation, Cory's shearwaters, *Calonectris borealis*, nesting in the Azores were displaced and released in open ocean at about 800 km from their colony, after being subjected to sensory manipulation. While magnetically disturbed shearwaters showed unaltered navigational performance and behaved similarly to unmanipulated control birds, the shearwaters deprived of their sense of smell were dramatically impaired in orientation and homing. Our data show that seabirds use olfactory cues not only to find their food but also to navigate over vast distances in the ocean.

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INTRODUCTION

Procellariiformes (that is albatrosses, petrels and shearwaters) are pelagic birds, which wander in the oceans most of the year and are tied to land only for breeding. Their colonies are mostly on small oceanic islands and, as central place foragers, these species commute between oceanic foraging sites and their nest (Warham, 1996). Their surprising navigational abilities allow them to pinpoint their colony following straight routes (Jouventin and Weimerskirch, 1990) even if their island is located within an apparently homogeneous environment such as the open ocean.

Navigating in the open ocean is a challenge for birds, as high seas appear as a featureless environment without relevant visual cues helping them to reach their goals. Similar to homing pigeons displaced to distant non-familiar locations, pelagic birds are thought to rely on a position-finding mechanism based on cues other than those provided by the local topography. The most widespread hypothesis proposes that individuals rely on magnetic cues to pinpoint their goal in the middle of the ocean (Freake et al., 2006; Lohmann et al., 2007). However, all the experiments aimed at testing this hypothesis in seabirds have failed to demonstrate a navigational role for geomagnetic information. In particular, magnets did not interfere with the navigational abilities of Procellariiformes (Benhamou et al., 2003a; Benhamou et al., 2003b; Bonadonna et al., 2003b; Bonadonna et al., 2005; Massa et al., 1991; Mouritsen et al., 2003). As an alternative, olfactory cues have been proposed as being the basis of the navigational map over the sea (Benhamou et al., 2003a; Benhamou et al., 2003b; Bonadonna et al., 2003a; Wallraff and Andreae, 2000). In the early seventies, the crucial role of olfaction in avian navigation was discovered in homing pigeons (Papi, 1989). A large body of evidence collected in the last 40 years has shown that homing pigeons are able to develop an odour-based navigational map, by associating the wind-borne odours at home with the direction of the winds; once at the release site, they are able to determine the direction of displacement on the basis of the local odour information (Papi, 1989; Wallraff, 2005). However, the investigations on the possible use of olfactory cues in wild species are still at an early stage, and evidence for olfactory navigation has been reported only in three species of migratory terrestrial birds: starlings, *Sturnus vulgaris*, swifts, *Apus apus*, and grey catbirds, *Dumetella carolinensis* (Fiaschi et al., 1974; Holland et al., 2009; Wallraff et al., 1995). Among birds, Procellariiformes have the most highly adapted olfactory neuroanatomy for performing olfactory tasks, and use of the sense of smell has been demonstrated in foraging, nest recognition and even mate recognition (Bonadonna et al., 2004; Bonadonna and Nevitt, 2004; Nevitt et al., 1995). For this reason they have been suggested as the most suitable candidates for long range olfactory navigation (Wallraff and Andreae, 2000).

Among Procellariiformes, Cory's shearwater, *Calonectris borealis* (Sangster et al., 2012), is a good candidate for studying oceanic navigation, as most of the populations of this species nest on small oceanic islands in the North-Eastern Atlantic Ocean and then disperse widely during their post-breeding migration (Dias et al., 2011; González-Solís et al., 2007). In order to test the role of geomagnetic and olfactory information in Cory's shearwater navigation, we displaced – in the open ocean – adult birds subjected to a magnetic disturbance ('magnetic' birds), birds subjected to

olfactory deprivation ('anosmic' birds) and untreated control birds. The movements of the displaced birds were tracked using either GPS data loggers or satellite (PPT) transmitters.

MATERIALS AND METHODS

Birds

This study was conducted under licence (permit nos 39/2010/DRA and 53/2011/DRA issued by the Direcção Regional do Ambiente from the Azores). Twenty-four Cory's shearwaters breeding at the colony of Capelinhos on Faial Island (38.584°N, 28.817°W, Azores Archipelago) were used in this study, conducted in June 2010 and 2011 (12 birds each year were displaced). The birds were incubating their eggs at the time of the experiment. In each accessible nest, the two pair mates were ringed at the start of the incubation period. During the 5 days prior to the experiment the colony was monitored daily, to check whether the incubating individuals had been relieved by their partner during the previous night. Only those individuals that had returned to the colony during the last two nights before the experiment were captured. This was done in order to displace only birds that were highly motivated to return to the nest, and with presumably no or low motivation to forage: indeed, after returning to the nest to relieve its partner during incubation, a bird normally fasts during the 7–10 days it spends on its egg (Thibault et al., 1997). The eggs of the captured birds were replaced with plaster eggs and kept in an incubator until the displaced parent or its mate came back to the colony. In the case of non-homed birds whose mates abandoned the nest, the eggs were given to pairs about to fail during incubation (pairs that were incubating a broken, infertile or addled egg). After capture, the birds were kept and transported in individual cardboard boxes.

