Mediterranean storm petrels rely on nest position for homing after migration: a test with artificial nestboxes

Petrels are highly philopatric and return from migratory journeys of thousands of kilometres to breed in the same burrow year after year. During the breeding season, some burrowing petrel species rely on their sense of smell to locate their nest at night, but the mechanisms involved in the homing behaviour after several months at sea are virtually unknown. To understand whether the sense of smell is involved in nest finding at the return from migration and to study the interplay with other positional cues, we explored the homing behaviour and nest choice by Mediterranean storm petrels (*Hydrobates pelagicus melitensis*). During two consecutive winters, we conducted our research in a colony with a long-lasting population study which contains well-used artificial nestboxes. We experimentally displaced previously occupied nestboxes in late winter and then checked for nest choice and occupancy by breeding individuals in the following breeding season. This experimental design allowed the manipulation of the location of the burrow, and the olfactory information contained within, without manipulating other positional cues. We observed that almost all individuals nested in the box located at the same position as the year before, disregarding whether the box was the same as the one they had previously occupied or another one. During the breeding period, we also tested in a Y-maze the olfactory preference for the occupied nestbox with respect to another random one. Again, storm petrels did not show any olfactory preference for their nest. Our study implies that storm petrels breeding in a cave rely on other positional cues rather than olfactory to home and suggests a mechanism combining tactile and proprioceptive cues to find the nest in the dark.

Keywords: homing, *Hydrobates pelagicus*, olfaction, migration, procellariiform seabird, short-range orientation

Procellariiform seabirds are renowned among birds for their stunning olfactory capabilities, which play a vital role in their life. Many petrel species use their sense of smell to locate foraging areas over the ocean surface (i.e. Grubb 1972, Hutchison and Wenzel 1980, Nevitt 2000, Dell'Arciccia et al. 2014), for oceanic navigation (Gagliardo et al. 2013), to recognize their partner (Bonadonna and Nevitt 2004) and, probably, to avoid inbreeding during mate selection (Bonadonna and Sanz-Aguilar 2012). In addition, several species have the capacity to distinguish between their own and a conspecific's nest burrow only by the odour, and tested burrowing petrel species need the sense of olfaction to home at night (Bonadonna and Bretagnolle 2002, Bonadonna et al. 2003a, Bonadonna et al. 2003b, Bonadonna et al. 2004, Dell'Arciccia and Bonadonna 2013).

Petrels are highly philopatric and show remarkable nest site fidelity, returning to breed year after year to the same nest, after a winter migration of thousands of kilometres (Warham 1990, 1996). They form long-lasting pair bonds and the partners are able to find and recognize their own nest after one year of absence. During breeding, when the nests are occupied by an incubating adult or later, visited to feed the chick, nest recognition is done using olfactory cues. In fact, individuals are attracted by the odour of their own nest (Bonadonna et al. 2003a, Bonadonna et al. 2004), and when nocturnal petrels are deprived of their smelling capabilities, their homing ability is strongly impaired or completely null (Bonadonna et al. 2001, Bonadonna and Bretagnolle 2002, Bonadonna et al. 2003b, Dell'Arciccia and Bonadonna 2013). However, studies specifically aimed to investigate the mechanisms underlying nest recognition at the return from migration, when nests have been left empty during months, have not yet been carried out.

Ecological traits of petrel species influence the type of stimuli relevant for a given behaviour, and the reaction to the stimulus considered. For instance, species nesting in burrows and crevices are generally nocturnal and employ olfaction to home; while species nesting on the surface are generally diurnal and rely on vision to find the nest (Warham 1990, 1996). In foraging, not all petrel species are sensitive to odours linked to food and species vary in their attraction to different odorants associated with food (Dell'Arciccia et al. 2014). Finally, besides the importance of species ecology, the response

to odours has been suggested to be also age dependent (Bonadonna and Sanz-Aguilar 2012). In fact, in species tested for the response to personal odours, chicks appear to be attracted by self-odours (de León et al. 2003) while, on the contrary, adults avoid their own smell as well as that of kin (Bonadonna and Nevitt 2004, Mardon and Bonadonna 2009, Bonadonna and Sanz-Aguilar 2012).

