

Review

Sensory ecology on the high seas: the odor world of the procellariiform seabirds

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Summary

Procellariiform seabirds wander the world's oceans aided by olfactory abilities rivaling those of any animal on earth. Over the past 15 years, I have been privileged to study the sensory ecology of procellariiforms, focusing on how olfaction contributes to behaviors, ranging from foraging and navigation to individual odor recognition, in a broader sensory context. We have developed a number of field techniques for measuring both olfactory- and visually based behaviors in chicks and adults of various species. Our choice of test odors has been informed by long-term dietary studies and geochemical data on the production and distribution of identifiable, scented compounds found in productive waters. This multidisciplinary approach has shown us that odors provide different information over the ocean depending on the spatial scale. At large spatial scales (thousands of square kilometers), an olfactory landscape superimposed upon the ocean surface reflects oceanographic or bathymetric features where phytoplankton accumulate and an area-restricted search for prey is likely to be successful. At small spatial scales (tens to hundreds of square kilometers), birds use odors and visual cues to pinpoint and capture prey directly. We have further identified species-specific, sensory-based foraging strategies, which we have begun to explore in evolutionary and developmental contexts. With respect to chemical communication among individuals, we have shown that some species can distinguish familiar individuals by scent cues alone. We are now set to explore the mechanistic basis for these discriminatory abilities in the context of kin recognition, and whether or not the major histocompatibility complex is involved.

Key words: olfaction, Procellariiformes, seabirds, sub-Antarctic.

Introduction

The tube-nosed seabirds (order: Procellariiformes) are noted for their wide-ranging, pelagic lifestyle. This order covers a diverse range of species groups including the storm-petrels, albatrosses, gadfly petrels, diving petrels, fulmars, prions and shearwaters (Warham, 1990; Warham, 1996). These birds spend most of their lives in flight over the ocean, and are tied to land for only a few months each year or every other year to breed and rear a single offspring. Most species have lifespans ranging from four to six decades, and tend to remain faithful to both their mate and nest site throughout their adult life. Like mustelids (the family that includes the weasels, badgers and ferrets), procellariiforms are renowned for their strong, musky personal scent (Bonadonna et al., 2007), which perfumes their oily plumage, their nest material and even their eggs. Not surprisingly, procellariiforms have among the largest olfactory bulbs of birds (Bang, 1966) and their neuroanatomy suggests a highly developed sense of smell in the few species that have been examined at the cellular level. For example, the olfactory bulbs of Northern fulmars (*Fulmarus glacialis*) have twice as many mitral cells as rats (120 000 vs 60 000) and six times as many as mice (120 000 vs 20 000) (Wenzel and Meisami, 1987). These cells are fundamental to olfactory processing and play a key role in odor contrast enhancement (reviewed by Shepherd et al., 2007). While such comparisons suggest a multitude of questions to explore with respect to anatomy and function, my current research program has been directed towards investigating the sensory ecology of these birds,

focusing on how olfaction, combined with other sensory modalities, contributes to behaviors ranging from foraging and navigation to individual odor recognition. This mini-review highlights some of our major findings and future directions.

An overview of foraging

Most procellariiforms forage over immense areas of the ocean for patchily distributed prey, including various species of fish, squid and krill. Their survival depends on finding the proverbial needle in a haystack on a daily basis. Depending on the species, procellariiform diets can be highly variable, and can vary with respect to prey availability (Reid et al., 1997; Reid et al., 1996) or time of year (Ainley et al., 1984). During the breeding season, procellariiforms are central place foragers (Stephens and Krebs, 1986), meaning that they are temporally constrained to return to their nest either to relieve a mate or to provision a hungry chick. Results from satellite tracking studies of larger species have revealed that species use different strategies to efficiently accomplish this task, including opportunistic and commuter foraging strategies (Weimerskirch, 1998). Opportunistic foragers such as wandering albatross (*Diomedea exulans*) tend to hunt for prey along continuous, looped paths covering many thousands of kilometers of pelagic and neritic water even on a single foraging trip (Fig. 1A). These birds forage mainly on fish (myctophids) and various squid species. A large fraction of their diet tends to be squid in the form of carrion (Croxall and Prince, 1994), which they track using a combination

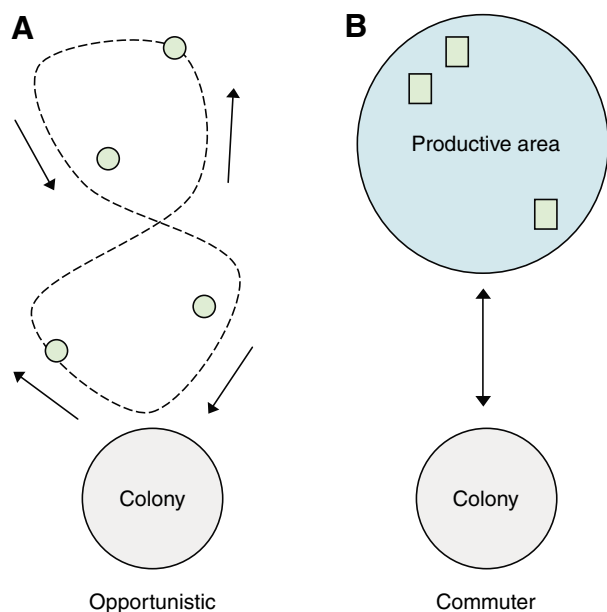


Fig. 1. Different long-range foraging strategies. In each diagram, the gray circle represents a colony site. (A) Opportunistic foraging strategy. The bird leaves the colony on a wide-ranging loop that can span thousands of kilometers. Prey items (green circles) are encountered opportunistically along the path (broken line). Arrows represent flight direction. (B) Commuter foraging strategy. The bird leaves the colony to forage at one of several productive areas, which can be located thousands of kilometers from the colony. The diagram shows one such area as the larger green circle. Within the productive area, prey patches (green squares) are more likely to be found. Elements in the diagram are not to scale.

