Testing olfactory foraging strategies in an Antarctic seabird assemblage

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Summary

Procellariiform seabirds (petrels, albatrosses and shearwaters) forage over thousands of square kilometres for patchily distributed prey resources. While these birds are known for their large olfactory bulbs and excellent sense of smell, how they use odour cues to locate prey patches in the vast ocean is not well understood. Here, we investigate species-specific responses to 3-methyl pyrazine in a sub-Antarctic species assemblage near South Georgia Island (54°00′ S, 36°00′ W). Pyrazines are scented compounds found in macerated Antarctic krill (*Euphausia superba*), a primary prey item for many seabird species in this region. To examine behavioural attraction to this odour, we presented birds with either scented or 'unscented' vegetable oil slicks at sea. As a positive control for our experiments, we also compared birds' responses to a general olfactory attractant, herring oil. Responses to pyrazine were both highly species specific and consistent with results from earlier studies investigating responses to crude krill extracts. For example, Cape petrels (*Daption capense*), giant petrels (*Macronectes* sp.) and white-chinned petrels (*Procellaria aequinoctialis*) were sighted at least 1.8–4 times as often at pyrazine-scented slicks than at control slicks. Black-browed albatrosses (*Diomedea melanophris*) were only sighted at pyrazine-scented slicks and never at control slicks. Wilson's storm-petrels (*Oceanites oceanicus*), black-bellied storm-petrels (*Fregetta tropica*), great shearwaters (*Puffinus gravis*) and prions (*Pachyptila* sp.) were sighted with equal frequency at control and pyrazine-scented slicks. As expected, responses to herring oil were more common. With the exception of great shearwaters (*Puffinus gravis*), each of these species was sighted up to five times as often at slicks scented with herring oil compared with control slicks. Together, the results support the hypothesis that Antarctic procellariiforms use species-specific foraging strategies that are inter-dependent and more complex than simply tracking prey by scent.

Key words: procellariiform seabird, olfaction, smell, odour cue, pyrazine, petrel, albatross, shearwater.

Introduction

Procellariiform seabirds (petrels, albatrosses and shearwaters) forage over thousands of kilometres for patchily distributed prey resources using their sense of smell. Procellariiforms have among the largest olfactory bulbs of any bird (Bang, 1965, 1966; Wenzel, 1987; Wenzel and Meisami, 1990). While the olfactory abilities of many tubenosed species have been noted in the scientific and popular literature for well over 100 years (reviewed by Warham, 1996), we are only beginning to understand the variety of complex behavioural strategies that different species use to hunt by smell.

Current theory suggests that procellariiform seabirds use olfactory cues to forage at both large and small spatial scales (Nevitt and Veit, 1999; Nevitt, 2000, 2001). Over large scales (hundreds or thousands of square kilometres), procellariiform seabirds detect productive areas for foraging by changes in the odour landscape. Dimethyl sulphide (DMS) has been implicated as one of the odorants that birds use to identify areas of high primary productivity (Nevitt et al., 1995; Nevitt, 1999, 2000; reviewed by Hay and Kubanek, 2002). Once a productive area is found, birds switch to an area-restricted search strategy to pinpoint ephemeral prey patches (see Nevitt and Veit, 1999). During area-restricted search, hunting strategies vary according to species and feeding conditions. For example, some species may track prey using their sense of smell whereas others may be better adapted to use visual cues to locate prey patches, either by spotting prey directly or by seeing aggregations of other foraging seabirds alighting on the water (Silverman et al., in press).

We have been investigating foraging strategies used in area-restricted search in the procellariiform seabird assemblage in the Atlantic sector of the Antarctic, near South Georgia Island (54°00′ S, 36°00′ W). This assemblage is made up of a number of species that feed to a greater or lesser extent on a patchily distributed prey resource, Antarctic krill (*Euphausia superba*; e.g. Prince and Morgan, 1987). Thus, this species assemblage offers a relatively simple system for investigating how different species use olfactory cues associated with krill to exploit prey patches. Given the extensive information on

