

Jérôme Mardon<sup>1&2</sup> and Francesco Bonadonna<sup>1</sup>

Atypical homing or self-odour avoidance? Blue petrels (*Halobaena caerulea*) are attracted to their mate's odour but avoid their own.

1) Behavioural Ecology Group, CEFÉ - CNRS, 1919 route de Mende, F-34293 Montpellier, Cedex 5, France

2) AECR Group, School of Biomedical, Biomolecular and Chemical Sciences UWA, 35 Stirling Highway, Crawley WA 6009, Australia

Corresponding author: Jérôme Mardon

Email: [jerome.mardon@cefe.cnrs.fr](mailto:jerome.mardon@cefe.cnrs.fr)

Phone: (0061) 8 6488 4440

Fax: (0061) 8 6488 1005

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## Abstract

Among procellariiform seabirds, many burrowing petrels show good olfactory abilities especially in recognising their nest. In particular, it has been reported that Antarctic prions (*Pachyptila desolata*) discriminate their own and their mate's odours, and in Y-maze experiments prefer the odour of a conspecific bird to their own. While traditionally examined from the perspective of homing mechanisms, these recent results have drawn attention to the possible use of chemical signals in birds' social behaviours. Indeed, the life-history of petrels suggests that a mate choice mediated by olfactory mechanisms may have evolved in this group to ensure genetic compatibility.

This study was undertaken to validate and extend results obtained on petrels' olfactory discrimination capabilities. Following the Y-maze experiment protocol, blue petrels (*Halobaena caerulea*) were offered three different choices: 1) mate versus conspecific's odour, 2) own versus mate's odour and 3) own versus conspecific's odour. We discovered that birds prefer the odour of their mate not only when presented against conspecific's odour, but also against their own. We further verified that blue petrels also avoid their own odour when presented against conspecific's odour. Our results confirm that olfactory discrimination in burrowing petrels goes beyond self-recognition and that self-odour avoidance may be widespread. We use two mutually non-exclusive behavioural frameworks for the interpretation of our results, homing and mate choice; and explain why homing mechanisms can not account for all of our observations. This study opens the door to further research on olfactory mechanisms that in petrels might mediate individual recognition and mate choice.

**Keywords:** petrel; olfaction; individual recognition; behaviour; seabirds

1 Signals broadcasting quality of individuals govern optimal mate choice processes, just as  
2 signals broadcasting identity are used for individual recognition. In the literature, visual or  
3 acoustic based communication systems are frequently noted as preferential channels to  
4 acquire information on the identity and quality of a signalling individual (Maynard Smith and  
5 Harper 2003). This is particularly true in birds, where vision and hearing are considered the  
6 principal communication means for a wide range of behavioural processes. Calls may  
7 broadcast information on sex, species, body condition and identity (Bretagnolle 1989;  
8 Genevois and Bretagnolle 1994; Galeotti et al. 1997; Aubin et al. 2000), and colours may  
9 indicate parasitic loads, age, hierarchical status, sex (Fenoglio et al. 2004; Nolan et al. 2004;  
10 Pryke and Griffith 2006; Nicolaus et al. 2007). However, an increasing number of studies  
11 indicates that chemical signals are also broadly used in vertebrates' recognition systems  
12 (Brown and Eklund 1994; Yamazaki and Beauchamp 2005). Indeed such signals may  
13 constitute reliable cues of quality and compatibility and could thus be used for social  
14 interactions (Wyatt 2003).

