

S29-1 Olfactory foraging strategies of procellariiform seabirds

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Abstract The study of olfactory foraging ability in procellariiform seabirds is now beginning to explore how species are morphologically and behaviorally adapted to track odor plumes, and to relate these findings to models of odor transport in natural situations. According to the models, odors in atmospheric flow tend to be dispersed laterally and downwind in turbulent plumes. Because turbulent transport processes operate more rapidly than molecular diffusion, plumes of airborne odors have an irregular, patchy distribution of concentrations. For a foraging seabird, tracking the distribution of high concentration, scented eddies over the ocean to a source is thus a complex problem. This paper explores this topic, first by reviewing current understanding of olfactory foraging by procellariiform seabirds at large and small spatial scales. I then discuss different behavioral mechanisms that procellariiform species use to track odors, and show that adaptive solutions to this problem vary considerably between species, depending on olfactory ability and flight style. I also review how different olfactory and visual modalities mediate intra- and inter-specific interactions between foraging seabirds at small spatial scales.

Key words Olfaction, Procellariiform seabirds, Foraging strategies, Petrel

1 Introduction

Antarctic procellariiform seabirds roam over the oceans of the world in search of patchily distributed food resources. Satellite telemetry and other remote monitoring techniques have now proven that many species routinely travel distances ranging from hundreds to thousands of kilometers during foraging trips (Weimerskirch, 1998). While satellite telemetry has provided substantial information about where species forage, little is known about the underlying sensory and behavioral mechanisms that contribute to foraging success. How do procellariiforms know where to forage, or recognize productive areas on the open ocean? While other sensory modalities should not be overlooked, well-developed olfactory systems, and the ability to detect odors associated with potential prey, has been well established for several species (Bang, 1965, 1966; Bang and Cobb, 1968; Grubb, 1972; Hutchison and Wenzel, 1980; Nevitt, 1999a; Nevitt et al., 1995; Wenzel, 1967; reviewed by Nevitt, 2001; Warham, 1996). There is an emerging picture that a keen sense of smell is fundamental to foraging success in many species; yet the strategies used to hunt prey by smell are more complex than simply tracking odors of target prey.

This paper provides a brief overview of some of the new developments in our understanding of olfactory foraging by procellariiform seabirds and offers some ideas for future investigation. I first address a new conceptual model which suggests that olfactory foraging occurs at different spatial scales over the ocean. I then review several underlying issues indicative of adaptations for optimizing olfac-

tory search at small spatial scales. Finally, I review how different olfactory and visual modalities mediate intra- and inter-specific interactions between foraging seabirds at small spatial scales.

2 Foraging at different spatial scales

Based largely on studies conducted in the southern oceans, current understanding perceives olfactory foraging as occurring at both large and small scales. This model has been reviewed in detail elsewhere with a more comprehensive explanation (Nevitt, 1999b, 2000, 2001). According to it, procellariiform seabirds use changes in the odor landscape at large scales of hundreds or thousands of kilometers to alert themselves that they have arrived at a productive area for foraging. Elevations in scents associated with primary production such as dimethyl sulfide (DMS) have been implicated as landscape indicators of productive foraging grounds (Nevitt, 1999a, 2000; Nevitt et al., 1995). The new model suggests that birds do not track changes in odor gradients over great distances, but rather that potentially rich feeding grounds share an olfactory signature which the long distance forager recognizes upon arrival.

Once a seabird has arrived at a productive area, the problem becomes one of locating exploitable prey patches (Fig. 1). A change in the large-scale olfactory landscape may trigger a bird to begin a relatively small-scale area-restricted search of the region using a combination of visual, olfactory, and other sensory cues to pinpoint a prey patch (Nevitt and Veit, 1999). Once an odor plume is detected, some species may zigzag upwind to sense out the odor

source of the prey patch (Hutchison and Wenzel, 1980). Other species are more likely to use visual cues to locate prey patches, either by spotting prey directly or by seeing aggregations of other foraging seabirds at the patch.

