

Evidence for nest-odour recognition in two species of diving petrel

Francesco Bonadonna^{1,*}, Gregory B. Cunningham², Pierre Jouventin¹, Florence Hesters¹ and Gabrielle A. Nevitt²

¹*Behavioural Ecology Group, Centre d'Ecologie fonctionnelle et Evolutive, CNRS, F-34293 Montpellier Cedex 5, France* and ²*Center for Animal Behavior and the Department of Neurobiology, Physiology and Behaviour, University of California, One Shields Avenue, Davis, CA 95616, USA*

*Author for correspondence (e-mail: bonadonna@cefe.cnrs-mop.fr)

Accepted 17 July 2003

Summary

In nearly every procellariiform species, the sense of smell appears to be highly adapted for foraging at sea, but the sense of smell among the diving petrels is enigmatic. These birds forage at considerable depth and are not attracted to odour cues at sea. However, several procellariiform species have recently been shown to relocate their nesting burrows by scent, suggesting that these birds use an olfactory signature to identify the home burrow. We wanted to know whether diving petrels use smell in this way. We tested the common diving petrel *Pelecanoides urinatrix* and the South-Georgian diving petrel *Pelecanoides georgicus* to determine whether diving petrels were able to recognise their burrow by scent alone. To verify the efficacy of the method, we also tested a bird that is known to use olfaction for foraging and nest

recognition, the thin-billed prion *Pachyptila belcheri*. In two-choice T-maze trials, we found that, for all species, individuals significantly preferred the odour of their own nest material to that of a conspecific. Our findings strongly suggest that an individual-specific odour provides an olfactory signature that allows burrowing petrels to recognize their own burrow. Since this ability seems to be well developed in diving petrels, our data further implicate a novel adaptation for olfaction in these two species that have been presumed to lack a well-developed sense of smell.

Key words: homing, orientation, olfaction, petrel, *Pelecanoides urinatrix*, *Pelecanoides georgicus*, olfactory recognition, Kerguelen archipelago.

Introduction

In procellariiformes, olfaction is used in two different ways: to help birds locate prey items and to help birds locate their nesting sites. At-sea experiments have demonstrated that these seabirds are attracted to prey-related odours such as krill and cod liver oil (Grubb, 1972; Verheyden and Jouventin, 1994; Lequette et al., 1989; Hutchison and Wenzel, 1980). Smaller procellariiformes, such as petrels and prions (Procellariidae), are also attracted to dimethyl sulphide (Nevitt et al., 1995; Nevitt and Haberman, 2003), a compound associated with primary production in the ocean (reviewed in Nevitt, 2000). Procellariiformes use their sense of smell to help locate dense regions of prey within productive areas of the ocean.

Odours emanating from the burrow help birds locate the nest site when returning under the cover of darkness. Arriving at night is critical to a bird's survival since burrow-nesting petrels tend to be small and susceptible to predation by skuas (*Catharacta skua lönnbergi*; Stercorariidae; Mougeot et al., 1998; Warham, 1996; Thoresen, 1969; Payne and Prince, 1979). Birds find their burrow at night despite poorly developed night vision (Brooke, 1989; Martin and Brooke, 1991), suggesting that cues other than those obtained visually may be important. The characteristic smell of an individual's

burrow is thought to assist returning birds in relocating their burrow quickly and efficiently among the thousands of others (Thibault and Holyoak, 1978; Warham, 1996).

The ability of individuals to recognise their burrow by smell has been established in several species of petrels, including storm petrels (Hydrobatidae), Cory's shearwaters (*Calonectris diomedea*), blue petrels (*Halobaena caerulea*) and prions (*Pachyptila* spp.) (Grubb, 1973, 1974, 1979; Benvenuti et al., 1993; Minguez, 1997; Bonadonna et al., 2001; Bonadonna and Bretagnolle, 2002). Bonadonna and Bretagnolle (2002), in particular, highlighted that species returning to colonies at night need an intact sense of smell to relocate their nest, whereas species that return during the day relocate the nest even if they are experimentally rendered anosmic. It has also been suggested that the olfactory signature of the nest is critical for nest relocation [Antarctic prion (*Pachyptila desolata*), Bonadonna et al., 2003; blue petrels (*Halobaena caerulea*), Bonadonna et al., in press). Using T-maze techniques, these studies demonstrated that birds can distinguish the odour of their own nest from that of a conspecific; however, birds fail if odours are absent or if the sense of smell is blocked. Since feathers and faeces are the primary bird-derived material found

