Behavioral attraction of Leach's storm-petrels (*Oceanodroma leucorhoa*) to dimethyl sulfide

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Summary

A recent model for olfactory foraging by procellariiform seabirds suggests that these birds use biogenic sulfur compounds to locate productive areas for foraging in the southern oceans. The present study refines a simple approach to test birds' responses to odors on land and extends our knowledge to a northern species, the Leach's storm-petrel (*Oceanodroma leucorhoa*). Rather than working at sea, we tested the behavioral response to dimethyl sulfide (DMS) at night in breeding colonies on Kent Island, New Brunswick, Canada. Birds were presented with either 5 ml DMS (100 μmol l^{-1} concentration) or control (water) solutions from a platform 1.5 m in height positioned in a flyway 10 m from a breeding colony. We also tested birds' responses to cod liver oil, a well-established olfactory attractant of procellariiforms foraging at sea. Leach's storm-petrels approached DMS presentations nearly twice as frequently as they approached controls. We next compared the distribution of approaches against a Poisson process to test for evidence of social cueing. We found that approaches to DMS were significantly clustered. By contrast, the distribution of approaches did not depart significantly from a Poisson distribution for either cod liver oil or control presentations. Taken together, these results suggest that Leach's storm-petrels can smell DMS and potentially use it as a foraging cue. The results are consistent with the hypothesis that the detection of biogenic sulfur compounds in combination with other cues assists birds in locating foraging hotspots.

Key words: dimethyl sulfide, DMS, procellariiform seabird, olfaction, Leach's storm-petrel, *Oceanodroma leucorhoa*, smell.

Introduction

Leach's storm-petrels (*Oceanodroma leucorhoa* Vieillot) are one of the most common procellariiform seabirds breeding in the Northern hemisphere (for a review, see Huntington et al., 1996). Like other members of this order, these birds are highly pelagic, coming to land only to breed. At sea, Leach's storm-petrels are opportunistic surface feeders and are known to forage on a variety of plankton and nekton, including fish, krill and squid. These birds are commonly seen foraging at upwelling zones in zooplankton-rich areas where they capture prey at or near the surface of the water (Brown, 1988; Grubb, 1972; Haney, 1987).

The sensory mechanisms that Leach's storm-petrels use to locate food have not been well characterized, but several lines of evidence suggest that olfaction is critical to this behavior. Anatomically, these birds have among the largest olfactory bulbs of any bird (Bang, 1966). Behavioral observations suggest that, while visual cues may be used to locate feeding aggregations, odor cues aid birds in locating prey (Grubb, 1972) or productive areas where prey aggregate (Nevitt, 2000). Foraging in low light levels is implied, since many types of

prey catalogued in diet samples migrate vertically to the surface at night but typically occur at depths beyond the range of petrels foraging during the day (Vermeer and Devito, 1988). Behavioral experiments performed at the mouth of the Bay of Fundy, off New Brunswick, Canada have demonstrated an attraction of Leach's storm-petrels to cod liver oil (Grubb, 1972) and krill fractions (Clark and Shah, 1992). Results from preliminary cardiac conditioning experiments also indicate a physiological sensitivity to component odorants of krill, including carboxylic acids, amines and phenols (Clark and Shah, 1992), suggesting a highly sensitive olfactory system in this species.

Recently, Nevitt (2000) proposed a new model for olfactory foraging by procellariiform seabirds. This model suggests that olfactory foraging occurs at both large and small scales (Nevitt, 1999b, 2000, 2001). Over large scales (hundreds or thousands of kilometers), procellariiform seabirds use changes in the odor landscape as signals that they have arrived at a productive area to forage. Scents associated with primary production that contribute to this odor landscape include biogenic sulfur

compounds such as dimethyl sulfide (DMS; Nevitt, 1999a, 2000; Nevitt et al., 1995). Encountering such odors triggers birds to begin a small-scale, area-restricted search (tens of kilometers) to locate prey either directly, by olfactory tracking or glimpsing prey in the water, or indirectly, by locating aggregations of feeding seabirds (Nevitt and Veit, 1999). While the model has implications for procellariiforms worldwide, the data supporting it are based solely on detailed studies of Antarctic procellariiform species assemblages (see also Nevitt, 1999a, in press; Nevitt et al., 1995).

