

The use of Odors at Different Spatial Scales: Comparing Birds with Fish

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Abstract Salmon travel hundreds of kilometers of open ocean and meandering rivers to return to their natal stream to spawn; procellariiform seabirds soar over thousands of kilometers of the ocean's surface searching for foraging opportunities and accurately return to their nesting islands. These large-scale olfactory-guided behaviors are among the most dramatic examples of animal navigation ever described. At much closer ranges, the sense of smell can be used for behaviors as diverse as tracking prey, nest location, and mate selection. Both fish and birds face similar problems interpreting olfactory information in fluid mediums where odors are dispersed as filamentous patches. Similar to insects, which have served as model organisms for investigating olfactory related behaviors, the few fish and bird species that have been studied tend to use olfactory information in conjunction with other sensory modalities. Similar to insects, fish and birds also employ oscillatory or cross-stream movement as sampling mechanisms. This review compares and contrasts the use of odors by fish

and birds over a range of spatial scales that span from thousands of kilometers to less than a meter. In so doing, we identify behavioral similarities and new questions that need to be addressed regarding the olfactory ecology of these diverse groups of organisms.

Keywords Odor tracking · Fish · Birds · Odor plume · Pigeon · Procellariiform · Vulture · Salmon · Lamprey · Eel

Introduction

Both fish and birds use olfactory information over a range of spatial scales. At large spatial scales on the order of hundreds of kilometers, olfactory-guided behaviors are among the most dramatic examples of animal navigation ever described. For instance, salmon require olfaction to relocate their natal streams, and pigeons released in unfamiliar territory are able to set a course for their home loft by using information derived from odors at the release site. At much closer ranges, the sense of smell can be used for behaviors as diverse as foraging and mate selection. Although one group swims and the other flies, both fish and birds face similar problems interpreting olfactory information in natural environments. Both groups have evolved to operate in three-dimensional space, in fluid mediums that share similar characteristics relevant to odor transport. Water and air both move in currents, and these currents distribute odors such that plumes have a filamentous, discontinuous structure (Zimmer-Faust et al. 1995; Finelli et al. 1999). As these odor filaments move away from a source, they can be widely dispersed depending on the turbulence of their environment (Zimmer-Faust et al. 1995; Moore et al. 2000); the higher the turbulence, the more irregular and patchier the distribution of odor filaments.

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How organisms decipher reliable information from such discontinuity has consequently been a topic of much interest.

Not surprisingly, many advances in this field have been informed by previous work with insects, which have served as model organisms for investigating olfactory-related behaviors in freely flying organisms (see Willis 2005; Cardé and Willis 2008). As with insects, the few fish and bird species that have been studied tend to use olfactory information in conjunction with input from other sensory modalities. While insects combine odor cues with visual flow to direct upwind flight, a variety of environmental cues provide directional information to fish and birds, and these cues can vary, depending on the spatial scale of the problem. In many fish species, olfactory information is interpreted with respect to input from the lateral line system, whereas in birds (pigeons, for example), olfactory, visual, and geomagnetic information are likely used together in different ways, depending on whether the bird is homing from familiar territory near to its loft or from unfamiliar territory hundreds of kilometers away. Like insects, many species of fish and birds use up-current or up-wind movement coupled with zigzagging or casting movements to focus search activity to the source of a plume (Fig. 1), but given that most of these species cannot be

studied easily in laboratory conditions, the dynamics of odor tracking are not as well characterized as they are in moths and other insects. Unlike insects, where tracking behavior can be induced by the controlled release of well-defined, species-specific pheromone blends, in most fish and bird species, potential odor cues tend to be poorly defined or characterized, and information about their distribution, production, and decay in the natural environment is typically lacking. This mini-review will compare and contrast the use of odors by fish and birds over a range of spatial scales, spanning from thousands of kilometers to less than a meter, to better define similarities in the use of scent and identify new questions that need to be addressed.

Olfactory-Mediated Behaviors in Fish

Fish use their sense of smell for behaviors that are performed over both large and small spatial scales, the dimensionality of which is relative to the species in question. For example, many species of salmon (*Oncorhynchus* spp.) use olfactory cues to home over hundreds of kilometers to a natal river (reviewed by Dittman and Quinn 1996), whereas black rockfish (*Sebastes inermis*) experimentally displaced as little as 4 km also require olfaction to return to their original,

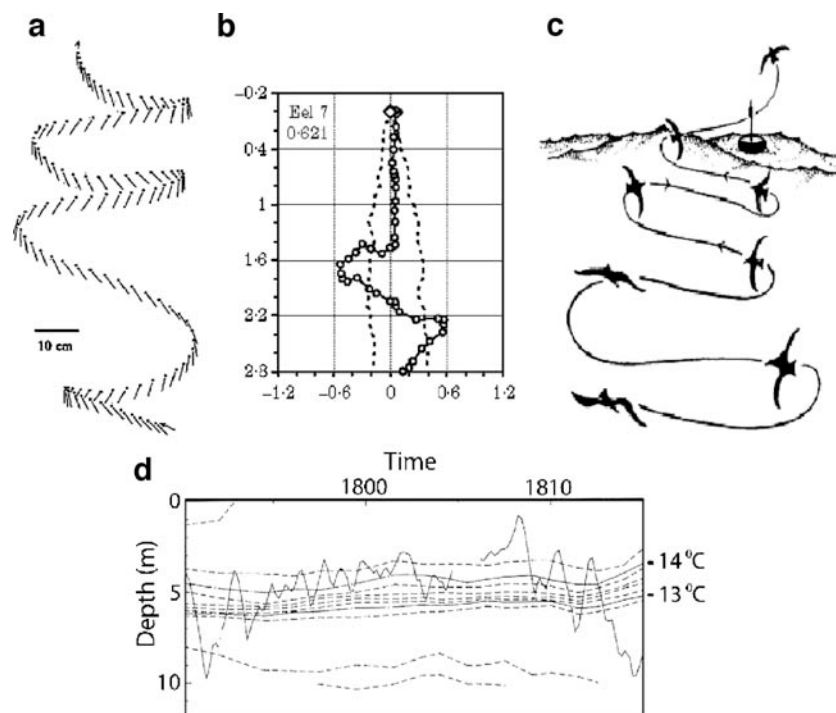


Fig. 1 A comparison of olfactory-search behaviors from moths, fish, and birds. **a** A moth exhibits cross-wind casting behavior (adapted from Belanger and Willis 1996). **b** A freshwater eel shows similar counter-turning behavior within the boundaries of an odor plume (adapted from Carton and Montgomery 2003). **c** Procellariiform

seabirds show counter-turning behavior in response to prey odors (courtesy of Hutchison and Wenzel 1980). **d** Atlantic salmon show vertical oscillations across water layers of different temperatures (courtesy of Døving et al. 1985)

familiar home range (Mitamura et al. 2005). How fish use olfactory information to locate a goal over such large distances is not yet well understood despite considerable research effort. By contrast, olfactory cues mediate other types of behaviors at much closer ranges. For example, single amino acids introduced into a flow tank almost instantaneously increase foraging-related activity (e.g., surfacing and jumping) in lake charr (*Salvelinus namaycush*; Hara 2006), whereas specific alarm pheromones elicit anti-predator behaviors in fathead minnows (*Pimephalus promelas*) even in the absence of a visual cue (Hartman and Abrahams 2000). At close range, odors can also aid some species in identifying potential mates. For example, living in turbid environments where visibility is limited, Lake Malawi cichlids (*Pseudotropheus emmiltos*), depend on olfaction to identify conspecifics (Plenderleith et al. 2005).

Although considerable research effort has focused on investigating large-scale, olfactory-guided migrations, with particular attention paid to commercially important fish species, the most detailed investigations of olfactory tracking to date have been conducted in laboratory or flume settings. These studies have focused on behaviors that can be elicited by olfactory cues that operate at close range. The emphasis on flume studies is, in part, due to logistic considerations of tracking animals in the field, yet no fish species has been studied in as much detail as moths at any spatial scale (see Cardé and Willis 2008). A consideration of data across insect and fish species suggests that olfactory tracking is highly adapted to and constrained by characteristics of odor dispersal linked to flow (Belanger and Willis 1996; Vickers 2000). Not surprisingly, many fish species have well-developed peripheral olfactory systems (Caprio 1988), including elaborate sniffing apparatuses (Nevitt 1991), and olfactory detection thresholds can be quite low. For instance, sea lamprey (*Petromyzon marinus*) can detect larval bile acids at 10^{-10} M (Bjerselius et al. 2000), and sablefish (*Anoplopoma fimbria*) can detect dilute squid extract made up of free amino acid concentrations between 10^{-13} and 10^{-17} M (Davis et al. 2006). In the following sections, we review recent advances that have been made in our understanding of how fish use olfactory information under natural conditions over relatively large and small spatial scales.

Large Spatial Scales

Olfactory-guided behaviors that occur over large spatial scales (which we will define as on the order of tens to hundreds of kilometers for this discussion) have been studied primarily in the context of homing (Hasler et al. 1978; Dittman and Quinn 1996; Ueda et al. 1998; Døving and Stabell 2003; Mitamura et al. 2005; Nordeng and Bratland 2006; Keefer et al. 2006). In fisheries studies,

homing typically refers to the directed movement of displaced fish back to an original location or home range. A number of these investigations have used tracking methods to study how fish move through the water as they home, and certain trends emerge. For example, when navigating over these large distances to locate a goal, various species have been shown to move vertically up and down in the water column (Fig. 1d; Døving et al. 1985; Døving and Stabell 2003). These behaviors have suggested to researchers that, in order to home, fish need to sample the water column for olfactory cues released from a particular habitat or odor source even when they are kilometers or even tens of kilometers from that source. Other studies have attempted to identify these ‘habitat’ cues and suggest that they are produced, in part, by conspecifics or by specific populations of fishes that reside within the given habitat. For example, sea lamprey (*Petromyzon marinus*) have been shown to home to specific rivers that carry scented compounds produced by larval sea lamprey (Bjerselius et al. 2000; Vrieze and Sorensen 2001; Sorensen et al. 2003).