foraging ecology and diet of seabirds in this area (e.g. Croxall et al., 1984, 1997; Croxall and Prince, 1987), we can also begin to formulate and test hypotheses about the sensory ecology of how different species forage. For example, it has been suggested that larger, more aggressive species are likely to be attracted to scents associated with macerated krill in combination with social cueing by other birds. By contrast, smaller, less aggressive species may be better adapted to hunting prey opportunistically, primarily by tracking scents linked to krill or zooplankton grazing, such as DMS (Nevitt et al., 1995; Nevitt, 1999).
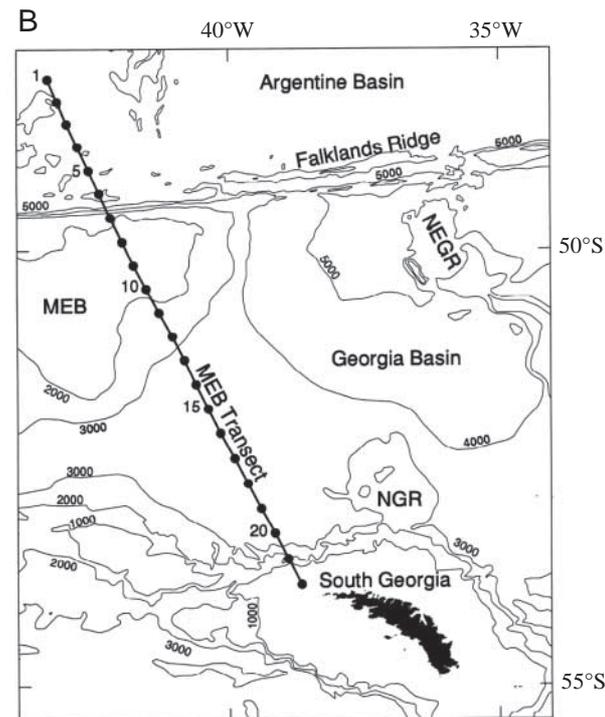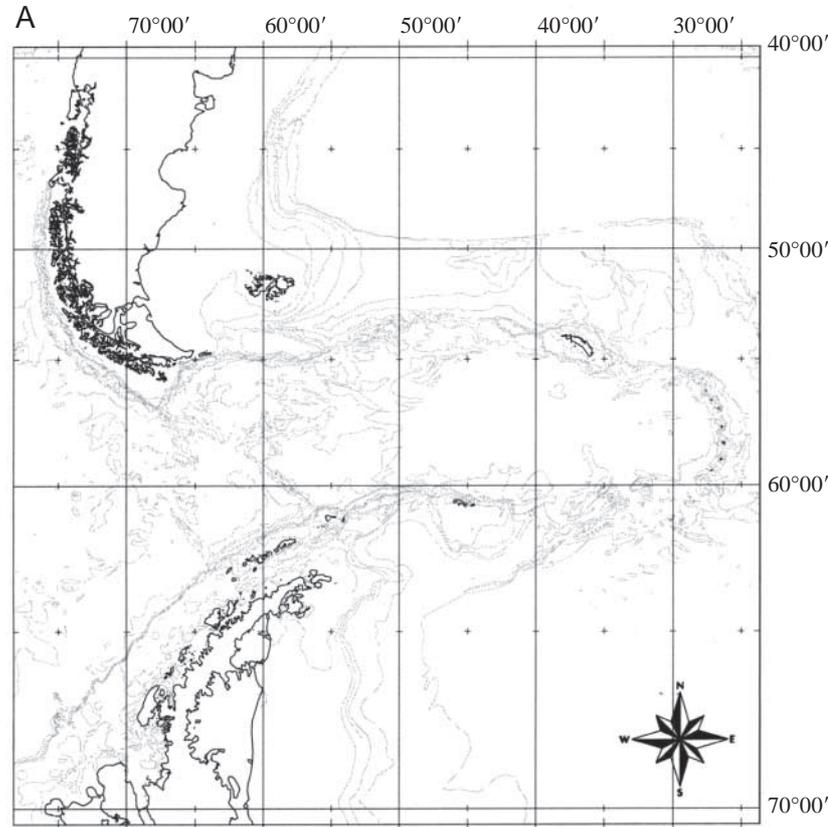
The present study was designed to test this idea by surveying responses of a much broader range of foraging procellariiforms to 3-methyl pyrazine, a scented compound found in extracts of macerated Antarctic krill (Kubota et al., 1989). Unlike crude extracts, 3-methyl pyrazine is colourless, and its concentration can be tightly controlled. Thus, in this study, we were able to examine the behavioural responses to the odour cue independent of any visual cues associated with prey. Since many species in the area are conditioned to fishy-smelling compounds (Nevitt et al., 1995), we also tested birds' responses to herring oil as a positive control for the experiment.

Materials and methods

The study was carried out as part of the British Antarctic Survey's Marine Life Science Core Program (Cruise # JR17; December 1996 – January 1997). Experimental trials were conducted along the Maurice Ewing Bank (MEB) where previous olfactory studies on DMS sensitivity were performed (Nevitt et al., 1995; Fig. 1). The transect runs north towards the Sub-Antarctic Front (43°40′ W, 48°10′ S) and south to the Willis Islands (west of Bird Island; 38°00′ W, 54°00′ S.) As in previous studies (Nevitt et al., 1995), working along this transect allowed us to sample olfactory responses from a wide range of species (Fig. 2) under variable environmental conditions that foraging birds typically encounter (Table 1).