The purpose of our current study was to begin to extend this research to an easily accessible northern species, the Leach's storm-petrel. Leach's storm-petrels are abundant and could serve as a model species for studying a variety of problems pertinent to olfactory foraging at sea. In addition, we wanted to assess the utility of a simple behavioral assay that can be performed in breeding colonies on land rather than at sea. This assay was introduced by Clark and Shah (1992) in a preliminary study. They showed that Leach's storm-petrels will investigate krill-derived odors presented on high platforms along flyways in breeding colonies. In our study, we used similar methods to test two odors – DMS and cod liver oil – against unscented controls. We predicted that if Leach's storm-petrels investigated DMS more frequently than unscented control presentations, this would indicate an ability to smell DMS and potentially use it as a foraging cue over the ocean. We chose cod liver oil as a second test odor for this behavioral assay because it is already known to attract Leach's storm-petrels and other procellariiforms at sea (e.g. Grubb, 1972). As in earlier studies, cod liver oil might thus serve as a convenient positive control for the utility of the assay itself (e.g. Nevitt et al., 1995).

Materials and methods
Study site
This experiment was conducted between 8 July and 25 July 1996 at the Bowdoin College Biological Research Station, Kent Island, New Brunswick (44°35′ N, 66°45′ W). Experiments were conducted on clear nights between 23.00 h and 03.30 h. Wind speeds were negligible (<5 knots) during experimental trials; thus, wind directions were not recorded.

Experimental trials
We adapted methods described elsewhere (Clark and Shah, 1992) to test Leach's storm-petrels' attraction to odors in the field. This technique is loosely based on studies designed to assay attractiveness of procellariiforms to odors at sea (e.g. see Hutchison and Wenzel, 1980; Lequette et al., 1989; reviewed by Nevitt, 2001).

Experimental set-up
We mounted a small (10 cm×15 cm) plywood platform on a pole approximately 1.5 m high over an open field within 10 m of an active breeding colony (near 'petrel path'). A small amount (5 ml) of test odor [DMS (100 μmol l^{-1}), undiluted cod

liver oil (Bristol-Myers Squibb, New York, NY, USA) or control solution (plain water)] was placed in a small (25 mm) Petri dish and positioned on the platform. An observer, positioned 25 m crosswind from the platform, recorded activity of each bird as it approached the platform. Observations were assisted by a night vision scope (Model MKF28; Startron Mfg., Freeport, PA, USA) and recorded into a dictaphone.

Experimental protocol
A team of two people carried out experiments. One person was responsible for setting up the experiment while the second person recorded observations. The basic protocol was as follows: a test substance (odor or control) was deployed on the platform. This marked the beginning of an observation period. Observation periods lasted 5 min. During this period, the observer recorded the number of approaches to the platform. Birds were counted if they approached within 1 m of the platform or circled around it; flight trajectories could generally be seen, so that care could be taken to count each individual only once. At the end of 5 min, the trial ended. The odor was removed from the platform and placed in a double Zip-lock™ bag. Following a rest period of at least 10 min, the procedure was repeated. Each test odor (DMS or cod liver oil) was paired sequentially with a control, but the order of stimulus presentation (odor or control) was randomized; thus, all observations were made blind to the treatment being tested.

Rationale
Response criteria (observation period, intervals between trials and scoring method to avoid repeated measures) were determined in a series of preliminary trials. We concluded that recording detailed tracking (turning rate, instantaneous orientation with respect to wind direction) was not possible given the speed with which the birds approached the target. We limited observation periods and separated them by intervals of at least 10 min to avoid eye fatigue. Since birds tended to travel through the testing area on the way to the colony, this technique also helped to reduce testing individuals more than once. Finally, we determined that tests should be made over several nights to avoid pseudo-replication between trials.