Many fish species also navigate across the expanse of oceans, lakes, and rivers, at times without obvious visual reference points. The mechanisms by which fish determine direction in these often visually homogeneous environments are not yet well understood. While it commonly has been assumed that odors mediate rheotaxis, more integrative hypotheses have been proposed to explain how fish track odors up-current without a fixed point of reference. These questions have been studied in salmonids, freshwater eels, and sea lamprey, which we will review in more detail in the following sections.

Salmonids Salmon (e.g., *Salmo* spp., *Oncorhynchus* spp.) are anadromous fishes. They start and end their lives in freshwater but typically spend most of their sub-adult lives foraging at sea. During sensitive periods of development linked to surges in plasma thyroid hormone, juveniles imprint to the scent of their natal stream (e.g., Dittman et al. 1996; reviewed by Dittman and Quinn 1996; Lema and Nevitt 2004; Nevitt and Dittman 2004). After undergoing a physiological metamorphosis (parr–smolt transformation) that prepares them for life in seawater, juvenile fish out-migrate to the ocean. Toward the end of their life cycle, depending on the species, salmon navigate over hundreds of kilometers to return to spawn in their natal stream. It is not known how fish return to the appropriate river system; however, numerous studies have shown that olfaction is essential in the freshwater homing migration (Hasler et al. 1978; Dittman et al. 1996; Courtenay et al. 1997; Nordeng and Bratland 2006).

Westerberg (1982) and Døving’s laboratory in Norway (Døving et al. 1985; Døving and Stabell 2003) have

provided some of the most intriguing results to date to suggest how salmon track odors at large spatial scales. In Norway, Atlantic salmon (*Salmo salar*) must navigate fjords before entering the river system on the homeward migration. The fjord portion of the migration, thus, provides an excellent opportunity to track salmon before they reach their home river, as fish can be followed more easily in the confines of fjords than in the open ocean. Moreover, in fjords, as in the ocean, there are micro-structured, horizontal layers in the water column, and these layers vary in temperature, thickness, and other parameters (Westerberg 1982). By using passive sonic tracking methods to follow individually tagged fish, Døving et al. (1985) have convincingly demonstrated that salmon oscillate vertically through these layers, which the authors speculate to have distinct origins (Westerberg 1982; Døving and Stabell 2003). According to this idea, as the fish moves up and down in the water column, it comes into contact with layers of water that originate from different sources.

Westerberg (1982) reasoned that these layers provide different chemical information to fish that is presented in conjunction with directional information via the thermal fluctuations that result from current shear. In support of this idea, Døving et al. (1985) found that unmanipulated (olfactory-intact) salmon limited their oscillatory swimming behavior to specific temperature layers of the water column, typically between the surface and 30 m in depth, whereas anosmic salmon did not restrict their swimming behavior and continued to oscillate between the surface and 80 m in depth. Furthermore, Døving and co-authors showed that olfactory-intact salmon made brief, vertical dives (Fig. 1d). They hypothesized that the purpose of these explorations was to sample the fine-structure of different water layers for both olfactory cues and directional cues provided by thermal shear or other input (i.e., infrasound; see Sand and Karlsen 2000).

In conjunction with these studies, Johnsen (1982) proposed a mechanism to explain how salmon locate their home streams within the river system. He suggested that familiar home-stream waters trigger positive rheotaxis and zigzag swimming behavior, whereas the absence of home-stream odor triggers either downstream drift or negative rheotaxis. In support of this hypothesis, Nordeng and Bratland (2006) found that juvenile salmonids displaced to neighboring river systems, which each emptied into the Salangen Fjord approximately 10 km apart, returned to their natal rivers with high precision. They reasoned that these fish homed by swimming up-current in response to odorants of their own population and down-current in the absence of population odors. Døving and Stabell (2003) have since postulated that salmon will exhibit positive or negative rheotaxis in response to a set of chemical signals, depending on the physiological state of the fish. According to this idea, fish use the same

chemical cues for foraging as they do to find the direction of their natal river when in a migratory state.

Salmon homing can, thus, be explained as a two-step process. As salmon enter the fjords, they sample odors by swimming in a pattern of vertical oscillations through the water column. This behavior occurs in conjunction with a combination of positive and negative rheotaxis in response to specific odors. Olfactory-mediated rheotaxis then persists as individuals enter the river system and find their way home to spawn.

Freshwater Eels Freshwater eels (*Anguilla* spp.) have a catadromous life history in that they are spawned in saltwater, migrate as juveniles to freshwater, then out-migrate to spawn in the Sargasso Sea. Yellow-phase American eels (*Anguilla rostrata*) initially migrate into the river system. During most of this stage of their life history, they reside as brackish or freshwater bottom-dwellers, moving between estuaries and river systems where they stay until they sexually mature. Similar to salmon, American eels undergo a physiological metamorphosis before out-migration that prepares them for life in seawater. These silver-phase eels migrate from freshwater and estuary habitats back to the Sargasso Sea. Both yellow and silver-phase eels use selective tidal stream transport, or STST, to travel into and out of the estuary during the appropriate migratory phase of their life cycle (Barbin 1998; Barbin et al. 1998). By using STST, eels can travel horizontally over tens of kilometers (between 12 and 32 km in these studies) with energetic efficiency, so long as they are able to choose the appropriate tide. Barbin et al. (1998) found that this ability depended on the eel having an intact sense of smell, although other sensory modalities also contributed to this behavior. Similar to the situation in fjords, in estuaries, differences in temperature and salinity lead to layering of water masses with a defined density boundary, or pycnocline. The depth of the pycnocline varies depending on hydrographic conditions but, in this study, ranged from 0.7 to 10.7 meters, with the bottom depth ranging from approximately 5 to 18 m (Barbin 1998). Barbin (1998) showed that olfactory-intact yellow-phase eels ascended to the surface and descended to the pycnocline with equal frequency as they used STST; ascents and descents were defined as a change in depth of greater than 3 m (Barbin 1998). In contrast, anosmic eels moved sporadically throughout the water column, rarely reaching the depth of the pycnocline, and ascended to the surface more frequently than olfactory-intact eels.

The results of Barbin et al. (1998) showed that anosmic, silver-phase (out-migrating) eels were less able to use STST and failed to choose the correct tidal currents. Only two of the eight anosmic silver-phase eels migrated out of the estuary within 7 days of release, and the other six had not left after 9 days (Barbin et al. 1998). In contrast, olfactory-

intact silver-phase eels timed their vertical movements with the tidal cycle and were able to move out of the estuary (over 32 km) in 4 days, on average, which is only slightly longer than the time it takes for water to move through the estuary on ebb tides (three nights on average). Behavioral differences between anosmic and olfactory-intact eels were similar to what Døving et al. (1985) observed with Atlantic salmon in fjords.

Sea Lamprey Like salmon, sea lamprey (*Petromyzon marinus*) are anadromous fish that begin life in the river as suspension feeding larvae and then make their way to lakes and oceans as fish parasites. Years later, they use olfactory cues that guide them back to an appropriate river to spawn. In contrast to salmon, this river is not necessarily their natal river. Instead, adult sea lamprey use pheromones released by larval lamprey to find suitable spawning streams (Bjerselius et al. 2000; Sorensen et al. 2003). A major advance that facilitates working with this system is that the pheromone blends have been characterized (Vrieze and Sorensen 2001). Consequently, the dynamics of odor search can be explored with respect to a known cue that can be identified as present or absent in natural water systems.

With this goal in mind, Sorensen et al. (2003) have studied movement patterns of sea lamprey in the process of searching for appropriate spawning rivers. As part of this study, the researchers tracked both anosmic and sham-treated lamprey in the Great Lakes by using acoustic telemetry (see Vrieze and Sorensen 2001; Sorensen et al. 2003). Similar to what Døving et al. (1985) reported for salmon, they found that lamprey actively swam on constant bearings while vertically migrating or oscillating through the water column of the lake. Once a lamprey encountered a river plume, it would begin circling before swimming upstream into the river. Though movement patterns were not reported for anosmic lamprey, stream capture rates revealed that only 10% of anosmic lamprey located streams, whereas nearly half of the sham-treated lamprey succeeded (see Vrieze and Sorensen 2001). Laboratory trials that used two-choice mazes have also shown that lamprey prefer waters from rivers and streams where larval pheromones are present (see Bjerselius et al. 2000; Vrieze and Sorensen 2001; Sorensen et al. 2003). Taken together, results from both sea lamprey and eels provide more general support for Døving's and Westerberg's hypotheses originally proposed in salmon, suggesting that vertical oscillations aid fish in determining the direction of an odor source when navigating over distances of kilometers.

Small Spatial Scales

By far, the majority of investigations have been carried out at much smaller spatial scales (typically less than 10 m

from the odor source). Most studies suggest that fish are capable of tracking odor plumes to the source within this more-limited range and that this behavior requires other sensory modalities, including the lateral line system. The use of olfaction in tandem with the lateral line system to direct movement up-current contrasts with insects that tend to use optical feedback to progress upwind to an odor source (Willis 2005). Our understanding of small-scale olfactory-mediated behavior comes from a combination of field manipulations and flume experiments, which we review below.

