

COULD OSMOTAXIS EXPLAIN THE ABILITY OF BLUE PETRELS TO RETURN TO THEIR BURROWS AT NIGHT?

FRANCESCO BONADONNA*, JÉRÔME SPAGGIARI AND HENRI WEIMERSKIRCH

Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique, F-79360 Villiers en Bois, France

*e-mail: bonado@cebc.cnrs.fr

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Summary

Like many other species of petrel, blue petrel (*Halobaena caerulea*) are able to return to their nest burrows at night in complete darkness. Since petrels have a well-developed olfactory system, we carried out an experiment to test whether blue petrels use olfaction to localise their nest burrows. Incubating birds were injected intranasally with a zinc sulphate solution, which reversibly impairs the sensitivity of the olfactory mucosa; control birds were

treated with physiological saline solution. None of the anosmic birds returned to their burrows, whereas all the birds treated with saline solution did. Our results suggest that olfactory cues are necessary for blue petrels to find their burrows.

Key words: homing, orientation, olfaction, blue petrel, *Halobaena caerulea*, zinc sulphate, anosmia, Kerguelen archipelago.

Introduction

Most petrels nest in crowded colonies and return to their nest burrows at night, often when light intensity is reduced by clouds and fog or on moonless nights when it is completely dark (Warham, 1990; Mougeot and Bretagnolle, 2000). This raises the question of what cues these birds use to locate first the colony and then their own burrow.

A number of cues may be important. Visual cues, echolocation, calls from the burrow and olfaction have all been suggested (Grubb, 1974). In recent years, it has been shown that olfaction plays a role in pigeon navigation (for references, see Papi, 1992; Roper, 1999), and it is implicated in homing for two other species of bird, swifts *Apus apus* (Fiaschi et al., 1974) and European starlings *Sturnus vulgaris* (Wallraff and Hund, 1982; Wallraff et al., 1995). Thus, it is reasonable to suppose that olfaction could be involved in homing processes in other species of bird. Olfaction as a mechanism for homing makes intuitive sense in procellariiforms because they possess a well-developed olfactory system (Bang, 1966; Bang, 1971; Bang and Wenzel, 1985; Healy and Guilford, 1990). Furthermore, it has been found that different species of petrel can respond to food-related odour cues (Jouventin, 1977; Jouventin and Robin, 1984; Lequette et al., 1989; Verheyden and Jouventin, 1994; Nevitt et al., 1995; Nevitt, 1999a).

Surprisingly, only a relatively small number of studies have investigated the role of olfaction in locating nest burrows (Table 1). The results of these studies clearly suggest the use of olfaction for homing only for species of the Hydrobatidae (storm petrels) family (Grubb, 1973; Grubb, 1974; Minguez, 1997). Storm petrels are known to respond to food-related odours, implying that these birds might use large-scale odour

cues to locate foraging areas (Nevitt et al., 1995). Grubb (Grubb, 1974) tested the olfactory homing hypothesis on Leach's storm petrel, *Oceanodroma leucorhoa*, using olfactory nerve section, plugged nostrils and Y-maze experiments. His findings strongly support the use of olfactory cues in homing processes in this species. Working on the British storm petrel *Hydrobates pelagicus*, Minguez (Minguez, 1997) suggested an olfactory homing ability in chicks exploring the immediate confines of the nest site. Little information is available on the use of olfaction for homing in the other families of petrel, although several species are known to use olfaction as a foraging cue (Jouventin, 1977; Jouventin and Robin, 1984; Lequette et al., 1989; Verheyden and Jouventin, 1994; Nevitt et al., 1995; Nevitt, 1999a). Shalleberger (Shalleberger, 1975) found that sectioning the olfactory nerves of wedge-tailed shearwaters, *Puffinus pacificus*, did not prevent the birds from relocating their burrows. James (James, 1986) further demonstrated that interfering with the smell of the burrows did not affect the ability of Manx shearwaters, *Puffinus puffinus*, to locate their nests. These studies used highly invasive techniques, probably resulting in high stress levels for the birds, or the strong manipulations of the nest sites, which could disrupt not only the cue under investigation but also several others. However, working on Cory's shearwater, *Calonectris diomedea*, Benvenuti and co-workers (Benvenuti et al., 1993) used zinc-sulphate-induced anosmia, a non-invasive chemical technique, to produce a reversible impairment of the olfactory mucosa. Their results provided evidence that Cory's shearwaters used olfaction to find their burrows.