15 Procellariiform seabirds have become notorious for their well developed olfactory  
16 neuroanatomy (Bang 1966) as well as for the attraction exhibited by some species for food-  
17 related scents (reviewed in Nevitt and Bonadonna 2005). Among procellariiforms, hypogean  
18 petrels nest in burrows they dig and to which they come back year after year. Returning from  
19 a foraging trip at sea, most of the burrowing species approach the nesting colony at night and  
20 without singing probably to escape avian predators such as gulls and skuas (Mougeot and  
21 Bretagnolle 2000a; Mougeot and Bretagnolle 2000b). Olfaction thus became critical in the  
22 homing processes of these petrels which are able to find and recognise their nest through an  
23 olfactory signature (Grubb 1974; Minguez 1997; Bonadonna et al. 2003a; Bonadonna et al.  
24 2003b; Bonadonna et al. 2004; Jouventin et al. 2007). This is for instance the case of  
25 European storm petrel chicks, *Hydrobates pelagicus*, coming back to their burrow after night  
26 exploring walks (Minguez 1997). Using a T-maze experiment, De Leon and co-workers  
27 (2003) showed that these chicks are able to recognize their own odour and that this odour  
28 leads them back to the nest. This study therefore demonstrated the first required step for  
29 individual recognition to proceed: self/non-self discrimination. Further work on the question  
30 was carried out on a subantarctic petrel species, the Antarctic prion - *Pachyptila desolata*  
31 (Bonadonna and Nevitt 2004). Using a similar kind of maze experiment, the authors first  
32 showed that birds preferred their own odour when presented against an odourless blank, thus  
33 checking for the birds' capacity to perceive self-odour. The study also showed that whilst  
34 adult prions prefer their mate's odour to the odour of an unknown conspecific, they also

35 prefer the odour of an unknown conspecific to their own odour. This work brought the debate  
36 beyond a simple self-discrimination process by highlighting the ability of burrowing petrels to  
37 recognise not only their own, but also their mate's odours (see also Jouventin et al. 2007).  
38 Moreover, the presence of a 'random conspecific' preference over self-odour in Antarctic  
39 prions was unexpected as it is not consistent with homing motivations that appear to explain  
40 results on European storm petrel chicks. Interpretation of such finding is therefore difficult  
41 and should be approached cautiously.

42 In a recent review, Zelano and Edwards (2002) suggested that a genetically based mate-choice  
43 system, particularly ones involving Major Histocompatibility Complex (MHC) preferences,  
44 might be expected in long-lived species engaged in lifetime monogamy, such as many  
45 procellariiform seabirds. MHC-dependent mating preferences can indeed potentially increase  
46 the genetic compatibility between mates (Penn 2002) and have been documented in  
47 mammals, fish and reptiles (Tregenza and Wedell 2000; Olsson et al. 2003). Several studies  
48 on birds also reported that female mate choice may be driven by genetic compatibility in  
49 some species (Johnsen et al. 2000; Blomqvist et al. 2002; Bonneaud et al. 2006) although it  
50 remains unclear in most cases how females may identify the genetic makeup of potential  
51 partners. As olfactory signals from urine or body odours have been associated with MHC  
52 genotypes in several species of vertebrates (Singh 2001), a role for chemical signalling in  
53 mediating mate choice and inbreeding avoidance is not out of the question for birds although  
54 it has received relatively little attention. Indeed, evidence of a functional olfaction has been  
55 found in every bird species tested so far (Roper 1999). Moreover, with their very acute  
56 olfactory capabilities, procellariiform seabirds are certainly the best candidates for the  
57 exploration of such processes in birds (Zelano and Edwards 2002; Bonadonna 2008).

58 If a genetically-based mate choice relying on olfactory cues has evolved in burrow nesting  
59 petrels, it is reasonable to expect two major behavioural processes in these species: olfactory  
60 individual discrimination and kin odours avoidance during mate choice. Therefore, before  
61 starting any further research on mate choice in petrel seabirds, we considered important to  
62 confirm and validate results obtained with Antarctic prions regarding olfactory discrimination  
63 capabilities and preferences. To do so, we repeated and extended our maze experiments to  
64 blue petrels, *Halobaena caerulea*, phylogenetically close to Antarctic prions.