Field Experiments Relatively little work has been conducted under natural, field conditions. However, the research that has been done indicates that current olfactory information is needed for fish to locate odor sources. For example, Montgomery et al. (1999) examined olfactory search tracks in Antarctic fish (*Trematomus bernacchii*), which are adapted to forage in low light conditions under Antarctic ice sheets. Working in the field, they made video observations of benthic Antarctic fish tracking an experimental odor plume from 5 m to the source. The odor plume was created by passing a solution of minced fish through a hose. By using computer simulations, they determined what search strategies fish used to find the source of this odor plume. The matching of field observations to computer simulations suggested that fish could not locate the source unless a combination of chemosensory and current information was provided.

Elliott et al. (1995) conducted an elegant test of olfactory-guided host-selection in anemonefish (*Amphiprion* spp.). Anemonefish lay their eggs next to the trunk of their host anemone where the adults tend to them until they hatch into pelagic larvae. Most species of anemonefish are obligate symbionts to a species-specific host anemone. This means that the pelagic larvae must settle and re-locate a host anemone after their pelagic life-stage concludes. Elliott et al. (1995) found that when they released juvenile anemonefishes greater than 1 m down-current from a host anemone, they would swim in zigzag patterns or counterturns in the direction of the anemone, turning less frequently as they got closer. If the anemonefish were instead released within 1 m down-current of its anemone, it would swim in a straight path toward it. If an anemonefish were released either perpendicular or up-current with respect to the anemone, it frequently was unable to locate its host. Interestingly, in these situations, the fish swam either laterally or drifted until it was down-current of the anemone. It would then descend to the substrate and swim up-current until it reached its host. At distances of half a meter or more, anemonefish were not visually attracted to their host anemones and required down-current chemical cues to locate them. These experiments went on to illustrate how currents effectively increase the

range of detection by fishes. With no current, anemonefishes' ability to locate their host anemones was severely reduced. At current velocities greater than 2.5 cm s^{-1} , fish were attracted to host anemones from up to 8 m down-current. From these and other experiments, Elliott et al. (1995) suggested that anemonefish used "decision rules" to locate a host anemone (i.e., if downstream from a host, swim directly upstream staying within 1 to 5 cm from the substrate, or if the odor plume is lost, turn and swim laterally across and down-current in a zigzag fashion until the stimulus is encountered again).

Another elegant field system has been developed to study foraging behavior of cod (*Gadus morhua*). Løkkeborg and Fernø (1999) tagged cod with acoustic transmitters and tracked them while the fish searched for a baited line, again in the fjords of Norway. Their tracks ran for several hundred meters, with an average of 262 m between the baited line and tagged fish. Cod found the bait line through chemically mediated rheotaxis (Løkkeborg 1998). Cod increased their swimming speed when heading up-current, and these faster swimming fish also tended to succeed in locating the baited line. The faster the fish were swimming, the higher the probability that they would encounter the odor plume and head up-current to the source. As fish also found the bait much more quickly during the day, the authors concluded that visual cues were probably used in conjunction with olfaction and rheotaxis to mediate bait search.

Thus far, the picture presented from field studies is that fish use olfaction in combination with other cues, that include rheotactic and visual cues, to locate odor sources in close proximity. Next, we will review results from flume studies that have examined olfactory search mechanisms with greater precision.

Laboratory Flume Experiments Blind cave fish (*Astyanax fasciatus*) are an ideal system for studying problems related to multimodal search in the absence of vision. These fish evolved in dark environments where they have become adapted to forage by using information from water movements and chemical cues. Baker and Montgomery (1999) found that both odor and current stimuli are required for blind cave fish to locate an odor source (for similar results in nocturnal banded kokopu *Galaxias fasciatus*, see Baker et al. 2002). If an appropriate odor stimulus was presented, fish oriented or swam upstream when current velocities were as low as 0.4 cm s^{-1} . The rheotactic threshold increased to 3 cm s^{-1} if olfactory cues were absent. In no-current conditions, fish tended to position themselves randomly throughout the tank and showed little attraction to the odor source. Because they used an experimental tank with a water inflow that was physically separated from an odor injection site, they could also determine how current

and odor worked together to trigger olfactory search. Interestingly, they found that, when an odor stimulus was paired with a unidirectional current, fish tended to cluster around the current inflow and not the odor injection site. This experiment showed that blind cave fish need a combination of olfactory and rheosensory input to locate an odor source.

Flume work with other species has provided evidence for horizontal casting behavior during olfactory search. For example, Carton and Montgomery (2003) looked at the behavioral reactions of freshwater eels (*Anguilla australis* and *Anguilla dieffenbachii*) in response to food odors in a semi-natural, turbulent flow raceway (5 m in length). They found evidence for both odor-mediated rheotaxis and cross-stream casting in response to experimental odor injections (Fig. 1b). At distances greater than 0.9 m from the odor source, eels swam up-current. Eels seemed to detect and track the edges of the odor plumes, as they initiated cross-stream, horizontal casting behaviors one second after moving beyond the lateral margins of the plume. These casting movements were slower than direct, up-current movements, and eels spent more time casting and searching closer to the odor source than farther away.

In summary, these flume experiments support field observations in suggesting that fish typically use a combination of olfaction and rheotaxis to locate the source of an odor plume. Although subtle differences appear in each of the studies described here, common themes are to use cross-stream casting behaviors to search for the odor source or to stay within the plume and to head up-current when the plume is detected. We now review how fish locate odor sources in no-flow and variable flow situations.

No-Flow or Variable-Flow Situations Although all of the studies we have discussed so far have concluded that currents are required for fishes to locate an odor source, species probably differ in their ability to locate odor sources depending on their specific adaptations. For example, working with brown bullhead catfish (*Ameiurus nebulosus*), Sherman and Moore (2001) showed that these fish were always successful in locating an odor source under no-flow conditions, whereas success rate diminished when current was present.

There also is evidence for area-restricted search (ARS) in response to odors in non-uniform flow situations. Bonnethead sharks (*Sphyrna tiburo*) showed behavioral responses to chemical stimuli in experimental circular tanks (1.8-m-diameter pools; Johnsen and Teeter 1985). When these fish were presented with blue crab homogenate in still water, they began turning in tight circles near the stimulus site, even in the absence of a distinct visual cue. Johnsen and Teeter (1985) speculated that this searching behavior functioned to keep the shark near its initial point of contact

with the stimulus. In contrast, when the same experiment was done with the addition of a current, sharks would reverse direction when they contacted the cue. Sharks would then swim in loops that extended progressively down-current, giving the impression that they were tracking the stimulus within the flow structure of the tank. How bonnethead sharks use odors to mediate ARS in natural situations requires further study.

Sniffing Fish are also able to sample odors through active sniffing—a behavior that resembles a cough in some species (Nevitt 1991). During a sniffing event, a spontaneous jaw protrusion increases water flow to accessory olfactory sacs. Nevitt (1991) recorded pressure fluctuations in the nasal sacs of flounders during spontaneous coughing and respiration. These experiments demonstrated that ventilation over the olfactory epithelium was mechanically linked to respiration. In controlled behavioral studies, coughing behavior was elicited as flounders sampled a defined odor plume within a flow tank. From these and other investigations, Nevitt concluded that coughing was analogous to “sniffing” in air-breathing organisms. Coughing in fishes has since been used as a measure of olfactory responsiveness in laboratory situations (e.g., Nevitt 1991; Murphy et al. 2001; Belanger et al. 2006). Ventilation rates in round gobies have been shown to correspond to voltage changes in electro-olfactograms recorded at the olfactory epithelium. Murphy et al. (2001) suggested that these changes were due to odor-induced ventilation. Further support for this connection between olfaction and ventilation rate was provided through olfactory deprivation studies in gobies (Belanger et al. 2006). They found that rendering fish anosmic, either through copper sulfate treatment or nasal occlusion with dental impression material, inhibited their reaction to pheromones as measured by gill ventilation rate. These results suggest that the increase in ventilation is another mechanism by which fish sample the aquatic environment for pertinent olfactory cues, especially in those species that are benthic or less active.

Olfactory-Mediated Behaviors in Birds

Questions related to the use of olfaction in birds have been hampered by the erroneous yet common assumption that most birds are anosmic. Consequently, compared to fish, little is known about how birds are able to track odors in natural situations (for review, see Roper 1999). Unlike insects that sense odors through olfactory receptor neurons housed on complex filamentous structures, the olfactory systems of birds are enclosed and, like fish, accessed typically through paired naral openings. In some groups

such as the procellariiform seabirds, these naral openings are sometimes modified into a single, tube-like structure at the top of the bill. By contrast, in turkey vultures and ducks, naral openings laterally traverse the bill, thus allowing continuous airflow between them. From a comparative perspective, the sense of smell in birds continues to be relatively overlooked (for exceptions, see Bang 1960, 1971; Bang and Wenzel 1985; Wenzel 1987; reviewed by Roper 1999), but nearly every species that has been investigated behaviorally for olfactory abilities has been shown to have them, from highly specialized species such as ground dwelling Kiwis (Wenzel 1960) and Kokapo (Hagelin 2004) to even the most pedestrian—starlings, chickens, and ducks (reviewed by Roper 1999; Van Buskirk and Nevitt 2007). Birds may present the next advance in understanding how olfactory information is used across an enormous range of spatial scales. In this paper, we review three of the best-described systems: homing pigeons, procellariiforms, and turkey vultures.

Homing Pigeons

One of the most intensely studied problems in animal navigation is the homing ability of the domesticated rock pigeon (*Columba livia*), and nearly all olfactory work in birds has focused on this problem. Pigeons released hundreds of kilometers from their home loft will fly home in a goal-oriented way, even when released from completely unfamiliar territory (for reviews, see Papi 1990; Able 1991, 1995; Walcott 1996). This behavior requires multimodal integration of an array of environmental cues, conceptualized in the navigation literature as the ‘compass’ (an orientation mechanism) and ‘map’ (a spatial coordinate system) senses (Kramer 1952). With respect to the compass, it is now generally accepted that pigeons use redundant, more-or-less condition-dependent mechanisms for orientation. For example, displaced birds orient by using either a sun compass or earth-strength magnetic field depending on whether or not the sun is visible (for review, see Walcott 1996; Wiltschko and Wiltschko 1998). With respect to the map, the physical substrate continues to be hotly debated with researchers arguing for both magnetic and olfactory input (see Wallraff 2000; Wiltschko and Wiltschko 2000). This discussion focuses on the olfactory map, but we refer readers to numerous, more comprehensive treatments of the field (e.g., Able 1991, 1995; Roper 1999; Alerstam 2006; Papi 2006).