The blue petrel *Halobaena caerulea* is a small burrowing

Table 1. Summary of the results of burrow-homing experiments on petrels

Reference	Species (family)	Olfactory effect	Technique employed
Grubb (1974)	<i>Oceanodroma leucorhoa</i> (Hydrobatidae)	Yes	Nerve section, sealed nostrils, Y-maze
Shallemberger (1975)	<i>Puffinus pacificus</i> (Procellariidae)	No	Nerve section
James (1986)	<i>Puffinus puffinus</i> (Procellariidae)	No	Nest manipulation
Benvenuti et al. (1993)	<i>Calonectris diomedea</i> (Procellariidae)	Yes	ZnSO ₄ -induced anosmia
Minguez (1997)	<i>Hydrobates pelagicus</i> (Hydrobatidae) (chicks)	Yes	Sealed nostrils, T-maze

petrel breeding in circumpolar Antarctic zones (Warham, 1990). These birds nest in large crowded colonies, often in mixed colonies with other burrowing petrel species (Jouventin et al., 1984; Jouventin et al., 1985; Fugler et al., 1987), and their activity on land is strictly nocturnal. Blue petrels tend to avoid moonlit nights in approaching the colony to elude predation risks (Mougeot and Bretagnolle, 2000), which suggests that vision cannot be the only cue they use for precise location of the burrow entrance. Blue petrels are thus a good candidate for evaluating the use of olfactory cues in locating their burrows.

Our aim in this study was to investigate whether blue petrels depend on olfaction to find their own burrows (short-range homing). To do this, we conducted a controlled experiment in which some birds were deprived of their sense of smell using zinc sulphate solution, and the homing abilities of this group were compared with those of a sham-manipulated group.

Materials and methods

Preliminary tests

The method of olfactory deprivation using a zinc sulphate solution has been successfully used on homing pigeon by several groups (Benvenuti et al., 1992; Benvenuti and Gagliardo, 1996; Bingman and Benvenuti, 1996; Bingman et al., 1998; Guilford et al., 1998). The method involves irrigating the olfactory mucosa with a solution of zinc sulphate heptahydrate (ZnSO₄·7H₂O). This solution is injected into the choanae using a short curved needle. This treatment produces only a temporary and variable impairment of the olfactory sense (for references, see Cancalon, 1982). However, Benvenuti and co-workers (Benvenuti et al., 1993) found that choanal injection was ineffective in the case of Cory's shearwaters and suggested injecting zinc sulphate directly into the nostrils.

To verify which method would be the most appropriate for our study and to find the correct shape for the curved needle, we performed a series of preliminary tests on blue petrels that had been killed by skuas, *Catharacta skua lönnbergi*. The petrels were collected at Kerguelen Islands (southern Indian Ocean) during austral summer 1997/1998, injected with a Methylene Blue solution, and the etmoidal region inspected surgically (Benvenuti et al., 1993). It was observed that the coloured liquid entered the nasal conchae and reached the olfactory mucosa only if injections were made directly into the

nostrils of the birds. A 40 mm long needle was than shaped to fit to the pathway between the nostrils and the nasal conchae, thus ensuring effective perfusion of the mucosa during the field experiments.

Study site and birds

The experiment took place in November 1999, during the egg incubation period of blue petrels, on Mayes Island (49°28'S, 69°57'E) in the Kerguelen archipelago, where more than 100 000 pairs of blue petrels breed. Parent birds alternate at the nest, with shifts lasting 8–12 days, and eggs can be temporarily abandoned (Chaurand and Weimerskirch, 1994). Birds spend the day foraging at sea or incubating in the burrow, and foragers only return to the burrow after complete darkness has fallen (Mougeot and Bretagnolle, 2000).

Several nests were inspected, and 12 incubating birds whose mass was similar to the mass at the start of an incubating shift (calculated by Chaurand and Weimerskirch, 1994) were chosen. Heavy birds were selected since they were likely to be strongly motivated to home to their burrow after release. The birds were banded for individual identification and weighed. Birds were then assigned randomly to the experimental ($N=6$) or control ($N=6$) group. Burrows were fitted with a window over the incubating chamber to facilitate recapture during the experiment.

The decision to use a small number of animals was made for ethical reasons: in the case of a positive response to the use of olfactory cues, experimental birds would not return home for several days after their release (until their olfactory perception regained a minimal functional level), thereby affecting their breeding success for the year.

Bird treatment and releases

Not all the birds were released on the same night since not all the burrows were found at the same time, but for each release equal numbers of control and experimental birds were used (see Table 2). Treatments were carried out in the early morning. Experimental birds were captured, weighed and injected with 4 ml of zinc sulphate solution in water (4% w/v) into each nostril, using the prepared curved needle. Birds were held by keeping the bill open and towards the ground to allow the solution to flow out from the choanae. Control birds received the same treatment, but the zinc sulphate solution was replaced with a physiological saline solution. After treatment, the bird was placed in an individual cloth bag and held there for 20–30 min in the dark to let them recover from the stress

of the manipulation. Birds were then returned to their own burrows through the normal burrow entrance.