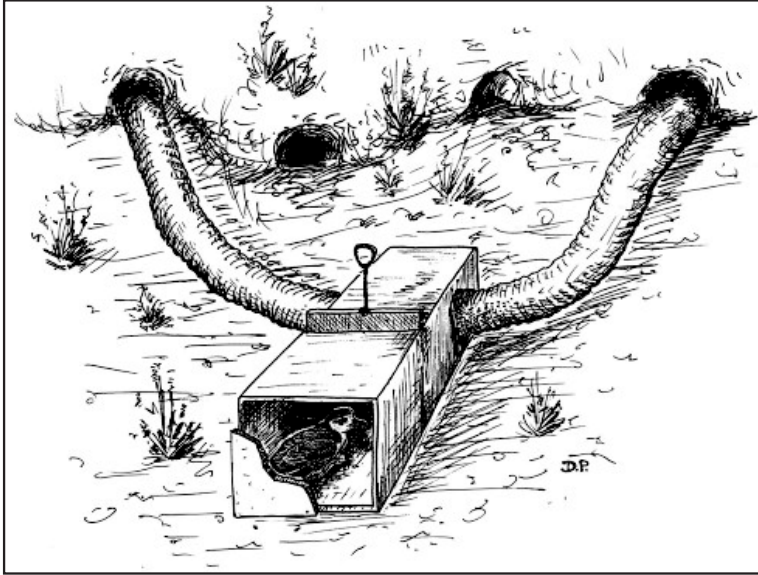


Fig. 1. Maze used to test thin-billed prions. In the case of common diving petrels, one arm of the maze was not connected directly to a burrow but contained nest material at the end. In the case of South-Georgian diving petrels, both arms of the maze were not connected to burrows and contained nest material at the end.

in the burrows, these results collectively suggest that birds recognise a burrow-specific odour for burrow recognition.

A group of burrow-nesting species that have not been studied with respect to nest recognition are the diving petrels (Pelecanoididae). Researchers have assumed that these birds have a poor sense of smell since they have relatively small olfactory bulbs compared with other procellariiformes (Bang and Cobb, 1968). Specifically, the relative olfactory bulb ratios of 18, South-Georgian diving petrels (*Pelecanoides georgicus*) and 23, common diving petrels (*Pelecanoides urinatrix*) were the smallest measured in the procellariiformes (Warham, 1996). Diving petrels also fail to recruit to prey-related odours at sea (Nevitt et al., 1995; Nevitt, 2000). Additionally, a recent study showed that 'sleeping' common diving petrel chicks do not respond to prey-related (dimethyl sulphide) and novel (phenyl ethyl alcohol) odourants, suggesting a lack of sensitivity to odourants, at least at an early age (Cunningham et al., 2003).

Our aim in the present study was to test the ability of two species of diving petrels to distinguish the odour of their own nest. An additional experiment on a species that uses olfaction both for foraging and for burrow locating was also performed for comparison.

Materials and methods

Tests took place during the birds' incubation period in the Kerguelen archipelago, southern Indian Ocean. We tested 22 common diving petrels (*Pelecanoides urinatrix* Gmelin) and eight thin-billed prions (*Pachyptila belcheri* Matthews) during December 2000 and January 2001 on Mayes Island (49°28' S, 69°57' E). 25 South-Georgian diving petrels (*Pelecanoides georgicus* Murphy and Harper) were tested in January and December 2002 on Verte Island (49°51' S, 70°05' E). The burrows of all species tested consist of an access gallery and an incubating chamber. Burrows were fitted with an access

window over the incubating chamber to facilitate capture of the bird and inspection of the nest during the experiments. When access was not needed, or during testing, this access window was closed with a rock.

In both field seasons, the maze had the same design and consisted of a box with two flexible, expandable, corrugated pipes (10 cm diameter) that were separated from the central chamber by a removable divider (Fig. 1). The first 20–30 cm of the two pipes were placed perpendicular to the box wall to reduce a possible visual effect on the choice.

Birds were captured and kept in a cloth bag during the arrangement of the maze. The subject's burrow was randomly assigned to either the left or the right arm of the maze. After the maze was set up, the bird was put in the box. Five minutes later, the divider was removed. The test ended when the bird arrived at the end of one pipe or after 15 min if the bird did not choose. The choice was assessed by the noise of the bird walking in the corrugated pipe. The time elapsing between the removal of the divider and the bird's choice was recorded. The protocol and the maze employed during the two field seasons had small differences as follows.