In this study, we investigated whether olfactory or other positional cues are employed to locate the home nest after the winter migration using the Mediterranean storm petrel (*Hydrobates pelagicus melitensis*). Several species of storm petrels are sensitive to and use a large variety of odour cues (Grubb 1973, 1974, Bonadonna and Sanz-Aguilar 2012, Dell'Ariccia et al. 2014). In particular, chicks of Mediterranean storm petrels exploring the immediate environs of their nest have been shown to use olfaction to relocate the nest, where their parents will feed them (Mínguez 1997). These characteristics make this species particularly suitable to explore the homing cues employed by breeders after the winter absence and the potential role of olfaction in this task. While previously studied storm petrel species breed exclusively on rocky grounds on slopes and stacks or in soil between the tree roots, the Mediterranean storm petrel has the ecological peculiarity of breeding also inside caves (del Hoyo et al. 1992, Brooke 2004). Breeding in caves can provide supplemental cues or modify cues used to home, as observed for other petrel species (i.e. hypogean vs superficial nesters).

For our study, we selected the breeding colony on Benidorm islet. This colony is object of a detailed and long-lasting population survey. Since 1993, breeding adults and their chicks have been ringed in their nests, which allow a thorough understanding of individual histories, pair members, nest occupancy and breeding success over the years (Sanz-Aguilar et al. 2009, Sanz-Aguilar et al. 2010). In 1996, the colony was provided with artificial nestboxes to increase nests sites. Nestboxes have widely been adopted by breeding storm petrels in all these years (de León and Mínguez 2003, Libois et al. 2012), and offer a unique opportunity for experimental studies. Thanks to this setting, we employed an experimental design allowing the manipulation of the location of the burrow, and the olfactory information contained within, without manipulating other positional or visual cues. We

expected that if Mediterranean storm petrels rely on olfaction to identify their nest when returning from migration, they would nest in the previously occupied nestbox, even when it had been displaced. On the contrary, if other positional cues play a major role in nest location, storm petrels would breed in the nestbox located at the original location, regardless as to whether or not it is the one previously occupied. Finally, we verified the response to nest odours during the breeding season in a Y-maze.

METHODS

This study was conducted on Isla de Benidorm, Spain (38° 30' 05.15" N, 0° 07' 48.68" W, approximately 6.5 ha). Here, there are two high-density colonies of Mediterranean storm petrels (*Hydrobates pelagicus melitensis*) inside two different caves, located on the opposite sides of the islet. The first cave (cave 1) is home to approximately 200 breeding pairs while the second cave (cave 2) houses around 100 pairs (Sanz-Aguilar et al. 2009, Sanz-Aguilar et al. 2010). In 1996, 87 artificial nestboxes were installed, 45 in cave 1 and 42 in cave 2, which have been widely adopted by breeding storm petrels, mainly in cave 2 (From cave 1, 23 nestboxes were subsequently removed in 2004). During the breeding season 2011, at the beginning of our experiment, 33 nestboxes in cave 2 and 6 in cave 1 were occupied (For details on nestboxes, occupancy rates and nesting success see de León and Mínguez 2003, Libois et al. 2012).

Experiment 1: Nestboxes Displacement

To test whether Mediterranean storm petrels use olfactory or other spatial cues for locating their nest after the winter migration, we artificially displaced the nestboxes before the birds' return for the breeding season (in early March 2012). To explore whether the distance of displacement may have impacted nest choice, we divided displaced nests into two categories: 10 nestboxes were displaced over a short distance (SD), which mean that two adjacent boxes were simply inverted in their respective positions (mean $\pm$ SEM = 25 $\pm$ 5 cm). Ten other nestboxes were displaced over a long

distance (LD. 248 ± 67 cm). Finally, 19 boxes remained untouched and used as controls (C. Fig. 1). During the subsequent breeding season (June 2012), all the nestboxes were checked for birds' presence and nesting; all breeding petrels were captured and identified, or ringed in case of unknown individuals. All natural nests were also checked during the normal population survey (Sanz-Aguilar et al. 2009, Sanz-Aguilar et al. 2010), so that we could find out the location of the individuals previously nesting in the experimental nestboxes but absent at the time of the study. In the breeding season 2012, the number of recaptured birds in the whole colony was lower (66%) with respect to the two previous years (71% in 2010 and 73% in 2011) in both artificial (70%) and natural (63%) nests, probably because of a slight increase in the number of birds that did not return to the colony that year, i.e. took sabbatical (Sanz-Aguilar, n.d.). Thus to test the repeatability of results, we replicated the experiment in the following year. In March 2013, we displaced another nine nestboxes over a short distance and eight over a long distance. A supplemental nestbox was occupied in 2012, so a total of three boxes remained as never displaced "permanent-controls". None of the nestboxes displaced during the first experimental season was displaced again in the second, therefore these boxes acted as controls in year 2. All nestboxes were checked during the subsequent breeding season (June 2013). The annual colony survey in the summer of 2014 allowed us to check for the nesting of birds that took a sabbatical in 2013, and so to complete the nest occupancy data for the second experimental year. This additional check to the experiment also provided the information of nest occupancy after no further nest displacements.

