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Journal

Marine Ecology-Progress Series, 315

ISSN

0171-8630

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Publication Date

2006

Peer reviewed

The potential role of ammonia as a signal molecule for procellariiform seabirds

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ABSTRACT: Procellariiform seabirds (petrels, albatrosses and shearwaters) navigate vast distances over seemingly featureless ocean habitat by mechanisms that are not well understood. These birds have large olfactory bulbs, and the use of smell has been implicated in both foraging and homing behavior. While many olfactory cues relevant to these behaviors have been identified, ammonia is a potentially significant, biogenic, scented compound that has not been studied in this context. Ammonium (NH_4^+) constitutes a primary waste product produced by many of the prey species on which procellariiforms forage. Nitrogen waste products, including volatilized ammonia (NH_3), also scent the terrestrial landscape of sub-Antarctic islands where newly breeding procellariiform seabirds recruit and raise their young. Since an ability to smell ammonia may be relevant to both prey detection and locating colonies or islands, we used a non-invasive, behavioral assay to examine whether this scented compound is detectable by a candidate test species, the blue petrel *Halobaena caerulea* Gmelin. Our results suggest that these birds can detect volatilized ammonia within a concentration range that they may naturally encounter (10^{-11} to 10^{-5} M), and point to ammonia as a potential signal molecule in the sub-Antarctic.

KEY WORDS: Petrel · Ammonia · Homing · Foraging · Antarctic · Navigation

INTRODUCTION

Procellariiform seabirds navigate the world's oceans by mechanisms that are not well understood. These birds have an excellent sense of smell, and olfaction has been linked to both foraging and homing to specific nest sites, particularly in burrowing species. With respect to foraging, the use of olfaction has been studied in greatest detail in sub-Antarctic species (for review see Nevitt 2000, Nevitt & Bonadonna 2005a). Our current understanding is that procellariiforms use odor cues at both larger (1000s of square kilometers), and smaller (10s or 100s of square kilometers) spatial scales (Nevitt 2000). At large spatial scales, changes in the odor profile over the ocean demarcate productive zones in what appears as a featureless landscape to humans. These productive zones are areas where prey patches are likely to be encountered. Once a bird arrives at a productive area, the changing odor landscape triggers a shift in behavior to a small-scale, area-restricted search. Birds then use a combination of visual and olfactory cues to pinpoint prey patches. Observational and experimental evidence collected from species assemblages near South Georgia suggests that the sensory modality that a bird typically uses depends on both the bird species and the foraging context (e.g. Nevitt 1999, Nevitt & Veit 1999, Nevitt et al. 2004). Some species zigzag upwind to focus activity to odor sources (e.g. Nevitt et al. 1995, Nevitt 2000), whereas others use visual cues provided by aggregations of prey, foraging seabirds and marine mammals (Silverman et al. 2004).

Procellariiform seabirds respond to a variety of scented compounds associated directly or indirectly with prey, including dimethyl sulfide (DMS), a sulfur-

based compound released by phytoplankton. DMS emissions become elevated in surface seawater associated with oceanic features such as upwelling zones and shelf waters, where both phytoplankton and prey tend to aggregate (for review see Nevitt 2000). DMS emissions also increase locally during cell destruction associated with zooplankton grazing (e.g. Dacey & Wakeham 1986, Daly & DiTullio 1996, Kasamatsu et al. 2004). A range of other scented compounds are also released, either through excretion or maceration, as organisms are broken up during the predation process (see discussion in Nevitt et al. 2004). These compounds include nitrogen waste products which, like DMS, may provide birds with proximate cues for detecting krill swarms. For example, freshly caught Antarctic krill *Euphausia superba* Dana excrete ammonium (NH_4^+) on the order of 1.6 to 2.8 nmol mg^{-1} dry mass h^{-1} (Atkinson & Whitehouse 2000). Calculations from laboratory, ship-based, experiments suggest that copepods and small euphausids excrete ammonium into the pelagic zone around South Georgia Island at a rate of approximately 1 mmol $m^{-2}\,d^{-1}$ (Atkinson & Whitehouse 2001).