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## METHODS

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This study was conducted on a small sub-Antarctic island (Ile Verte, 49°51'S, 70°05'E) in the Kerguelen Archipelago between November 2006 and January 2007. Blue petrels are a common burrow-nesting species in this region and a study colony made of 70 burrows has been followed since 2001 on this island. Burrows are fitted with a closable aperture over the incubating chamber to facilitate capture. During incubation partners alternate incubation shifts, relieving each other from the nest every 8 to 12 days (Warham 1996). Incubating birds were presented with odour choices in a Y-maze. To trap individual odours, incubating birds were collected from their burrows and held individually in cotton bags (23 x 23 cm) for half an hour. Bags were then stored separately in plastic storage bags (ziplock ®) and kept in the dark in a cardboard box. Bags were stored between 2 and 20 days at ambient temperatures (5 - 10°C) before being used in experiments.

Choice experiments between two scented bags were carried out using a standard Y maze. The maze was made from opaque PVC wire housing and had three symmetrical arms (arm length: 60 cm; width: 12 cm; height: 11 cm). The angle between each arm was ~120 degrees. One arm was used as starting point, and was fitted with two trap doors (30 cm apart) to provide a temporary holding compartment for the bird to be tested. The end of each odour choice arm was equipped with a separate compartment for the odour source (a scented cotton bag), also accessible via a trap door to the outside. A second partition was positioned at 20 cm from each end, and was equipped with a CPU cooling fan (Globe Fan Technology Co. Ltd., product number S05010, Taiwan) to provide low-noise and controlled airflow (9 CFM; 243 l.min<sup>-1</sup>) through each choice arm. Thus the bird did not have direct access to scented bags, but was in contact with scented air flowing over the bags at a constant rate. The maze was washed after each trial with methanol (70%) to remove any odour residue. Odour stimuli were alternated between arms for each trial to eliminate possible bias between either the choice arms themselves or their spatial positions. Birds were removed from burrows, transported to the maze in a cotton bag (different from scented bags), placed in the entryway of the maze, and allowed to settle down for a 3 min period. At the end of this period the inner trap door was lifted and the bird was allowed to make a choice. The choice was easily assessed by the noise of the bird walking in the maze. Birds that either never settled down or sat calmly in the holding compartment facing away from the maze arms were removed after 15 min and reported as no-choice birds (n = 4). Three different odour choice experiments were performed

100 on subject birds in a random order: 1) mate versus conspecific's odour, 2) own versus mate's  
101 odour and 3) own versus conspecific's odour.

102 Ten occupied burrows were selected, and the incubating birds found inside were held in  
103 cotton bags to collect their odour. Two days minimum after odour collection, burrows were  
104 checked again and birds inside were picked to perform one of the choice experiments. When  
105 partners were found in the burrow, they were held in turn in clean cotton bags to collect their  
106 odour before performing one of the experiments. From then on, burrows were visited every  
107 second day (except on very windy and/or wet days), and the bird inside was tested in one of  
108 the three experiments according to the availability of odour bags. Our sampling design was to  
109 test each bird once for each type of experiment. However experiments were stopped with a  
110 given pair of birds as soon as the chick started to hatch. Consequently some individuals did  
111 not perform all three experiments.

112 As already shown by previous studies on petrels (Bonadonna et al. 2003a; Bonadonna et al.  
113 2003b; Bonadonna and Nevitt 2004; Bonadonna et al. 2004), removing birds does not appear  
114 to affect incubation behaviour or the hatchability of the eggs. In the present study, no petrel  
115 deserted the nest following experiment, and hatching success has been of 80% for the study  
116 burrows (eight nest out of 10), about 70% for control burrows in the same colony (11 nests  
117 out of 15), and between 30% and 40% in a control study colony in another island, 6 km apart  
118 (Mayes island, more than 100 burrows).