Because storm petrels from Benidorm have lower partner fidelity than other storm petrels and the formation of new pairs is relatively common (Bried et al. 2003; Sanz-Aguilar n.d.), we did not use the "pair" as the unit of our statistical tests of nest choice but rather analysed individual choices. First, we investigated whether our experiment influenced the rate of non-recaptured birds employing a Fisher's exact test, exploring whether the proportion of non-recaptured individuals was the same in the control and in the displaced nests. Then, to understand whether storm petrels followed their previously occupied nests when displaced or they rather nested in a different nestbox,

we performed a Fisher's exact test, testing the independence between the nesting-box choice and the experimental condition (displaced vs. control nests). Finally, we performed a multiple correspondence analysis (MCA), to test whether there was an association between the nest choice and other factors that may have influenced the birds' choice besides the nest displacement, i.e. the distance of nest displacement, the presence of the partner of the previous year, the sex, the colony or the returning to the nest after a sabbatical year. Variables and their levels tested are summarized in table 1. MCA was performed using R package ade4 v. 2.15.3 (R Development Core Team 2011).

Experiment 2: Y-Maze Choice Test

To test for storm petrels' ability to recognize and choose their own nest versus another nest odour, we presented them with a binary odour choice in a classic Y-maze test, during the brooding period in June 2013. The Y-maze was a modified version of the one previously used in this colony (Bonadonna and Sanz-Aguilar 2012). It was made of three stainless steel symmetrical arms (Arm length: 35 cm; width: 11 cm; height: 8 cm; angle between each arm: about 120°). The end of each odour choice arm was equipped with a 20 cm stainless steel tube allowing the maze to connect directly to a nestbox entrance (Fig. 2). The tubes were equipped with a computer cooling fan (Globe Fan Technology Co. Ltd., product number S05010, Taiwan) to provide low-noise, controlled airflow (9 CFM; 243 litres/min) through each choice-arm before the subject bird was tested. The maze was placed immediately outside the nesting cave, with the choice-arms towards the colony entrance and the entry-arm towards the sea, in order to simulate the homing direction and, thus, increasing the motivation of birds to leave the starting point and move toward one of the choice-arms. One experimenter removed two individuals from their nestboxes, put them into two separated bird-bags and transported them and the empty nestboxes to the maze. During the tests, the eggs were removed from the experimental nests and put in two separate boxes to keep them safe. A second experimenter placed the nestboxes at the end of each of the choice-arms and turned on the fans for 60 s. The fans were then turned off before the bird was placed in the entryway of the maze. Birds

were tested one at a time and only one time. At the end of the experiment we immediately returned the nest to its proper location, replaced the egg in its place and then returned the adult to the nest. Adults were returned to their nest within a maximum of 30 min, where they immediately resumed incubating the egg in a normal fashion. For each trial, the petrel was placed in the entryway of the maze and allowed to make a choice for a maximum of 10 min or until it reached the goal arm. Movement of a bird along the maze was easily tracked by the sound of walking, and confirmed visually when a bird reached one of the two choice-arms by an opening on top of the maze's arms. An arm choice was scored when a bird travelled halfway down a choice-arm and stopped for at least 30 s; however, the majority of birds walked to the end of the choice-arm and stopped. No-choice birds (removed after 10 min) sat calmly in the entry-arm facing away from the maze arms. The maze was washed thoroughly after each trial with ethanol (70%) to remove any odour residue and let evaporate until dry. All experiments were performed during daylight, when there were no free-flying birds at the colony. This procedure eliminated any possible bias between either the choice-arms themselves or their relative positions with respect to the colony, shoreline or other physical features in the environment.

Y-maze preferences were analysed using the Binomial test. We then checked for differences in choice time of birds expressing different preferences in the maze using Wilcoxon-Mann-Whitney test for independent samples and, finally, we checked for lateral preference of the maze's choice-arms with the Fisher exact test (Zar 1996).