Nitrogen waste products may also play a role in how birds navigate to colony sites or islands. Islands provide breeding habitat for marine mammals and seabirds and consequently receive substantial quantities of marine-derived nitrogen as wastes. These wastes give rise to both atmospheric (volatilized NH_3) and marine ammonium (NH_4^+/NH_3) plumes that are often detectable by humans kilometers downwind (Erskine et al. 1998, see also Rankin & Wolff 2000). In a review of population sizes of penguins, seals, and their associated excrement rates on Macquarie Island, Erskine et al. (1998) calculated that over 3 700 000 t of dry mass excrement was deposited annually, and this converted to nearly 240 t of nitrogen. Moreover, the contribution of ~60 000 burrowing petrels of various species (see Shirihai 2002) was not included in this calculation because uric acid from birds is rapidly mineralized, releasing ammonia gas. On another sub-Antarctic island (Marion Island), Lindeboom (1984) estimated that over 10% of nitrogen from penguin colonies eventually reached inland vegetation as volatilized ammonia. Thus, from a human perspective, increased volatilized ammonia contributes substantially to the odor landscape associated with the island habitat on which birds nest. Even though ammonia is both a potent olfactory and trigeminal stimulant to humans, most bird species that have been tested (including rock doves *Columbia livia*, red-winged blackbirds *Agelaius phoeniceus*, European starlings *Sturnus vulgaris* and gray partridges *Perdiz perdix*) cannot physiologically or behaviorally detect this compound (for review see Clark 1997).

Since volatilized ammonia may be important in both prey detection and locating colonies or inhabited islands, the aim of this study was to determine whether ammonia is detectable to a candidate procellariiform species within a concentration range that is potentially biologically relevant to both foraging and navigation. Therefore, although absolute sensitivity thresholds in birds typically range from 10^{-7} to 10^{-5} M across a variety of olfactory stimuli and species (see Roper 1999 for review), the lowest concentration we tested was 4 orders of magnitude lower (10 pM or 10^{-11} M) than the lowest expected threshold value. Experiments were performed on the blue petrel *Halobaena caerulea* Gmelin, a common species that nests in burrows throughout the sub-Antarctic. To reliably test a concentration series in the field, we used a non-invasive, behavioral assay that was developed to test responses of domestic chicks to odor stimuli in laboratory situations (Porter et al. 1999). We have previously adapted this method to examine olfactory sensitivity in both blue petrels and diving petrels (Cunningham et al. 2003). Based on our findings, we explore two potential roles for ammonia as signal molecule for procellariiform seabirds.

MATERIALS AND METHODS

The study was conducted at Ile Verte (49° 51' S, 70° 05' E) from January 8 to 16, 2004. Ile Verte is situated on the eastern side of the Kerguelen Archipelago, just south of the Antarctic Convergence. Breeding populations of blue petrels at Kerguelen have been estimated to approach 1 to 2 million pairs (Weimerskirch et al. 1989).

The Porter method. We tested the olfactory responses of 24 blue petrel chicks using the Porter method. This method was developed as a relatively simple technique for testing responses of domestic chicks to odors in laboratory settings (Porter et al. 1999). Chicks enter a sleep-like state and responses are recorded as test odors are puffed onto their nostrils. This technique has several advantages for our applications in that it is completely non-invasive, does not deleteriously impact fledging success, and has previously been used to test the responses of blue petrel chicks in the field (Cunningham et al. 2003). While the Porter method does not work well with adult birds, results from earlier work suggest that chick responses to odor stimuli reflect those of adults in at-sea experiments (Cunningham et al. 2003).

To run a trial, a chick was removed from its burrow, placed in a cotton bag and transported to a well-ventilated field hut (4×6 m) within 500 m of the colony. The chick was then placed in a holding chamber lined with a clean paper towel. The holding chamber was made of black, flexible corrugated plastic folded to form a rec-

tangular box (approximately $10 \times 5 \times 5$ cm) open at both ends. The chamber was placed on a small platform to allow easy access to the chick's nostrils. The chick was positioned so that its head protruded from one end and the chamber walls were in contact with the bird's body. Once the chick was positioned in the chamber, it quickly (within 3 min) entered a sleep-like state in which its head drooped slightly and its eyes closed. As in earlier studies, chicks were considered to be 'asleep' when their eyes were closed, their head became droopy, and their legs and wings relaxed. Chicks were left to sleep for at least 3 min before initiating a trial.