Treatments

Before displacement, the experimental birds were subjected to sensory manipulation. The anosmic birds (N=8) were deprived of their sense of smell by washing their olfactory mucosa with a 4% zinc sulphate solution (Bonadonna et al., 2001). Zinc sulphate washing specifically affects olfactory cells, inducing their necrosis (Cancalon, 1982). For instance, the specific effect of zinc sulphate in odour-guided behaviours has recently been shown in Cory's shearwaters nesting at the Salvages islands (Dell'Ariccia and Bonadonna, 2013). The olfactory neurons are replaced by new neurons, so that the olfactory mucosa is completely regenerated a few weeks after the treatment. The treatment was performed by inserting a curved needle with a rounded tip into each nostril and injecting 2.5 ml of zinc sulphate solution.

The magnetically treated birds (N=8) had a semi-cylindrical PVC box (diameter 1 cm, length 3.5 cm) containing a strong cylindrical neodymium magnet (diameter 5 mm, length 10 mm, total mass 3.9 g, magnetic moment 0.1 A m^2) glued on their head. The magnet was free to tumble inside the box, thus producing a randomly variable artificial magnetic field, which was stronger than the natural one throughout the bird's head. The artificial field produced was about 60,000 nT at 7 cm from the magnet, with the natural field being around 45,000 nT in the study area. The same kind of magnets have previously been used in sea turtle experiments, producing an impairment in the homing abilities of displaced turtles (Luschi et al., 2007).

The control birds (N=8) were not subjected to sensory manipulation, as we did not want to include manipulated control groups (birds bearing dummy magnets and birds subjected to nasal washing with physiological solution) in order to minimise the impact on the colony. Such control groups were not strictly necessary as it has previously been reported that carrying dummy magnets (Benhamou et al., 2003b; Bonadonna et al., 2003b; Bonadonna et al., 2005), washing the olfactory mucosa with physiological solution (Bonadonna et al., 2001; Luschi et al., 2007) or even washing the non-olfactory nasal mucosa with zinc sulphate (Benvenuti et al., 1993) does not affect the behaviour of petrels.

Tracking system

The birds used in the experiment belonged to the Atlantic species, *Calonectris borealis*, of the 'Cory's shearwater complex [Cory's shearwater was formerly considered a polytypic species, with one subspecies in the Atlantic and the other in the Mediterranean, but it was recently split into two distinct species (Sangster et al., 2012)]. *Calonectris borealis* is characterised by a larger body size and heavier body mass compared with the Mediterranean species, Scopoli's shearwater, *Calonectris diomedea* (Thibault et al., 1997), thus allowing the use of the tags reported below (Phillips et al., 2003). Control and magnetic birds were equipped with Technosmart (in the 2010 release) or E-obs (in the 2011 release; www.e-obs.de) GPS data loggers, fixed to the back feathers with water-resistant Tesa tape. All the loggers acquired a fix every minute. The E-obs loggers featured remote UHF data download capability through a base station placed at the colony, so that in 2011 we were able to detect the presence of the birds at the colony and download the tracking data, even if we were not able to recapture the birds. As it is known that petrels deprived of their sense of smell have difficulty in finding their burrows (Benvenuti et al., 1993; Bonadonna and Bretagnolle, 2002; Bonadonna et al., 2001), making tag recovery difficult, the anosmic birds were equipped with Argos satellite transmitters (model PTT-100-30 Argos GPS from Microwave Telemetry, 30 g, Microwave PTT-100, 32 g), some of which had a GPS receiver (supplementary material Table S1). The solar-powered transmitters (N=5) were attached on the back of the birds using a Teflon ribbon harness crossed on the breast, while the battery-supplied transmitters (N=3) were attached to the back feathers with water-resistant Tesa tape (supplementary material Table S1). Although the use of Argos satellite transmitters, GPS tags and harnesses might reduce the foraging efficiency of petrels, particularly in small species (Phillips et al., 2003), these devices have been successfully used for navigational studies as they do not seem to affect flight and navigational/migratory performance (Benhamou et al., 2003b; Bonadonna et al., 2005; Mouritsen et al., 2003; Ristow et al., 2000). The harnesses employed in this experiment were the same as those used in a study on the smaller Scopoli's shearwater (Ristow et al., 2000), whose long distance migration was successfully tracked for months. Because the Technosmart GPS loggers were lighter than the other tags, additional mass was added to their packages to make it about the same for all birds (total mass, 30 g).