Mayes Island: December 2000 and January 2001

All the birds were tested while the mate was at sea to forage. The maze's central chamber was a cardboard box measuring 20 cm×40 cm×20 cm. In the case of thin-billed prions, one pipe was connected to the nest of the subject bird and the second pipe to the nest of a conspecific neighbour. The owner of the neighbouring nest was kept in a cloth bag far from the maze during the whole experiment. Consequently, both burrows were empty during the trial. In the case of common diving petrels, the second pipe was connected to a box containing material from another common diving petrel nest. This was necessary due to the difficulty of finding diving petrels' nests within a reasonable distance. The length of the two pipes was similar within each single trial and ranged between 50 cm and 130 cm depending on the position of the nests. Tests were performed in the night-time for prions and in the daytime for diving petrels. In the latter case, the apparatus was covered with a thin black blanket to keep the box and the pipes in the dark.

Verte Island: January and December 2002

All the birds were tested while the mate was at sea to forage. All tests took place at night. The maze's central chamber was a wooden box of 20 cm×47 cm×20 cm. The difficulty of finding

Table 1. Results from maze experiments on three petrel species

Species (N)	Maze's arm leading to			Binomial distribution	Choice delay time (mean \pm s.d.) (min)
	own odour	neighbour's odour	No-choice		
Common diving petrel (22)	7	0	15	$P=0.0078$	8 ± 2.7
South-Georgian diving petrel (25)	11	2	12	$P=0.011$	7 ± 4.18
Thin-billed prion (8)	7	1	0	$P=0.035$	13.6 ± 11.14

South-Georgian diving petrels' nests within a reasonable distance obliged us to modify the experimental protocol for this species. All the experiments were performed at least 4 m from the tested bird's nest, and both 30 cm-length pipes were closed at the end with a metal dish containing nest material (from the tested bird and from a conspecific neighbour).

Results

Most of the tested diving petrels did not choose an arm of the maze (up to 60% of common diving petrels and up to 48% of South-Georgian diving petrels; Table 1), whereas all of the thin-billed prions did choose. Diving petrels that did not choose were inactive after removal of the divider, remaining immobile inside the main central chamber throughout the experiment. To compare frequencies of choices between the two species of diving petrels we considered three types of choice: own nest, neighbour's nest and no-choice. We found no significant differences in the frequencies of the three choices (likelihood ratio χ^2 test, $P=0.15$). When a choice was made, both species of diving petrel preferred the arm of the maze issuing odours from their own nest (binomial test, own nest vs neighbour's nest: South-Georgian diving petrels, $P<0.05$; common diving petrels, $P<0.01$). All the tested thin-billed prions preferred the maze's arm leading to their own burrow (binomial test, own nest vs neighbour's nest, $P<0.05$).

Discussion

These data suggest that two species of diving petrels are able to recognise the scent of the home burrow. Both common diving petrels and South-Georgian diving petrels significantly preferred the arm of the maze that contained nest material from their own burrow over material from a conspecific. This is the first experimental evidence demonstrating that at least two species of diving petrels have a functioning sense of smell. We also tested thin-billed prions, a species that is attracted to food-related odours (Nevitt et al., 1995) and uses olfaction in nest recognition (Bonadonna and Bretagnolle, 2002). Our results indicate that this species also uses odours to identify the home nest.

While a significant number of diving petrels were attracted to the scent of their particular nests, many failed to choose an arm of the maze. This failure to choose may reflect that diving petrels were more stressed by the manipulation than thin-billed prions. When placed in the maze, most diving petrels tended to huddle in a corner of the central chamber without moving,

whereas prions tended to always choose an arm. We have noted similar behaviours when walking in the colony at night. When startled, diving petrels tend to freeze while thin-billed prions and other larger burrowing petrels tend to run away (F. Bonadonna, personal observation). This behaviour may reflect different adaptations to avoid predation in colonies (Mougeot et al., 1998; Thoresen, 1969; Payne and Prince, 1979). Since diving petrels are darker in colour than thin-billed prions, they may be better hidden from skuas if they remain immobile. Thus, a tendency to freeze under stressful conditions may account for the differences recorded in the percentage of no-choice between diving petrels and other burrowing petrels that have been tested in this manner (Bonadonna et al., 2003, in press).