Experimental design

Controlled experiments were designed to identify whether any procellariiform species might be attracted to 3-methyl pyrazine ('pyrazine'), a scented component of macerated Antarctic krill (Euphausia superba; Kubota et al., 1989; Clark and Shah, 1992). As in other studies (Nevitt et al., 1995), our aim was to produce a downwind odour concentration in the nanomolar range. We did this by deploying pyrazine-scented

Fig. 1. (A) The location of South Georgia Island relative to the Antarctic Peninsula. (B) Detail of the Maurice Ewing Bank (MEB) transect line and 23 stations. Experiments were conducted at stations 3, 4, 8, 9, 10, 13, 15, 19 and 20. Abbreviations: NGR, Northwest Georgia Rise; NEGR, Northeast Georgia Rise.
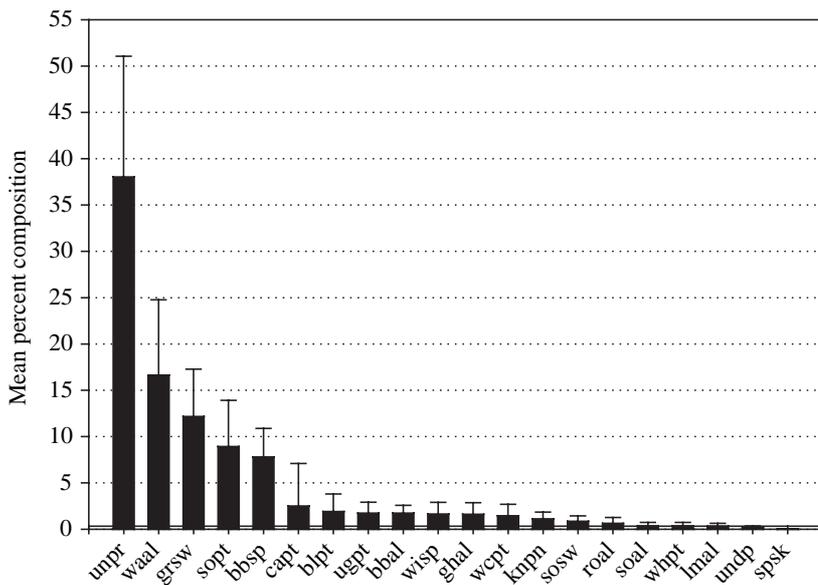
Fig. 2. Species composition of birds along the Maurice Ewing Bank (MEB) transect as determined by survey counts leading up to experimental stations (see text). Species codes are: unpr, unidentified prion (*Pachyptila* sp.); waal, wandering albatross (*Diomedea exulans*); grsw, great shearwater (*Puffinus gravis*); sopt, soft-plumaged petrel (*Pterodroma mollis*); bbsp, black-bellied storm-petrel (*Fregetta tropica*); capt, Cape petrel (*Daption capense*); blpt, blue petrel (*Halobaena caerulea*); ugpt, unidentified giant petrel (*Macronectes* sp.); bbal, black-browed albatross (*Diomedea melanophris*); wisp, Wilson's storm-petrel (*Oceanites oceanicus*); ghal, grey-headed albatross (*Diomedea chrysostoma*); wcpt, white-chinned petrel (*Procellaria aequinoctialis*); knpn, king penguin (*Aptenodytes patagonicus*); sosw, sooty shearwater (*Puffinus griseus*); roal, Southern royal albatross (*Diomedea epomophora*); soal, sooty albatross (*Phoebetria fusca*); whpt, white-headed petrel (*Pterodroma lessonii*); lmal, light-mantled sooty albatross (*Phoebetria palpebrata*); undp, unidentified diving petrel (*Pelecanoides* sp.); spsk, South polar skua (*Catharacta maccormicki*).

vegetable oil slicks on the ocean surface at seven different locations along the MEB transect (Fig. 1B). Because environmental conditions varied and surface slicks also presented visual cues to seabirds, pyrazine-scented slicks were always paired with unscented 'control' slicks. We reasoned that if birds used pyrazine as a foraging cue, then more birds would be attracted to slicks scented with pyrazine than to control slicks. Since we have previously established that many species in the area are conditioned to fishy-smelling compounds (Nevitt et al., 1995), we reasoned that if birds were attracted to pyrazine, then their response should be qualitatively similar to their response to herring oil. Thus, we also tested birds' responses to herring oil at six locations to provide a positive control for interpreting our results.

While the ship was positioned into the wind, either a control, pyrazine- or herring-scented oil slick was deployed off the stern. Slicks usually drifted about 100 m from the ship, allowing easy observation of approaching birds. Prior to deployment, a count was made of all birds within a 180° arc with a radius of 300 m from the stern of the ship. Once a slick was deployed, one person using binoculars made observations at 1-min intervals for 12 min; data were recorded by a second person standing close by. Birds were counted if they (1) flew upwind over the slick within approximately 1 m of the surface, (2) landed, (3) milled or (4) pattered on the slick. To avoid

bias, the order of slick presentation (control, pyrazine or herring) was randomised at each location, and deployments were separated by at least one hour. We generally tested only two slicks at a location due to time constraints imposed by the ship's schedule. To eliminate inter-observer bias, the same observer recorded data for all trials and was kept blind with respect to the treatments being tested. Slicks were tested one at a time and dissipated within 20 min. Standard meteorological data were recorded during all trials using shipboard instrumentation (Table 1).