Releases

On the evening of the capture day, the cardboard boxes containing the birds were embarked on a cargo ship, travelling from Faial to Lisbon. The release sites were about 800 km east of the colony and over 500 km from the easternmost island of the Azores. The releases began about 24 h after departure in 2010, and about 39 h after departure in 2011, because the cargo ship stopped for several hours in Ponta Delgada (São Miguel Island, Azores). The birds were released astern at about 20 min intervals, alternating individuals belonging to the three groups. After release, the nests of the displaced birds were monitored daily to check for homed birds and to recover the tracking devices. Original track data are available on Movebank (movebank.org) and are published in the Movebank Data Repository with doi 10.5441/001/1.nf80477p.

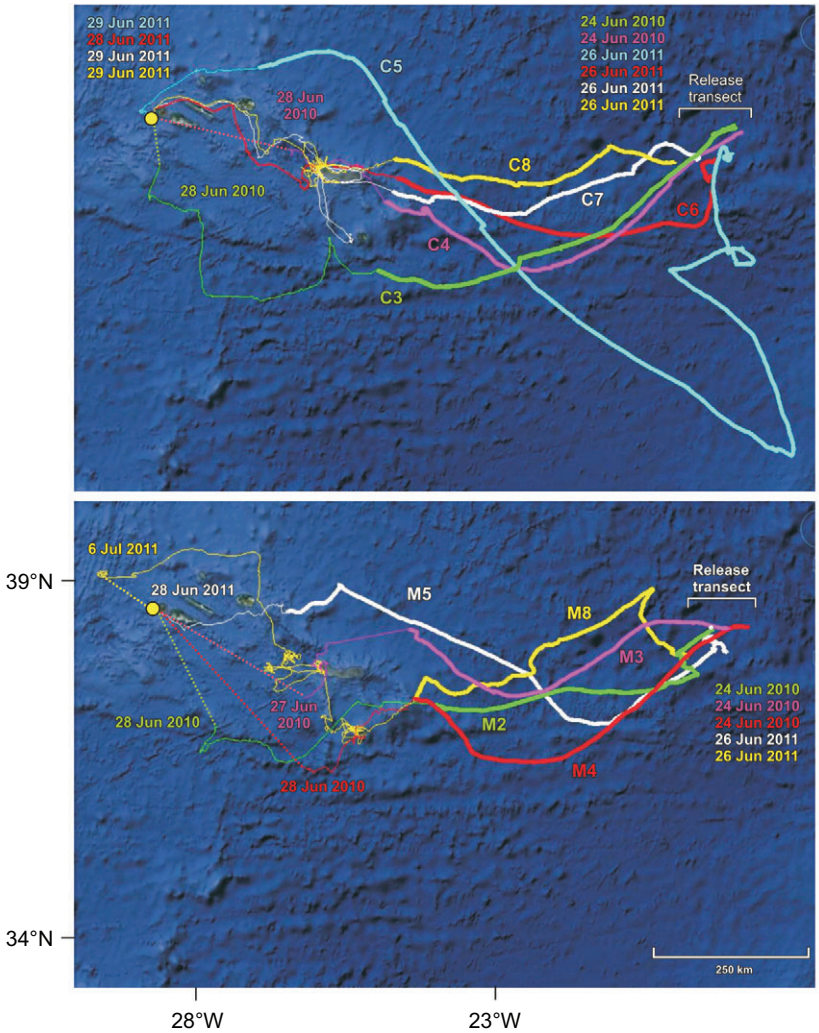

Fig. 1. Homing paths of unmanipulated control birds (C3, C4, C5, C6, C7, C8, upper panel) and birds carrying mobile magnets (M2, M3, M4, M5, M8, lower panel) plotted over a Google Earth map. See supplementary material Table S1 for details. The yellow circle indicates the home colony. For birds that homed but were not tracked as far as the home island, broken lines link the last location obtained and the colony. Thick lines represent the oceanic journey; thin lines represent the track recorded after the bird got closer than 50 km to any one of the islands of the Azores Archipelago. For each bird, colour-coded dates of release and of the last fix recorded are reported.