of visual and olfactory cues (Nevitt et al., 2008). On the other hand, commuters such as black-browed albatross (*Thalassarche melanophrys*) may travel thousands of kilometers to a shelf break or seamount where prey are likely to be more concentrated (Fig. 1B). Upon arrival, these birds engage in area-restricted search (ARS) to locate prey (Fig. 2A,B) (reviewed by Nevitt, 2000). This particular species tends to forage on a combination of squid, krill and fish in roughly equal proportions during the breeding season (Rodhouse and Prince, 1993). Thus, foraging strategies tend to operate over different spatial scales. At larger scales, the task is to localize productive areas within the vast, seemingly featureless oceanic environment where prey are likely to be encountered, whereas at small scales, birds must pinpoint and capture prey using whatever proximate cues are available to them (Fig. 2).

I have proposed that natural scent cues in the marine environment present guideposts to aid seabirds in foraging and navigation (Nevitt, 2000). At large spatial scales, I have suggested that seabirds use changes in the olfactory landscape to recognize potentially productive foraging opportunities as they fly over them (Fig. 3) (Nevitt et al., 1995). These changes in the olfactory landscape reflect bathymetric features, which tend to accumulate phytoplankton and therefore prey, and we speculate that birds build up a map of these features over time (Nevitt, 2000). Thus, in the context of foraging, a bird might navigate to a historically rich productive area (a shelf break, a seamount or an upwelling zone) using mechanisms that we have yet to work out. The bird knows that it has arrived, however, by a predictable variation in the way the ocean smells (Fig. 2A). This change in the background scent triggers the bird to begin ARS at a much smaller scale (tens to hundreds of square kilometers). For

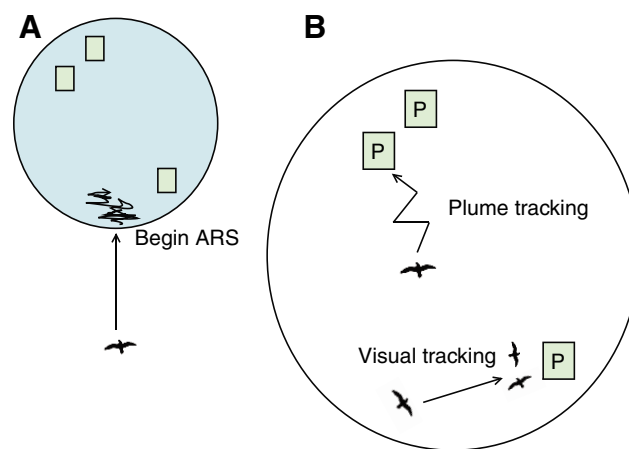


Fig. 2. Locating prey in a vast ocean. (A) The bird travels to a productive area using navigation mechanisms that have not yet been defined. Upon arriving, the bird may recognize the productive area by a change in the odor landscape, depicted here as a change in color. This change in the way the ocean smells triggers the bird to begin area-restricted search (ARS). (B) ARS may involve tracking odor plumes upwind to a prey patch or item (P), in combination with visually monitoring the foraging activity of other birds (Nevitt, 2000).

ARS, birds might use olfactory, visual or a combination of signals, including the foraging activity of other birds, to locate and capture prey (Fig. 2B) (Nevitt, 1999a; Nevitt et al., 2008).

This conceptual model stems from the discovery that seabirds and other marine predators can smell trace concentrations of sulfur compounds, which are naturally associated with oceanic features where prey tend to aggregate. Most critically, we have established that dimethyl sulfide (DMS), and its precursor dimethylsulfoniopropionate (DMSP), can be detected by a variety of marine organisms including procellariiforms (Nevitt and Haberman, 2003; Nevitt et al., 1995) and some species of fish (DeBose et al., 2008). This work has been extended by others to include harbor seals (Kowalewsky et al., 2006) and whale sharks (reviewed by Martin, 2007). DMS is a scented compound that is involved in climate regulation through the production of cloud condensation nuclei (reviewed by Simó, 2001). Biogenic marine

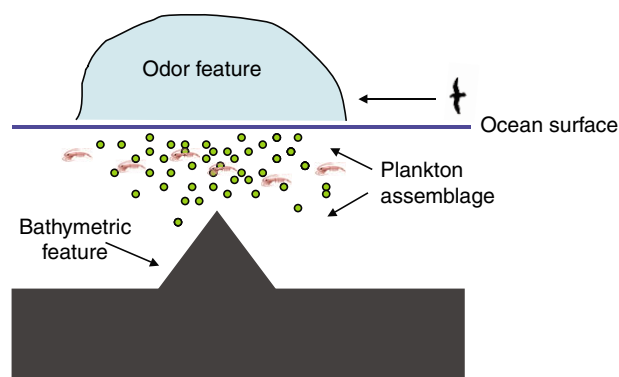


Fig. 3. An olfactory feature. A bathymetric feature (in this case, a seamount) where phytoplankton accumulate leads to a change in the odor landscape over the seamount that a bird might recognize upon arrival [adapted from Nevitt (Nevitt, 2000)].