During a trial, we exposed the chick to a series of 3 increasing ammonia solution concentrations (10 pM, 10 nM, 10 µM in water, pH 7.0) with a control (water) inserted randomly into the sequence. Vapor concentrations were not measured, but were conservatively estimated to be 1 order of magnitude less than solution concentrations (e.g. Sawyer & McCarty 1978). Stimuli were presented by puffing odor above the chicks' nostrils using a 500 ml Nalgene® squeeze bottle. The tip of the bottle was positioned ~3 cm from the nostrils. The bottle was then squeezed 1 to 2 times in 5 s, producing brief puffs of odorant-saturated air near the bird's nostrils. Responses to odorant presentations were recorded for 1 min and scored categorically as positive (Score = 1; biting movements, vocalizations, distinct head or body movements) or negative (Score = 0; typically no reaction) for each bird (modified from Porter et al. 1999). Experimental observations and scoring were done 'blind': the person delivering the stimulus and recording the response did not know the identity or concentration of the stimulus being delivered. In addition, the person who set up the odor sequence was not present during the experimental trial. If the chick woke up during a test, we waited for up to 3 min for it to return to a sleep-like state. We then allowed the bird to sleep for 1 min before proceeding with the next stimulus. If the bird did not fall asleep within 3 min, we aborted the experiment and returned the bird to its burrow.

All experiments were conducted within a narrow temperature range (10 to 13°C) during daylight hours, when parents were absent from the burrow. Chicks were transported and tested one at a time and spent less than 30 min away from the nest. Each chick was weighed after testing, returned to its burrow, and was tested only once. Burrows were monitored again prior to fledging to check for any deleterious effects of the experimental procedure. Although we left the island just prior to fledging, we observed no mortality among the chicks that were tested; weight gain and wing chord growth were within normal parameters (Jouventin et al. 1985).

Odors. Odorant stimuli (100 ml) were prepared in serial dilution from stock solutions (1 mM; Sigma-Aldrich). Solutions were prepared using new Hamilton syringes and glassware. During preliminary trials, we noticed that distilled water prepared from local sources in the Kerguelen laboratories had an ammonia odor. Thus, to avoid potential contamination from ambient water sources, all solutions were prepared in bottled spring water (Evian®) imported from France rather than locally available distilled water. Test solutions were transferred to clean Nalgene® squeeze bottles. Bottles were allowed to sit for at least 3 h at ambient temperature to equilibrate the headspace.

Statistical analysis. To determine whether there was a difference among treatment effects, scores were analyzed using a Friedman test (in essence, a nonparametric, blocked ANOVA). Dunnett's multiple comparison test was used to determine which of the non-control treatments differed significantly from the control treatment (Daniel 1990). We next used a rank ANOVA to examine whether the condition of being fed the previous night impacted the dose response. Fed status was indicated by a marked distension of the crop. This analysis followed the structure of a repeated-measures ANOVA, with feeding status considered as a between-subject factor, and dose considered as a within-subject factor (Daniel 1990).

As in earlier studies (Cunningham et al. 2003), we also investigated the relationships between age indicators (chick weight and tarsus length) and chick responsiveness to treatments. Here we calculated Spearman's ρ coefficient, a measure of association based on ranked data. We looked at mean behavioral response by averaging each chick's scores for control and ammonia treatments. A significant test statistic indicated a nonzero rank correlation (Zar 1996). All analyses were performed using SYSTAT software.

RESULTS

The 24 *Halobaena caerulea* chicks we tested ranged in weight from 85 to 215 g (mean ± SE was 166.9 ± 6.5 g), suggesting that chicks were mid-way through their development to fledging at the time of testing; (Jouventin et al. 1985). Average (±SE) wing chord and tarsus measurements were consistent with this approximation (wing chord: 45.4 ± 2.1 mm; tarsus: 28.2 ± 0.8 mm).

Mean scores for control and the 3 test stimuli were significantly different (Fig. 1, Friedman test, $F = 3.21$; df = 3; p < 0.03); All application concentrations differed significantly from the control (p < 0.05, Dunnett's multiple comparison test), suggesting that chicks could detect ammonia at solution concentrations from 10 pM to 10 µM (10^{-11} to 10^{-5} M).