Data analysis

The homing success of the three groups of birds was compared with the χ^2-goodness of fit test. The homing performance was also evaluated by considering the ability of the birds to approach the home colony over the first 5 days after release. Between-group differences were tested using two-way RM ANOVA and Student–Newman–Keuls test for multiple comparisons. In the analysis of the GPS data, we only considered the fixes for which the calculated speed was lower than 80 km h^{-1}, which is considered to be the maximum flight speed of a Cory's shearwater (Paiva et al., 2010), and higher than 10 km h^{-1}, chosen to eliminate the periods during which the birds were not travelling but were likely to rest on the sea surface. For the Argos locations, the same maximum speed threshold was used to filter out the locations that determined an implausible speed. For the minimum speed, locations for which a speed lower than 10 km h^{-1} was determined were discarded only if the distance between the two fixes was lower than 5 km, corresponding to a time lag of 30 min. As we aimed to evaluate the navigational performance in the open ocean, we excluded from the analysis the locations recorded after a bird got closer than 50 km to any of the islands of the Azores Archipelago. For each track, we calculated a mean vector of the directions taken by the bird while moving from one recorded fix to the next. Each mean vector is therefore representative of the flight path of the shearwater in the open ocean. In addition, a further analysis was conducted for the Anosmic group on the portion of the tracks recorded in the first 5 days after release. This was done in order to evaluate the behaviour of the birds during a period in which their motivation to feed was likely to be low. The mean vector distributions were tested for randomness with the one-sample Hotelling test. In order to evaluate the difference in orientation exhibited by the three experimental groups, we performed a one-way ANOVA applied on the deviation of the mean vector directions from the home direction. Between-group differences in tortuosity of the flight path were tested by applying the one-way ANOVA on the mean vector lengths. Multiple comparisons were performed with the Bonferroni *t*-test. Wind data were obtained from NCEP-DOE Reanalysis 2 global weather model, provided by the NOAA/OAR/ESRL PSD (Boulder, CO, USA; www.esrl.noaa.gov/psd/) and were accessed through Movebank (www.movebank.org).

RESULTS

All the control shearwaters released were able to fly back to the breeding colony. Similar performances were displayed by the magnetic birds, as only one of them did not return to the colony. In contrast, only two of the anosmic shearwaters released could find their way back home during their breeding period (comparison of the number of homed and non-homed birds in the three experimental groups χ^2 goodness of fit, $P<0.01$).

At the end of the experiment we obtained six tracks of control (C) birds, five tracks of magnetic (M) birds and six tracks of anosmic (A) birds suitable for the analysis, because of technical failures: the

GPS logger of the bird C1 partially failed and only recorded for 8 h; birds C2 and M1 lost their logger; bird M7 escaped from its box during transportation with the logger still switched off; the transmitters on birds A1 and A4 stopped transmitting within a few hours of release.

Both control and magnetic birds displayed homeward-oriented routes generally flying within a narrow corridor (Fig. 1), while the anosmic shearwaters wandered across the ocean for thousands of kilometres (Fig. 2). Consistently, both control and magnetic shearwaters approached their home island faster than the anosmic birds (Fig. 3), as shown by the analysis of the distance of the single birds from the colony in the first 5 days after release (two-way RM ANOVA $P<0.001$; Student–Newman–Keuls test $P<0.001$ anosmic *versus* magnetic and anosmic *versus* control; $P>0.05$ control *versus* magnetic). In both 2010 and 2011, winds in the area around the release sites in the 2 days following release were mostly from the north or north-east, the only exception being the day of release in 2010 when winds were blowing from west-north-west. However, they were weak ($<3\ \mathrm{m\,s^{-1}}$) and rapidly shifted towards north-west and then north.

The analysis of the portion of the tracks in the open ocean is reported in Fig. 4. The mean vector distributions of both control (second-order mean vector length $r=0.672$, direction $\alpha=265$ deg) and magnetic birds ($r=0.669$, $\alpha=267$ deg) were significantly different from random (Hotelling test, $P<0.01$), and were oriented in a direction close to that of the breeding island. By contrast, the anosmic shearwaters' mean vectors ($r=0.070$, $\alpha=339$ deg) were randomly distributed (Hotelling test, $P>0.05$). The three experimental groups displayed a difference in orientation with respect to the home direction (one-way ANOVA applied on the angular distance between each vector and the home direction, $F=5.498$, $P<0.02$; mean angular distance control 13 deg, magnetic 10 deg, anosmic 83 deg). In particular, the anosmic group exhibited a greater deviation from home than both control and magnetic shearwaters (Bonferroni *t*-test, $P<0.05$), while no difference emerged between control and magnetic birds ($P=1$). Furthermore, a significantly greater tortuosity of the flight path was observed in the anosmic group in comparison with the two other groups (one-way ANOVA applied on the mean vector lengths, $P<0.001$, $F=46.549$; mean length control $r=0.687$, magnetic $r=0.678$, anosmic $r=0.130$; Bonferroni *t*-test: anosmic *versus* magnetic $P<0.001$; anosmic *versus* control $P<0.001$; magnetic *versus* control $P=1$).