Statistical analysis
We used a Wilcoxon paired-sample test to determine whether odor treatment (DMS or cod liver oil) attracted Leach's storm-petrels more than the paired control treatment (Zar, 1996). The analysis was performed on 12 paired trials (odor-control) for DMS and 11 paired trials for cod liver oil.

We then examined whether birds recruited independently to odor or control presentations. Here we used a two-tailed G-test to compare the distribution of the rate of attraction during each of the 12 (or 11) trials with the distribution predicted by a Poisson process (Zar, 1996). The distributions for each treatment (DMS, cod liver oil, DMS-control, cod liver oil-control) were considered separately.

Results

General observations

In trials where wind was detectable, Leach's storm-petrels tended to approach the platform from downwind in a zigzag flight pattern characteristic of olfactory responses of procellariiforms observed at sea (e.g. Nevitt, 2001, in press). Upon reaching the platform, birds tended to circle it briefly once or sometimes twice. Although vocalizations (contact calling) were commonly heard in the colony, we did not notice any obvious tendency for storm-petrels to call in association with either odor or control presentations. Birds were never observed to contact the platform or Petri dish and tended to leave the vicinity after a single investigation.

Quantitative observations

Leach's storm-petrels approached DMS presentations nearly twice as frequently as they approached controls (Fig. 1; $P<0.05$, $N=12$; Wilcoxon paired-sample test). By contrast, storm-petrels approached cod liver oil and controls at the same frequency (Fig. 2; $P>0.1$, $N=11$; Wilcoxon paired-sample test).

We next examined the distribution of approach rates of Leach's storm-petrels between experimental trials within each of the four treatments (DMS, DMS-control, cod liver oil, cod liver oil-control). If birds arrived in groups, or if the presence of an initial individual enhanced the probability of more arrivals during a 5-min test period, then we would expect the pattern of arrivals to differ significantly from a chance (Poisson) distribution.

Fig. 3A illustrates that the distributions of approach rates differed significantly from that predicted by a Poisson distribution for DMS presentations ($G=17.18$, $P<0.001$, d.f.=6). Thus, the behavior of some individuals may have enhanced the attraction of others. By contrast, Fig. 3B shows that Leach's storm-petrels approached cod liver oil at random ($G=2.3$, $P>0.1$, d.f.=3). Similarly, birds approached both
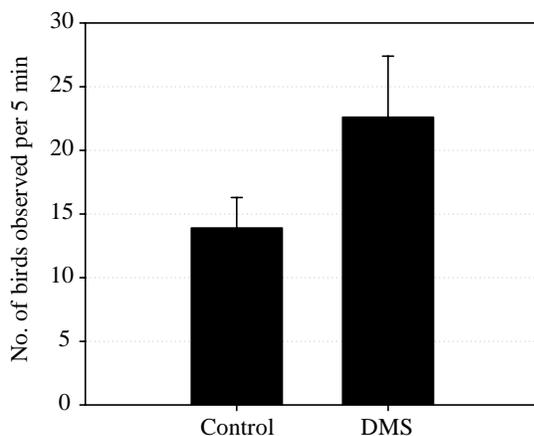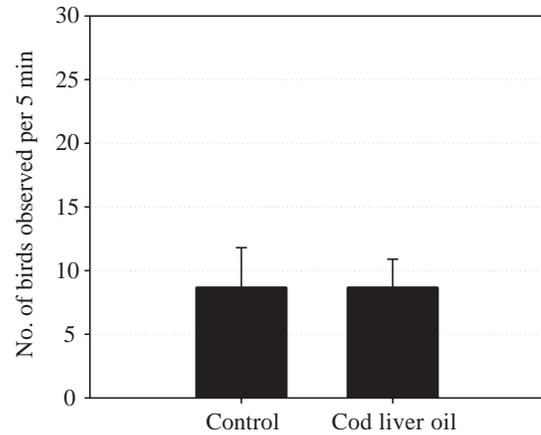

Fig. 2. Means ± S.E.M. of responses to cod liver oil and associated control presentations ($N=11$ paired trials). These data show that Leach's storm-petrels were attracted in similar numbers to cod liver oil and control presentations than to plain water in colony tests (see text for details).

control treatments at random (DMS-control, $G=3.79$, $P>0.1$, d.f.=3; cod-control, $G=7.43$, $P>0.05$, d.f.=3; data not shown but appear similar to Fig. 3B).