Odours

Pyrazine (200 mmol l^{-1} 3-methyl pyrazine in 2.5 litres of vegetable oil; 0.5 moles total; Sigma-Aldrich, St Louis, MO, USA), herring (50 ml commercial herring oil; diluted to 2.5 litres in vegetable oil) and control (2.5 litres of vegetable oil) slicks were prepared approximately 1 h before experiments. Because turbulent plume dynamics are not easily predicted under natural conditions (Dusenbury, 1992), we adapted a simple but well-established sector model derived from empirically sampling turbulent odour plumes in nature to estimate average odour profiles downwind of slicks (Elkinton and Cardé, 1984). This approach is conservative: it assumes that the odour disperses as a cone-shaped plume downwind of the slick with edges 20° from the axis and that dispersal is continuous and rapid (5–10 m s^{-1}) due to wind. The wind speed recorded during our experiments ranged from approximately 8 to 20 knots (3.85–10.28 m s^{-1}; Table 1). Thus, even over the short (12 min) time course of the experiment, the odour gradient established is predicted to extend kilometres downwind of the slick.

As in other studies (Nevitt et al., 1995), we used this model to calculate a theoretical maximum for the average concentration that a bird might encounter traversing a plume extending 1 km downwind of the slick. To do this, we

Table 1. *Environmental parameters during experimental trials*

Environmental parameter	Range
Air temperature (°C)	2.3–9.4
Surface sea temperature (°C)	2.7–10.6
Barometric pressure (hPa)	980.3–1009.4
Wet bulb temperature (°C)	96.6–96.7
Dry bulb temperature (°C)	4.3–11.0
Wind strength (m s^{-1})	3.85–10.28

calculated what would happen if the entire amount of odour deployed was instantaneously concentrated in a plume extending 1 km downwind of the slick. While turbulent odour plumes are not homogeneous, even this exaggerated scenario predicts an average concentration of <10 nmol m^{-3}. Naturally occurring levels of 3-methyl pyrazine are not known; however, based on studies of other scented compounds that have been measured over the southern oceans (Berresheim, 1987) and recent studies of sensitivity thresholds (G.N., unpublished data), we considered this concentration to be within biologically relevant levels.

Underway observations

To determine background species compositions along the MEB (Fig. 2), we counted all birds within a 100 m-wide 'box' 100 m off the bow of the ship using standard strip transect methodology while the ship was underway (Tasker et al., 1984). Using binoculars, one observer continuously scanned the area while a second person entered data directly into a portable computer. Birds were counted for 3 km prior to arriving at stations where slicks were deployed.

Statistical analysis

Our goal was to compare the attractiveness of scented slicks and control slicks. An inherent difficulty to performing behavioural studies at sea is that, since individuals cannot be marked, observations of individuals are not strictly independent. In addition, responses tend to be highly variable between species over time. Moreover, because experiments are usually performed in different geographical locations contingent upon ship availability, true replicates can seldom be performed. While such issues have generally been ignored in the literature (e.g. Hutchison and Wenzel, 1980), our analysis was designed to deal with these concerns more directly. First, we defined the response that each species gave to a particular slick in terms of 'slick attentiveness' over the 12-min observation period. Attentiveness was determined by summing counts per minute (or 'bird-minutes') over time. We reasoned that if experimental and control slicks were equally attractive to birds, then the two slicks should also have equal

probabilities of attracting birds for an additional bird-minute throughout the 12-min observation period. For each species, we then tested whether the proportion of bird-minutes spent on scented slicks (either pyrazine or herring) was equal to the proportion of bird-minutes spent on control slicks (G-test for pooled data; Zar, 1996). Analyses were performed on pooled data to accommodate variability in weather parameters and bird distributions down the length of the MEB transect.

Results

Species-specific attraction to odour cues

During surveys between testing stations, we identified 18 different species of procellariiforms along the MEB transect (Fig. 2). Of these 18 species that made up the 'background' population, nine routinely recruited to scented slicks (Table 2). The species composition of the experimental recruits did not correlate to the nine most abundant species sighted along the transect (Spearman rank correlation: r_s=0.26; P>0.1) or to the species composition of ship followers surveyed prior to the start of experimental trials (see Materials and methods; r_s=0.22; P>0.1). These comparisons suggest that scented slicks attracted a sub-sample of species in the area rather than simply those individuals that happened to be in the area.