The mean vector distribution of the anosmic birds limited to the first 5 days after release (see Fig. 4) turned out to be significantly oriented (Hotelling test, $P<0.01$, second-order mean vector: $r=0.348$, $\alpha=315$ deg), but in a direction significantly different from the home direction. In fact, the 99% confidence limits (290 deg, 354 deg) of the distribution of the mean vectors do not include the direction of the home colony (273 deg). This anosmic bird distribution was compared with the distributions of the other two groups used in the previous analysis, as all the controls and magnetic shearwaters approached the archipelago in under 5 days. This comparison revealed that the anosmic group oriented in a significantly different direction from the other two groups (one-way ANOVA applied on the angular distance from home, $P<0.001$, $F=29.485$; mean angular distances control 13 deg, magnetic 10 deg, anosmic 41 deg; Bonferroni *t*-test, $P<0.001$ in both comparisons) and that they flew along a significantly more tortuous path (one-way ANOVA applied on the mean vectors lengths, $P<0.001$, $F=15.892$; mean length control $r=0.687$, magnetic $r=0.678$, anosmic $r=0.352$; anosmic *versus* magnetic $P=0.001$; anosmic *versus* control $P<0.001$).

Most control and magnetic birds changed their behaviour after reaching any one of the islands of the Azores Archipelago, shifting from the straight path displayed during the oceanic leg to much more tortuous routes, either staying in the vicinity of the coasts or making excursions outside the shelf (Fig. 5). Both homed anosmic birds first approached other islands before getting to Faial (see Fig. 2, insets). Bird A5 initially moved along a tortuous path for 10 days

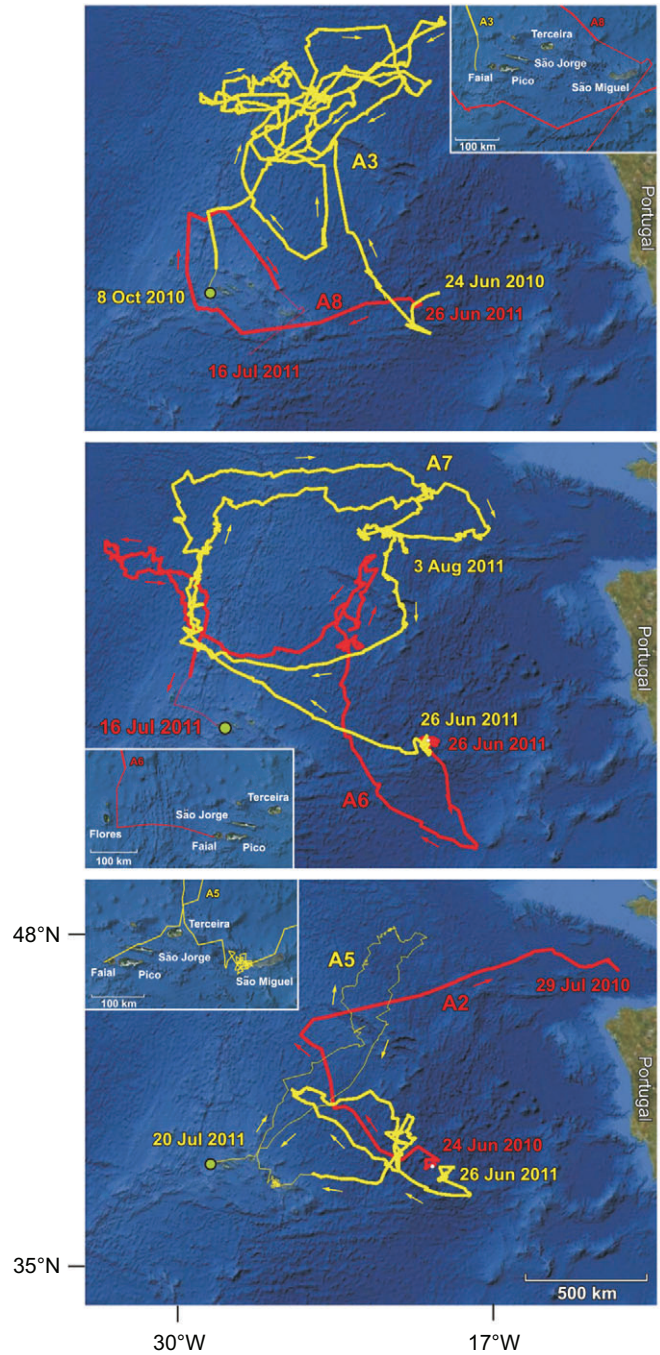

Fig. 2. Tracks of anosmic birds (A2, A3, A5, A6, A7, A8) (see supplementary material Table S1 for details). The green circle indicates the home colony. The insets show the area near the Azores islands at greater magnification (see Results for other explanations). Faial is the home island. The A3 track is reported only until the bird approached the colony site more than 3 months later, when the reproductive period was over and its olfactory mucosa should have been reconstituted. The complete track of this bird is reported in supplementary material Fig. S1. Other explanations as in Fig. 1.