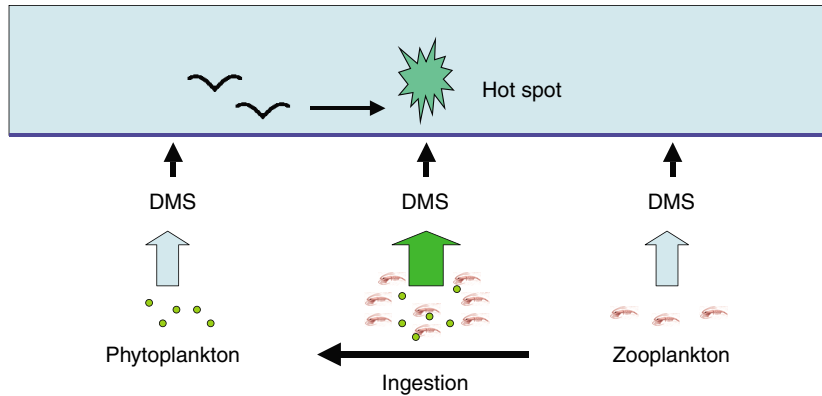


Fig. 4. Dimethyl sulfide (DMS) emissions increase when phytoplankton are grazed by zooplankton. Its precursor, dimethylsulfoniopropionate (DMSP) is a metabolite of phytoplankton, and an excretion product of zooplankton and other predators (Dacey and Wakeham, 1986; Hill and Dacey, 2006).

DMS is a major contributor to geochemical sulfur cycling. Thus, considerable effort has been directed towards understanding and monitoring its production and distribution in the marine environment, extending from local (prey patch size) to global spatial scales (reviewed by Simó, 2001). It is arguably unprecedented to have such detailed information on the production and distribution of a biogenic signal molecule, and these data have provided important insights into how seabirds and other marine organisms might use scented compounds in foraging and navigation at both local and global spatial scales.

DMS is largely produced as a byproduct of the metabolic decomposition of DMSP in marine phytoplankton (notably *Phaeocystis* in the Southern ocean) and other marine algae (including zooxanthalae in coral reefs) (Nevitt, 2000). In the Southern ocean, DMS is frequently associated with oceanic features where phytoplankton are plentiful (including upwelling zones, seamounts and shelf breaks) (Berresheim et al., 1989; Daly and DiTullio, 1996; McTaggart and Burton, 1992). These are areas where seabirds and other marine predators tend to aggregate and forage (Nevitt and Bonadonna, 2005b; Nevitt et al., 1995). DMSP tends to be released when phytoplankton cells are crushed and it is then rapidly converted to DMS *via* processes within the marine microbial food web (reviewed by Pohnert et al., 2007). As Fig. 4 illustrates, it is now well established that DMS emissions increase when phytoplankton are grazed by protozoans (Wolfe and Steinke, 1996), metazoans (Dacey and Wakeham, 1986) and krill (Daly and DiTullio, 1996), suggesting that, during ARS at small spatial scales, local elevations in DMS may opportunistically alert higher order predators (including birds) to rapidly accumulating aggregations of zooplankton (e.g. krill) and zooplankton predators (fish and squid).

Different sensory-based foraging strategies

To test these ideas experimentally, we conducted a multi-year study of small-scale foraging in the Atlantic sector of the Southern ocean, which confirmed that birds tend to be attracted not to prey scents *per se* but rather to odors such as DMS that are released during feeding interactions (Nevitt, 1999a; Nevitt, 1999b; Nevitt et al., 2004; Nevitt et al., 1995). To put it more colloquially, predators tend to be messy eaters, and procellariiform species are adapted to pay attention to who is eating whom (Hay and Kubanek, 2002; Nevitt, 1999b; Nevitt et al., 2004). For example, when DMS was presented to seabirds in controlled experimental trials performed at sea, several species of storm-petrels (*Oceanodroma* sp.), prions (*Pachyptila* sp.) and gadfly petrels (*Procellaria* sp.) responded by tracking this odor to its source, using a zigzag, upwind search behavior characteristic of olfactory tracking in organisms as diverse as fish, moths and crustaceans (DeBose and Nevitt, 2008;

Montgomery et al., 1999; Moore and Crimaldi, 2004; Nevitt et al., 1995; Willis, 2005; Zimmer-Faust et al., 1995). Surprisingly, these species tended to ignore krill odors, even though krill contributes significantly to their diets. By contrast, other typically larger and more conspicuous species recruited to visual cues and to odors associated with crushed krill (pyrazines). Nearly every species recruited to fishy scents, presumably through conditioning to fishing boats (Nevitt, 1999b; Nevitt et al., 2004; Nevitt et al., 1995).