We found that being fed the previous night had no impact on the dose response to ammonia, suggesting that chicks were just as likely to respond to volatilized
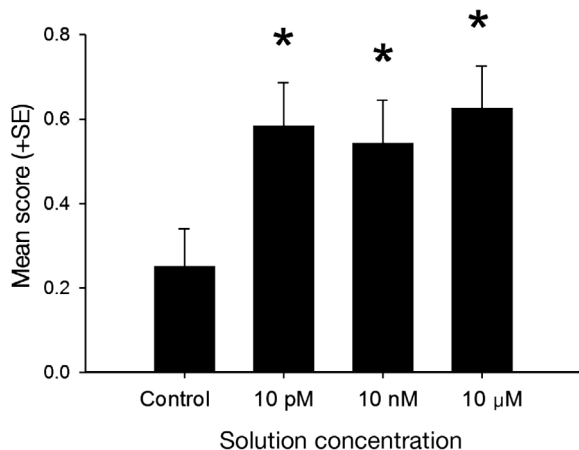
Fig. 1. *Halobaena caerulea.* Average behavioral responses of 24 blue petrel chicks to ammonia using the Porter method. Mean (+SE) scores are plotted for responses to control and to each solution concentration. *Significant difference from control response (p < 0.05)
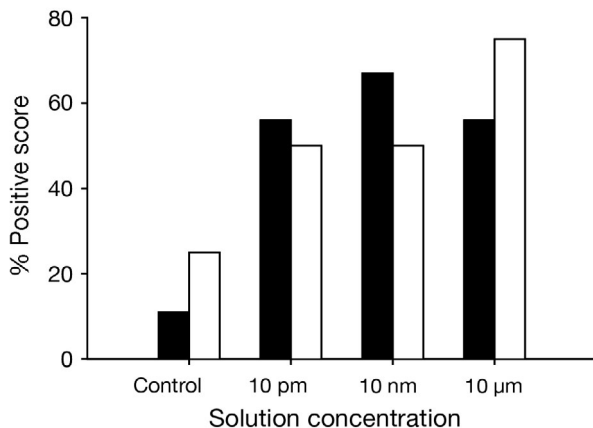

Fig. 2. *Halobaena caerulea.* Responses to ammonia of fed (black bars; N = 9) vs. unfed (white bars; N = 12) chicks, showing percentage of positive scores for control and for each solution concentration. Feeding status of 3 birds could not be determined and these were therefore not included in this analysis

ammonia at the concentrations tested, regardless of whether or not they were hungry (Fig. 2, Fed: N = 9; Unfed: N = 12; rank ANOVA: F = 0.46; p = 0.98; We had no data for feeding state for 3 chicks). Similarly, we found no correlation between average score and either weight (Spearman's ρ = 0.06; p = 0.73; N = 24) or tarsus length (Spearman's ρ = −0.15; p = 0.50; N = 24), suggesting that chicks responded similarly to test stimuli, regardless of their age.

DISCUSSION

Our results demonstrate that blue petrel chicks can detect volatilized ammonia at solution concentrations as low as 10 pM (10^{-11} M). While this concentration is well below the detection range that has typically been reported for other avian species (10^{-7} to 10^{-5} M, reviewed by Roper 1999), the dose response curve did not reach threshold, suggesting that blue petrels can probably detect even weaker concentrations than those we tested (see Nevitt & Bonadonna 2005a). In earlier experiments in which we used this technique to test blue petrel chicks' responses to a single concentration of DMS, we found that response depended on satiation state (Cunningham et al. 2003) and, potentially, age (Cunningham unpubl. data). In the present experiment, our results showed no significant correlation with these variables, suggesting that neither hunger nor age influenced responsiveness. In interpreting our results, we caution that a limitation of this non-invasive, behavioral assay is that it does not discriminate between an olfactory and a nociceptive (trigeminal or common chemical sense) response. Humans experience this sense in response to various spices (capsassin in chili peppers, horse radish, or garlic, for example), whereas birds are sensitive to different compounds that may or may not also stimulate the olfactory system (for review see Clark 1998). In any event, both pathways may be involved in mediating the detection of scented compounds in natural situations, depending on the context and the concentration (Clark 1997). With respect to our study, we did not observe chicks recoiling from stimulus presentations as might be expected for a trigeminal irritant, and chicks responded at stimulus concentrations that are more typically attributed to olfactory perception ($<10^{-5}$ M, Kirifides et al. 2004). Behavioral responses were also qualitatively similar to those we have observed in similar tests using established foraging odors (e.g. DMS, Cunningham et al. 2003).