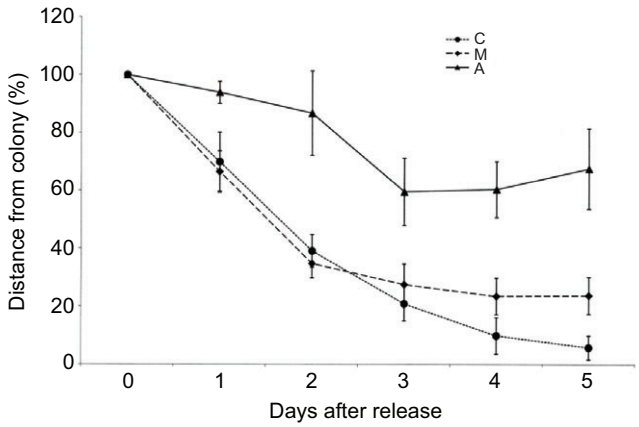

Fig. 3. Mean ± s.e.m. distance from the colony, expressed as a percentage of the distance at the release site, of the three groups of shearwaters (C, un-manipulated controls; M, birds bearing mobile magnets; A, anosmic birds) from the time of release (indicated by 0) up to day 5 after release.

before approaching São Miguel Island, where it remained for 2 days in the proximity of the coast, probably foraging. In the following days, A5 flew north-west to Terceira Island, and then started a 1100 km long northward journey, subsequently homing back to the breeding colony with a very straight path. Bird A6 arrived in the vicinity of Corvo Island, West of Faial, where it suddenly changed its flight direction, heading towards the home colony. Bird A8, conversely, did not return home even after having approached São Miguel Island (Fig. 2).

The reproductive success of the pairs involved in the experiment was compared with that of other accessible nests in the colony. We estimated that the impact of our experiment on breeding success resulted in four fewer chicks produced each year. However, we conducted our experiment on a small sample every year (our 12 experimental nests represent *ca.* 10% of the colony from Capelinhos), and in long-lived species such as Cory's shearwater, the parameter having the greatest influence on population dynamics is adult survival rate and not breeding success (Fontaine et al., 2011). Therefore, we are confident that our experiment should have no significant long-term effect on the dynamics of the Capelinhos colony.

DISCUSSION

The first displacement experiment of Procellariiformes subjected to magnetic disturbance or olfactory deprivation clearly highlighted the crucial role of olfactory cues in oceanic navigation. We confirmed that magnets attached to the head of the birds, purportedly masking any geomagnetic information, do not interfere with homing behaviour, as already shown in albatrosses and other Procellariiformes (Benhamou et al., 2003a; Benhamou et al., 2003b; Bonadonna et al., 2003b; Bonadonna et al., 2005; Mouritsen et al., 2003), including the closely related Scopoli's shearwater in the Mediterranean (Massa et al., 1991). Conversely, olfaction seems to be necessary for shearwaters to determine the direction of displacement. As it is known that olfaction helps Procellariiformes to locate patches of prey abundance at sea (Nevitt et al., 1995), it might be argued that the tortuous paths displayed by the anosmic birds were not due to a home-searching behaviour but were related to difficulties in locating food. We consider this interpretation very unlikely on the basis of the results of our analysis of the portion of the track of the anosmic birds in the first 5 days after release. This clearly showed that even when the birds' motivation to feed was still presumably low (as they were captured at the beginning of their incubation stint, these birds had reserves for fasting for at least 6–7 days), their paths were tortuous and not homeward oriented.

The ability of Procellariiformes to exploit olfactory environmental information for navigation has often been hypothesised, and how olfactory information might be used by these birds in a spatial task has been the subject of theoretical speculation. Reporting the navigational performance of displaced white-chinned petrels, *Procellaria aequinoctialis*, Benhamou and colleagues proposed that at a relatively short distance from the colony the birds might have followed an odour plume originating from the home island (Benhamou et al., 2003b). Such osmotactic behaviour cannot explain the performance of our control and magnetic shearwaters, which oriented towards the colony island soon after release, at a distance of 800 km, and in the presence of winds not blowing from the home direction. Alternatively, Cory's shearwaters may learn an olfactory map on the basis of wind-borne odours, similar to homing pigeons (Wallraff and Andreae, 2000; Papi, 1989). As these birds display a high fidelity to the natal colony both as prospectors and reproducing individuals, such a learning phase might take place during the post-fledging period, when juveniles can remain around the colony island for several days, before starting their first migratory flight (P. Lambardi and J.B., unpublished data). Alternatively, shearwaters may learn the olfactory landscape of the ocean during their foraging trips from the colony and their migratory flights outside the breeding season and use it for navigation (Nevitt and Bonadonna, 2005). As petrels are able to locate foraging areas in the open sea by exploiting odours associated with prey abundance (Dacey and Wakeham, 1986; Nevitt, 2008; Nevitt et