These and other results suggested that procellariiforms within this sub-Antarctic assemblage exploit at least two fundamentally different sensory strategies for ARS. DMS responders are adapted to forage opportunistically on small or less concentrated prey patches, whereas more aggressive species (e.g. albatross, Diomedidae, and giant petrels, Macronectes) are better adapted to exploit multi-modal cues, which include scents from crushed prey and visual cues associated with the activity of other birds and marine predators (Nevitt, 1999b; Nevitt and Bonadonna, 2005b; Nevitt et al., 2004).

Evolutionary questions

We have now categorized search strategies for a number of species and species groups, and have begun to explore these behaviors using phylogenetic techniques (Van Buskirk and Nevitt, 2008). These analyses show that odor responsiveness is linked to life history strategy (Fig. 5). This surprising result has suggested to us that the early environment that chicks experience may be linked to the evolution of different sensory-based foraging strategies among the procellariiforms. Compared with other birds, procellariiforms have a lengthy chick-rearing period that can last from 6 weeks in some species to nearly a year in some of the larger albatrosses (Warham, 1990). Thus, chicks reared in burrows spend their early life in a dark, underground nest, where odors are likely to dominate their early sensory experience. Moreover, because predation on chicks tends to be extreme in breeding colonies, burrow-nesting chicks usually remain deep underground in the dark until just before fledging. By contrast, chicks reared above ground or in surface crevices grow up with early access to light, and are exposed to a wide range of stimuli, including visual, auditory and olfactory inputs. In an evolutionary framework, these differences in rearing environment could lead to differences in sensory function.

Conveniently for our needs, the procellariiforms have been the subject of several phylogenetic analyses (Bretagnolle et al., 1998; Imber, 1985; Kennedy and Page, 2002; Nunn and Stanley, 1998), and the underlying phylogenetic relationships between the subgroups are well researched. Using comparative methods, we found that burrow nesting was significantly correlated to DMS tracking

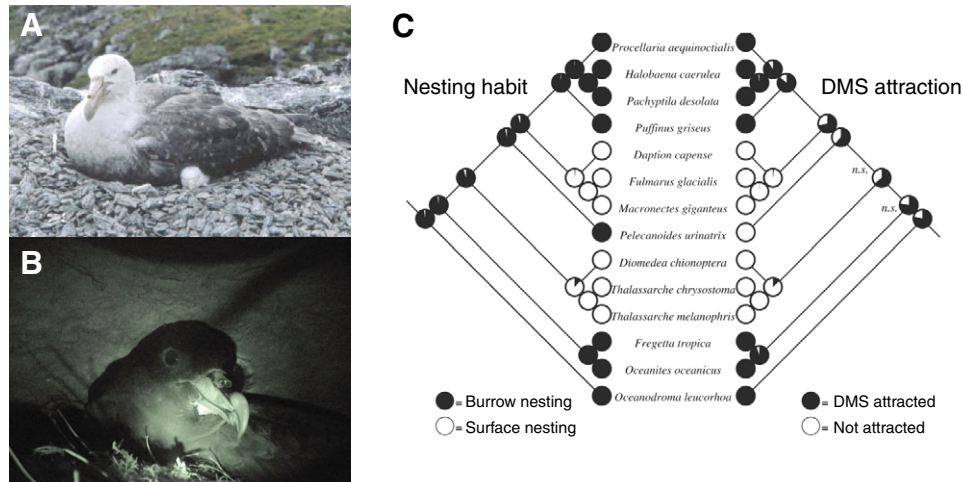


Fig. 5. Burrow nesting is correlated to behavioral sensitivity to DMS. (A) Southern giant petrel (*Macronectes giganteus*) brooding a chick on a surface nest. Photograph courtesy of R. Van Buskirk. (B) White-chinned petrel (*Procellaria aequinoctialis*) incubating an egg in its dark, underground burrow. Photograph provided by G.A.N. (C) Marginal probability reconstructions of ancestral states for nesting habit and DMS responsiveness using the topography of Nunn and Stanley (Nunn and Stanley, 1998). Each tree uses a global analysis and a Markov k -state one-parameter model (Pagel, 1999). Areas of pie charts indicate relative support for each ancestral state. Positive DMS attraction indicates those species that showed a statistically significant behavioral response to DMS in experimental trials. Log likelihood scores for the trees are -6.869894700 for nesting habit and 7.607159452 for DMS behavioral sensitivity. All reconstructions are significant for the ancestral state occupying the majority of each node, except for two nodes labeled as not significant (NS) [reproduced with permission from Van Buskirk and Nevitt (Van Buskirk and Nevitt, 2008)].

behavior, but not to a behavioral attraction to odors more directly associated with macerated krill or fish (including pyrazines or trimethylamine) (Van Buskirk and Nevitt, 2008) (Fig. 5C). Ancestral trait reconstruction further indicated that the procellariiforms arose from a burrow-nesting lineage, with the albatrosses and the fulmarine petrels independently adopting a surface-nesting strategy (Fig. 6). The implication is that the move to the surface may have constituted a life history innovation that presented new opportunities for selection to act on the development of other sensory modalities (most likely vision), while relaxing the need to track prey by scent, and offers new questions to explore. For example, surprisingly few studies have investigated anatomical or functional differences in eye structure among the procellariiforms, and our results suggest that a more complete characterization of these structures is warranted (see discussion in Nevitt et al., 2008). Equally interesting is that burrow nesting appears to be an ancestral trait, suggesting that some degree of DMS sensitivity may also have been an ancestral condition for the Procellariiformes and their sister order, the Sphenisciformes

(penguins). Penguins are generally not thought to be particularly olfactory birds, but since they also forage in productive areas that are characterized by high levels of DMS (Culik, 2001), their olfactory abilities should be further investigated. Interestingly, little penguins (*Eudyptula minor*) not only nest underground but also show tube-like structures on their nares during development (Kinsky, 1960).