The releases were performed during the night following the treatment, 1 h after complete darkness. In this way, we could eliminate subjects with a low motivation to return home since the birds had sufficient time to abandon their nest in response to any excessive stress due to the manipulation. Animals were taken from their burrows and transported in tissue bags from the colony to the sea-shore approximately 100 m from the nest. They were then released towards the sea in the flow of birds that were commuting between the sea and the colony. This protocol was chosen rather than releasing the birds on the ground in the colony since blue petrels suffer heavy predation from skuas that can kill them in the colony at night (Mougeot et al., 1998). Moreover, these birds normally fly until in close proximity to the burrow entrance and thus searching for a nest whilst walking on the ground is not a normal activity.

The morning after the release, and over subsequent days, the burrows were checked for the presence of birds and the mass of returned birds was recorded. All burrows were monitored for at least three mornings following the release, until our departure from the study site (on 9 November). Throughout the study period, the colony and the skuas that nested in proximity to the colony were checked for ringed carcasses.

Statistical methods

Differences in the homing performances between control and experimental birds were tested using a one-tailed (predicting lower homing success in anosmic birds) Fisher's exact test. A Mann-Whitney *U*-test was used to compare the masses of the two groups of birds upon return (Siegel, 1956).

Results

On the night of the release, six experimental birds and five

control birds were found in the burrows, one control bird having abandoned its burrow. Each individual was incubating its egg and exhibiting normal behaviour indistinguishable from that of unmanipulated birds. The mass of birds at the release is given in Table 2; the mean mass of the experimental group was 201.6 ± 11.4 g ($N=6$) and that of the control group was 200.8 ± 8.1 g ($N=6$; means \pm s.d.). A Mann-Whitney *U*-test showed no difference in mass between the two groups ($U=18.5$, $N_1=6$, $N_2=6$, not significant). Upon release, all birds flew towards the open sea and vanished from sight in a few seconds.

On the morning following the release, three of the five control birds and none of the six experimental birds had returned home during the night (one-tailed Fisher's exact test, $P<0.05$). Two more control birds were found in the burrow on the second morning after release. In contrast, none of the experimental birds returned, nor were any found dead in the colony. The mass of birds upon their return was in all cases lower than the mass at release (Table 2).

Discussion

Ethical reasons limited the sample size in our experiment, but the results are sufficiently clear to show that the use of olfaction is critical for blue petrels to locate their own burrow. To date, the evidence for the use of olfactory cues for homing tasks in petrels was limited to species belonging to the Hydrobatidae family (Grubb, 1974; Minguéz, 1997), in which olfaction probably plays an important role in locating feeding zones at sea (Nevitt et al., 1995). Although the results of homing studies in other species are more controversial, other petrel species respond to food-related odour cues, indicating the importance of olfaction in their biology. In particular, Nevitt (Nevitt, 2000) correlated the presence of flocks of blue petrels with naturally elevated dimethyl sulphide levels at sea.

Table 2. Measurements of mass and homing results following release of $ZnSO_4$ -treated (experimental) and saline-treated (control) blue petrels

	Bird	Release date	Mass at release (g)	Mass at return (g)	Day						
					0	1	2	3	4	5	6
Experimental group	1	2/12/99	201	•	–	–	–	–	–	–	–
	2	3/12/99	199	•	–	–	–	–	–	–	NR
	3	4/12/99	218	•	–	–	–	–	–	NR	NR
	4	5/12/99	212	•	–	–	–	–	NR	NR	NR
	5	6/12/99	190	•	–	–	–	NR	NR	NR	NR
	6	6/12/99	190	•	–	–	–	NR	NR	NR	NR
Control group	7	4/12/99	195	194	+	+	+	+	Des	NR	NR
	8	2/12/99	201	189	+	+	+	Des	NR	NR	NR
	9	5/12/99	213	204	–	+	–	+	NR	NR	NR
	10	6/12/99	196	181	–	+	+	NR	NR	NR	NR
	11	6/12/99	208	203	+	+	+	NR	NR	NR	NR

+, present; –, absent; Des, deserted nest; NR, not recorded.

One control bird (bird 12) abandoned its burrow before the release.

Individual nest site recognition in burrowing birds could also involve auditory cues, such as the song of their partner or recognition of the voice of their chick calling from the burrow. In blue petrels, egg desertions lasting 1–2 day have been observed under normal conditions; frequently, the incubating bird departs without waiting for the partner to change over because energy reserves have become depleted (Chaurand and Weimerskirch, 1994). In this case, incoming birds have to locate their empty nest. Thus, the experimental task imposed on the birds in our study is a problem that blue petrels must normally confront.