Preference for scented over control slicks varied with respect to odour (Fig. 3). Of the nine species that were attracted to slicks, four species clearly exhibited a special interest in pyrazine-scented slicks as compared with control slicks (Fig. 3, black bars). Cape petrels, giant petrels and white-chinned petrels, for example, were sighted 1.8–4 times as often at slicks scented with pyrazine than at control slicks; black-browed albatrosses were sighted only at pyrazine-scented slicks and never at control slicks. The remaining five species were sighted just as frequently at pyrazine-scented as at control slicks. These species included great shearwaters, prions, wandering albatrosses, black-bellied storm-petrels and Wilson's storm-petrels.

By contrast, eight of the nine species participants recruited to herring-scented slicks in significantly higher numbers than to control slicks (Fig. 3, grey bars). Cape petrels, giant petrels,

Table 2. *Comparison of the composition of species present before and during experimental trials*

Common name	Species	Pre-trial survey (%)	Experimental recruits (%)
Prion	*Pachyptila* sp.	78.7	40.8
Giant petrel	*Macronectes* sp.	6.3	9.0
Wandering albatross	*Diomedea exulans*	5.8	2.5
Great shearwater	*Puffinus gravis*	5.1	2.7
White-chinned petrel	*Procellaria aequinoctialis*	2.0	3.9
Black-bellied storm-petrel	*Fregetta tropica*	0.6	5.0
Black-browed albatross	*Diomedea melanophris*	0.6	1.2
Cape petrel	*Daption capense*	0.5	6.2
Wilson's storm-petrel	*Oceanites oceanicus*	0.4	24.7

Data are presented as percent of total observations (pre-trial survey of ship followers, N=2048; experimental recruits, N=2361). Species composition of ship followers was determined from pre-trial surveys (see Materials and methods).
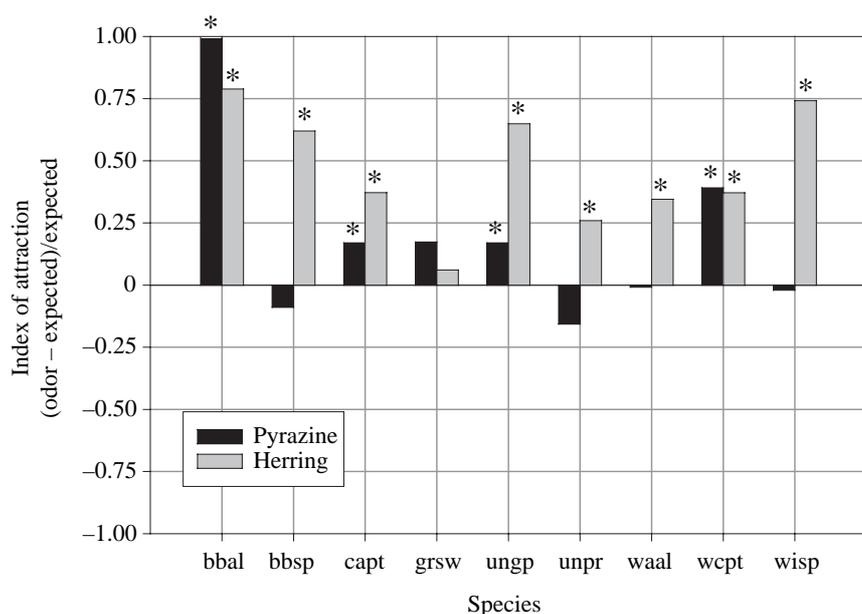
Fig. 3. Relative attraction to experimental (pyrazine, black bars; herring, grey bars) and control slicks. Positive values (upward bars) indicate a positive attraction to pyrazine- or herring-scented slicks whereas negative values (downward bars) indicate a positive attraction to control (plain vegetable oil). So, for example, a value of +1 indicates that a species was only observed at an experimental slick and never at a control slick. An asterisk (*) indicates a significant attraction in the direction indicated (G-test for pooled data, $P<0.05$; Zar, 1996).

black-browed albatrosses, white-chinned petrels, prions, wandering albatrosses, black-bellied storm-petrels and Wilson's storm-petrels were sighted 2–5 times as frequently at herring-scented slicks than at control slicks. Only great shearwaters failed to discriminate between herring-scented and control slicks.

Nine procellariiform species were recorded in transect surveys but were not attracted to slicks. These species were soft-plumaged petrels, blue petrels, sooty shearwaters, Southern royal albatrosses, sooty albatrosses, light-mantled sooty albatrosses, grey-headed albatrosses, white-headed petrels and common diving petrels. Non-procellariiform species noted in the area included king penguins and South polar skuas, neither of which recruited to slicks.