The idea behind the olfactory map is that pigeons learn to associate windborne olfactory information with compass direction before they leave the loft. Papi was the first to suggest that pigeons form what was later termed a ‘mosaic’ map of the olfactory environment that surrounds the loft, which is then extended during exploratory flights

(e.g., Papi et al. 1971; reviewed by Papi 1990). In an effort to explain the ability of pigeons to home from distant (greater than 100 km), unfamiliar sites, Wallraff further proposed that odors form large-scale, two-dimensional gradient maps (e.g., Wallraff 1989; reviewed by Wallraff 2004, 2005). According to this model, scented winds provide directional information that the bird learns before leaving the loft area. From this information, the bird can extrapolate relative positional information at an unfamiliar release site by comparing spatial variation in relative odor concentrations between the release site and the loft. In search of a physical substrate, the model assumes spatially explicit, monotonic gradients in odor profiles that run along a bi-coordinate axis surrounding the loft and extending to distant sites.

Elements of these two models are summarized as follows: (1) Pigeons are exposed to a radial spectrum of wind-borne odor blends at or in the vicinity of the loft; (2) they learn to associate the directions of the scented winds with general compass headings (either by using the sun compass or the magnetic compass); (3) upon release, pigeons sample the air and make a mental comparison of the ambient odor blend (or ratio, according to Wallraff) with the blend at the release site; and (4) they then use this information to set a course for home. According to Papi, this would be achieved by following a simple set of learned rules (i.e., in response to odor blend X at the release site, go in the opposite direction from which odor blend X was experienced at the loft). According to Wallraff, a pigeon would deduce a course home at the release site by comparing the ratio of odors at the release site with the memory of the ratio at the loft and extrapolating relative positional information to set a course for home.

In support of each of these theories, a variety of carefully conducted research documents that pigeons require an intact sense of smell to home and that homing does not involve simply tracking an odor or odor blend to its source (reviewed by Able 1995; Papi 1990; see also Gagliardo et al. 2001a). Similar to studies with salmon, rendering birds anosmic (either by olfactory nerve transection, chemical removal of cilia, or by application of a local anesthetic) interferes with homing (for example, see Bingman and Benvenuti 1996; Bingman et al. 1998). Homing ability is also impacted by changes in rearing environment in that pigeons must have access to windborne odors at or in the vicinity of the loft to later be able to home from unfamiliar areas (for example, see Gagliardo et al. 2001b). Among numerous studies, Papi has demonstrated that olfactory homing is seasonally and geographically variable, and limited to distances of 500 km in some locations, and that range can be extended if birds are allowed access to the odor environment during transport (reviewed by Papi 1990). As with salmon, a major stumbling block has been

to identify and characterize the odor cues involved, which is, in the case of pigeons, the biogenic substrate for the putative map (for a more complete discussion on this topic, see Roper 1999).

To better define an odor map, Wallraff's model suggests a spatially explicit gridwork of odor gradients, which offers predictive value in estimating location relative to the loft. To pin this gridwork to a genuine, physical substrate, Wallraff and Andreae (2000) collected air samples over three consecutive years from 96 rural sites distributed within a 400-km-diameter circle around an experimental pigeon loft near Wurzburg, Germany. They then used gas-chromatography to measure a suite of largely anthropogenic hydrocarbons distributed over the landscape and analyzed their spatial distribution as a proxy for the spatial distribution of natural odor blends that pigeons might use to home. Their data show rising and falling profiles in the proportions of volatile hydrocarbons in the spatial domain that were fairly consistent from year to year and resilient to changing wind conditions (Fig. 2). They went on to document a systematic, directional relationship between wind direction at the loft and relative amounts of aromatics correlated to positional direction.

While this experiment was clearly monumental, potential limitations that the authors pointed out are that, with the exception of isoprene (Fig. 2), the study focused on aromatics that were not natural, biogenic compounds but rather long-lived, anthropogenic pollutants, and there was no demonstration that birds could smell these or other, more appropriate compounds at the concentrations measured. By necessity, air was collected along roads and much closer to

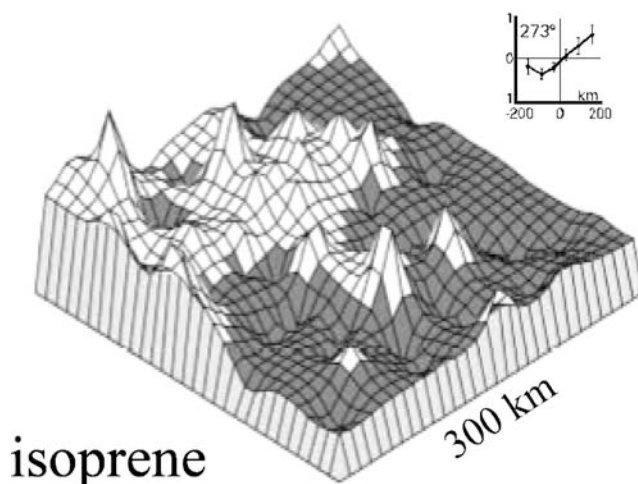


Fig. 2 Isoprene concentrations expressed as a proportion of six hydrocarbons (adapted from Wallraff and Andreae 2000). Data were collected from 96 rural locations in a 200-km radius around a pigeon loft in Wurzburg, Germany. Complete landscapes were computed by interpolation. Areas with above-average values have lighter shading, while areas with below-average values have darker shading (for further details, see Wallraff and Andreae 2000)

the substrate (4.5 m) than a pigeon normally flies. The physical association between point sources (potential emission sites such as roads, factories, or mining operations) and the ratios measured could not be considered in the analysis. Finally, samples were not taken synchronously, and sampling duration and volume (48 l of air over 2 h), as well as subsequent analysis, averaged out fine-scale structure (odor filaments), the unit the bird is likely to be sampling (Wallraff and Andreae 2000; reviewed by Wallraff 2005).

However, somewhat analogously to the work of Døving et al. (1985) with salmon, this approach is among the first to attempt a description of the spatial complexity in the odor landscape through which pigeons navigate. Further work is needed to determine flux rates of volatile substances produced by that landscape and to make clear-cut associations between what can be measured and what can be smelled. While the compounds analyzed were fairly stable, the properties of biogenic odorants are likely to vary with respect to lifetime and decay time. Thus, it will be critical to show that biogenic odor blends that are produced in a given area retain some spatial homogeneity and that pigeons can link that homogeneity to a compass direction back at the loft via experience with windborne delivery. In an alternative scenario, depending on the dynamics of fine-scale mixing and odor transport, a pigeon might get an occasional whiff of source concentration produced some distance away and still learn to associate those occurrences with compass direction. In this hypothetical example, intermittency of the pigeons' encounter rate with source concentration might also encode distance from the loft. The possibility that the fine-scale, filamentous nature of odor transport could add a different dimension to the problem ought to be considered.

The monotonic gradient model provides a starting point for humans who tend to lack an intuitive framework (and vocabulary) to describe and understand how olfactory features are related over large spatial scales on the order of hundreds of kilometers (we are reminded of the 'aroma of Tacoma', a paper mill city south of Seattle). However, this framework currently imposes unrealistic constraints on the spatial distribution of odors. Wallraff's relief maps showing standardized ratios of hydrocarbons reinforce this idea—they are as complex as mountain ranges, depending on which way an axis is drawn. However, this is not a shortcoming and only illustrates that the problem presents challenges comparable to those presented by other sensory features. For example, characteristics of visual landscapes that seem intuitively obvious to humans can be difficult to parameterize in the context of pigeon homing (e.g., Lau et al. 2006). Thus, a major strength of this study (Wallraff and Andreae 2000) is that it illustrates that identifiable, relatively stable features occur in the chemical realm,

opening up new avenues for inquiry into an age-old problem.

Procellariiforms

Like pigeons, procellariiforms present an attractive model for investigating olfactory navigation over large distances. This Order, commonly referred to as the tube-nosed seabirds, is represented by the petrels, albatrosses, and shearwaters, which are in many ways like fishes of the air. These birds live highly pelagic lifestyles, coming to land only for a few months each year or every other year to breed and rear a single offspring (for comprehensive review of procellariiforms, see Warham 1990, 1996). These birds generally mate for life and routinely forage over hundreds and thousands of square kilometers of open ocean in search of patchily distributed prey. Not surprisingly, they have among the largest olfactory bulbs of any bird and, depending on the species, rely more or less upon their unusually highly developed sense of smell to find their prey. Procellariiforms use odors to forage over vast distances of open ocean, and much research has focused on understanding the mechanisms different species use to find prey (reviewed in Nevitt and Bonadonna 2005a). We have shown, for example, that procellariiforms can use olfactory cues at both large (hundreds to thousands of square kilometers in this case) and small (less than a hundred square kilometers) spatial scales for foraging. Our current understanding is that, at large spatial scales, birds use odors to identify productive areas for foraging, whereas at smaller spatial scales, they use odors in combination with other cues to track prey directly (reviewed by Nevitt 2000; Nevitt 2008).