Laboratory experiments on wild birds, such as carrying out Y-maze tests, is a difficult task since the stress imposed on the animals often produces a large number of birds that fail to respond to the test (Grubb, 1974). It is, therefore, preferable to carry out field experiments involving manipulation of the senses of the animals or of the odour coming from the nest. The latter possibility is difficult to realise since we do not know what kind of odour signal the birds rely on and, consequently, we cannot be sure of totally obstructing their perception of the appropriate odour. Olfaction can also be impaired by sealing the nostrils or by olfactory nerve section (Grubb, 1974; Shalleberger, 1975). In the first case, birds can still perceive odours through the choanae; the second technique is highly invasive and can stress the animals, thus giving a non-specific effect.

We used a non-invasive chemical technique that has been demonstrated to be effective on other birds (Benvenuti et al., 1992; Benvenuti et al., 1993; Benvenuti and Gagliardo, 1996; Bingman and Benvenuti, 1996; Bingman et al., 1998; Guilford et al., 1998) to impair the olfactory sense of blue petrels. This technique produces a temporary anosmia while leaving the anatomy of the birds intact; animals can breathe freely through their nostrils and are not subjected to a surgical operation. Thus, the stress to which birds are subjected during and after manipulation is reduced. The experimental protocol used in our work ensured that the birds studied were highly motivated since they were at the beginning of their incubation period and were given the opportunity to abandon their nest before release. The fact that one control bird abandoned its burrow before release suggests that some birds might become less motivated to return home after handling. Such a difference in motivation could result in a non-specific effect influencing the results.

After they had been released, birds flew towards the sea, but the fact that all birds showed a decrease in their mass when they returned indicated that the manipulated birds had not foraged but had remained at sea in the vicinity of the colony. Blue petrels are known to forage at a distance from the colony and never close to shore. The negligible distance between the release site and the colony excludes the involvement of mechanisms to localise the colony site, focusing instead on the task of finding the burrow.

The results of this study support previous work proposing that birds use olfactory cues to identify their nesting burrows (Grubb, 1974; Benvenuti et al., 1993; Minguéz, 1997).

However, two authors have contested this possibility. Shalleberger (Shalleberger, 1975) concluded that olfactory ability is not critical for successful burrow-homing in wedge-tailed shearwaters, although just three out of 12 experimental birds with sectioned olfactory nerves were able to home compared with seven out of 10 sham-operated birds (one-tailed Fisher exact test, $P < 0.05$). James (James, 1986) rejected the olfactory hypothesis and proposed visual guidance as a leading cue for burrow-homing in Manx shearwaters, but anatomical studies had convinced Lockie (Lockie, 1952) that the eyes of this shearwater are not dark-adaptable. Moreover, the visual disturbance created in the experiments of James (James, 1986) apparently failed to prevent the birds from locating their burrows, and the manipulation he used to block out the nest scent may not have masked the natural olfactory signature the birds used for orientation to their nests. These authors criticise previous studies but conclude that, under different conditions of illumination, petrels could show an evolutionary divergence in their homing mechanism. It is curious in our opinion, that birds with a highly developed olfactory system (Bang, 1966; Bang, 1971; Bang and Wenzel, 1985; Healy and Guilford, 1990) and eyes that are not highly adapted for nocturnal vision (for references, see Warham, 1996) should use visual guidance in some cases and olfactory mechanisms in others.

So far, the only model proposed for olfactory homing in birds is that suggested for pigeons, in which the olfactory theories of navigation postulate the existence of an odour-based map sense (for references, see Papi, 1992; Roper, 1999). We do not think that our results with blue petrels can be interpreted in relation to this model, although a similar process could be proposed for navigation at sea (Nevitt, 1999b). We believe that the mechanism involved in this short-range homing is osmotaxis, which requires a direct sensory (in our case olfactory) contact with the goal. Birds could approach the colony smelling the colony odour, land in the proximity of their burrow led by their own nest odour, and search using olfaction for its entrance. Grubb (Grubb, 1973; Grubb, 1974) observed a similar behavioural sequence for Leach's storm petrels. Incoming petrels attracted to a different area of the colony by material collected in the burrows (Grubb, 1973) were observed to perform hovering flights over the vicinity of their burrow and preferred nest material in a Y-maze test (Grubb, 1974).

It has been reported that several procellariiforms are able to home after active or passive displacement over hundreds or thousands of kilometres (for references, see Warham, 1996), although it is still a major problem to identify which senses may be involved in this task. Our findings, together with those of other groups on localising food (Jouventin, 1977; Jouventin and Robin, 1984; Lequette et al., 1989; Verheyden and Jouventin, 1994; Nevitt et al., 1995; Nevitt, 1999a; Nevitt, 2000) and burrows (Grubb, 1973; Grubb, 1974; Benvenuti et al., 1993; Minguéz, 1997), further suggest the importance of the olfactory sense in this order of birds and suggest that olfactory navigation could be an important homing mechanism for these animals.

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