Potential role of ammonia as a foraging cue

The sensitivity range suggests that the blue petrel *Halobaena caerulea* may be able to use ammonia as a signal molecule for detecting prey patches, and this is a topic that deserves further research. Ammonium is the major excretion product of seabird prey, including schooling mesopelagic fish and krill swarms. Although ammonium is taken up by phytoplankton through nitrogen recycling, it has also been shown to accumulate in surface seawater for at least several hours in association with dense krill swarms. For example, Johnson et al. (1984), measured ammonium (NH_4^+) levels within a krill swarm to be on average 0.75 mmol m^{-3} (7.5×10^{-7} M) higher than in adjacent seawater and suggested that these levels were generated by excretion over a period of 15.5 h.

While it is not known how much of this ammonium is volatilized, the discovery that blue petrels are responsive to picomolar solution concentrations suggests that they may be able to use trace emissions to identify productive foraging areas. Marine ammonia emissions have not been as well studied in the sub-Antarctic as emissions of other trace gases. However, empirical measurements taken in the remote Pacific (Quinn et al. 1988, 1990, as cited by Nightingale & Liss 2004) suggest that the sea-to-air flux of NH_3 is similar in size to DMS emissions. Blue petrels are sensitive to DMS at sea, and chicks also respond to it using the Porter method (e.g. Nevitt et al. 1995, Nevitt 2000, Cunningham et al. 2003). Moreover, the foraging behavior of blue petrels involves searching remote, offshore areas for patchily distributed prey in pelagic waters (e.g. Chaurand & Weimerskirch 1994), where the signal-to-noise ratio for ammonia and other trace gases emitted into the atmosphere in association with zooplankton aggregations is likely to be high (see discussion in Larsen et al. 2001). Large fetch, wave action and wind, all typical of the Southern Ocean environment, should increase the rate of transfer between seawater and air. Wave spray will tend to aerosolize ammonia in solution, while low temperatures will tend to reduce the atmospheric equilibrium concentration and the extent of volatilization (Liss & Galloway 1993, Liss et al. 2004).

With respect to signaling prey availability to birds, we speculate that signals should be strongest when prey is closest to the surface, since it has previously been established that ammonium concentrations in surface seawater reflect vertical migratory patterns of mesozooplankton. For example, Priddle et al. (1997) showed that ammonium concentrations in near-surface (top 30 m) water around South Georgia varied diurnally, with maximum values reaching 1.3 mmol m^{-3} (1.3×10^{-6} M) near local midnight, dropping to as low as 0.1 mmol m^{-3} (1×10^{-7} M) around noon. Thus, if blue petrels can detect volatilized ammonia at sea and use it to locate, recognize, or otherwise evaluate potential prey hotspots, then this ability may be most useful at night when prey is closest to the surface and when visual cues are obscured. In support of this hypothesis, the correlation between prey availability and diet implies that at least some foraging occurs at night (e.g. Croxall et al. 1999, Cherel et al. 2002). However, the mechanisms by which blue petrels locate prey are not completely understood, particularly in terms of elucidating the interaction between olfactory and visual cues with respect to prey capture (see Nevitt 2000). Clearly, the combined evidence suggests that volatilized ammonia may be an important signal molecule for this species, but whether blue petrels and other procellariiforms can use it as a foraging cue at sea will require further investigation.