Discussion

DMS was a stronger attractant than control presentations but, surprisingly, cod liver oil was not. We initially considered that cod liver oil might have attracted fewer birds because it is less volatile than DMS and, therefore, not as noticeable to passing birds. However, a human standing several meters downwind of the platform was capable of distinguishing cod liver oil from control presentations, suggesting that birds could also smell the difference from downwind. Considering that Leach's storm-petrels are attracted to cod liver oil at sea, our interpretation is that birds could probably detect the cod liver presentations, but that DMS presented a more compelling stimulus for them to investigate in the colony setting. Given the low-wind conditions during testing (0–5 knots), the downwind DMS concentration detected was probably consistent with the DMS concentration that birds would encounter in natural foraging situations (nanomolar range: Dacey et al., 1984; Nevitt et al., 1995). However, because approaches tended to be clustered only with DMS, we suspect that birds were attracted to behaviors elicited by the odor in addition to the odor itself.

The interpretation that birds are recruiting to a scent as well as to social cues provided by conspecifics is consistent with a multimodal foraging strategy involving both olfactory and visual cues (Nevitt and Veit, 1999). Leach's storm-petrels forage opportunistically at upwelling zones and are often observed congregating in zooplankton-rich areas (Huntington et al., 1996). Prey species include fishes (myctophids), cephalopods, crustaceans (euphausids, decapods, amphipods, isopods, mysids and copepods) and jellyfish (Scyphozoa)

Fig. 1. Means ± S.E.M. of responses to dimethyl sulfide (DMS) and associated control presentations ($N=12$ paired trials). These data show that Leach's storm-petrels were attracted in significantly higher numbers ($P<0.05$) to DMS presentations than to plain water in colony tests (see text for details).
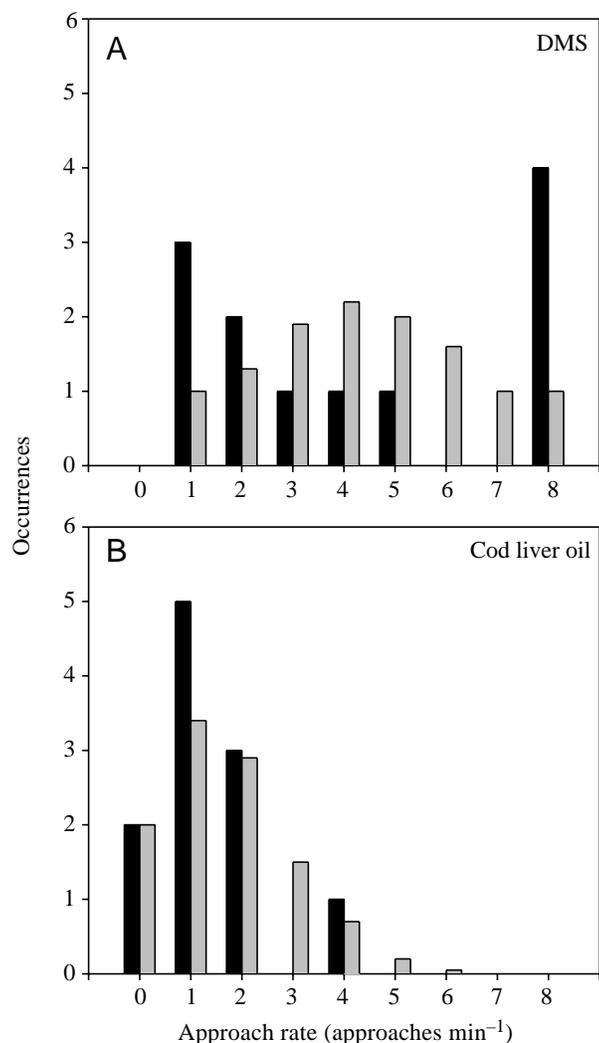
Fig. 3. Distributions of rates of attraction to (A) dimethyl sulfide (DMS) and (B) cod liver oil compared with distributions predicted by relative Poisson processes. These graphs compare the observed distributions of approach rates (black bars) to distributions predicted if birds were approaching the platforms at random (gray bars). The approach rate (approaches min^{-1}) was calculated by taking the total number of approaches recorded in a 5-min observation period and dividing by five. We then tallied the frequency of occurrence of each rate to generate the curves for DMS (N=12) and cod liver oil (N=11). The distribution of approach rates departed significantly from a Poisson distribution for DMS but not for cod liver oil presentations; approaches to DMS were clustered, whereas approaches to cod liver oil occurred at random (Zar, 1996).