Large Spatial Scales Results from extensive behavioral testing performed mostly at sea have led to classifications of olfactory responsiveness to prey-related odors among different species (reviewed by Nevitt 2008). These differences in behavior have provided us with a better understanding of the various ways different species use scent, both in terms of long-distance navigation and tracking prey. Toward this end, we have overcome a major stumbling block that confronts researchers working in the area of pigeon navigation by identifying a measurable, biogenic, scented compound that contributes to stable and predictable landscape features on the ocean surface. Dimethyl sulfide (DMS) is a breakdown product of dimethylsulfoniopropionate (DMSP), which is, in turn, a metabolite produced by various species of phytoplankton (most notably, *Phaeocystis* in the sub-Antarctic). Phytoplankton tend to aggregate where upwelling occurs, and, during senescence or consumption by phytoplankton grazers

(e.g., krill, fish, and squid), DMSP and DMS are released. DMS is not very soluble in seawater, and so it is quickly emitted into the atmosphere where it also can serve as a local, small-scale foraging cue for seabirds (Nevitt et al. 1995; see also Nevitt et al. 2004). Biogenic DMS has been shown to be a significant source of biogenic sulfur on a planetary scale and plays a key role in global climate regulation, so considerable research has been devoted to mapping regions noted for DMS production and flux (Kettle et al. 1999). The elucidation of such areas suggested to us that predictable odor features are superimposed upon the ocean, thus offering seabirds olfactory landmarks to identify useful foraging regions such as shelf breaks, sea mounts and upwelling zones (reviewed by Nevitt 1999; 2000). We coined the term “olfactory landscape” to describe this idea (Nevitt et al. 1995). We have since shown through physiological, behavioral, and observational tracking studies that procellariiforms respond to DMS at biogenic concentrations and will orient to it in non-foraging contexts (for example, Nevitt et al. 1995; Nevitt and Haberman 2003; Nevitt and Bonadonna 2005b).

With respect to olfactory navigation and foraging over large (hundreds and thousands of square kilometers) spatial scales, the current hypothesis driving our work is that birds build a map of their familiar surroundings through experience, first with odors in the nest, and then with odors associated with foraging experience at sea (Cunningham 2005). We have recently shown, for example, that Antarctic prion (*Pachyptila desolata*) chicks will orient to DMS and other prey-related odors at biogenic concentrations (10^{-12} M) even before fledging, and currently, we are testing the idea that this is a learned behavior through contact with parents in the nest (Bonadonna et al. 2006; Nevitt et al., unpublished). As chicks leave the nest to forage for the first time without parental assistance, we reason that knowledge of scents that are typically associated with prey prepares them to recognize productive foraging grounds (Cunningham 2005; Cunningham et al. 2006; Bonadonna et al. 2006). Once birds fledge, we hypothesize that they build up an association of potential foraging locations with scented compounds through experience, including interactions with con- and hetero-specifics (Silverman et al. 2004). Since birds routinely forage over expansive distances, this hypothesis suggests that, over time, the foraging landscape that may span thousands of square kilometers for some species becomes predictable through familiarity, despite it seeming so large from a human perspective. Because ocean features that are not strictly tied to the bathymetry (physical structure of the ocean floor) can be spatially more variable, we speculate that odor cues associated with productivity allow birds an effective means of recognizing ocean features that may vary

spatially with season or weather conditions (for a more complete review, see Nevitt 2008).

Small Spatial Scales Many species of procellariiforms perform characteristic zigzag upwind search in response to odor cues. Researchers commonly have reported that procellariiforms are attracted to experimental deployments of prey-related scents from distances of several hundred meters to kilometers (for example, Grubb 1972; Hutchison and Wenzel 1980; Nevitt and Haberman 2003; Nevitt et al. 2008). Results from several studies suggest that olfactory tracking is more typical of burrow-nesting rather than surface-nesting species (Nevitt et al. 1995, 2004; Nevitt 1999) and that this behavior may be linked to differences in developmental environments in the nest (Van Buskirk and Nevitt 2008; reviewed by Nevitt 2008). However, surface-nesting procellariiforms also have large olfactory bulbs, and new evidence suggests that hunting by smell is a principal foraging strategy for at least one albatross species. This study involved examining the tracks of freely ranging wandering albatross (*Diomedea exulans*) for evidence of olfactory search (Nevitt et al. 2008). Tracks were analyzed from 19 birds equipped with miniature global positioning systems (GPS) and stomach temperature recorders (Weimerskirch et al. 2007). This combination of devices provided high-precision location data (GPS, 10-s sampling rate; Weimerskirch et al. 2002) in combination with data on the size and location of prey ingestion (Wilson et al. 1995).

On a typical foraging trip, wandering albatrosses fly in vast, looped paths, which often cover thousands of square kilometers of open ocean. Wandering albatrosses are known to forage primarily on squid, often in the form of carrion floating on the surface of the water (Croxall and Prince 1994). This suggested to us that scent might be an important cue for these birds to locate prey opportunistically. We predicted that if olfaction were used in prey capture, then wandering albatross should show a tendency to fly crosswind, since this would optimize the likelihood of encountering an odor plume and that we should see evidence for upwind, zigzag turning before prey capture (Dusenbery 1992). By contrast, if birds were using visual search, then we should see evidence of them bee-lining to prey items, irrespective of wind direction. To avoid bias, tracks were first analyzed blind with respect to wind direction in a radius of 10 km from the touchdown point. We calculated this distance to be beyond the visual range at which a bird was likely to be able to easily see a prey item or a conspecific on the water.

The analysis confirmed that wandering albatrosses tend to fly cross-wind, a behavior that had previously been shown and considered primarily as an adaptation for energetic efficiency (Weimerskirch et al. 2000; see discussion in Nevitt et al. 2008; Fig. 3). We found that initial

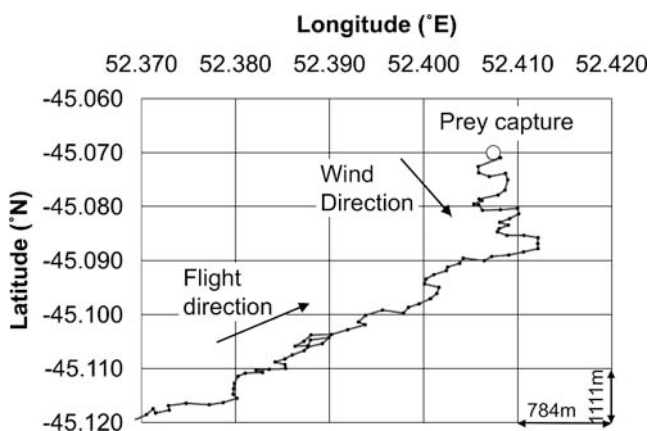


Fig. 3 GPS track of a wandering albatross equipped with a stomach temperature recorder to monitor feeding events. This track illustrates crosswind flight followed by zigzag upwind flight preceding a feeding event (open circle). Arrows refer to flight and wind direction as indicated. The horizontal and vertical distances represented by the smallest grid rectangle are shown in the lower right corner

olfactory detection was implicated in nearly half (46.8%) of all flown approaches that preceded prey capture events, thus accounting for 45.5% of the total prey mass captured by in-flight foraging. We further showed that zigzag approaches were initiated, on average, approximately 2.5 km ($2,401 \pm 346$ m) downwind of the prey capture site, with maximum detection distances observed at 5 km (5,002 m). This result suggested to us that, as a wandering albatross flies along a foraging transit, the area of ocean it surveys is extended, on average, approximately 2.5 km upwind via olfaction. However, when we examined tracks beyond the 10-km spatial limit of the original analysis, we occasionally observed upwind tracks that originated as far as 20 km from the point of prey capture, suggesting that prey detection may be possible from further distances. Finally, it should be noted that, while this discussion focuses on olfactory search in flight, wandering albatrosses also use sit-and-wait strategies to forage (e.g., Weimerskirch et al. 2007). Odors may be useful in this context for identifying productive areas where prey are likely to surface (see Nevitt 2000).

Apart from foraging, olfaction is used for a variety of other behaviors that operate at more localized (within 1 km) spatial scales. Within this range, several species of burrow-nesting petrels have been shown to require a sense of smell to relocate their nest, and individual-specific odors are likely to be involved in the context of nest-site recognition (reviewed by Nevitt and Bonadonna 2005b; see also Bonadonna and Nevitt 2004). When birds are displaced from their burrows at night, they typically sweep their heads from side to side in a manner consistent with olfactory search. This behavior can be elicited in chicks as well as in adults. For example, O'Dwyer et al. (2008) report that when Leach's storm petrel (*Oceanodroma*

leucorhoa) chicks are presented with a choice between nest material from their own burrow and nest material from a neighboring burrow, they will sweep their heads in broad arcs around their body. This behavior is accompanied by rapid biting movements and coughing, with the bill placed close to the substrate (O'Dwyer et al. 2008; see also Cunningham et al. 2003). In simple wind tunnel experiments, we have shown in other species (thin-billed prions *Pachyptila belcheri* and blue petrels *Halobaena caerulea*) that chicks increase their turning rate in response to prey-related odors, suggesting that simple wind tunnels may provide a useful means for investigating olfactory tracking in more precocial species (e.g., Cunningham et al. 2006). We are clearly only scratching the surface of the questions that can be addressed in this fascinating order of birds.

Turkey Vultures

Turkey vultures (*Cathartes aura*) are one of the few terrestrial birds that are commonly accepted as having a remarkable sense of smell. Like procellariiforms, turkey vultures have among the largest olfactory bulbs of any bird (Bang 1960; Bang and Cobb 1968). These birds forage exclusively by scavenging for viscera and muscle tissues of dead animals, and humans have co-opted their abilities for practical purposes. In the late 1930s, for example, the Union Oil Company of California introduced ethyl mercaptan ($\text{CH}_3\text{CH}_2\text{SH}$), a sulfur-based compound associated with animal decay, into 40-mile gas lines so that they could use the presence of turkey vultures as an easy means to locate leaks in the lines in the remote backcountry (reviewed by Stager 1964). Similarly, black vulture (*Coragyps atratus*), a species noted for its visual rather than olfactory abilities, has been reported to use turkey vultures to find carcasses (Buckley 1997).