Differences in response profiles

The temporal response profiles over the 12-min observation period were distinctive for different species and odours. By subtracting controls from experimental values, we could get a clearer picture of the patterns of responses over time that could be attributed to the odour cue alone. Fig. 4 illustrates three characteristic patterns that we observed using this technique. In the first pattern, recruitment to an odour cue increased over time and then stabilised. Fig. 4A illustrates this pattern for Wilson's storm-petrels in response to herring oil (open circles); black-bellied storm-petrels showed a similar pattern of recruitment in response to herring oil slicks. Note that because the response to pyrazine was indistinguishable from the control response for this species, the plot of the pyrazine response yields a flat line or 'null' response (Fig. 4A, filled circles).

In a second pattern, the relative proportion of birds responding to an odour cue peaked rapidly within 3–4 min and then diminished to near zero levels over the remainder of the 12-min observation period. This pattern most likely reflects conspecific visual cueing initiated by the odour

presentation. Fig. 4B illustrates this pattern. Here, giant petrels in the visual area accumulated rapidly at both herring- (open circles) and pyrazine-scented slicks (filled circles) and then just as quickly disbanded. We observed similar, though less dramatic, profiles for wandering albatrosses in response to herring oil.

Fig. 4C illustrates the third type of response profile that we observed. Here, the proportion of birds responding to an odour cue peaked rapidly and cyclically throughout the observation period, most likely reflecting birds milling over the slick. This pattern is illustrated for white-chinned petrels in response to both herring oil (Fig. 4C, open circles) and pyrazine (Fig. 4C, filled circles). For this species, response profiles to pyrazine and herring oil showed very similar periodicity. Cape petrels, black-browed albatrosses and prions exhibited similar patterns.

Discussion

We found that responses of seabirds to pyrazine near South Georgia mirrored responses to macerated krill that we have previously reported near Elephant Island (61°00′ S, 56°00′ W; Nevitt, 1999). In both studies: (1) Cape petrels and giant petrels were sighted up to four times more frequently at scented slicks than at control slicks, suggesting that these birds were attracted to olfactory cues from macerated krill; (2) black-browed albatrosses were sighted only at scented slicks and never at control slicks and (3) Wilson's storm-petrels and black-bellied storm-petrels were sighted with equal frequency at pyrazine and control slicks. Combined, these results suggest that 3-methyl pyrazine is one of the scented compounds in macerated krill that is attractive to some procellariiforms. Great shearwaters (indifferent to pyrazine) and white-chinned petrels (attracted to pyrazine) were not numerous in the Elephant Island study area, so no comparisons are possible for these two species.

Other studies

Although euphausids are common prey to procellariiforms worldwide (reviewed by Warham, 1996), only a few other studies have tested responses of seabirds to krill-related odours in the context of foraging at sea (Hutchison and Wenzel, 1980; Hutchison et al., 1984; Nevitt, 1994, 1999; Nevitt et al., 1995). Working in the coastal waters off southern California,
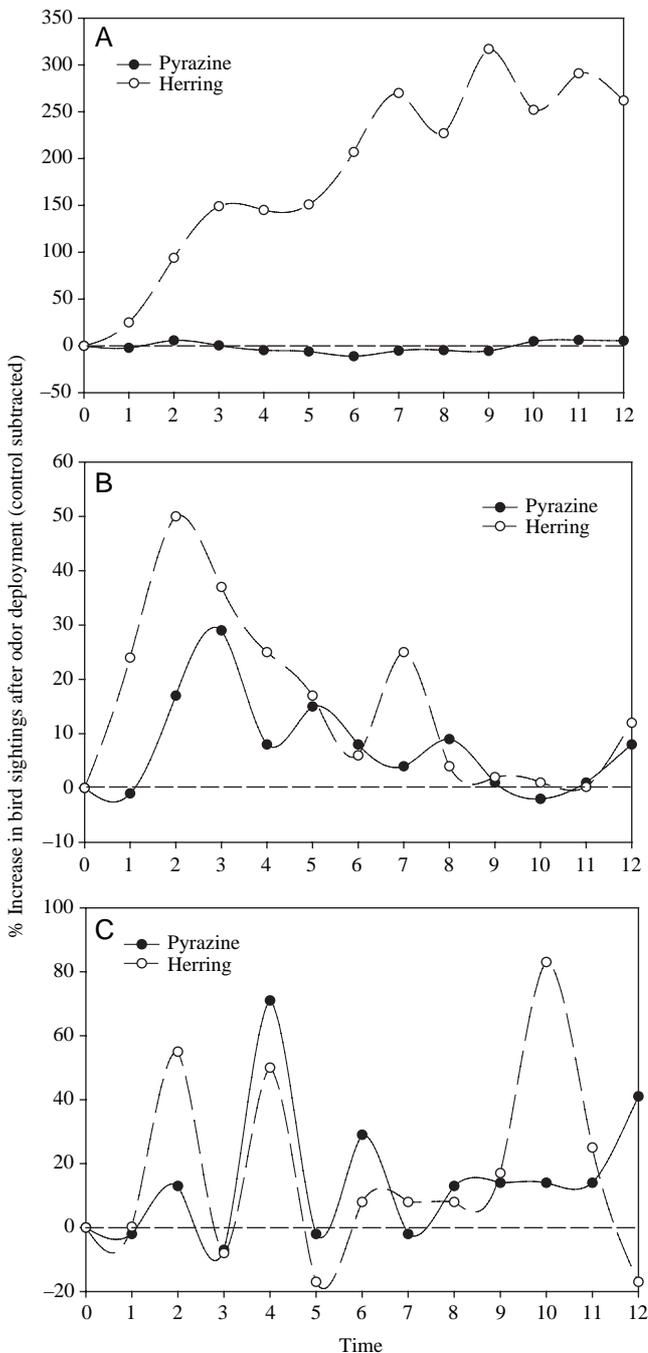