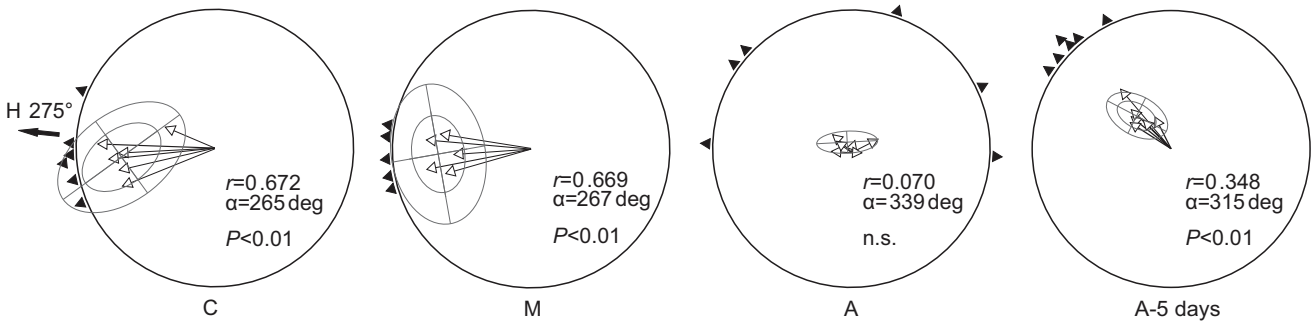

Fig. 4. Orientation of the tracks in open ocean (C, control birds; M, birds bearing magnets; A, anosmic birds; A-5 days, anosmic birds in the first days after release). Each mean vector indicates the mean orientation of a bird's track. The mean vector distributions were tested for randomness with the Hotelling test (confidence ellipses are shown). Triangles at the periphery of the circles represent the mean directions of the tracks. Second-order mean vector length (*r*) and direction (α) are given.

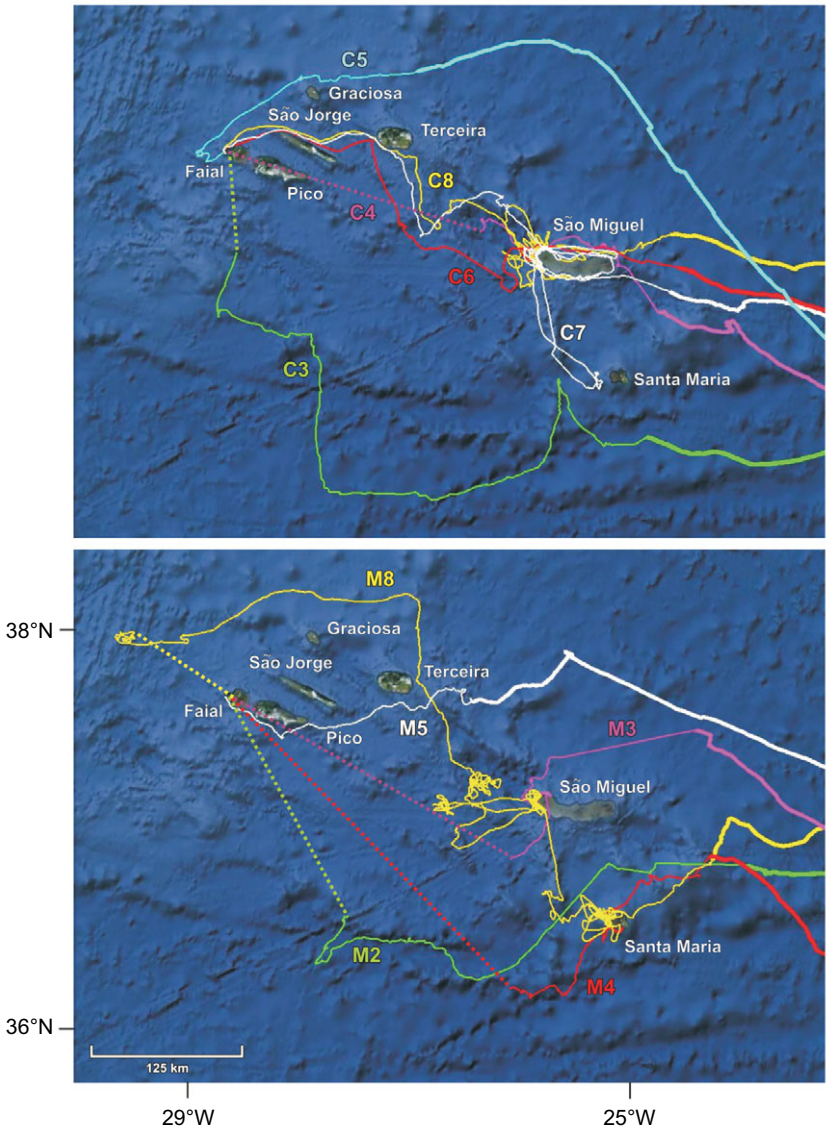

Fig. 5. Sections of tracks of control (upper panel) and magnetic (lower panel) shearwaters after the birds had approached any island of the archipelago. The tracks are plotted over a magnified map of the Azores Archipelago area. Other explanations as in Fig. 1.