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## RESULTS

122 Six males and ten females performed experiment 1 (mean choice time $\pm$ SD: 3.5 $\pm$ 2.2 min),  
123 seven males and nine females performed experiment 2 (mean choice time $\pm$ SD: 4.2 $\pm$ 2.9 min),  
124 ten males and seven females performed experiment 3 (mean choice time $\pm$ SD: 2.9 $\pm$ 2.1 min).

125 Both sex confounded, birds significantly preferred the odour of their mate over the odour of a  
126 conspecific in experiment 1 (binomial test,  $p < 0.01$ , Fig 1a), the odour of their mate over their  
127 own in experiment 2 (binomial test,  $p < 0.001$ , Fig 1b), and the odour of a conspecific bird  
128 over their own odour in experiment 3 (binomial test,  $p < 0.01$ , Fig 1c). Figure 1 also displays  
129 sex-specific results for the 3 experiments.

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## DISCUSSION

132  
133 Our results show that blue petrels are able to recognize and discriminate individual odour  
134 cues, in particular their mate's and their own odours. This behaviour is consistent with  
135 behaviours observed in Antarctic prions (Bonadonna and Nevitt 2004) for which the existence  
136 of an individual olfactory signature has recently been suggested (Bonadonna et al. 2007).  
137 However, if these clear cut results provide an unambiguous demonstration of blue petrels'  
138 olfactory discrimination capabilities, the birds' motivation underlying these choices are more  
139 challenging to explain. Traditionally, burrowing petrels' olfactory abilities have been  
140 investigated within the framework of homing behaviours (Grubb 1974; Minguéz 1997;  
141 Bonadonna et al. 2003a; Bonadonna et al. 2003b; Bonadonna et al. 2004). As the birds used  
142 for our experiment were displaced from their nest and placed in the novel environment of the  
143 Y-maze, the prime hypothesis is, therefore, that birds' decisions were driven by desires to  
144 escape and/or return to the nest.

145  
146 In blue petrels, breeding partners alternatively leave the burrow to forage at sea for up to 12  
147 days (Warham 1996). It follows that the last bird to occupy the nest before an individual  
148 comes back from its foraging trip is its partner. Therefore, the partner's scent should be the  
149 strongest odorous signal from the nest at that time, representing a major part of the burrow  
150 olfactory signature. When given a two-way choice, blue petrels preferred their mate's odour  
151 to the one of an unknown conspecific (experiment 1). A similar olfactory preference for the  
152 mate's odour has recently been reported for Wilson's storm petrels (*Oceanites oceanicus*)  
153 (Jouventin et al. 2007). Such preference is consistent with the 'homing' hypothesis in that it  
154 would drive a bird back to its burrow under natural conditions. The novel finding of the birds'  
155 preference for their mate's odour over their own (experiment 2) could similarly be explained  
156 by this mechanism. Yet, we did not expect such an unequivocal preference for the partner's  
157 scent as observed in this second experiment. Indeed, orienting to self-odour has been shown  
158 to be an efficient homing mechanism leading European storm petrel chicks back to their nests  
159 (Minguéz 1997; De Leon et al. 2003). In adult petrels, it would also be useful in specific cases  
160 when the partner skipped an incubating shift or gave up breeding. In this regard, results of  
161 experiment 3 are striking. The preference for an unknown conspecific odour over self-odour  
162 observed in both blue petrels and Antarctic prions (Bonadonna and Nevitt 2004) challenges  
163 De Leon and co-workers' results (2003) on European storm petrel chicks and more generally  
164 the 'homing' hypothesis. Indeed, such an olfactory mechanism would drive a homing bird  
165 away from its nest. Different behavioural processes that could explain this apparent self-odour

166 avoidance need to be discussed. First, birds may simply not be able to perceive their own  
167 odour and are therefore just attracted to the only odour perceived ('perception hypothesis'). It  
168 is also possible that self-odour detection is perceived by the bird as an indication that it has  
169 already explored this arm of the maze ('confusion hypothesis'). However, several arguments  
170 challenge these two hypotheses. First, it was shown in both Antarctic prions (Bonadonna and  
171 Nevitt 2004) and European storm petrels (De Leon et al. 2003) that birds do perceive their  
172 own odour as they preferred it to an odourless blank. The latter result, together with the short  
173 length and simplicity of the Y-maze approach we used, also advocates against the 'confusion  
174 hypothesis'. Finally, these two hypotheses would not constitute a satisfying explanation of our  
175 data as they are both inconsistent with results on self-odour perception obtained from  
176 European storm petrel chicks (De Leon et al. 2003).