Although research exploring the use of olfaction by turkey vultures has been debated by scholars as notable as Audubon and Darwin, it was K. E. Stager who carried out the most comprehensive studies on this subject (Stager 1964). Working with vulture populations mainly in California and Mexico, he designed several different foraging challenges, which he carefully controlled for visual cues. These tests involved presenting birds with open containers of ethyl mercaptan or covered baits. He found that turkey vultures tended to be attracted to odor cues whether or not a visual stimulus was also present but not to visual cues (mounted specimens) in the absence of odor cues.

Pertinent to olfactory tracking, Stager (1964) also noted the flight patterns of turkey vultures in response to carcasses and ethyl mercaptan in the absence of visual cues. He reports that vultures approached odor sources from downwind and that they tended to circle the source at elevations estimated by eye to be within 100 m off the

ground. If a visual cue (in this case, an actual carcass) was also present, birds eventually tended to approach it and sometimes landed; in the absence of a visual cue, they typically circled for about 20 min and then left the area. To Stager, these observations suggested that turkey vultures located a potential prey item, first, by using olfaction, whereas visual cues allowed them to deduce its exact location.

In an effort to better understand the characteristics of the odor stimuli that are attractive to turkey vultures, other studies have suggested that the age of the carcass comes into play. Although humans often associate turkey vultures with rotting flesh, results from controlled studies suggests that they have a much more discriminating palate. For example, Owere and Northington (1961) showed that captive vultures consistently preferred freshly killed chicks over decaying food. In field studies, Houston (1986) confirmed that 1-day-old carcasses attracted more vultures than either fresh or 4-day-old carcasses, whereas putrid carcasses were ignored. Thus, for turkey vultures, olfaction may be important not only in locating potential prey but in assessing the age of the carcass.

Given the technical challenges involved, much less is known about the detailed behavioral mechanisms turkey vultures use to locate odor sources, in part because soaring altitudes typically exceed 50 m (see Estrella 1994). Unfortunately, one of the only published attempts to explain how they might accomplish this feat used a Gaussian plume model and concluded that turkey vultures should be unable to detect prey by smell above an altitude of 17 cm (Smith and Paselk 1986). The short-coming of this approach is that a Gaussian dispersion model estimates average concentration for a given distance (altitude in this case) and is thus not well suited to the biological problem. The actual situation is much more complex and requires different predictive tools (for example, large eddy simulation, or LES, Dardoff 1972). In the real atmosphere, odors from a carcass will be lifted as discrete patches that present pockets of high concentration that vultures should be able to detect. Moreover, turkey vultures typically soar on sequences of updrafts generated by thermals and ridges. Since these thermal updrafts also provide a means of vertical transport of odor patches, a more detailed examination of their use of thermals in relation to odor tracking coupled to a more rigorous treatment of atmospheric boundary layer modeling may be a starting point. We are currently exploring this problem.

Summary and Future Directions

Olfactory-mediated behaviors operate over a wide range of spatial dimensions for both fish and birds. By organizing

our discussion into spatially explicit terms, specific themes emerge. In this paper, we summarize consistent findings among these seemingly disparate groups and suggest future directions to explore.

At large spatial scales, odor search reflects physical features of the fluid medium. As we have described, fish as diverse as salmon, eels, and lamprey all show patterns of vertical, oscillatory swimming as they travel through estuaries and fjords. In marine and brackish systems, water tends to be stratified by temperature or salinity gradients, and a number of studies suggest that fish actively sample different water masses as they swim through these layers. The situation is much less clear in birds, where researchers do not have as detailed an understanding of how odors might be distributed in the environment with respect to a physical substrate. Proposed mechanisms include the use of large-scale gradients for navigating distances of hundreds of kilometers. However, in some systems (procellariiforms), the physical evidence points to odors occurring as landscape features associated with sources of odor production. Following the example of Døving and others, future work with birds should be directed toward individual tracking with respect to such features.

Equally important to this problem will be developing more realistic models of atmospheric transport of odors at the spatial scales pertinent to olfactory sampling. Unlike fishes, the bird species that have been looked at do not generally fly in vertical oscillations (with the exception of the Kerguelen petrel *Lugensa brevirostris*), suggesting that birds do not need to sample air masses in the same way that fish are presumed to sample water layers (e.g., salmon and freshwater eels). This likely reflects the different stabilities of thermal or density layers in water as compared to air due to the greater degree of turbulent mixing in the atmospheric boundary layer. However, analogous to fish sampling water layers in fjords, birds that soar on thermal updrafts (e.g., vultures) may have the opportunity to sample thermals (i.e., vertical stratifications) for their odor content.

Another trend we see is that both fish and birds use olfaction in combination with other sensory cues, and attempts to study behaviors with respect to one cue in isolation are problematic. In fish, olfactory-mediated tracking has been shown convincingly to work in combination with both the lateral line and visual systems in a number of species (e.g., Baker and Montgomery 1999; Baker et al. 2002; Carton and Montgomery 2003), and recent evidence suggests involvement of the otolith system as well (Sand and Karlsen 2000; see Døving and Stabell 2003). In birds, olfaction may be used in combination with visual cues or geomagnetic information, depending on the species and the spatial scale of the behavior. The take-home message is that, in natural situations, olfaction works in combination with a range of other sensory modalities. An

understanding of how organisms interpret multimodal cues should take precedence over focusing on any one modality.

Finally, the distribution of natural cues and how these odorants disperse in turbulent environments remain largely unknown (see Zimmer-Faust et al. 1995; Moore and Crimaldi 2004), and yet the few systems where cues have been identified have led to significant advances in our understanding of how animals make sense of olfactory information in natural contexts (e.g., Nevitt et al. 1995; Carton and Montgomery 2003; Sorensen et al. 2003). Since the challenges will require understanding how cues are produced, released, and decay over time and space, progress will depend on researchers being able to think across disciplines and draw on expertise from various fields, including marine and atmospheric chemistry. Already, considerable information is available about the production and distribution of compounds not normally associated with olfaction. For example, DMSP, which is typically studied in the context of sulfur cycling in the ocean, recently has been identified as a potentially important foraging cue for fishes over coral reefs (DeBose and Nevitt 2007; DeBose et al. 2008). Gaining insight into how animals glean information from naturally occurring, biogenic odorants at appropriate biological concentrations remains a top priority for olfactory ecology.

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References

- ABLE, K. P. 1991. Common themes and variations in animal orientation systems. *Am. Zool* 31:157–167.
- ABLE, K. P. 1995. Orientation and navigation: a perspective on fifty years of research. *Condor* 97:592–604.
- ALERSTAM, T. 2006. Conflicting evidence about long-distance animal navigation. *Science* 313:791–794.
- BAKER, C. F., and MONTGOMERY, J. C. 1999. The sensory basis of rheotaxis in the blind Mexican cave fish, *Astyanax fasciatus*. *J. Comp. Physiol. A* 184:519–527.
- BAKER, C. F., MONTGOMERY, J. C., and DENNIS, T. E. 2002. The sensory basis of olfactory search behavior in banded kokopu (*Galaxias fasciatus*). *J. Comp. Physiol. A* 188:553–560.
- BANG, B. G. 1960. Anatomical evidence for olfactory function in some species of birds. *Nature* 188:547–549.
- BANG, B. G. 1971. Functional anatomy of the olfactory system in 23 orders of birds. *Acta Anat* 58:Suppl.1–76.
- BANG, B. G., and COBB, S. 1968. The size of the olfactory bulb in 108 species of birds. *Auk* 85:55–61.
- BANG, B. G., and WENZEL, B. M. 1985. Nasal cavity and olfactory systems, pp. 195–223, in J. S. King, and J. McClelland (eds.). *Form and Function in Birds*, vol. 3 Academic, New York.
- BARBIN, G. P. 1998. The role of olfaction in homing and estuarine migratory behavior of yellow-phase American eels. *Can. J. Fish. Aquat. Sci* 55:564–575.
- BARBIN, G. P., PARKER, S. J., and MCCLEAVE, J. D. 1998. Olfactory cues play a critical role in the estuarine migration of silver-phase American eels. *Environ. Biol. Fish* 53:283–291.
- BELANGER, J. H., and WILLIS, M. A. 1996. Adaptive control of odor-guided locomotion: behavioral flexibility as an antidote to environmental unpredictability. *Adapt. Behav* 4:217–253.
- BELANGER, R. M., CORKUM, L. D., LI, W., and ZIELINSKI, B. S. 2006. Olfactory sensory input increases gill ventilation in male round gobies (*Neogobius melanostomus*) during exposure to steroids. *Comp. Biochem. Phys. A* 144:196–202.
- BINGMAN, V. P., and BENVENUTI, S. 1996. Olfaction and the homing ability of pigeons in the southeastern United States. *J. Exp. Zool* 275:186–192.
- BINGMAN, V. P., ALYAN, S., and BENVENUTI, S. 1998. The importance of atmospheric odours for the homing performance of pigeons in the Sonoran Desert of the southwestern United States. *J. Exp. Biol* 201:755–760.
- BJERSELIUS, R., LI, W., TEETER, J. H., SEELYE, J. G., JOHNSEN, P. B., MANIAK, P. J., GRANT, G. C., POLKINGHORNE, C. N., and SORENSEN, P. W. 2000. Direct behavioral evidence that unique bile acids released by larval sea lamprey (*Petromyzon marinus*) function as a migratory pheromone. *Can. J. Fish. Aquat. Sci* 57:557–569.
- BONADONNA, F., and NEVITT, G. A. 2004. Partner-specific odor recognition in an Antarctic seabird. *Science* 306:835–835.
- BONADONNA, F., CARO, S., JOUVENTIN, P., and NEVITT, G. A. 2006. Evidence that blue petrel, *Halobaena caerulea*, fledglings can detect and orient to dimethyl sulphide. *J. Exp. Biol* 209:2165–2169.
- BUCKLEY, N. J. 1997. Experimental tests of the information-center hypothesis with black vultures and turkey vultures. *Behav. Ecol. Sociobiol* 41:267–269.
- CAPRIO, J. 1988. Peripheral filters and chemoreceptor cells in fishespp. 313–338, in J. Atema, R. R. Fay, A. N. Popper, and W. N. Tavolga (eds.). *Sensory Biology of Aquatic Animals* Springer, New York.
- CARDÉ, R. T., and WILLIS, M. A. 2008. Navigational strategies used by insects to find distant wind-borne sources of odor. *J. Chem. Ecol.* (this issue)
- CARTON, A. G., and MONTGOMERY, J. C. 2003. Evidence of a rheotactic component in the odour search behaviour of freshwater eels. *J. Fish Biol* 62:501–516.
- COURTENAY, S. C., QUINN, T. P., DUPUIS, H. M. C., GROOT, C., and LARKIN, P. A. 1997. Factors affecting the recognition of population-specific odours by juvenile coho salmon. *J. Fish Biol* 50:1042–1060.
- CROXALL, J. P., and PRINCE, P. A. 1994. Dead or alive, night or day-how do albatrosses catch squid? *Antarct. Sci* 6:155–162.
- CUNNINGHAM, G. B. 2005. Development of olfactory behaviors in procellariiform seabirds. Dissertation in Physiology Graduate Group, University of California, Davis, pp. 155.
- CUNNINGHAM, G. B., VAN BUSKIRK, R. W., BONADONNA, F., WEIMERSKIRCH, H., and NEVITT, G. A. 2003. A comparison of the olfactory abilities of three species of procellariiform chicks. *J. Exp. Biol* 206:1615–1620.
- CUNNINGHAM, G. B., VANBUSKIRK, R., HODGES, M. J., WEIMERSKIRCH, H., and NEVITT, G. A. 2006. Behavioural responses of blue petrel chicks *Halobaena caerulea* to a food-related and novel odour in a simple wind tunnel. *Antarct. Sci* 18:345–352.
- DAVIS, M. W., SPENCER, M. L., and OTTMAR, M. L. 2006. Behavioral responses to food odor in juvenile marine fish: acuity varies with species and fish length. *J. Exp. Mar. Biol. Ecol* 328:1–9.
- DEARDORFF, J. W. 1972. Numerical investigation of neutral and unstable planetary boundary layers. *J. Atmos. Sci* 29:91–115.