al., 1995), it is likely that different areas of the oceans are remembered by the birds on the basis of their olfactory characteristics, so as to build a cognitive map on the basis of olfactory signals (Jacobs, 2012). One of the candidate substances as a food indicator is dimethyl sulphide (DMS) (Nevitt et al., 1995), which originates in high quantity from phytoplankton grazed by zooplankton (Dacey and Wakeham, 1986). It has been suggested that DMS and other biogenic odours whose concentration varies predictably in space may contribute to form an olfactory landscape used in spatial tasks (Bonadonna et al., 2003a; Nevitt and Bonadonna, 2005).

On the basis of a number of experimental findings, we can exclude the possibility that the impairment of the olfactory-deprived shearwaters might be due to a non-specific effect of anosmia affecting their motivation to home. It has been shown recently at the Salvages islands that anosmic Cory's shearwaters displaced within the colony are able to locate their nest during the day, but not at night when olfactory cues are needed (Dell'Ariccia and Bonadonna, 2013). The possible non-specific effects of anosmia treatment resulting in the disruption of birds' navigational performance have largely been debated in homing pigeon studies (Jorge et al., 2009; Wiltschko, 1996). However, since the discovery of the role of olfaction in bird navigation in pigeons (Papi et al., 1972), the specific role of environmental odours in navigation has been successfully demonstrated by many subsequent experiments, speaking against a non-specific effect of anosmia (Benvenuti and Wallraff, 1985; Gagliardo et al., 2011; Ioalè et al., 1990; Papi et al., 1974). Additionally, it has been argued (Mora et al., 2004) that experimental manipulations of the olfactory system might have accidentally affected the putative magnetoreceptor described by some authors in the pigeon's upper beak (Fleissner et al., 2003) (but see Treiber et al., 2012). However, no effect on pigeon navigational performance emerged when the trigeminal innervation of the putative magnetoreceptor in the upper beak was severed (Gagliardo et al., 2006; Gagliardo et al., 2008; Gagliardo et al., 2009).

In our experiment, two anosmic subjects (A5, A6) eventually homed after about 3 weeks of wandering (Fig. 2; see also supplementary material Fig. S1) and another anosmic bird (A3) approached the home island 3 months after the displacement, when the breeding season was over and its olfactory function was probably fully recovered. The behaviour of these anosmic birds that flew long tortuous paths, probably searching for the colony island, indicates that olfactory deprivation does not affect the motivation to home. This is consistent with observations in homing pigeons (Wallraff, 2005).

As the birds of our study were likely to be very familiar with the Azores Archipelago, it is reasonable to assume that the local topography provided navigational information for the two anosmic birds that succeeded in returning to their nest. Indeed, bird A6 deflected its route by about 90 deg once it had passed close to Corvo and Flores Islands, clearly reorienting towards home. Also, bird A5 changed its behaviour after arriving near São Miguel, shifting from wide range wandering movements in the open ocean to small scale movements around the island. Subsequently, this bird left the archipelago for a long loop, which was very similar in shape and location to the 'long' foraging trips normally performed by breeding Azorean Cory's shearwaters (Magalhães et al., 2008) and which was substantially different from the wandering movements shown by the same bird soon after release. As this bird started this northward journey 16 days after the zinc sulphate treatment, it is also possible that its olfactory function had partially recovered by that time. Conversely, bird A8 apparently did not take advantage of its landfall at São Miguel Island, as it never returned home.

Our findings show that geomagnetic information is neither sufficient nor necessary for shearwater navigation over the ocean, because magnetic disturbance did not affect the birds' navigational performance, and magnetic cues were not sufficient to allow navigation in the anosmic birds. These results reveal that Cory's shearwaters rely on olfactory cues for oceanic navigation, and thus challenge the notion that ocean navigators use a magnetic map. Olfactory navigation may be a widespread mechanism in birds and odours may also constitute a reliable source of information for other oceanic navigators.

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AUTHOR CONTRIBUTIONS

F.B. conceived the study; A.G., P. Luschi, F.B. and M.W. designed the study; A.G., J.B and P. Lambardi carried out the experiments; A.G., P. Luschi and F.B. analysed the data; A.G., F.B., P.Luschi and M.W. interpreted the findings and wrote the paper.

COMPETING INTERESTS

No competing interests declared.

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