OLFACTORY GUIDANCE IN FORAGING BY PROCELLARIIFORMS

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ABSTRACT.—Systematic field experiments show that procellariiform birds, viz., Black-footed Albatrosses (*Diomedea nigripes*), shearwaters (*Puffinus griseus, P. creatopus, P. puffinus, P. bulleri,* and *P. tenuirostris*), Northern Fulmars (*Fulmarus glacialis*), and storm-petrels of several species, are consistently attracted to sources of food-related odors under natural conditions at sea with controlled visual cues. They approach predominantly from downwind, in proportions above control levels, when food odors are presented as surface slicks, slicks spread in large shallow pools of plastic floating on the ocean, and by saturated wicks on free-floating rafts. Control stimuli and odorous materials unrelated to food do not attract procellariiforms. Birds of other orders are not attracted by any odorous stimulus, and approach the areas from all directions only when discrete visual stimuli are added. Observations and photographs reveal a flight pattern displayed only by procellariiforms in their apparent foraging approaches to food-related stimuli. Tube-nosed birds are most numerous under conditions of reduced visibility, high winds, large swells, and turbulent ocean surface. The results of this study strongly support the view, previously based on comparative anatomy and uncontrolled observations, that procellariiforms use olfaction in locating food.

The ethology of olfaction is still largely unexplored in all vertebrates, and notably so for birds. Among avian olfactory systems, the nasal architecture and olfactory bulbs of the procellariiforms are impressive (Bang 1965, 1966, 1971). Cobb's (1960) measure, the ratio of olfactory bulb diameter to the largest diameter of the cerebral hemisphere, places tube-nosed species in 10 of the first 12 ranks for the 151 species among 23 orders on which measurements have been made (Bang 1971). These high values range from 0.27 for the Northern Fulmar (*Fulmarus glacialis*) to 0.37 for the Snow Petrel (*Pagodroma nivea*). The two other highest-ranking species, the Brown Kiwi (*Apteryx australis*) in rank 2 and the Turkey Vulture (*Cathartes aura*) in rank 10, have already been shown to respond discriminatively to appropriate food odors (Stager 1964, Wenzel 1969, 1971). The Rock Dove (*Columba livia*), now thought to be partly dependent on olfactory cues for homing (Papi et al. 1978, Keeton 1979), falls in midrange with a ratio of 0.17.

Anecdotal evidence has long suggested that procellariiforms can distinguish odors (for review see Wenzel, in press). Some species can be attracted over long distances by griddle drippings, especially bacon fat, poured on the ocean surface and they often collect more quickly when the fat or oil has been heated (Murphy 1936, Miller 1942,

Kritzler 1948). Several species of albatrosses discriminate between slicks of paint or petroleum and bacon fat or whale oil (Murphy 1936, Miller 1942). Two Snow Petrels in captivity accurately found hidden pieces of herring either outside in the snow or concealed inside a room (Jouventin 1977).

In addition to feeding, other features of procellariiform biology also suggest the possibility of olfactory guidance. Many species eject redolent stomach oil when disturbed. Secretion from the uropygial gland is typically odorous, accounting for the well-known musky scent of many procellariiforms. Such compounds might serve as olfactory markers to aid in identifying individual nesting burrows, chicks, and mates in densely populated breeding colonies (Stager 1967). Members of several species must find their burrows when they are obscured by fog, clouds, overlying forests, darkness, or snow cover.

Few controlled experiments have been attempted on the olfactory behavior of procellariiforms. Grubb (1974, 1979) studied the role of olfaction in the return of Leach's Storm-Petrel (*Oceanodroma leucorhoa*) to its nesting burrow. After approaching their island upwind at twilight or after dark and crashing through the heavy wooded cover, breeding birds typically walked upwind to their burrows, in contrast to the inconsistent orientation of nonbreeders. Grubb found

that cutting the olfactory nerve or plugging the nares prevented return, while unoperated and sham-operated control birds came back within a week or less. Storm-petrels at sea seem to have been attracted to surface slicks of vegetable oil (R. S. Crossin, unpubl. data from 1968 Pacific Ocean Biological Survey Program), and storm-petrels and shearwaters approached elevated sponges soaked in cod liver oil more often than they did sponges soaked in sea water (Grubb 1972).

The experiments reported here were designed to answer three questions. First, can procellariiforms be attracted to an odor source when visual stimuli are controlled or absent? Second, do these birds differ from others in frequency of visits to odor sources and in behavior patterns? Third, does attractiveness differ among various odorous stimuli including natural foods, foods not usually eaten by pelagic birds, and compounds unrelated to food?