Ethical note

This study was authorized by the Environmental Monitoring Service of Benidorm Island (Serra Gelada Natural Park, Generalitat Valenciana). All aspects of the study were performed according to guidelines established by the Centre National de la Recherche Scientifique for the ethical treatment of animals, were approved by the ethical committee during the evaluation of the Marie Curie Intra-European Fellowship proposal [PIEF-GA-2010-272282 - SOMA] to GDA and complied with current

French and Spanish regulations. The experiments were performed according to the Certificado de aptitud para el anillamiento y marcado de aves silvestres Categoría 'Anillador Especifico: *Hydrobates pelagicus*' de Ministerio de Medio Ambiente y Medio Rural y Marino n° Anillador: 410049 to ASA. A new survey of the colony at chicks fledging, showed that breeding success of manipulated nestboxes during both experimental years (85% in 2012 and 60% in 2013) was not lower from that of unmanipulated nestboxes (60% in 2012 and 59% in 2013) and comparable to the mean breeding success for the colony since 1997 (68%). Also survival at cave 2, where the majority of nestboxes were located, during the experimental years (85% in both years) was similar to the previous 10 years (83%).

RESULTS

Experiment 1: Nestboxes Displacement

During the breeding season of 2012, we recaptured 71% ($N=77$) of the known individuals nesting in the experimental nests the previous year, 76% ($N=37$) from control nests and 68% ($N=40$) from displaced nests. The following year, during the breeding season of 2013, we recaptured 79% ($N=67$) of the known individuals nesting in the experimental nests, 80% ($N=35$) from control and permanent-control nests (86%, $N=29$ and 50%, $N=6$ respectively) and 78% ($N=32$) from displaced nests (Table 2 and Figure A1). In both years, the proportion of recaptured birds was not statistically different in control and displaced nests (Fisher's exact test: $P > 0.5$ in both years). In 2013, we also recaptured 10 individuals (6 from long distance and 4 from control nests) non-recaptured in 2012, suggesting that they took a sabbatical year from breeding on that year (Table 2). In 2014, we recaptured two individuals (both from control nests) that took a sabbatical the previous year (Table 2). During the normal nest survey in 2014, after no further nests displacement, we recaptured 96 individuals all in the same nestbox and same location as the previous year, except for a pair that nested in a new one.

Mediterranean storm petrels did not follow the previously occupied nestbox when it was displaced. In fact, during the first experimental year, 93% ($N=28$) of the individuals from the control nestboxes were recaptured in the previously occupied nests, but only 15% ($N=27$) of the individuals whose nestbox was displaced nested in the previously occupied nestbox (Fisher's exact test: $P = 2.3 \cdot 10^{-9}$). The same pattern was observed during the second experimental year: 100% ($N=28$) of the control individuals nested in the previously occupied nestbox, while only 4% ($N=25$) of the individuals whose nestboxes were displaced nested again in the previously occupied nestbox (Fisher's exact test: $P = 3.2 \cdot 10^{-14}$). In the ten years preceding the experiment, the average nest fidelity, i.e. the proportion of recaptured birds found nesting in the same nest as the previous year, was 96% (Sanz-Aguilar, n.d.; Figure A2), highlighting that individuals from the control nestboxes showed a usual pattern of nest use. On the contrary, this pattern was disrupted in individuals from the displaced nests.

Multiple correspondence analysis showed that none of the tested variables but the experimental condition influenced nest choice. Results were similar in the two experimental years. The first 2 factorial axes of the MCA explained 80.6% of the total variation in 2012, and 79% in 2013. These axes are highly correlated with the nest choice and the experimental condition, but not with the other tested variables (Table 1). To a lesser extent, the second axis was also correlated to the partner. This exception is due to the association between breeding with a new partner and nesting in a new nest, i.e. individuals that chose a completely new nest tended to be with a new partner. Figure 3 illustrates the association between each variable and its levels on both axes and the eigenvalues. A detailed description of the analysis output and correlation values is provided in the appendix.

Experiment 2: Y-Maze Choice Test

In the Y-maze, we tested 53 storm petrels for nest odour choice, of which 38 (72%) entered one arm successfully, thereby making a choice. There was no significant preference for a given arm: 16 petrels chose the maze arm leading to the own nest, while 22 chose the arm connected to the other nest (Two tailed binomial test: $N = 38$, $P = 0.42$; Fig. 4). Choice time (the time that the bird took to

walk halfway down the arm) was similar for birds choosing the arm leading to their own or to the other nest. Median choice time to the own nest was 35 sec (range 5 sec to 3.5 min), median choice time to the other nest was 25 sec (range 2 sec to 7.5 min) (Wilcoxon-Mann-Whitney for independent samples: $W = 176.5$, $N_1 = 16$, $N_2 = 22$, $P = 0.4$). Overall, birds showed no lateral preference (own nest: 8 right and 8 left arm; other nest: 13 right and 9 left arm. Fisher exact test: $P = 0.74$). No-choice birds were mainly inactive, remaining immobile inside the entry arm throughout the experiment, often facing away from the maze arms.