Fig. 4. Three 'typical' response profiles over time to pyrazine (filled circles) and herring oil (open circles); control data are subtracted. Profiles are illustrated for (A) Wilson's storm-petrels (*Oceanites oceanicus*), (B) giant petrels (*Macronectes* sp.) and (C) white-chinned petrels (*Procellaria aequinoctialis*) (see text).

Hutchison et al. (1984) compared the attractiveness of a volatile fraction of cod liver oil to homogenates of squid (*Loligo opalescens*) and Antarctic krill. Their results showed that sooty shearwaters were strongly attracted to floating wicks scented with these food-related compounds, suggesting that odours from squid and krill homogenates could serve as foraging cues under more natural situations. In our study, sooty shearwaters did not recruit to either scented or unscented slicks. However, these birds were sighted only incidentally during transect surveys (Fig. 2), suggesting that there were not many of them around to participate in our experiments.

By contrast, Hutchison et al. (1984) found that Northern fulmars (*Fulmaris glacialis*) were not attracted to food-related cues. Northern fulmars do not occur in the Southern oceans, and a related species, the Antarctic fulmar (*Fulmaris glacialoides*), was absent from the transect during the present study. They have, however, been found to be unresponsive to macerated krill in previous work conducted in the Elephant Island study grid near the Antarctic Peninsula (Nevitt, 1999).

With respect to storm-petrels, Hutchison et al. (1984) provide no data concerning attraction of this species to macerated krill at sea. However, whole-krill homogenates and component odours derived from krill (including pyrazine) have been shown to attract Leach's storm-petrels, *Oceanodroma leucorhoa*, in other land-based behavioural experiments (Clark and Shah, 1992). These researchers tested birds' responses to krill odours presented on platforms positioned within breeding colonies in New Brunswick. Because these behavioural trials were not performed at sea, their relevance to foraging is unclear (see discussion in Nevitt and Haberman, 2003). Even so, Clark and Shah (1992) were the first to use simulation techniques to predict the dispersion profiles of pyrazine and other volatiles released by macerating krill. Their model inferred that a patch of krill 0.5 m in diameter might be detectable to foraging Leach's storm-petrels from distances in the order of kilometres. Such detection ranges are greater than the visual range of a petrel foraging within a metre of the surface of the water in seas that are routinely metres high (Clark and Shah, 1992; Haney et al., 1992; see also review by Nevitt and Veit, 1999).

More precise data on sensory thresholds to specific natural scented compounds is needed to get a clearer understanding of olfactory detection ranges. But to start to answer these questions, we need to know what specific compounds seabirds respond to in real-life foraging situations. The present study illustrates that responses elicited by pyrazine and krill extracts (Nevitt, 1999) are similar across species, even in different regions of the sub-Antarctic. Thus, pyrazine is a good candidate to examine behavioural response thresholds (e.g. Cunningham et al., 2003) and will undoubtedly serve as a useful probe to facilitate future work modelling odour dispersal and transport associated with krill swarms.

Inter-specific differences in olfactory foraging

While it is commonly assumed that procellariiform seabirds conduct olfactory-mediated area-restricted search by tracking

odour cues emitted from prey, understanding the dynamics of olfactory foraging is turning out to be more complex than simply determining detection thresholds for particular prey-related odorants. For example, an intriguing feature of the results presented here and elsewhere (Nevitt, 1999) is that inter-specific differences in the response to krill-derived odours do not reflect the proportions by mass of krill in these birds' diets (Table 3). Species whose diets comprise 30–90% Antarctic krill by mass are not preferentially attracted to krill odours. Thus, an olfactory foraging model that assumes an increased attraction to krill-derived odours by krill-eating species is probably a naïve representation of the complex interactions driving area-restricted search.