METHODS

Our observations were made from 10 to 80 km off the California coast (120°–122°W, 35°–36°N). Cruises lasting two to six days ranged within an 80-km radius of Estero Bay on at least four days each month from April 1977 to August 1978. We presented stimuli in three ways, as surface slicks, as surface slicks in translucent plastic enclosures floating on the ocean, and by saturated wicks on free-floating rafts. The test stimuli included substances with different visual characteristics and with odorous properties a) related to natural food of pelagic birds (fish oils and squid homogenate), b) related to foods not normally ingested by these birds (vegetable oil and bacon fat), and c) unrelated to food (petroleum oil and mineral oil).

In the first experiments, open slicks were made by spreading 3–10 l of a single substance on the ocean surface. One of two control conditions was a designated area of ocean approximately comparable to the area of a slick and empty of birds at the start of observation, and the other was such an area where procellariiforms were already feeding naturally. In some of the experiments using bacon fat, puffed cereal was added as a specific visual stimulus.

Procellariiforms, especially storm-petrels, may approach slicks because of small organisms (e.g., euphausids, copepods, and larval fish) that could be attracted to them (Crossin, unpubl.). Therefore, a second set of experiments used isolated slicks. Two identical circular enclosures were made of flexible, translucent plastic with limited reflective properties to diminish the potential salience of visual cues. Since the plastic was not transparent, it was very unlikely that marine organisms would have been drawn by seeing the oil in it and, hence, have been visible to birds. The enclosures were 6.15 m in diameter with an inner surface area of approximately 30 m² depending on wave action. The perimeter of each enclosure was a flotation collar 25.4 cm in diameter. Enclosing slicks in this manner provided a surface area large enough for birds to land as they had in open slicks and also permitted isolation of stimulus material from direct contact with the ocean surface by means of a bottom membrane. In such en-

closures, we made both successive and simultaneous comparisons between tuna oil as the test stimulus and ocean water as the control. In simultaneous comparisons, the two enclosed slicks were presented approximately 75–100 m apart in open sea at the same time; for successive comparisons, stimuli were presented individually in a sequence that was reversed on alternate days of each cruise. In all tests, the enclosures contained 3–10 l of stimulus material.

In a third set of experiments, odor was diffused by mounting a wick on a floating vertical pole 1 m high. The pole was attached to a wooden floor that filled the center of an inflated inner tube 0.7 m in diameter. A gimbal on top of the pole held a polyethylene bottle, filled with stimulus or control material, from which a cotton wick protruded about 15 cm. This method insured continuous saturation of the wick and proved highly effective in dispersing the stimulus with no differential visual cues. In our first series with saturated wicks, the experimental stimuli were the same unrefined substances that had been presented as surface slicks. In the later experiments, however, we added squid homogenate and the major complex fraction of tuna oil. The latter was prepared by gas chromatography and dissolved in hexane. In this set of experiments sea water, hexane, and mineral oil were presented as controls and petroleum oil as potentially aversive in contrast to the edible oils.

In most tests the boat was stationed where procellariiforms had been sighted either on the same or a prior cruise, but some experiments were conducted at new locations where these birds had yet to be seen. No experimental stimuli were deployed until at least 10 min had elapsed without sighting a procellariiform in any direction, either with or without binoculars. During at least one day of each cruise, usually the first, prolonged observations were made under baseline conditions (i.e., no stimulus presented) before beginning any experiments. The observation boat remained crosswind approximately 50–100 m from the stimuli throughout the experiments. Occasional maneuvering under power was necessary to compensate for drift, or wave and wind action. The orders of stimulus presentation and of boat stations at sea were typically reversed on successive days.

Observation periods usually lasted at least two hours. Shorter periods occurred only when birds became too numerous for reliable counts, as often happened after deployment of slicks with puffed rice and bacon fat. Following each experiment, the boat was moved to a new station, downwind and/or farther to sea, at least 3 km from the preceding one. Experiments were repeated at the same stations in different seasons of the year.

Birds were counted as having visited the area if we could see them without binoculars. Each bird sighted and its subsequent behaviors were recorded as new events, unless it was clear that the same bird was approaching repeatedly. Procellariiforms were identified by family for overall data analysis. The more readily identifiable species were noted but precise identification of every bird sighted was not attempted. Birds belonging to other families, e.g., gulls, terns, pelicans, and cormorants, were identified only as nonprocellariiforms.