DISCUSSION

Our data suggest that Mediterranean storm petrels returning at their colony from migration rely on nest position rather than on nest odour for homing. Accordingly, in the Y-maze, tested birds showed no behavioural preference for their nest odour over that of a random nest.

With very few exceptions, displacing the nestboxes showed that birds nested in the same location rather than in the same nestbox, even when this was just the adjacent entrance. Also those birds that took a sabbatical year (i.e. who did not reproduce during one year but returned to breed the year after) returned to the nestbox in the same location as their previous breeding, irrespective of whether the nestbox was the same or another one. The proportion of non-recaptured birds in control and displaced nests was independent from our experiment in both experimental years. MCA analysis showed that, besides the experimental condition (i.e. the displacement of nestboxes), none of the other variables tested were correlated to the nest choice. The only exception was that individuals that chose a completely new nest tended to be with a new partner. This association is stronger in 2012 than in 2013 because of the higher number of non-recaptured and divorced birds moving to new nests in 2012. Indeed, we observed that of the 11 individuals who chose a completely new nestbox (or moved to a natural nest), only two bred with their previous year partner, i.e. the two partners of a pair moved together into a new nest. In all the other cases, a new pair was formed either because the pair divorced and we found both pair members in a new nest with a different partner ($n=4$), or because one of the partners was not recaptured (i.e. probably dead) and we found the other with a new partner breeding in a new nest ($n=5$). This suggests that nest change from previous years is mainly due to the forming of a new pair and was not linked to our experiment. MCA results also show a strong association between the control condition (i.e. unmoved nestboxes) and the nesting in the same nestbox (and thus also the same location) as the year before, in both years. In fact, almost all birds in 2012 and all in 2013 whose nest was not displaced continued to nest in their nestbox. The association between nesting in the own nestbox and its displacement on a short

distance highlight that birds were able to relocate their displaced nest only under this condition of displacement. Finally, long distance nest displacements are associated with the nesting in the same position, reflecting the observation that birds whose nest had been displaced over a long distance nested in the same location as the year before, in an alien nestbox. This statistical association appears evident only in 2013 because of the higher number of divorced birds moving to new nests in 2012 (see above). Taken together, results from this first experiment suggest that Mediterranean storm petrels do not rely on olfactory cues to home to the nest after the winter migration but that other positional cues (e. g. topography) are employed. It might be that, after the winter absence, no volatile and smelly compounds are left in the empty nests, so storm petrels have to rely on more stable cues to find again the nest in this particular context. However, other hypotheses attempting to explain why a species sensitive to odours behave in this way are also possible (see below).

In accordance with the results from our first experiment, Mediterranean storm petrels did not show a preference for their own nest over that of a random conspecific when tested during the breeding season in a Y-maze. In general, Y-maze choice experiments do not allow the discrimination between whether the experimental subjects were unable to detect the odours or if they did not show a behavioural preference for them. However, according to past literature, our results suggest a lack of preference rather than a lack of odour perception. Mediterranean storm petrels have already been shown to be able to perceive personal odours (de León et al. 2003, Bonadonna and Sanz-Aguilar 2012), and the olfactory nest signature in petrels is formed by mate's personal odour (Bonadonna and Nevitt 2004. See below). In addition, when there is no odour in the maze arms or when the birds are made anosmic, petrels do not make a choice in the maze, remaining mainly in the starting point, suggesting that the perception of any odour is necessary to motivate them to move inside the maze (Bonadonna et al. 2003b, Bonadonna et al. 2004). In our experiment, the majority of birds (72%) moved in the maze, leaving the entry-arm towards one of the choice-arms. This tendency to move in the maze suggests that the birds actually perceived some kind of odour that motivated them to enter one of the choice-arms, but either that they could not discriminate between the two

295 odours or that the two odours had the same importance and/or attractiveness for them.
296 Mediterranean storm petrels breeding in Benidorm caves nest in crevices between the rocks and,
297 often, the crevices are shared by several breeding pairs (Mínguez 1997, personal observation).
298 Homing birds thus have to be able to find their nesting crevice within the colony and, then, their nest
299 location within the crevice. It is possible to hypothesize that homing storm petrels may use olfaction
300 to recognize the area within the colony where they nest but then, once at the crevice, they use other
301 cues to identify and join their own nest-cup. Probably, each nest has an identifiable odour but, being
302 “open” in the crevice, the different odours are mixed in a bouquet of the crevice and birds cannot
303 really use the nest’s odour to arrive at their nest. It is realistic to imagine that a burrow has a
304 stronger odour because it is a “closed” environment in which the birds rub themselves on the whole
305 entry tunnel and on the incubation chamber walls, allowing odours to saturate and concentrate in
306 the nest. On the contrary, an “open” nest-cup in a crevice has few features that may saturate with
307 odours, and the walls of the crevice and of the entryway that connects to it may smell of all the birds
308 nesting in the same crevice. In this respect, storm petrels may be not accustomed to smell their own
309 nest odour from far, but still they respond to a generic nest odour to home. Therefore, it may be
310 that, in the maze, storm petrels smelled this generic nest odour, which they followed to find a
311 possible exit out of the maze, but without a specific response to their own nest odour.