In terms of their natural history, diving petrels may be particularly well adapted to finding their nests using their sense of smell. Diving petrels commonly feed along the outer coasts of Kerguelen Island (Bocher et al., 2000) and return to the burrow for incubating shifts or to provision chicks. Arriving at the burrow involves first locating the specific island within the bay, then the general region of the island and then the specific burrow. A returning bird could use a variety of other cues to assist with finding the burrow. These include visual, auditory and spatial cues, such as knowledge of the local topography. Although we do not know how much a bird relies upon each of these sensory modalities, we believe that olfaction plays a large role at close proximity to the burrow. Once an adult lands on the ground, they are at high risk of predation and thus it is essential to find the burrow quickly. Because survival depends on finding the burrow, diving petrels probably do not use visual cues as the primary method to locate burrows. On Mayes and Verte Islands, where the present study was conducted, for example, diving petrel burrows are often located in areas that contain large amounts of the plant *Acaena magellanica* (Rosaceae). These plants blanket the ground and cover the entrance to many burrows (F. Bonadonna, personal observation). It is unlikely that diving petrels are able to locate these burrows using visual cues, particularly since birds return to the colonies at night. Behavioural and anatomical data further suggest that these birds have relatively poor night vision (Brooke, 1989). Indeed, researchers working in the colonies at night are often hit by flying diving petrels, suggesting that diving petrels may be blind to objects even as large as humans (F. Bonadonna, personal observation).

Alternatively, returning diving petrels could use acoustic information to locate burrows, but we believe this to be unlikely. Although diving petrels are vocal in their burrows at night, it is

not known if they call to each other or if mates use calls to guide returning partners to the burrow. Furthermore, when depleted of reserves, incubating diving petrels will often leave the burrow to forage before their mate returns (Chaurand and Weimerskirch, 1994; Warham, 1996). In this case, the incoming adult must locate an empty, quiet nest. Relying solely upon acoustic information, therefore, may not allow the bird to successfully find the burrow in an efficient fashion. Additionally, since the burrows were empty during our experiments, birds could not use acoustic information to make their choices.

Another possible method for arriving at the home burrow could be the use of topological information, as suggested by Brooke (1989). Evidence from our experiment with South-Georgian diving petrels, however, suggests that they can recognize the burrow even when its location has been manipulated. In this case, birds were not being tested on their ability to return to their burrow but their ability to go towards a metal dish located away from their burrow that contained their specific burrow material. Other studies suggest that positional cues alone are not enough for a petrel to find its burrow. For example, in previous experiments, blue petrels and Antarctic prions were tested with the arms of the maze pointing towards the burrows, but the arms were closed off at the end. This prevented air from passing between the burrow and the maze. In these studies, birds were unable to recognise home burrows, suggesting that positional cues were not involved in burrow recognition (Bonadonna et al., 2003, in press). While these experiments do not rule out the possibility that positional cues are used under natural conditions, our experiments suggest that olfactory cues are sufficient for identifying the home nest.

Taken together, these results suggest that diving petrels are able to recognise an olfactory signature of their own nest, suggesting that pheromonal, individual odour recognition or the ability to recognise a burrow odour is well developed in these species. Further experiments are needed to clarify the nature of this olfactory signature.

We are especially indebted to the Institut Polaire Français Paul Emile Victor (IPEV) for financial and logistical support. Ethical Committee from IPEV approved the study. David Pinaud prepared Fig. 1. Dr Richard Van Buskirk and Rebecca Kihlslinger reviewed the manuscript and made helpful comments. G.B.C. and G.A.N. were supported by OPP 9814326 to G.A.N. We are grateful to an anonymous referee for valuable comments on an earlier draft of the manuscript.

References

- Bang, B. G. and Cobb, S.** (1968). The size of the olfactory bulb in 108 species of birds. *Auk* **85**, 55-61.