For every observation we recorded the exact position of the experimental station. Ambient conditions on the ocean surface, such as air and water temperature, wind direction and velocity, prevailing weather and visibility, as well as such other aspects of the immediate environment as ocean depth, bottom characteristics, and presence or absence of other marine life, were recorded continuously throughout the observations. Both still

TABLE 1. Procellariiform species sighted in study area.

Species	Relative abundance during year	
Black-footed Albatross	Common	March–July
	Uncommon	August–September
Northern Fulmar	Common	November–April
	Uncommon	May–June
Sooty Shearwater	Common	April–November
	Uncommon	December–March
Pink-footed Shearwater	Common	May–November
Short-tailed Shearwater	Rare	November–March
New Zealand Shearwater (*P. bulleri*)	Uncommon	September–October
Manx Shearwater	Uncommon	September–February
Ashy Storm-Petrel (*Oceanodroma homochroa*)	Uncommon	Year round
Black Storm-Petrel (*O. melania*)	Uncommon	April–November
Leach's Storm-Petrel	Uncommon	May–October
Fork-tailed Storm-Petrel (*O. furcata*)	Also observed	May–October
Least Storm-Petrel (*Halocyptena microsoma*)	Also observed	May–October

photographs and motion pictures were taken during most experiments. From the records, the experimental stimuli and particular environmental conditions such as wind direction and velocity could be related to bird frequency and such specific behavior patterns as foraging, flight, and feeding. Wind direction was centered on compass points corrected to the magnetic meridian. Arriving birds sighted within 40° on either side of the wind source were counted as upwind approaches, these arriving within 40° of the opposite point were scored as downwind.

Bird counts were transformed into percent frequency scores and organized into contingency tables incorporating control conditions and stimuli, direction (upwind-downwind), closeness of approach, and bird type (procellariiform-nonprocellariiform). Chi-square tests on the transformed scores showed significant results (χ^2 = 12.67–229.82; df = 1–7; P < .001) for the comparisons described below.

RESULTS

All three types of experiments were highly consistent in supporting the conclusion that procellariiforms detect and are attracted to sources of food-related odors. The procel-

lariiform species sighted and attracted across seasons are listed in Table 1, which shows their relative frequencies of occurrence based on our observations. The most frequently observed procellariids were Sooty and Pink-footed shearwaters (*P. griseus* and *P. creatopus*), and Northern Fulmars. Less commonly observed, storm-petrels were most numerous in late spring (May–June) and early fall (September). Black-footed Albatrosses (*Diomedea nigripes*), relatively uncommon in general, occurred in highest concentrations during early spring (April–May).

The proportions of procellariiforms to nonprocellariiforms visiting an area were greater when food-related odors were present than during control conditions (Table 2). More procellariiforms approached within 10 m of the stimulus (Fig. 1), landed on the water, and attempted to feed directly on or close to the sources of these odors. Neither
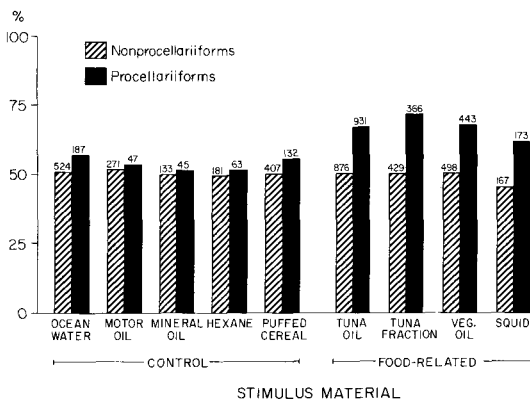

FIGURE 1.   Percentage of procellariiforms and nonprocellariiforms approaching from downwind that flew within 10 m of each stimulus. The total number flying upwind is shown above each bar.
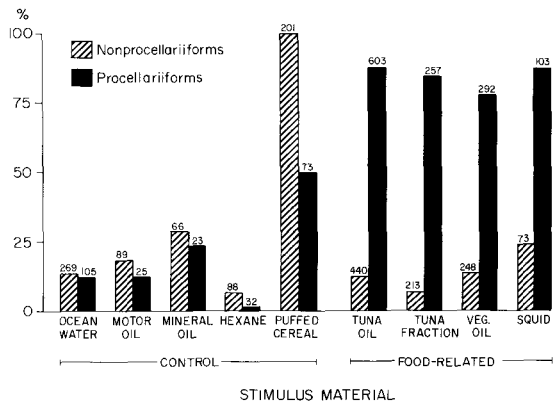

FIGURE 2.   Percentage of procellariiforms and nonprocellariiforms approaching each stimulus from downwind. The total number sighted, regardless of direction, is shown above each bar.