312 Our results seem to contrast previous findings which suggest olfactory nest recognition in
313 Mediterranean storm petrel chicks (Mínguez 1997). However, this earlier study reports, in
314 accordance with the idea that only the nest-cup may saturate with odour, olfactory recognition of
315 the nest as an effective method only at a very short distance. When artificially displaced from the
316 nest, the nestlings were able to get back to their nest only from 10 cm away. But even at 20 cm
317 away, only 54% of tested control chicks were able to reach their nest again and only 27% from 30 cm.
318 Yet, storm petrel chicks are reported to wander up to 1 m far in their usual exploratory activity
319 around the nest (Mínguez 1997), suggesting that additional cues are probably involved in chicks’
320 homing. Likewise, in adults’ homing other cues appear to have a greater importance than olfaction.

In addition, the discrepancy between our and previous results may reflect a different response to odours by chicks and adults. An age-dependence in odour responsiveness has already been proposed for this species concerning personal odours (Bonadonna and Sanz-Aguilar 2012). In fact, an opposite response to personal odours has been recorded in Mediterranean storm petrels, in which chicks appear attracted by self-related odours (de Léon et al. 2003) while adults avoid them (Bonadonna and Sanz-Aguilar 2012). This attraction to related conspecific odours has been observed in several sexually immature animals, including both birds and mammals (Hepper 1987, Todrank et al. 2005, Krause et al. 2012). On the contrary, studies carried out on different petrel species investigating the response to personal odours in sexually mature individuals evidence an opposite behaviour, i.e. an attraction towards non-related individuals (Bonadonna and Nevitt 2004, Mardon and Bonadonna 2009). Indeed, as for the response to related conspecific's odours, Mediterranean storm petrel adults may exhibit a different behaviour than the chicks in the use of olfactory cues to relocate the nest.

Personal odours of the individuals occupying the nest appear to be the chemical cue employed in nest recognition (Bonadonna et al. 2003b, Bonadonna et al. 2004). In particular, species in which olfaction plays a crucial role in homing, i.e. Blue petrels (*Halobaena caerulea*) and Antarctic prions (*Pachyptila desolata*), show a behavioural attraction to the odour of the partner while they tend to avoid their own (Bonadonna and Nevitt 2004, Mardon and Bonadonna 2009), suggesting that olfactory recognition of the burrow is based on the recognition of the partner's odour. Breeding adults of Mediterranean storm petrel have never been tested for the response to their own odour, but they avoid the odour of kin-related individuals (Bonadonna and Sanz-Aguilar 2012), which appear to be similar to the own odour (Célérier et al. 2011). So, as for other species, they probably do not rely on their own odour to recognize the nest. However, for them, the recognition of the partner's odour might not be a good strategy either. Like other petrels, Mediterranean storm petrels form long lasting pair bonds, and the same partners nest together year after year. However, petrel species with lower survival rates, i.e. smaller species, show lower levels of fidelity than other species. Such populations have a higher proportion of widowed individuals, which may induce the forming of new

pairs either because of the absence of the usual partner or because widowers may be attractive as potential mates for individuals involved in suboptimal mating, increasing the incidence of divorces (Bried et al. 2003). In Benidorm, during the two years of our experiment, we observed average partner fidelity of only 76.8% (similar to that calculated in the 1993-2011 period. Sanz-Aguilar, n.d.), which is lower than any of the species tested in a previous study on mate fidelity in petrels (Bried et al. 2003). As a consequence, the use of the partner's odour to recognize the nest would require the learning of different partners' odours and the cognitive capability to frequently update the target odour. The use of the partner's odour to recognize the nest might be a costly strategy, and not the most efficient one for nest discrimination.