Developmental mechanisms

In parallel with our phylogenetic work, we have been investigating how olfactory behaviors develop in burrow-nesting chicks. Blue petrels (*Halobaena caerulea*) are a common burrow-nesting species in the sub-Antarctic and they have served as an important model for these investigations. Adults forage opportunistically on a variety of crustaceans (including euphausiids, gammarid and hyperiid amphipods, mysids, decapods and copepods), squid and fish (Ridoux, 1994). We have shown that they respond to experimental deployments of DMS and fishy-smelling odors at sea (Nevitt et al.,

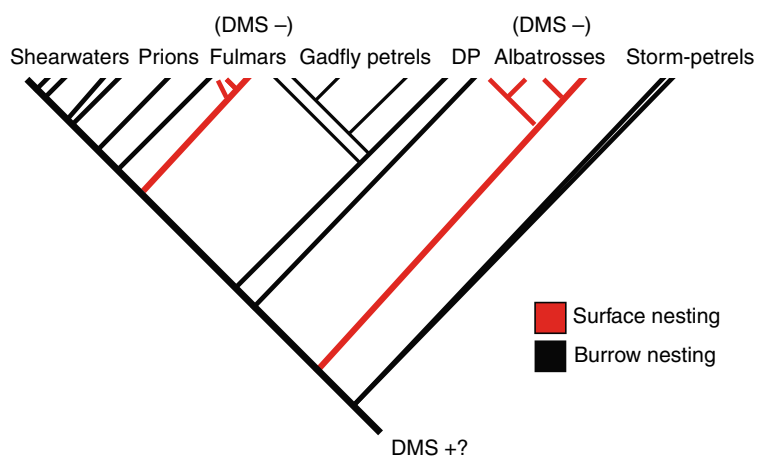


Fig. 6. Sketch illustrating the general phylogenetic relationships among the procellariiforms (see Kennedy and Page, 2002). DP indicates diving petrels. We have proposed that the procellariiforms may have arisen from a burrow-nesting lineage, with surface nesting arising independently in two groups (shown in red) as a derived condition. In the context of foraging, this change could have lessened the degree to which surface nesters rely on olfactory tracking to locate ephemeral prey patches (DMS-), while at the same time promoting a cascade of changes that ultimately led to a multi-modal foraging strategy, and the exploitation of distant and more consistently productive areas (Van Buskirk and Nevitt, 2008).

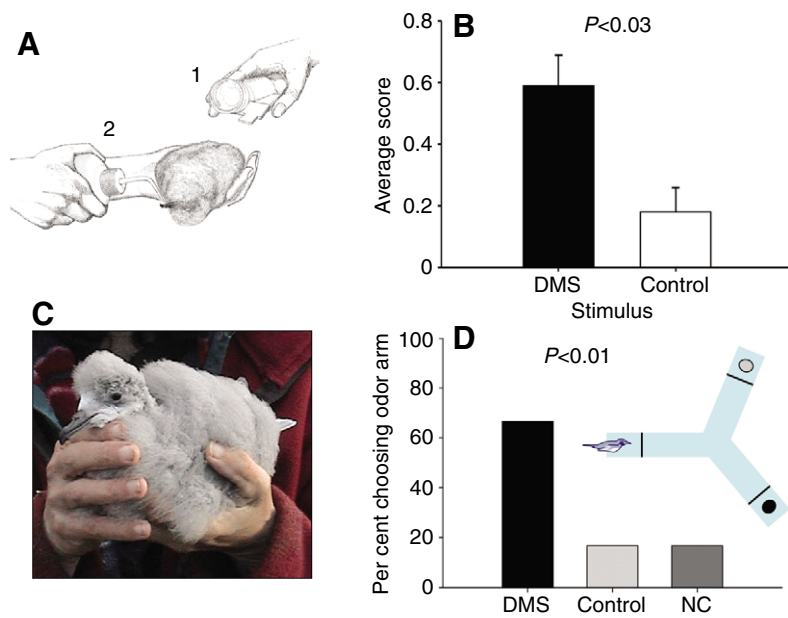


Fig. 7. Testing the response of blue petrel (*Halobaena caerulea*) chicks and fledglings to odors in the field. (A) The Porter method. A light bulb warms the chick to induce a 'sleeping' state (1). Puffs of odor are presented to the chick (2) and the reaction is scored following the convention of Porter et al. (Porter et al., 1999) [adapted from Cunningham et al. (Cunningham et al., 2003)]. (B) Responses to DMS using the Porter method. Average response scores to DMS (10 pmol l⁻¹, filled bar) and control (open bar, distilled water) solutions. Values are means + s.e.m. Differences are significant (Wilcoxon signed-rank test, $P < 0.03$, $N = 22$ chicks, 15–20 days old). (C) A blue petrel near fledging age. (D) Blue petrel fledglings orient towards DMS (10⁻¹² mol l⁻¹) in a Y-maze. The histogram shows the percentage of birds that chose DMS or control. NC indicates no-choice. $P < 0.01$, binomial test, $N = 24$. Photograph provided by G.A.N. [data from Bonadonna et al. (Bonadonna et al., 2006)].