We have proposed an alternative explanation based not on diet but on foraging behaviour (Nevitt 1999), and the data presented here support this model. Our model suggests that species that routinely forage in large, mixed-species feeding aggregations use odours associated with macerated krill to locate these aggregations from beyond the visual foraging range. These birds tend to rely heavily on visual cues (such as aggregations of birds foraging) to locate foraging hotspots. Smaller, less aggressive species use a different strategy: these birds track prey or productive hotspots by smell, tending to exploit scented compounds associated with primary productivity (e.g. DMS) to find prey opportunistically (Nevitt et al., 1995).

In support of this idea, the relative proportions of different species engaged in feeding aggregations near South Georgia reflect the species-specific responses we observed to both macerated krill and pyrazine (Harrison et al., 1991). Black-browed albatrosses, giant petrels and white-chinned petrels dominated mixed-species feeding aggregations and were also attracted to crude krill extracts or pyrazine in our studies. Wilson's storm-petrels and prions, however, were present in much smaller proportions (Harrison et al., 1991), possibly reflecting an increased risk of predation by species such as

giant petrels at such aggregations (Hunter, 1983; G.N., personal observation). These species were not attracted to krill scents and, again, this suggests an alternative foraging strategy for these smaller, more vulnerable species.

The key to this alternative foraging strategy may be found by considering the responses of these species to DMS. DMS is released by phytoplankton (e.g. *Phaeocystus* sp.) during grazing by Antarctic krill and other zooplankton (Dacey and Wakeham, 1986; Daly and DiTullio, 1996). Both Wilson's storm-petrels and prions have been shown to be attracted to DMS in experimental trials, whereas Cape petrels and other large species present at feeding aggregations are not (Nevitt et al., 1995). The implication is that DMS-responders may rely more on indirect indicators of krill to opportunistically exploit zooplankton-rich foraging areas independently of feeding aggregations. A familiarity with DMS as a foraging cue may also give smaller birds such as storm-petrels a competitive edge to locate and exploit ephemeral feeding patches independently of other species.

Little information is available about how large, mixed-species feeding aggregations develop under natural conditions, particularly in terms of which species arrive first. Verheyden and Jouventin (1994) have suggested that species such as storm-petrels may initiate these aggregations by being the first birds to locate krill swarms. If this is the case, our data suggest that stages of recruitment may be dictated by different odour cues and may be partially dependent on a species-specific response to these different cues. For example, recruitment of Wilson's storm-petrels may be initiated by tracking DMS hotspots that presumably develop as krill begin to graze, in consort with visual cueing by conspecifics (see discussion in Nevitt and Haberman, 2003). As other species join, subsequent recruitment may be facilitated by olfactory cues released from macerated krill, in addition to obvious visual signals provided by the aggregation itself.

Alternatively, pyrazine and other scented compounds in krill

Table 3. *Odour responses relative to the % by mass of krill in the diet of 13 Antarctic procellariiforms*

Common name	Species	% Krill	DMS	Krill	Fish
Blue petrel	*Halobaena caerulea*	75	+	+	+
White-chinned petrel	*Procellaria aequinoctialis*	47–59	+	+	+
Black-bellied storm-petrel	*Fregetta tropica*	5	+	−	+
Prion	*Pachyptila* sp.	1–87	+	−	+
Wilson's storm-petrel	*Oceanites oceanicus*	40–85	+	−	+
Diving-petrel	*Pelecanoides* sp.	15–78	0	0	0
Black-browed albatross	*Diomedea melanophris*	35–39	−	+	+
Giant petrel	*Macronectes* sp.	5–33	−	+	+
Wandering albatross	*Diomedea exulans*	10	−	+	+
Cape petrel	*Daption capense*	2–85	−	+	+
Grey-headed albatross	*Diomedea chrysostoma*	15–17	−	0	0
Antarctic fulmar	*Fulmarus glacialoides*	2–90	NA	+	+
Kerguelen petrel	*Pterodroma brevirostris*	<2	NA	+	+

+, positive response; −, no difference in response to experimental and control slicks or aerosols; NA, no data available; 0, no response from birds in the area to either experimental or control slicks as determined from transect surveys. Behavioural data are also included from Nevitt (1994, 1999) and Nevitt et al. (1995).

are presumably released when krill are macerated or damaged, a situation that is likely to occur when krill swarms are preyed upon by diving predators such as penguins and seals as well as other seabirds. Under such circumstances, krill are thought to be driven to the surface and thus present a profitable feeding opportunity to procellariiforms (e.g. Hunt et al., 1992). While visual cueing is certainly critical to this process (Haney et al., 1992; Bretagnolle, 1993; Veit, 1995; Silverman et al., in press), it is also possible that pyrazine and other scented compounds released during these feeding events direct distant pyrazine-responders to the area. Storm-petrels detecting pyrazine may simply choose to avoid it until the aggregation has disbanded whereas giant petrels and some albatross species may be highly attracted (see Fig. 4B). We suspect that multiple tactics come into play, given the variety of foraging scenarios that these birds routinely encounter. These behavioural strategies are likely to be more complex for many species than simply tracking prey by scent.

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