3 Tracking the plume to its source: optimizing search at small spatial scales

We are now beginning to explore the morphological and behavioral adaptations that different species use to track odor plumes, and to relate them to conceptual models of odor transport in natural situations. It is generally assumed that odors in atmospheric flow tend to be dispersed laterally and downwind in turbulent plumes. Because turbulent transport processes operate more rapidly than the dissipating eddies of molecular diffusion, plumes of airborne

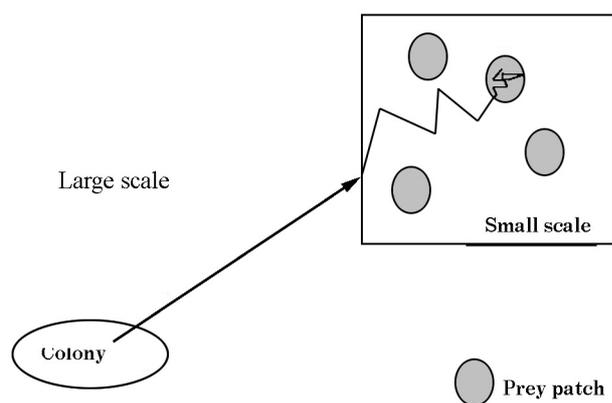


Fig. 1 Large and small scale search strategies
 Shaded (grey) areas indicate prey patches in a productive area (square outline) far from the colony. Lines with arrowheads indicate the theoretical flight trajectory of the seabird. As the seabird arrives at the foraging area, the changing olfactory landscape is predicted to trigger an area-restricted search (Nevitt and Veit, 1999).

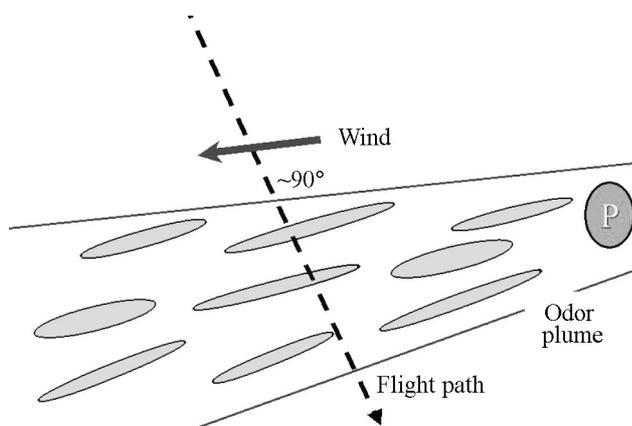


Fig. 2 Encountering the odor plume
 This diagram shows an odor plume emitted by a theoretical prey patch "P" on the right-hand side of the diagram. Scented eddies are indicated as grey ovals streaming downwind from the prey patch. For a foraging petrel, the probability of encountering the odor plume is maximized by flying directly cross-wind. This flight path is indicated by a dashed line perpendicular to the direction of the wind.

odors have an irregular, patchy distribution of concentrations. For a foraging seabird, tracking the distribution of high concentration, scented eddies over the ocean to a source is thus a complex problem that may be solved in different ways.

The basic algorithm for olfactory search is diagramed in Figs. 2 and 3 (Dusenbury, 1992). Odors emitted from a prey patch will disperse downwind and become subject to turbulent mixing. The odor plume is spatially discontinuous, presenting the bird with odor patches (eddies) that can be almost as concentrated as at the source. Energetic considerations aside, a bird foraging by smell should maximize its chances of encountering a random odor plume by flying directly crosswind (Fig. 2; Dusenbury, 1992). Once a scented eddy is encountered, the bird will travel upwind within that eddy until it loses the scent (Fig. 3). The bird then turns directly crosswind again to cast about for the odor. Such casting behavior is common among animals that track odor plumes (e.g., Carde, 1996 for moths) because it maximizes the likelihood of re-encountering a plume. Upwind, zigzag flight is commonly seen in many of the smaller procellariiforms in association with odor traces at sea (Hutchison and Wenzel, 1980; Warham, 1996).