1995), and that foraging activity is associated with areas of naturally elevated DMS concentrations (Nevitt, 2000).

Results from a number of studies have also shown that, even as chicks, blue petrels can detect and are attracted to prey-related odor cues well before they leave the nest. For example, we have used a simple non-injurious, behavioral assay to demonstrate that chicks can detect both DMS and ammonia, a urinary byproduct of most marine organisms, at concentrations ranging from 10⁻¹² to 10⁻⁶ mol l⁻¹ (Bonadonna et al., 2006; Nevitt et al., 2006) (Fig. 7A,B). However, they can also detect scents like rosy-smelling phenyl ethyl alcohol (PEA), which they would likely never encounter in nature (Cunningham et al., 2003; Nevitt et al., 2006). To test whether and which of these odors also elicit olfactory search, we studied chicks' responses to odors using a simple wind tunnel developed for field use. While we did not test DMS in this context, we found that blue petrel chicks responded to fishy-smelling odors but not to PEA by increasing their turning behavior (Cunningham et al., 2006). This search behavior was monitored in chicks 3–4 weeks before fledging, when their parents were still provisioning them, and is typical of olfactory search in other animals (DeBose and Nevitt, 2008; Moore and Crimaldi, 2004).

One of the questions we are currently exploring is whether odor preference is innate or, rather, learned through interactions with parents in the nest to prepare the chick to forage on its own after fledging. Like other procellariiforms, blue petrels provision chicks until a few weeks prior to fledging, at which time they are abandoned. Although other types of seabird provision and likely tutor their offspring at sea after fledging (Davoren and Montevecchi, 2003), procellariiform fledglings are adapted to forage on their own after leaving the nest. How they are able to accomplish this task is widely debated, and it is generally assumed that fledglings rely on the activity of other seabirds to find food (Ward and Zahavi, 1973). However, in a variety of other organisms, juveniles learn foraging odors through interactions with their parents (Hudson et al., 1999; Schaal et al., 2000; Vargas and Anderson, 1996). Although blue petrel chicks should be naive to DMS as they are growing up in the burrow, we have observed that adult birds often smell like DMS or phytoplankton when they return to the colony to provision chicks. This observation inspired us to test the response of more ambulatory

blue petrel fledglings to DMS at very low concentrations (10⁻¹² mol l⁻¹) just days before they were to leave the nest to forage. Using a simple Y-maze design, we found that blue petrel fledglings were attracted to DMS over a control odor, suggesting that a preference for DMS is already established before chicks leave the nest (Fig. 7C,D) (Bonadonna et al., 2006).

These results provide a framework for understanding how foraging behavior develops in blue petrels, and perhaps in other burrow-nesting species as well. Our current hypothesis is that, prior to fledging, chicks acquire information about prey-related odors through feeding interactions with their parents. Scents that the fledgling has previously associated with feeding may then serve to alert the bird to potential foraging opportunities as they are encountered at sea. These foraging opportunities will likely also involve interactions with hetero- or conspecifics (Silverman et al., 2004; Ward and Zahavi, 1973). As the fledgling gains foraging experience, it acquires a working knowledge of potential foraging locations by associating foraging success with other cues (e.g. scent cues associated with prey or productivity, visual cues provided by other seabirds, geomagnetic references associated with foraging location). It follows that a bird might thus develop a map of foraging locations, which are tied to spatially explicit features (such as a shelf break or seamount, for example). However, in the marine environment, productive foraging areas are dynamic. Foraging opportunities typically vary both temporally and spatially over large areas (for example, over upwelling and convergence zones), suggesting that any map cannot be strictly or entirely spatially explicit, but must be used together with proximate cues that allow the bird to recognize when it has arrived in a profitable zone to forage (Nevitt, 2000). Whether the foraging location is spatially fixed (such as a seamount) or dynamic (such as an upwelling or convergence zone), scent cues associated with trophic interactions would provide a foraging petrel with immediate feedback as to whether foraging is likely to be successful at that particular time or place.