- DEBOSE, J. L., and NEVITT, G. A. 2007. Investigating the association between pelagic fish and DMSP in a natural coral reef system. *Mar. Freshw. Res* 58:720–724.
- DEBOSE, J. L., LEMA, S. C., and NEVITT, G. A. 2008. Dimethylsulfoniopropionate as a foraging cue for reef fishes. *Science* 319:1356.
- DITTMAN, A. H., and QUINN, T. P. 1996. Homing of Pacific salmon: mechanisms and ecological basis. *J. Exp. Biol* 199:83–91.
- DITTMAN, A. H., QUINN, T. P., and NEVITT, G. A. 1996. Timing of imprinting to natural and artificial odors by coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci* 53:434–442.
- DØVING, K. B., and STABELL, O. B. 2003. Trails in open waters: sensory cues in salmon migration, pp. 39–52, in S. P. Collin, and N. J. Marshall (eds.). *Sensory Processing in Aquatic Environments* Springer, New York.
- DØVING, K. B., WESTERBERG, H., and JOHNSEN, P. B. 1985. Role of olfaction in the behavioral and neuronal responses of Atlantic salmon, *Salmo salar*, to hydrographic stratification. *Can. J. Fish. Aquat. Sci* 42:1658–1667.
- DUSENBERY, D. B. 1992. *Sensory Ecology*. Freeman, New York.
- ELLIOTT, J. K., ELLIOTT, J. M., and MARISCAL, R. N. 1995. Host selection, location, and association behaviors of anemonefishes in field settlement experiments. *Mar. Biol* 122:377–389.
- ESTRELLA, R. R. 1994. Group size and flight altitude of turkey vultures in two habitats in Mexico. *Wilson Bull* 106:749–752.
- FINELLI, C. M., PENTCHEFF, N. D., ZIMMER-FAUST, R. K., and WETHEY, D. S. 1999. Odor transport in turbulent flows: constraints on animal navigation. *Limnol. Oceanogr* 44:1056–1071.
- GAGLIARDO, A., ODETTI, F., and IOALÈ, P. 2001a. Relevance of visual cues for orientation at familiar sites by homing pigeons: an experiment in a circular arena. *Proc. Roy. Soc. Lond* 268:2065–2070.
- GAGLIARDO, A., IOALÈ, P., ODETTI, F., and BINGMAN, P. 2001b. The ontogeny of the homing pigeon navigational map: evidence for a sensitive learning period. *Proc. R. Soc. Lond. B* 268:197–202.
- GRUBB, T. C. 1972. Smell and foraging in shearwaters and petrels. *Nature* 237:404–405.
- HAGELIN, J. C. 2004. Short communication. Observations on the olfactory ability of the Kokapo *Strigops habroptilus*, the critically endangered parrot of New Zealand. *Ibis* 146:161–164.
- HARA, T. J. 2006. Feeding behaviour in some teleosts in triggered by single amino acids primarily through olfaction. *J. Fish Biol* 68:810–825.
- HARTMAN, E. J., and ABRAHAMS, M. V. 2000. Sensory compensation and the detection of predators: the interaction between chemical and visual information. *Proc. Royal Soc. London Ser. B—Biol. Sci* 267:571–575.
- HASLER, A. D., SCHOLZ, A. T., and HERRALL, R. M. 1978. Olfactory imprinting and homing in salmon. *Am. Sci.* 66:374–355.
- HOUSTON, D. C. 1986. Scavenging efficiency of turkey vultures in tropical forest. *Condor* 88:318–323.
- HUTCHISON, L. V., and WENZEL, B. M. 1980. Olfactory guidance in foraging by procellariiforms. *Condor* 82:314–319.
- JOHNSEN, P. B. 1982. Establishing the physiological and behavioral determinants of chemosensory orientation, pp. 379–386, in J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill (eds.). *Mechanisms of Migration in Fishes* Plenum, New York.
- JOHNSEN, P. B., and TEETER, J. 1985. Behavioral responses of bonnethead sharks (*Sphyrna tiburo*) to controlled olfactory stimulation. *Mar. Behav. Physiol* 11:283–291.
- KEEFER, M. L., CAUDILL, C. C., PEERY, C. A., and BJORN, T. C. 2006. Route selection in a large river during the homing migration of Chinook salmon (*Oncorhynchus tshawytscha*). *Can. J. Fish. Aquat. Sci* 63:1752–1762.
- KETTLE, A. J., ANDREAE, M. O., AMOUROUX, D., ANDREAE, T. W., BATES, T. S., BERRESHEIM, H., BINGEMER, H., BONIFORTI, R., CURRAN, M. A. J., DITULLIO, G. R., HELAS, G., JONES, G. B., MCTAGGART, A. R., MIHALOPOULOS, N., NGUYEN, B. C., NOVO, A., PUTAUD, J. P., RAPSOMANIKIS, S., ROBERTS, G., SCHEBESKE, G., SHARMA, S., SIMÓ, R., STAUBES, R., TURNER, S., and UHER, G. 1999. A global database of sea surface dimethylsulfide (DMS) measurements and a procedure to predict sea surface DMS as a function of latitude, longitude and month. *Glob. Biogeochem. Cycles* 13:399–444.
- KRAMER, G. 1952. Experiments on bird orientation. *Ibis* 94:265–285.
- LAU, K.-K., ROBERTS, S., BIRO, D., FREEMAN, R., MEADE, J., and GUILFORD, T. 2006. An edge-detection approach to investigating pigeon navigation. *J. Theor. Biol* 239:71–78.
- LEMA, S. C., and NEVITT, G. A. 2004. Evidence that thyroid hormone induces olfactory cellular proliferation in salmon during a sensitive period for imprinting. *J. Exp. Biol.* 207:3317–3327.
- LØKKEBORG, S. 1998. Feeding behaviour of cod, *Gadus morhua*: activity rhythm and chemically mediated food search. *Anim. Behav* 56:371–378.
- LØKKEBORG, S., and FERNÖ, A. 1999. Diel activity pattern and food search behaviour in cod, *Gadus morhua*. *Environ. Biol. Fish* 54:345–353.
- MITAMURA, H., ARAI, N., SAKAMOTO, W., MITSUNAGA, Y., TANAKA, H., MUKAI, Y., NAKAMURA, K., SASAKI, M., and YONEDA, Y. 2005. Role of olfaction and vision in homing behaviour of black rockfish *Sebastes inermis*. *J. Exp. Mar. Biol. Ecol* 322:123–134.
- MONTGOMERY, J. C., DIEBEL, C., HALSTEAD, M. B. D., and DOWNER, J. 1999. Olfactory search tracks in Antarctic fish *Trematomus bernacchii*. *Polar Biol* 21:151–154.
- MOORE, P., and CRIMALDI, J. 2004. Odor landscapes and animal behavior: tracking odor plumes in different physical worlds. *J. Mar. Syst* 49:55–64.
- MOORE, P. A., GRILLS, J. L., and SCHNEIDER, R. W. S. 2000. Habitat-specific signal structure for olfaction: an example from artificial streams. *J. Chem. Ecol* 26:565–584.
- MURPHY, C. A., STACEY, N. E., and CORKUM, L. D. 2001. Putative steroidal pheromones in the round goby, *Neogobius melanostomus*: olfactory and behavioral responses. *J. Chem. Ecol* 27:443–470.
- NEVITT, G. A. 1991. Do fish sniff? A new mechanism of olfactory sampling in pleuronectid flounders. *J. Exp. Biol* 157:1–18.
- NEVITT, G. A. 1999. Olfactory foraging in Antarctic seabirds: a species-specific attraction to krill odors. *Mar. Ecol. Prog. Ser* 177:235–241.
- NEVITT, G. A. 2000. Olfactory foraging by Antarctic procellariiform seabirds: life at high Reynolds numbers. *Biol. Bull* 198:245–253.
- NEVITT, G. A. 2008. Sensory ecology on the high seas: investigating the odor world of the procellariiform seabirds. *J. Exp. Biol.* (in press).
- NEVITT, G. A., and HABERMAN, K. L. 2003. Behavioral attraction of Leach's storm-petrels (*Oceanodroma leucorhoa*) to dimethyl sulfide. *J. Exp. Biol* 206:1497–1501.
- NEVITT, G. A., and DITTMAN, A. H. 2004. Olfactory imprinting in salmon: new models and approaches, pp. 109–127, in G. Von Der Emde, J. Mogdans, and B. G. Kapoor (eds.). *The Senses of Fish: Adaptations for the Reception of Natural Stimuli* Narosa, New Delhi.
- NEVITT, G. A., and BONADONNA, F. 2005a. Seeing the world through the nose of a bird: new developments in the sensory ecology of procellariiform seabirds. *Mar. Ecol. Prog. Ser* 287:292–295.
- NEVITT, G. A., and BONADONNA, F. 2005b. Sensitivity to dimethyl sulphide suggests a mechanism for olfactory navigation by seabirds. *Biol. Lett* 1:303–305.
- NEVITT, G. A., VEIT, R. R., and KAREIVA, P. 1995. Dimethyl sulphide as a foraging cue for Antarctic procellariiform seabirds. *Nature* 376:680–682.