Despite its simplification, the model shows that species adapted to search by olfaction should also be adapted to flying directly crosswind, simply because this behavior maximizes the chances of encountering an odor plume. Although our laboratory has not studied this issue, data reported by others support it. For example, Spear and Ainley (1997) made shipboard observations of flight direction relative to wind direction for a variety of procellariiform species. They found that storm-petrels tended to fly perpendicular to, or across, the predominant wind direction. These birds are highly olfactory, and commonly zigzag upwind towards odor patches deployed experimentally at sea (reviewed in Nevitt, 1999b).

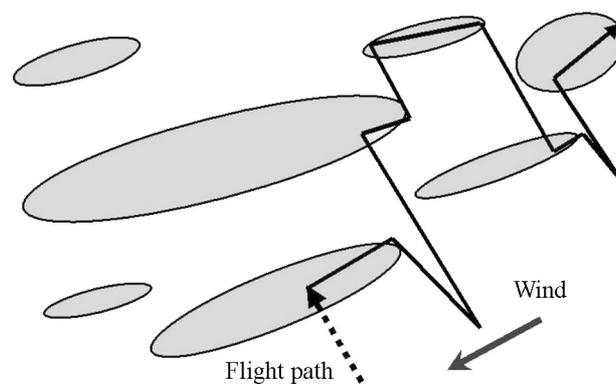


Fig. 3 Locating the source of the odor plume
 The figure shows the zigzag flight path used to track an odor plume to its source (upper right hand corner, not shown). Scented eddies are indicated as gray ovals, as in Fig. 2. The initial cross-wind flight path is indicated by a dotted line. The solid line indicates the flight path once the odor plume is encountered.

In contrast, Spear and Ainley's data indicate that dynamic soarers, such as albatrosses, fly more obliquely crosswind. Energetic considerations notwithstanding, this result is consistent with a foraging strategy that is less reliant on olfactory cues, in that constraints on the flight style may lessen the chances of encountering an odor plume. Elucidating the relationship between flight energetics and sensory ecology in driving different foraging strategies is clearly a ripe area for future study.

Incorporating technologies to track fine-scale movements of individual foraging birds gets over many of the limitations of shipboard observational studies (Weimerskirch et al., 2002). Although sample sizes are smaller, the fine scale resolution of the flight trajectories that individual birds follow allows for more refined predictions about search behavior under different foraging conditions. For example, Spear and Ainley's data (1997) indicate that albatrosses tend to fly obliquely to the wind, yet that behavior could change during active foraging events. Birds might choose flight directions that are energetically more costly if the chance of finding prey is high.

Fine-scale monitoring will help to elucidate such questions, and further determine when different sensory strategies are likely to be employed for finding prey. Species such as the wandering albatross (*Diomedea exulans*), for example, forage opportunistically, presumably on both dead and live prey, using a combination of sensory strategies including olfaction and sight. Because wandering albatrosses are sensitive to prey-related odors, detailing fine-scale flight trajectories with respect to wind direction should be useful in distinguishing olfactory from visual or multimodal search strategies (Fig. 4). Casting behavior may thus be restricted to highly productive areas, and to particular types of prey (e.g., squid carrion), or to foraging areas where specific prey types are likely to be found. Casting behavior may also vary with weather condition, or with the type of foraging trip being made, short or long (Weimerskirch, 1998). There are clearly a multitude of ques-