177  
178 The preference patterns described here, when compared with preferences observed in  
179 European storm petrel chicks (De Leon et al. 2003), suggest an alternative hypothesis. Petrels'  
180 olfactory preferences may vary with age and/or social contexts so that self-odour avoidance  
181 may be developed only at sexual maturity. In such case, olfactory preferences should be  
182 examined from the perspective of sexual behaviours and mate choice. Blue petrels are  
183 monogamous and faithful year after year to their mate and burrow (Bried and Jouventin  
184 2002). After breeding they disperse at sea until the next breeding season (Warham 1996). In  
185 September, males and females have to meet and recognise each other in the darkness of their  
186 burrow. Singing in the burrow is costly because of predation (Mougeot and Bretagnolle  
187 2000a) so that olfactory partner recognition may be adaptive to burrow-nesting petrels.  
188 Moreover, if petrels' odour constitutes an individually specific (Bonadonna et al. 2007) and  
189 honest signal reflecting the genetic make-up of a bird, it could be used as a secondary sexual  
190 trait. In such a case, one would expect blue petrels to prefer their mate's odour to the odour of  
191 a random conspecific (experiment 1) as would have been the case during pair formation.  
192 Consistent with this hypothesis is the preference of birds for their mate's odour over their own  
193 (experiment 2).

194 What is more, most petrel species breed on remote islands and are philopatric with regard to  
195 the colony (Warham 1996). Their life-history traits (philopatry, genetic lifelong monogamy)  
196 suggest that kin recognition may be important for discriminating between potential mates and  
197 to avoid inbreeding. Therefore, a kin-odour avoidance mechanism, based on a self-odour  
198 template, could account for the observed preference for an unknown conspecific odour over  
199 self-odour (experiment 3, Bonadonna and Nevitt 2004). Self-referent phenotype matching, the



200 so-called ‘armpit effect’ (Dawkins 1982), has been implicated as a mechanism for assessing  
201 relatedness in other systems including birds and rodents (Heth et al. 1998; Hauber et al. 2000;  
202 Mateo and Johnston 2000). To explore whether such a mechanism is used by burrowing  
203 petrels for olfactory discrimination among individuals is a fascinating prospect of future  
204 research.

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206 Our results clearly demonstrate that blue petrels can discriminate between their own, their  
207 mate’s and unknown conspecifics’ odours. To our knowledge, this is only the third bird  
208 species (after Antarctic prions and Wilson’s storm petrels) proven to possess olfactory  
209 mechanisms of individual recognition, beyond simple self-discrimination. We have developed  
210 two mutually non-exclusive behavioural frameworks for the interpretation of our results:  
211 homing and mate choice. Although simpler, the homing hypothesis can not account for all of  
212 our results. The mate choice hypothesis, or a combined effect of the two, therefore appears  
213 more robust. Zelano and Edwards’s (2002) suggestion of a MHC-based mate choice,  
214 mediated by olfactory mechanisms, in procellariiform seabirds is still the object of current  
215 research, but all these results taken together support this intriguing hypothesis.

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**Figure legend**

Figure 1: Absolute frequencies of the different choice outcomes in the three experiments. Sex specific results are shown (dashed areas: females, open areas: males). Sex specific p-values are indicated above the graphs and refer to binomial tests between the two choice options.

**Figure 1**