- NEVITT, G. A., REID, K., and TRATHAN, P. 2004. Testing olfactory foraging strategies in an Antarctic seabird assemblage. *J. Exp. Biol* 207:3537–3544.
- NEVITT, G. A., LOSEKOOT, M., and WEIMERSKIRCH, H. 2008. Evidence for olfactory search in Wandering albatross *Diomedea exulans*. *Proc. Nat. Acad. Sci. U.S.A* 105:576–4581.
- NORDENG, H., and BRATLAND, P. 2006. Homing experiments with parr, smolt and residents of anadromous Arctic char *Salvelinus alpinus* and brown trout *Salmo trutta*: transplantation between neighboring river systems. *Ecol. Freshw. Fish* 15:488–499.
- O'DWYER, T. W., ACKERMAN, A. L., and NEVITT, G. A. 2008. Examining the development of individual recognition in a burrow-nesting procellariiform, the Leach's storm-petrel. *J. Exp. Biol* 211:337–340.
- OWRE, O. T., and NORTHINGTON, P. O. 1961. Indication of the sense of smell in the turkey vulture from feeding tests. *Am. Midland Nat* 66:200–205.
- PAPI, F. 1990. Olfactory navigation in birds. *Experientia* 46:352–363.
- PAPI, F. 2006. Navigation of marine, freshwater and coastal animals: concepts and current problems. *Mar. Freshw. Behav. Physiol* 39:3–12.
- PAPI, F., FIORE, L., FIASHCHI, V., and BENVENUTI, S. 1971. The influence of olfactory nerve section on the homing capacity of carrier pigeons. *Monit. Zool. Ital* 5:265–267.
- PLENDERLEITH, M., VAN OOSTERHOUT, C., ROBINSON, R. L., and TURNER, G. F. 2005. Female preference for conspecific males based on olfactory cues in a Lake Malawi cichlid fish. *Biol. Lett* 1:411–414.
- ROPER, T. J. 1999. Olfaction in birds. *Adv. Study Behav* 28:247–332.
- SAND, O., and KARLSEN, H. E. 2000. Detection of infrasound by the Atlantic cod. *R. Soc* 125:197–204.
- SHERMAN, M. L., and MOORE, P. A. 2001. Chemical orientation of brown bullheads, *Ameiurus nebulosus*, under different flow conditions. *J. Chem. Ecol* 27:2301–2318.
- SILVERMAN, E. D., VEIT, R. R., and NEVITT, G. A. 2004. Nearest neighbors as foraging cues: information transfer in a patchy environment. *Mar. Ecol. Prog. Ser* 277:25–35.
- SMITH, S. A., and PASELK, R. A. 1986. Olfactory sensitivity of the turkey vulture (*Cathartes aura*) to three carrion-associated odorants. *Auk* 103:586–592.
- SORENSEN, P. W., VRIEZE, L. A., and FINE, J. M. 2003. A multi-component migratory pheromone in the sea lamprey. *Fish Physiol. Biochem* 28:253–257.
- STAGER, K. E. 1964. The role of olfaction in food location by the turkey vulture (*Cathartes aura*). *Los Angeles Cty. Mus. Contrib. Sci* 81:3–63.
- UEDA, H., KAERIYAMA, M., MUKASA, K., URANO, A., KUDO, H., SHOJI, T., TOKUMITSU, Y., YAMAUCHI, K., and KURIHARA, K. 1998. Lacustrine sockeye salmon return straight to their natal area from open water using both visual and olfactory cues. *Chem. Sens* 23:207–212.
- VANBUSKIRK, R., and NEVITT, G. A. 2007. Evolutionary arguments for olfactory behavior in modern birds. *ChemoSense* 10:2–6.
- VANBUSKIRK, R., and NEVITT, G. A. 2008. The influence of developmental environment on the evolution of olfactory foraging behavior in procellariiform seabirds. *J. Evol. Biol* 21:67–76.
- VICKERS, N. J. 2000. Mechanisms of animal navigation in odor plumes. *Biol. Bull* 198:203–212.
- VRIEZE, L. A., and SORENSEN, P. W. 2001. Laboratory assessment of the role of a larval pheromone and natural stream odor in spawning stream localization by migratory sea lamprey (*Petromyzon marinus*). *Can. J. Fish Aquat. Sci* 58:2374–2385.
- WALCOTT, C. 1996. Pigeon homing: observations, experiments and confusions. *J. Exp. Biol* 199:21–27.
- WALLRAFF, H. G. 1989. Simulated navigation based on assumed gradients of atmospheric trace gases (models on pigeon homing. Part 3). *J. Theor. Biol* 138:511–528.
- WALLRAFF, H. G. 2000. Path integration by passively displaced homing pigeons? *Anim. Behav* 60:F30–F36.
- WALLRAFF, H. G. 2004. Avian olfactory navigation: its empirical foundation and conceptual state. *Anim. Behav* 67:189–204.
- WALLRAFF, H. G. 2005. Beyond familiar landmarks and integrated routes: goal-oriented navigation by birds. *Connect. Sci* 17:91–106.
- WALLRAFF, H. G., and ANDREAE, M. O. 2000. Spatial gradients in ratios of atmospheric trace gases: a study stimulated by experiments on bird navigation. *Tellus* 52B:1138–1157.
- WARHAM, J. 1990. The Petrels: Their Ecology and Breeding Systems. Academic, London.
- WARHAM, J. 1996. The Behavior, Population Biology and Physiology of the Petrels. Academic, London.
- WEIMERSKIRCH, H., GUIONNET, T., MARTIN, J., SHAFFER, S. A., and COSTA, D. P. 2000. Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Phil. Trans. R. Soc. Lond. B* 267:1869–1874.
- WEIMERSKIRCH, H., BONADONNA, F., BAILLEUL, F., MABILLE, G., DELL'OMO, G., and LIPP, H. P. 2002. GPS tracking of foraging albatrosses. *Science* 295:1259–1259.
- WEIMERSKIRCH, H., PINAUD, D., PAWLOWSKI, F., and BOST, C. A. 2007. Does prey capture induce area-restricted search? A fine scale study using GPS in a marine predator, the wandering albatross. *Am. Nat* 170:734–743.
- WENZEL, B. M. 1960. The olfactory prowess of the Kiwi. *Nature* 220:1133–1134.
- WENZEL, B. M. 1987. The olfactory and related systems in birds. *Ann. N.Y. Acad. Sci* 519:137–139.
- WESTERBERG, H. 1982. The orientation of fish and the vertical stratification at fine- and micro-structure scales, pp. 179–204, in J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill (eds.). Mechanisms of Migration in Fishes Plenum, New York.
- WILSON, R. P., PUTZ, K., GREMILLET, D., CULIK, B. M., KIERSPEL, M., REGEL, J., BOST, C. A., LAGE, J., and COOPER, J. 1995. Reliability of stomach temperature changes in determining feeding characteristics of seabirds. *J. Exp. Biol* 198:1115–1135.
- WILTSCHKO, W., and WILTSCHKO, R. 1998. The navigation system of birds and its development, pp. 155–159, in R. P. Balda, I. M. Pepperberg, and A. C. Kamil (eds.). Animal Cognition in Nature. Academic, San Diego.
- WILTSCHKO, R., and WILTSCHKO, W. 2000. A strategy for beginners! Reply to Wallraff (2000). *Anim. Behav* 60:F37–F43.
- WILLIS, M. A. 2005. Odor-modulated navigation in insects and artificial systems. *Chem. Senses* 30:i287–i288.
- ZIMMER-FAUST, R. K., FINELLI, C. M., PENTCHEFF, N. D., and WETHEY, D. S. 1995. Odor plumes and animal navigation in turbulent water flow: a field study. *Biol. Bull* 188:111–116.