TABLE 2.   Number of procellariiforms (P) and nonprocellariiforms (NonP) sighted during each stimulus condition, rate of sighting, and proportion of procellariiforms sighted to nonprocellariiforms. The number of trials for each condition and the total duration in minutes are also shown.

Stimulus condition	No. trials	Total time	Total		No./10 min		P/NonP
			P	NonP	P	NonP	
Open slick							
P feeding	3	210	174	150	8.3	7.1	1.17
Ocean	13	1,770	388	515	2.1	2.9	0.72
Vegetable oil	6	780	222	230	2.9	3.0	0.97
Tuna oil	11	1,500	436	344	3.2	2.3	1.39
Bacon fat[a]	2	150	95	160	6.3	10.7	0.59
Bacon fat[b]	2	210	58	207	2.6	9.9	0.26
Enclosed slick: separate							
Ocean water	4	780	79	263	1.0	3.4	0.29
Tuna oil	4	780	231	291	2.8	3.6	0.78
Saturated wick							
Ocean water	11	1,590	187	524	1.2	3.1	0.39
Motor oil	4	570	47	171	0.8	3.0	0.27
Mineral oil	3	390	45	133	1.2	3.3	0.36
Hexane	4	570	63	181	1.1	3.1	0.35
Puffed rice[c]	3	240	132	407	5.5	17.0	0.32
Vegetable oil	13	1,860	443	498	2.4	2.6	0.92
Tuna oil	21	3,060	931	876	3.0	3.0	1.00
Tuna fraction	10	1,350	366	429	2.8	3.1	0.90
Squid	5	600	173	161	2.8	2.7	1.04

[a] Bacon fat with puffed rice added.
[b] Bacon fat and puffed rice deployed 100 m downwind from tuna oil slick spread 2 h earlier.
[c] Spread on ocean surface with no wick present.

the plastic enclosures nor the wicks attracted procellariiforms unless they were baited with food-related odors. These birds approached the observation area more often from downwind when we presented such odors (Fig. 2). Furthermore, we observed two instances of Black-footed Albatrosses, Sooty, Pink-footed, and Manx (*P. puffinus*) shearwaters, and Northern Fulmars feeding in mixed groups on small schools of bait fish, which they approached predominantly from downwind. Of the procellariiforms that landed and fed near the odor sources, a greater proportion had initially approached from downwind. The largest differences in approach direction between procellariiforms and nonprocellariiforms were observed when food-related odors were presented on saturated wicks. This difference was greatly reduced when a visual stimulus such as puffed cereal was also present on the water nearby.

Neither approaches to the observation area by gulls, terns, pelicans, cormorants, phalaropes, alcids, and other nonprocellariiform species nor the proportions of these birds landing or feeding was related to wind direction under any condition. Such birds usually arrived in the area of a food-related stimulus some time after procellariiforms had appeared. Groups of mixed species,

predominantly gulls, hovered at the periphery of surface slicks several meters above the procellariiforms that had either landed and were attempting to feed or were making very low foraging flights over the slick. Only procellariiforms regularly landed and fed on both fish and vegetable oils. Gulls and pelicans occasionally alighted briefly, close to procellariiforms that had rafted in the slick, but never attempted to feed. The proportion of nonprocellariiforms approaching within 10 m of the enclosed slicks or the saturated wicks was never above control levels unless procellariiforms were already in the area and making repeated foraging flights near the odor source.

When puffed cereal was presented, with or without oily slicks, nonprocellariiforms approached from all directions and landed in greater proportions than when cereal was absent (Table 2). With cereal alone, they were more numerous than were procellariiforms. The consistency of this difference in behavior is clear when bird frequency is expressed as a density measure over time (birds/10 min). The experiments with saturated wicks are most illustrative. When they were saturated with control materials, the rate of procellariiform sighting was approximately constant; with odorous edible materials, however, the rate increased at least

two-fold. The rate of nonprocellariiform sighting differed only slightly and showed no discernible trends across all experimental and control conditions except when puffed cereal was presented alone or in conjunction with surface slicks. Then their arrivals increased above control levels. Two experimental trials were conducted to test the difference more directly. We presented a combined visual and olfactory stimulus, bacon fat with puffed rice, about 100 m downwind from a fish oil slick that had been spread 2 h before. No procellariiforms moved from the old to the new slick for at least 45 min nor were there any new arrivals. Conversely, nonprocellariiforms approached almost immediately from all directions, especially from the area of the original slick, landed, and eagerly fed on the fat and cereal mixture.