Mediterranean storm petrels may, therefore, disregard olfactory information in favour of more constant and reliable cues. For instance, the topographic features of the cave remain constant in space and time and they could serve as landmarks to relocate the nest crevice. To understand how these birds find their nest, we observed the behaviour of homing storm petrels at night with infrared binoculars. The typical hovering behaviour of homing petrels (Grubb 1974) was observed only outside the cave 2 and in the cave entrance of cave 1, where the cave vault is high enough to allow such flights and the lights of the city of Benidorm just in front (less than 4 km away) illuminate the cave. Once storm petrels have chosen the direction to the nest in cave 1 or entered in cave 2, birds were observed either walking or pattering on the ground, flapping in the typical storm petrel flying mode, hopping and regularly touching the ground until landing in front of the nest and then walking in. In cave 1, storm petrels often landed on some rock and disappeared walking between the rocks toward the nesting crevice or burrow, located at different depths. This observed behaviour may allow the formulation of a new hypothesis of an orientation strategy analogous to that observed and studied in blind people, who use locomotion to explore the environment and are able to integrate spatial information linking the tactile experience to their movements (for a review, see Ungar 2000). Similarly, storm petrels might locate nest position by a combination of tactile and proprioceptive cues in the dark, by pattering on the rocks and walking between them, after identifying the correct

area within the colony. Some specifically designed experiments to test such hypothesis would be of great interest.

Finally, our results cannot exclude some use of visual cues. Behavioural experiments supported an influence of vision in the homing process in Manx shearwater (*Puffinus puffinus*; Brooke 1978, James 1986); and Leach's storm petrel (*Oceanodroma leucorhoa*) seems to have sufficient visual capabilities for prey seizing on moon-lit nights (Mitkus et al. 2014). Especially in cave 1, which is in front of the city of Benidorm, some light is available which could be comparable to a full moon and allow the visual perception of at least shapes and shadows. Inside a cave, the presence of the cave vault and of other obstacles, i.e. rocks, may have provided the evolutionary pressure to (at least partially) night vision to avoid collisions. On this subject, specific studies would be necessary to definitely ascertain or rule out a possible use of visual cues.

In conclusion, our study is the first that specifically address the question of which cues are used for nest finding after migration, evidencing that Mediterranean storm petrels breeding in a cave rely on positional cues other than olfactory to home. This result provides an interesting piece in the understanding of chemical and sensory ecology in petrels, and probably in birds in general. The use and the importance of the sense of smell in many bird species is now acknowledged, however it is still poorly understood what avian olfaction is used for and in which situations it becomes a critical sense. Interestingly, Mediterranean storm petrels are known to respond to a variety of odours, and yet here we found that they did not use their sense of smell. This highlights for the first time that we must not only think about whether a certain species overall uses the sense of smell or not, but rather how their ecology shapes the circumstances in which olfactory cues are used. Our study reflects that space perception and the solution of spatial tasks depend upon a fusion of stimuli coming from different sensory systems. Vision and olfaction are only two of these senses and their use, fundamental under some ecological circumstances, is denied in others, when other cues become more profitable. This finding also highlights that it is not possible to establish the sensory ability of

birds irrespective of the adaptive forces that may shape these abilities, a fundamental point to correctly interpret results from future studies.

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TABLES AND FIGURES

Table 1. Variables and levels of the Multiple Correspondence Analysis (MCA)

Variable	Levels	Notes
Experimental condition (EC)	Control (C) Short-distance (SD) Long-distance (LD)	Unmoved nestbox Nestbox displaced on a short distance Nestbox displaced on a long distance
Nest choice (nest)	Same Own Other New	Same nestbox and same position of previous breeding Same nestbox in another position than previous breeding Same position but other nestbox than previous breeding New nestbox in a new position than previous breeding
Partner	Same New Unknown (uk)	Same partner as previous breeding Different partner than previous breeding Unknown partner
Sex	Male (M) Female (F)	
Sabbatical (sabb)	Yes No	Individuals skipping one breeding season Individuals breeding in consecutive years

Abbreviations in as in figure 3.

Table 2. Number of birds recaptured in the 3 experimental conditions and nestbox of recapture

Nest of recapture	Experimental Condition		
	C	SD	LD
2012			
Previous	26+4*	4	0
Different	2	15	8+6*
2013			
Previous	28+2*	1	0
Different	0	11	13

*Individuals recaptured after a sabbatical year (i.e. during the breeding season 2013 for the first experimental year and in 2014 for the second). C: control-unmoved nestboxes; SD: short-distance displaced nestboxes; LD: long-distance displaced nestboxes; Previous: nestbox occupied the previous year; Different: a different nestbox than that occupied the previous year.