- Benvenuti, S., Ialò, P. and Massa, B.** (1993). Olfactory experiments on Cory's shearwater (*Calonectris diomedea*): the effect of intranasal zinc sulphate treatment on short-range homing behaviour. *Boll. Zool.* **60**, 207-210.
- Bocher, P., Cherel, Y. and Hobson, K. A.** (2000). Complete trophic segregation between South Georgian and common diving petrels during breeding at Iles Kerguelen. *Mar. Ecol. Prog. Ser.* **208**, 249-264.
- Bonadonna, F. and Bretagnolle, V.** (2002). Smelling home: a good solution for burrow finding in nocturnal petrels? *J. Exp. Biol.* **205**, 2519-2523.
- Bonadonna, F., Hesters, F. and Jouventin, P.** (2003). Scent of a nest: discrimination of own-nest odours in Antarctic prions (*Pachyptila desolata*). *Behav. Ecol. Sociobiol.* **54**, 167-173.
- Bonadonna, F., Spaggiari, J. and Weimerskirch, H.** (2001). Could osmotaxis explain the ability of blue petrels to return to their burrows at night? *J. Exp. Biol.* **204**, 1485-1489.
- Bonadonna, F., Villafane, M., Bajzak, C. and Jouventin, P.** (in press) Recognition of burrow's "olfactory signature" in blue petrels, *Halobaena caerulea*: an efficient discrimination mechanism in the dark. *Anim. Behav.*
- Brooke, M. D. L.** (1989). Determination of the absolute visual threshold of a nocturnal seabird, the common diving petrel *Pelecanoides urinatrix*. *Ibis* **131**, 290-300.
- Chaurand, T. and Weimerskirch, H.** (1994). Incubation routine, body mass regulation and egg-neglect in the blue petrel *Halobaena caerulea*. *Ibis* **136**, 285-290.
- Cunningham, G. B., Van Buskirk, R. W., Bonadonna, F., Weimerskirch, H. and Nevitt, G. A.** (2003). A comparison of the olfactory abilities of three species of procellariiform chicks. *J. Exp. Biol.* **206**, 1615-1620.
- Grubb, T. C.** (1972). Smell and foraging in shearwaters and petrels. *Nature* **237**, 404-405.
- Grubb, T. C.** (1973). Colony location by Leach's petrel. *Auk* **90**, 78-82.
- Grubb, T. C.** (1974). Olfactory navigation to the nesting burrow in Leach's petrel (*Oceanodroma leucorhoa*). *Anim. Behav.* **22**, 192-202.
- Grubb, T. C.** (1979). Olfactory guidance of Leach's storm petrel to the breeding island. *Wilson Bull.* **91**, 141-143.
- Hutchison, L. V. and Wenzel, B. M.** (1980). Olfactory guidance in foraging by procellariiforms. *Condor* **82**, 314-319.
- Lequette, B., Verheyden, C. and Jouventin, P.** (1989). Olfaction in sub-Antarctic seabirds: its phylogenetic and ecological significance. *Condor* **91**, 732-735.
- Martin, G. R. and Brooke, M. D. L.** (1991). The eye of a procellariiform seabird, the Manx shearwater, *Puffinus puffinus*: visual fields and optical structure. *Brain Behav. Evol.* **37**, 65-78.
- Minguez, E.** (1997). Olfactory recognition by British storm-petrel chicks. *Anim. Behav.* **53**, 701-707.
- Mougeot, F., Genevois, F. and Bretagnolle, V.** (1998). Predation on burrowing petrels by the brown skua at Mayes islands, Kerguelen. *J. Zool. Lond.* **244**, 429-438.
- Nevitt, G. A.** (2000). Olfactory foraging by Antarctic procellariiform seabirds: life at high Reynolds numbers. *Biol. Bull.* **198**, 245-253.
- Nevitt, G. A. and Haberman, K.** (2003). Behavioral attraction of Leach's storm-petrels (*Oceanodroma leucorhoa*) to dimethyl sulfide. *J. Exp. Biol.* **206**, 1497-1501.
- Nevitt, G. A., Veit, R. R. and Kareiva, P.** (1995). Dimethyl sulphide as a foraging cue for Antarctic procellariiform seabirds. *Nature* **376**, 680-682.
- Payne, M. R. and Prince, P. A.** (1979). Identification and breeding biology of the diving petrels *Pelecanoides georgicus* and *P. urinatrix exsul* at South Georgia. *N.Z. J. Zool.* **6**, 299-318.
- Thibault, J. C. and Holyoak, D. T.** (1978). Vocal and olfactory displays in the petrel genera *Bulweria* and *Pterodroma*. *Ardea* **66**, 53-56.
- Thoresen, A. C.** (1969). Observations on the breeding behaviour of the diving petrel (*Pelecanoides u. urinatrix*, Gmelin). *Notornis* **16**, 241-260.
- Verheyden, C. and Jouventin, P.** (1994). Olfactory behavior of foraging procellariiformes. *Auk* **111**, 285-291.
- Warham, J.** (1996). *The Behaviour, Population Biology and Physiology of the Petrels*. London: Academic Press.