(Harrison, 1984; Montevecchi et al., 1992; reviewed by Huntington et al., 1996); however, myctophids constitute as much as 70% of prey taken by volume in Northeast Atlantic populations (Montevechhi et al., 1992). These and other species migrate to the surface at night to feed (Watanabe et al., 1999). It is commonly assumed that Leach's storm-petrels use visual cues such as streaks of foam (Brown, 1988; Haney, 1987) or feeding activity of other birds (Haney et al., 1992;

Silverman and Nevitt, 1995) to pinpoint productive areas. However, once a productive area is localized, it is likely that Leach's storm-petrels and other species perform an area-restricted search using whatever cues are available.

Because zooplankton feeding is associated with the production of DMS, we have proposed that DMS signals productive areas of ocean where foraging success is likely to be high (e.g. Beresshiem, 1987; for a review, see Bates et al., 1992; Nevitt, 1995; Nevitt and Veit, 1999). DMS is a by-product of the metabolic decomposition of dimethylsulfoniopropionate (DMSP) in phytoplankton (Nguyen et al., 1988; Turner et al., 1995; Yang et al., 1992). DMSP is released by phytoplankton as they are broken up during grazing and is enzymatically cleaved to form DMS (e.g. Wolfe and Steinke, 1996). DMS released into the atmosphere is thus linked to the presence of zooplankton (Daly and DiTullio, 1996; Tokunaga et al., 1997) and may alert birds to areas where prey is likely to be feeding (reviewed in Nevitt, 2000; Nevitt and Veit, 1999).

Multimodal cues may alert birds to subtle differences in foraging opportunities. Myctophids, for example, are bioluminescent, but this characteristic is likely to change when animals are stressed or macerated, as happens during feeding. Distinctive scents may also be released as prey items are macerated, and these scents may invoke different behaviors. Working in colonies, Clark and Shah (1992) have demonstrated that Leach's storm-petrels can detect a variety of scented compounds from macerated krill, including trymethylamine, pyrazine and carboxylic acids. However, working in the southern oceans, we have found that odor cues associated with maceration are not necessarily attractive to smaller seabirds but might instead serve as a deterrent in highly competitive situations. For example, although Antarctic krill (*Euphausia superba*) comprise as much as 95% of the diet of Wilson's storm-petrels (*Oceanites oceanicus*), experimental testing at sea suggests that these birds avoid scents associated with macerated krill. This result is consistent with the hypothesis that macerated krill signals an increased risk of predation for smaller petrels by larger species in mixed-species feeding aggregations (Nevitt, 1999a).

Identifying how complex sensory processes drive the foraging ecology of interspecific interactions is a topic of great interest. The technique we adopted for this project is relatively straightforward, but we caution that demonstrating that a bird is attracted to an odor in a breeding colony does not necessarily suggest that the odor operates as a foraging cue on the ocean. Cod liver oil is one of the most potent attractants to Leach's storm-petrels at sea, but birds ignored it here, suggesting that the salience of the stimulus presentation needs to be considered in testing situations. Still, the present study provides a clear demonstration that perhaps the most compelling questions in this field are not simply related to identifying what compounds birds can smell or how these compounds disperse over the ocean but rather in elucidating how procellariiforms make use of a complex variety of foraging cues under circumstances that are ecologically meaningful.

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