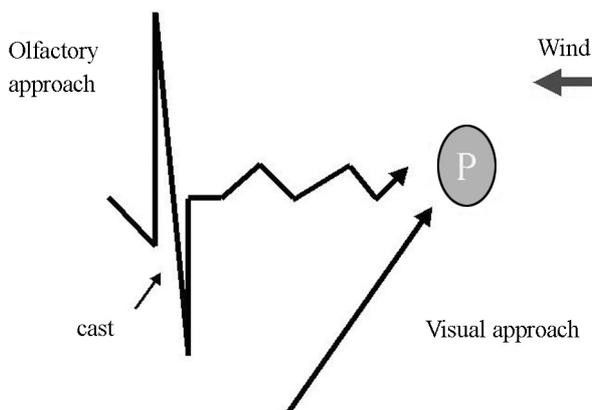


Fig. 4 Fine scale flight paths indicate differences between the sensory modalities used to locate a prey patch

The characteristic olfactory “cast” is indicated by a broad zig-zag sweep perpendicular to (across) the direction of the wind.

tions that will be intriguing to explore with GPS technology.

4 Interspecific interactions

It is becoming recognized that different olfactory abilities mediate intra- and inter-specific interactions among foraging seabirds at small spatial scales. Controlled behavioral experiments show that different species of procellariiforms are sensitive to a variety of naturally scented compounds associated with prey. Responses have been detailed for approximately 20 species of Antarctic procellariiforms to the following odors: krill (crude extract, trimethyl amine, pyrazine, 2,3-dimethyl pyrazine), squid, cod liver oil, herring oil and phenyl ethyl alcohol (Cunningham et al., submitted; Nevitt, 1999a, b; Nevitt et al., 1995), as well as to biogenic sulfurous compounds associated with phytoplankton (dimethyl sulfide, DMS) (Nevitt et al., 1995), and krill (Daly and DiTullio, 1996). I now review several basic trends that have been identified, particularly with respect to how different odor sensitivities are linked to foraging at mixed-species feeding aggregations near South Georgia Island (Nevitt, 2000; Nevitt and Veit, 1999).

The term “mixed-species feeding aggregation” is used to describe large gatherings of birds — often numbering hundreds — which exploit ephemeral food bonanzas, such as a krill swarm near the surface. How these aggregations form is not known, but results from empirical studies investigating the sensitivity of various procellariiform species to prey related odors near South Georgia Island suggest use of two competing strategies: “early detection” and “late detection”.

For early detectors such as storm-petrels, olfaction provides a means of opportunistically exploiting small prey patches or larger krill swarms before late detectors arrive to displace them. These species are highly sensitive to DMS and will track DMS plumes in experimental trials. As well as serving as a general indicator of high primary productivity, DMS emissions increase as phytoplankton are grazed by krill, particularly when krill swarms aggregate (Nevitt, 1999a). Thus the ability to detect and respond to DMS and other odors may give highly olfactory species such as storm-petrels an advantage in locating and exploiting available food resources quickly and efficiently.

In contrast, late detectors such as albatrosses and giant petrels take their cues from the activity patterns of other seabirds. In experimental trials, late detectors do not track DMS, but instead recruit to scents associated with macerated krill and are highly responsive to the activity of con- and heterospecifics (Nevitt, 1999a, 1999b). These species probably arrive after aggregations have started to form, and are primarily attracted by visual cues. Late detectors tend to be highly visible and aggressive at mixed-species feeding aggregations, and a nuisance for smaller species (Nevitt, 1999a). It is not surprising that late detectors often dominate mixed-species feeding aggregations (Harrison et al., 1991), and probably represent a threat to smaller, early detectors that could fall prey to them.

These patterns are significant because they suggest that procellariiform species have evolved different strategies for foraging based partly on sensory factors. Some species are clearly more highly adapted to exploit olfactory cues, and others better fitted to combine visual and olfactory cues, according to the situation. Because species that tend to be olfactory also nest in burrows, we are currently exploring whether the environment of the burrow predisposes chicks to learn olfactory cues brought back by the parents early in life. These and other questions suggest productive areas for future research.

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