Olfactory navigation

Because DMS is produced by phytoplankton, which often occurs in spatially predictable locations, a logical extension of this model

is that an ability to recognize predictable features such as shelf breaks or seamounts by scent may also be adaptive for navigation as the bird matures. Although olfactory navigation has been controversial in other avian systems, most notably in the context of pigeon homing (Able, 1995; Alerstam, 2006), much of the debate has centered on the inherent problems of identifying a biogenic scented compound or suite of compounds that pigeons can detect at appropriate concentrations and therefore utilize as a substrate for an olfactory map (reviewed by DeBose and Nevitt, 2008; Wallraff and Andreae, 2000). By contrast, in the marine environment, DMS is clearly linked to a physical source (phytoplankton) and association with predictable oceanic features is established (reviewed by Nevitt, 2000). Until recently, what was lacking was a clear demonstration that a procellariiform was sensitive enough to detect DMS at concentrations that would typically be encountered at sea (10^{-12} to 10^{-9} mol l⁻¹) since these concentrations are as much as a million times lower than previously reported odor sensitivities for birds (reviewed by Roper, 1999). We have since used heart rate monitoring techniques to demonstrate that Antarctic prions (*Pachyptila desolata*) can physiologically detect DMS at 5×10^{-9} mol l⁻¹, which was, for technical reasons, the lowest concentration we tested. We have also shown that these birds (as well as blue petrel fledglings, discussed earlier) will orient to DMS in non-foraging contexts in simple Y-maze experiments at concentrations as low as 10^{-12} mol l⁻¹ (Nevitt and Bonadonna, 2005b). Considering that many species routinely travel in the dark or under conditions where visibility is limited by fog or extreme cloud cover, these results provide some of the most compelling evidence to date that an olfactory landscape superimposed upon the ocean is detectable to seabirds, and may present navigational guideposts in non-foraging contexts.

Navigation systems tend to involve multimodal cues, however, and the spatial scales over which birds operate suggest that geomagnetic cues might be useful for cross-referencing positional information of olfactory features that are spatially predictable. Several albatross and petrel species [including black-browed albatross (*Diomedea melanophris*), waved albatross (*Diomedea irrorata*), wandering albatross (*Diomedea exulans*) and white-chinned petrels (*Procellaria aequinoctialis*)] have been investigated with this in mind, but do not apparently rely on earth-strength magnetic cues to navigate back to a nesting colony (Benhamou et al., 2003; Bonadonna et al., 2005; Mouritsen et al., 2003). Because navigation systems tend to be redundant (Able, 1995; Papi, 2006), these studies do not rule out the possibility that procellariiforms are sensitive to earth-strength magnetic fields. Many of the breakthroughs made in investigating geomagnetic orientation in marine organisms have been accomplished by manipulating test subjects (for example, sea turtles and spiny lobsters) in experimental coil systems (see Lohmann et al., 2008), and these methods have not yet been used to test procellariiforms even though they may be tractable for this type of investigation. While our research has focused on olfaction, how sensory information is integrated across different modalities is not known for this group of seabirds or, perhaps, for any marine organism (see discussion in DeBose and Nevitt, 2008; Nevitt et al., 2008). Gaining a more thorough understanding of the sensory worlds these birds inhabit will be an exciting area for future work.

Individual recognition

During the breeding season, procellariiforms must be able to relocate their nest or burrow, often in dense colonies among hundreds of other birds. This topic has been studied extensively in a variety of petrels, and the best evidence to date suggests that odor

cues are required for nest-site relocation in burrow-nesting species (for a review, see Nevitt and Bonadonna, 2005a). How this behavior develops has received much less attention, but may be a key to understanding how procellariiforms learn individual-specific odor cues for use in other social contexts. One of the few published studies addressing this topic found that European storm-petrel (*Hydrobates pelagicus*) chicks required an intact sense of smell to relocate their burrows after they had been displaced short distances (1 m) from them (Minguez, 1997). Subsequent experiments revealed that these chicks could distinguish their own body odor from a control scent, or even when tested against the scent of a conspecific (De Leon et al., 2003). The European storm-petrel population where these researchers worked was somewhat unusual for the species in that adults tended to nest in caves where chicks were observed wandering out of their burrows into enclosed, protected crevices. The researchers logically concluded that individual odor recognition was thus adaptive for homing behavior, because parents were only observed feeding chicks within the nest cavity, and chicks needed to return to the proper cavity to be fed (Minguez, 1997). As it turns out, however, this situation is not typical for European storm-petrels (e.g. Cramp et al., 1976). Due to heavy predation in colonies, storm-petrel chicks are much more likely to be confined to their burrow until they are ready to fledge. This more typical situation suggested to us that learning to recognize personal scents may be adaptive to the development of kin recognition in the context of both dispersal and mate choice (O'Dwyer et al., 2008).

We have since re-examined individual odor recognition using Leach's storm-petrels (*Oceanodroma leucorhoa*) as a model system. Leach's storm-petrels dig burrows up to 1 m deep where they lay a single egg, and chicks do not typically survive if they leave the burrow prior to fledging. In addition, our previous work indicates that Leach's storm-petrels are not natively philopatric to the nesting colony (E. Milot, L. Bernatchez and G.A.N., unpublished observations), suggesting that learning the scent of their own nest is not necessary for relocating the home colony once an individual reaches breeding age. Using simple choice tests, our results showed that Leach's storm-petrel chicks could recognize petrel-scented nest material, and could easily distinguish scents associated with their own nest material from scents associated with a conspecific's nest material. Given that an ability to recognize individual odor is not adaptive for homing at this life stage, these data suggest that the development of individual-specific odor recognition may serve other functions (O'Dwyer et al., 2008).