Procellariiform densities, regardless of seasonal variation and across experimental conditions, were greatest during and just after storms. High velocity west and northwesterly winds, low clouds, fog or overcast, and a turbulent ocean surface with ground swell of 1.5–2 m and whitecaps were present on over 80% of the days when procellariiform densities were above the median for all observations. By contrast, 78% of the lower procellariiform densities were associated with clear weather, calm seas, and variable low velocity winds, i.e., 18 mi/h or less from the east and south.

DISCUSSION

Few reports have described food hunting behavior of procellariiforms and most published information is anecdotal (e.g., Bent 1922, Murphy 1936, Palmer 1962). Although precise observations of modes of feeding in several species have been reported recently (e.g., Bourne 1976, Jones 1976, King and Simmons 1976, Brown et al. 1978), nearly all studies deal with the manner of catching the prey, i.e., diving, plunging, pursuit plunging, etc. (Ashmole 1971, Ainley 1977). Little or no research has been directed toward the guidance mechanisms involved in the location of feeding sites and, in particular, none toward the study of foraging behaviors enroute. Many species are most active nocturnally and during storms, the latter observation strongly supported by our own data, complicating the study of foraging behavior even more than the inherent unpredictability of site locations for natural feeding. Our reliable attraction of procellariiforms to the immediate area of a specific stimulus and our repeated observations un-
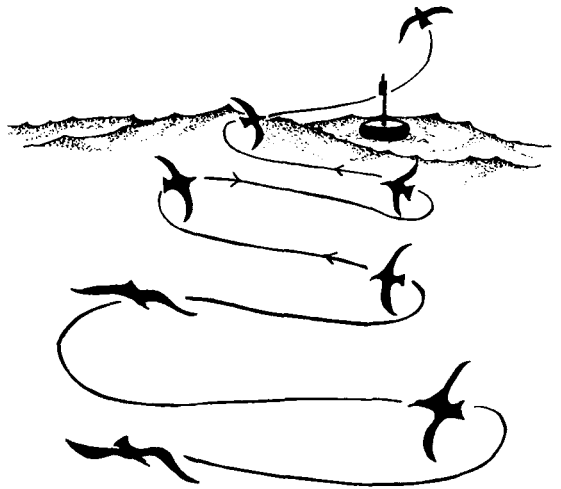

FIGURE 3.   Diagram of flight pattern of procellariiforms in approaching source of food-related odor.

der a wide range of weather conditions afforded a unique opportunity to observe flight and foraging patterns.

Each observation began with the initial sighting of a bird several hundred meters away and continued with visual and photographic monitoring of its approach to the stimulus. We verified a specific behavior pattern termed "foraging" (Kritzler 1948) shown only by procellariiforms. Kritzler characterized it as "not unlike a hound on a fresh trail" (p. 6) and elicited it with long slicks of heated salt pork spread to capture fulmars. We saw this behavior most clearly in approaches to the saturated wick, which served as a point source of odor (Fig. 3). Solitary low-flying birds, or small groups, were first sighted far downwind of the stimulus making broad zig-zag crosswind excursions while progressing steadily upwind. This approach pattern could be seen most clearly with albatrosses, shearwaters, and fulmars. Its stereotypy was notable despite the species differences in flight styles. Characteristically, the highest point was reached at the lateral extent of each excursion. A broad wheeling turn was followed by some brief but vigorous wing flapping, after which another low crosswind glide led to the next turn. The breadth of excursions narrowed as the bird came closer to the stimulus. Shortly after passing the wick, often within less than 10 m, the bird made a high arching 180° turn and circled back downwind of the stimulus to repeat the zig-zag upwind approach. This sequence was usually repeated several times, ending only after a number of low passes had been made

near the wick and the bird had landed downwind for a while before continuing upwind, apparently not to return.

Foraging approaches could be readily distinguished from the flight patterns observed during control conditions. Transit flights were marked by little deviation in course and were not consistently related to wind direction. Our experimental results suggest that the foraging pattern is a behavioral adaptation based on the ability to follow an airborne odor gradient.