Figure 2. The Y-maze. Lower part: starting arm. Upper part: the choice arms connected to nestboxes. The fans providing controlled airflow in the choice arms are placed at the intersection between the tubes leading to the nestboxes and the arms. The battery supplying the fans is placed behind the box supporting the maze and is not visible.

Figure 3. Multiple correspondence analysis. Projection of the variables on the first two dimensions with the eigenvalues (lambda) for the a) first (2011-2012) and b) second (2012-2013) experimental years. EC: Experimental Condition (C: Control; SD: Short Distance; LD: Long Distance); nest: nest choice (same: same nest-same position (nests non-displaced); own: same nest-other position; other: other nest-same position; new: new nest and new position); partner: partner choice (same: same partner as the previous year; new: new partner; uk: unknown, partner non-recaptured); sabb: sabbatical the previous year (yes; no); sex (M: male; F: female). Some vector labels are overlapped due to data distribution and not visible: EC.C is hidden behind nest.same in both figures; such overlap is complete in (b) due to a 100% correspondence between these two variable levels. In (b), sex.F is partially hidden behind sabb.no. A detailed description of the figure, the association between variables and axes and respective correlation values is provided in the appendix.

Figure 4. Nest choice in the Y-maze. The histogram shows the percentage of storm petrels choosing the own or the conspecific (other) nest in the Y-maze, as well as birds that made no choice (N=53). The proportion of birds choosing the own or the other nest was not significantly different (Two tailed binomial test: $N = 38$, $P = 0.42$).

Figure A1. Annual return rates. The graph evidences that the return rate (i.e. the proportion of birds captured in a given year and recaptured the following year) is relatively constant throughout the years (x axis), and higher in the nest-boxes than in natural nests. The average return rate in the nest-boxes in the decade preceding our experiment (2001-2010) was 77%. In the two experimental years, our recapture rates were of 71 and 79%, respectively, showing that the overall return rate was not different from previous years and that our experiment did not have an impact on the birds' return to nest-boxes.

Figure A2. Pattern of nest fidelity. The graph illustrates the high nest fidelity for nest-boxes and natural nests throughout the years (x axis). In the nest-boxes, in the 2001-2010 period, the average nest fidelity (i.e. the proportion of recaptured birds found nesting in the same nest as the previous year) was 96%, highlighting that storm petrels return to nest in the same nest-box year after year. Such pattern was maintained during our experiment in control nests, for which nest fidelity was 93% and 100% in the two experimental years, but completely disrupted in displaced nests. When the nest-boxes where moved, only 15% of birds the first year and 4% the second continued to nest in the nest-box previously occupied. Because of the manipulation of the colony, nest fidelity of nest-boxes in the experimental years is not showed.

APPENDIX

Detailed description of the Multiple Correspondence Analysis results

Multiple correspondence analysis gave similar results in the two experimental years. The first 2 factorial axes of the MCA explained 80.6% of the total variation in 2012, and 79% in 2013. The eigenvalues of the MCA for both years suggested that two main factors, F1 and F2, were important to the structure of the dataset. The first axis F1, the horizontal one, was highly correlated with the nest choice and the experimental condition, which had correlation values of 0.8 and 0.91, respectively, in 2012 and of 0.946 and 0.902 in 2013. The second axis F2, the vertical one, was also correlated to the nest choice (0.62 in 2012 and 0.52 in 2013) and the experimental condition (0.77 in 2012 and 0.52 in 2013). To a lesser extent, the second axis was also correlated to the partner (0.41 in 2012 and 0.37 in 2013). Figure 3 in the main text illustrates the association between each variable on both axes. In both years, on the first axis, the control condition (EC.C) is strongly correlated to the nesting in the same nest-box and location (nest.same). This association is even stronger in 2013 (Fig. 3b) in which 100% of control birds nested in the same nest and the two variables are perfectly superposed on the graph. Again in both years, nesting in a completely new nest (nest.new) is associated with the breeding with a new partner (partner.new). In 2012, we observe an association between the individuals nesting in their own nest-boxes but in a different location (nest.own) and the experimental condition with nests displaced at short distance (EC.SD. Fig. 3a). In 2013, on the second axis, nesting in the same location but in another nest (nest.other) is associated with the experimental condition in which nest-boxes were displaced at a long distance (EC.LD). Again in 2013, the variable nest choice for individuals nesting in their own nest-box displaced (nest.own) seems to be strongly correlated to axis F2; however, this last result must be carefully interpreted. In fact, only one individual in 2013 was captured in its own nest-box after this was displaced, so the length of the vector may be biased (Fig. 3b).