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

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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 well-used artificial nestboxes that has been studied for the past two decades. 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 nestbox located at the same position as the year before, regardless of whether the nestbox was 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 than olfactory ones to home and suggests a mechanism combining tactile and proprioceptive cues to find the nest in the dark.

Procellariiform seabirds are renowned among birds for their stunning olfactory capabilities, which play a vital role in their lives. Many petrel species use their sense of smell to locate foraging areas over the ocean surface (i.e. Dell'Ariccia et al., 2014; Grubb, 1972; Hutchison & Wenzel, 1980; Nevitt, 2000), for oceanic navigation (Gagliardo et al., 2013), to recognize their partner (Bonadonna & Nevitt, 2004) and, probably, to avoid inbreeding during mate selection (Bonadonna & 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, in tests, burrowing petrel species showed they needed the sense of olfaction to home at night (Bonadonna & Bretagnolle, 2002; Bonadonna, Cunningham, Jouventin, Hesters, & Nevitt, 2003; Bonadonna, Hesters, & Jouventin, 2003; Bonadonna, Villafane, Bajzak, & Jouventin, 2004; Dell'Ariccia & 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 1 year of absence. During breeding, when the nests are occupied by an incubating adult or, later, visited to feed the chick, nest recognition is by olfactory cues. In fact, individuals are attracted by the odour of their own nest (Bonadonna, Cunningham, et al., 2003; Bonadonna et al., 2004), and when nocturnal petrels are deprived of their smelling capabilities, their homing ability is strongly impaired or absent (Bonadonna & Bretagnolle, 2002; Bonadonna, Hesters, et al., 2003; Bonadonna, Spaggiari, & Weimerskirch, 2001; Dell'Ariccia & Bonadonna, 2013). However, studies specifically aimed at

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investigating 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'Ariccia et al., 2014). Finally, besides the importance of species ecology, the response to odours has been suggested to be also age dependent (Bonadonna & Sanz-Aguilar, 2012). In fact, in species tested for the response to personal odours, chicks appear to be attracted by self-odours (de Léon, Mínguez, & Belliure, 2003) whereas adults avoid their own smell as well as that of kin (Bonadonna & Nevitt, 2004; Bonadonna & Sanz-Aguilar, 2012; Mardon & Bonadonna, 2009).

In this study, we investigated whether the Mediterranean storm petrel, *Hydrobates pelagicus melitensis* employs olfactory or other positional cues to locate the home nest after the winter migration. Several species of storm petrels are sensitive to and use a large variety of odour cues (Bonadonna & Sanz-Aguilar, 2012; Dell'Ariccia et al., 2014; Grubb, 1973, 1974). 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 for exploring 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 tree roots, the Mediterranean storm petrel has the ecological peculiarity of breeding also inside caves (Brooke, 2004; del Hoyo, Elliott, & Sargatal, 1992). Breeding in caves can provide supplemental cues or modify cues used to home, as observed for other petrel species (i.e. hypogean versus superficial nesters).

For our study, we selected the breeding colony on Benidorm island. This colony has been the subject of a detailed and long-term population survey. Since 1993, breeding adults and their chicks have been ringed in their nests, which allows a thorough understanding of individual histories, pair members, nest occupancy and breeding success over the years (Sanz-Aguilar et al., 2009, 2010). In 1996, the colony was provided with artificial nestboxes to increase nest sites. Nestboxes have been widely adopted by breeding storm petrels in all these years (de Léon & 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. If other positional cues play a major role in nest location, however, storm petrels would breed in the nestbox located at the original location, regardless of whether 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 inside two 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 2) houses around 100 pairs (Sanz-Aguilar et al., 2009, 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 six in cave 1 were occupied (for details on nestboxes, occupancy rates and nesting success see de Léon & Mínguez, 2003; Libois et al., 2012).

Experiment 1: Nestbox 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, i.e. two adjacent boxes were simply inverted in their respective positions (mean ± SEM = 25 ± 5 cm). Ten other nestboxes were displaced over a long distance (248 ± 67 cm). Finally, 19 boxes remained untouched and used as controls (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 if they were unknown individuals. All natural nests were also checked during the normal population survey (Sanz-Aguilar et al., 2009, 2010), so that we could find 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

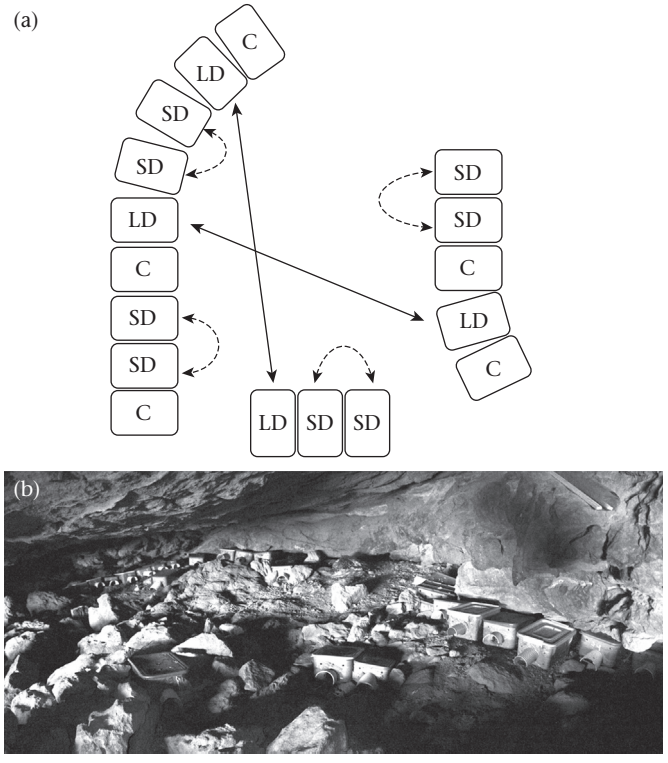

Figure 1. (a) Outline of nestboxes' displacements within the colony and (b) image of the nestboxes in the colony (cave 2). Arrows exemplify nest displacements: plain arrows are long-distance displaced nestboxes (LD), dashed arrows short-distance displaced nestboxes (SD) and C control, unmoved nestboxes.