Ammonia as a signal molecule in the terrestrial habitat

A common assumption is that procellariiform seabirds navigate to islands by simply seeing them in the distance, but this perspective overlooks the fact that other species do not share the same sensory world as humans (for reviews see Dusenbery 1992, Wiltschko & Wiltschko 1994 and Goodenough et al. 2000). For example, previous studies have suggested that olfactory features of island habitat are likely to be as distinctive for procellariiforms as visual features are for humans (reviewed by Nevitt & Bonadonna 2005a). With respect to homing, Grubb (1974) showed that Leach's storm-petrels *Oceanodroma leucorhoa* translocated just 500 m from their nesting colonies failed to relocate their burrows if their olfactory nerves were transected. Moreover, intact birds consistently approached colony sites by zigzagging upwind (Grubb 1974; see also Griffin 1940, Billings 1968, Grubb 1973), suggesting an olfactory-mediated search (see Dusenbery 1992 for detailed descriptions of olfactory search). More recent studies indicate that similarly displaced blue petrels *Halobaena caerulea* and thin-billed prions *Pachyptila belcheri* fail to relocate nest sites when rendered temporarily anosmic (smell-blind) (Bonadonna et al. 2001, 2004). While vocalizations are audible in colonies, these results indicate that auditory cues provided by mates and conspecifics were insufficient for nest site relocation at these spatial scales. At greater distances, procellariiforms may be able to use magnetic cues for orientation and navigation, but a variety of species can still home accurately, even when the local magnetic field has been experimentally disrupted (e.g. white-chinned petrels *Procellaria aequinoctialis*: Benhamou et al. 2003, Bonadonna et al. 2005).

Although procellariiform seabirds doubtless use a hierarchy of cues in long-distance navigation (Nevitt & Bonadonna 2005b), the demonstration that petrels can detect volatilized ammonia indicates that it is a potential odor landmark used for homing to islands, particularly at night or in fog when other cues are obscured. Sub-Antarctic islands are detectable by smell from a distance, even to humans, due to the large number of seabirds and marine mammals that tend to breed on them. A primary component of this characteristic odor can be attributed to nitrogen waste, and in particular, to volatilized ammonia. For example, on Macquarie Island, Erskine et al. (1998) found volatilized ammonia in the air spaces 1 m above penguin colonies, and were able to trace the transfer of this ammonia inland as well as out to sea. In Antarctica, ammonia transfer from penguin colonies has been traced as far as 15 km (Rankin & Wolff 2000). These data suggest that the odor signature around inhabited islands is a prominent feature for those animals that can detect it.

The association of ammonium with inhabited islands suggests that ammonia and associated scents may contribute to the sensory cues birds use to evaluate habitat before choosing to nest there for the first time. For example, nitrogen signatures also give local information about where nesting sites are or have been historically (see Lindeboom 1984, Erskine et al. 1998, Bergstrom et al. 2002). On Macquarie Island, soils from direct excrement zones of nesting animals, especially soils associated with burrowing petrels, had a substantially higher concentration of soluble nitrogen than soil samples collected away from such influence (Erskine et al. 1998). Total soluble nitrogen levels were highest (1.8 ± -0.4 µM g^{-1} dry wt) at a burrowing petrel site, surpassing those in soils collected from penguin colonies (1.61 ± 0.3 to 0.8 ± -0.1), elephant seal wallows (0.2 ± -0.1), light-mantled, sooty albatross, nesting sites (0.6 ± -0.2), and areas frequented by skuas and non-indigenous rabbits ($0. \pm -0.2$), giant petrels (1.2 ± -0.1) and humans (0.5 ± -0.2). The dominant soluble form of nitrogen was ammonium, whereas concentrations of other forms (nitrate, urea, uric acid and amino acids) were comparatively low. Soils sampled at the burrowing petrel site also contained 45% protein – double to that at any other site. These data are noteworthy, since urinary proteins have been linked to individual recognition in other species (mice, e.g. Hurst et al. 2001) and could also be explored in the context of burrow or individual recognition (Bonadonna et al. 2001, 2004, Bonadonna & Nevitt 2004).

CONCLUSIONS

The results presented here suggest that blue petrels can detect ammonia at concentrations pertinent to both foraging and navigation. The extreme sensitivity suggests that blue petrels may be able to use volatilized ammonia to detect prey patches at sea, and this is a topic that deserves further research. For example, with respect to multi-level ecological monitoring programs, our results suggest that examining the relationship between seabird distributions and seawater ammonium concentrations may provide insights into the foraging behavior of birds and other predators (Serebrennikova & Fanning 2002, Chapman et al. 2004), particularly with respect to the mechanisms used to find prey. In the context of homing, a picture is emerging that sub-Antarctic islands represent prominent olfactory features in the sensory landscape in which blue petrels and other procellariiforms operate. Our results thus establish volatilized ammonia as a measurable, biogenic, scented compound in the hierarchy of cues that these birds have available to them to relocate their home islands. The possibility that petrels use ammonium as a cue for evaluating potential breeding areas needs to be further explored.

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