In line with this idea, we have also demonstrated that adult Antarctic prions (*Pachyptila desolata*) can perform individual choice tests based on scent alone (Fig. 8) (Bonadonna and Nevitt, 2004). Like other burrow-nesting procellariiforms, Antarctic prions return to colonies at night, and most interaction on land occurs underground, in dark burrows, suggesting that a chemically mediated identification system would be adaptive. The behavioral tests again employed a simple Y-maze design that allowed us to test responses to individual odors, collected from birds by first placing them in clean cotton bird bags and then passing air over the scented bags in the maze. We found that the majority of test birds preferred conspecific odor to their own odor, suggesting that birds were attracted to less familiar scents (Fig. 8A). This result was surprising because, like other procellariiforms, pairs are socially and biologically monogamous and philopatric to a single burrow. What is more, incubating birds do not typically explore other burrows because predation pressure can be severe in colonies even for adult birds that wander outside their burrows (e.g. Warham, 1996). In combination with these experiments, we also tested whether birds

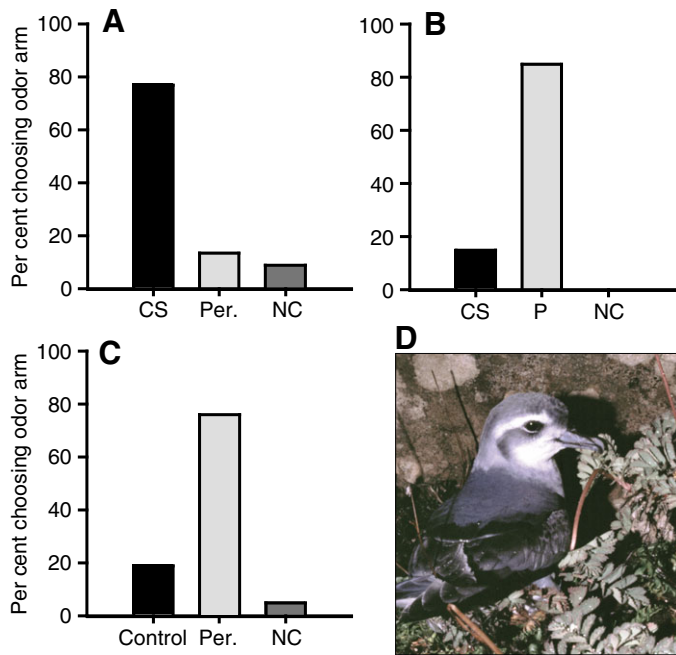


Fig. 8. Evidence for individual odor recognition in Antarctic prions. (A–C) Each histogram shows the percentage of birds that chose a particular odor from three Y-maze experiments. (A) Conspecific (CS) vs personal (Per.) odor ($N=22$). (B) Conspecific vs partner (P) odor ($N=20$). (C) Control vs personal odor ($N=21$). NC indicates no-choice. P values were determined by a binomial test. Note that experiments were not conducted sequentially but were dove-tailed depending on the availability of birds. (D) Photograph of an Antarctic prion (*Pachyptila desolata*). [Adapted from Bonadonna and Nevitt (Bonadonna and Nevitt, 2004).]

could recognize the scent of their mate. Here we found that birds tended to prefer the scent of their partner to the odor of a random conspecific (Fig. 8B). Additional tests showed that prions preferred their own personal odor, but only when tested against a blank odor (Fig. 8C).

Future directions

Together, these results have led us to wonder whether odors may also play a role in mate choice (Zelano and Edwards, 2002). The potential that scent-based cues contribute to mate choice decisions has been typically overlooked in birds [for exceptions, see Douglas (Douglas, 2008); Hagelin (Hagelin, 2004) and Hagelin and Jones (Hagelin and Jones, 2007)] but kin recognition is mediated by scent in a wide range of vertebrates, including humans (Wedekind et al., 1995), mice (Yamazaki et al., 1976; Yamazaki et al., 1979), fish (Reusch et al., 2001) and lizards (Olsson et al., 2003). Given that breeding birds form long-term pair bonds, producing just one egg per season with, presumably, little or no extra-pair paternity (Austin and Parkin, 1996; Quillfeldt et al., 2001; Swatscheck et al., 1994), selecting an appropriate mate is critical to lifetime reproductive success. Although we know little about how procellariiforms choose mates and establish long-term pair bonds (Jouventin et al., 1999), the fact that many procellariiform species are natively philopatric to remote islands (Warham, 1990) suggests that mechanisms may have evolved to avoid breeding with close kin and to enhance genetic diversity.

Although work in this context is still in its infancy, this new avenue of research suggests that the odor world of the

procellariiforms may be much richer than we originally suspected. Scents are used not only in foraging, homing and, potentially, navigation, but also within social and familial interactions. The data that we have collected so far suggest that petrels can learn familial odors as chicks in the nest, and that adults learn to recognize odors associated with their partner. While the underlying mechanisms are unclear, it is well established that genes of the major histocompatibility complex influence individual odors in other systems (Penn and Potts, 1998). This highly polymorphic set of genes encodes a range of molecules involved in immune responses and self–non-self recognition. Characteristics of the major histocompatibility complex, in turn, influence mating preferences in a diverse range of vertebrate groups (Carroll et al., 2002; Milinski et al., 2005; Penn and Potts, 1999). Thus, an intriguing future area of research will be to explore the mechanistic basis of individual recognition in the context of mate choice, and whether or not the major histocompatibility complex is involved.

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