In introducing his description of the olfactory anatomy of the Short-tailed Shearwater (*P. tenuirostris*), Wood Jones (1937) wrote that the well-developed olfactory structures and characteristic odor of tubenosed birds implied retention of some odor usage by this family in contrast to birds in general, which he considered as "the pioneers in obtaining emancipation from the dominance of the olfactory sense" (p. 281) as a result of their excellent visual system. The present report adds to the very sparse experimental literature on this topic by providing data on olfactory guidance of procellariiforms to odor sources at sea. Systematically collected under a range of conditions and with control of visual cues, the data support the impression that olfaction plays a role in the regulation of at least one important aspect of the natural behavior of procellariiforms.

ACKNOWLEDGMENTS

LITERATURE CITED

AINLEY, D. G. 1977. Feeding methods in seabirds: A comparison of polar and tropical nesting communities in the eastern Pacific Ocean, p. 664–685. *In* G. A. Llano [Ed.], Adaptations within Antarctic ecosystems. Smithsonian Institution, Washington, DC.

ASHMOLE, N. P. 1971. Sea bird ecology and the marine environment, p. 224–286. *In* D. S. Farner, and J. R. King [Eds.], Avian biology, Vol. 1. Academic Press, NY.

BANG, B. G. 1965. Anatomical adaptations for olfaction in the snow petrel. Nature 205:513–515.

BANG, B. G. 1966. The olfactory apparatus of tubenosed birds (Procellariiformes). Acta Anat. 65:391–415.

BANG, B. G. 1971. Functional anatomy of the olfactory system in 23 orders of birds. Acta Anat. Suppl. 1 58:1–76.

BENT, A. C. 1922. Life histories of North American petrels and pelicans and their allies. U.S. Natl. Mus. Bull. 121.

BOURNE, W. R. P. 1976. Plunge-diving and porpoising by aquatic seabirds. Br. Birds 69:188–189.

BROWN, R. G. B., W. R. P. BOURNE, AND T. R. WAHL. 1978. Diving by shearwaters. Condor 80:123–125.

COBB, S. 1960. Observations on the comparative anatomy of the avian brain. Perspect. Biol. Med. 3:383–408.

GRUBB, T. C., JR. 1972. Smell and foraging in shearwaters and petrels. Nature 237:404–405.

GRUBB, T. C., JR. 1974. Olfactory navigation to the nesting burrow in Leach's Petrel (*Oceanodroma leucorrhoa*). Anim. Behav. 22:192–202.

GRUBB, T. C., JR. 1979. Olfactory guidance of Leach's Storm Petrel to the breeding island. Wilson Bull. 91:141–143.

JONES, W. E. 1976. Manx Shearwaters plunge-diving. Br. Birds 69:513–514.

JOUVENTIN, P. 1977. Olfaction in Snow Petrels. Condor 79:498–499.

KEETON, W. T. 1979. Avian orientation and navigation. Annu. Rev. Physiol. 41:353–366.

KING, B., AND K. E. L. SIMMONS. 1976. Feeding habits of certain seabirds. Br. Birds 69:512–513.

KRITZLER, H. 1948. Observations on behavior in captive fulmars. Condor 50:5–15.

MILLER, L. 1942. Some tagging experiments with Black-footed Albatrosses. Condor 44:3–9.

MURPHY, R. C. 1936. Oceanic birds of South America. American Museum of Natural History, New York.

PALMER, R. S. [Ed.] 1962. Handbook of North American birds. Vol. 1. Yale University Press, New Haven, CT.

PAPI, F., W. T. KEETON, A. I. BROWN, AND S. BENVENUTI. 1978. Do American and Italian pigeons rely on different homing mechanisms? J. Comp. Physiol. A 128:303–317.

STAGER, K. E. 1964. The role of olfaction in food location by the Turkey Vulture (*Cathartes aura*). Los Ang. Cty. Mus. Contrib. Sci. 81:1–63.

STAGER, K. E. 1967. Avian olfaction. Am. Zool. 7:415–419.

WENZEL, B. M. 1969. The olfactory prowess of the kiwi. Nature 220:1133–1134.

WENZEL, B. M. 1971. Olfactory sensation in the kiwi and other birds. Ann. N.Y. Acad. Sci. 188:183–193.

WENZEL, B. M. 1980. Chemoreception in sea birds, p. 41–67. *In* J. Burger and B. L. Olla and H. E. Winn [Eds.], Behavior of marine animals: Current perspectives in research. Vol. 4. Marine birds. Plenum Press, New York.

WOOD JONES, F. 1937. The olfactory organ of the Tubinares. I. Emu 36:281–286.

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