

OLFACTORY BEHAVIOR OF FORAGING PROCELLARIIFORMS

CHRISTOPHE VERHEYDEN AND PIERRE JOUVENTIN

Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique,
79360 Beauvoir-sur-Niort, France

ABSTRACT.—Olfactory foraging, although very rare among birds, is frequently found in members of the Procellariiformes; this finding is based on a small number of field studies using a standardized method (i.e. raft tests). Reactions of seven species previously tested under artificial conditions were tested again under natural feeding conditions (fish-oil slicks) to check validity. Concurrently, we compared the flight behavior of two groups of species (with and without olfactory capacities) when approaching an odor source. A large-scale experiment was then conducted in pelagic waters to test the reaction of a community of procellariiforms (15 species) to a food-related odor diffusing within a principal feeding area. We observed the same reactions (attraction or indifference) to oil slicks as to test rafts in all species evaluated. Results obtained with the standardized method thus hold under natural conditions. Species guided by olfaction approached the odor source by flying against the wind very close to (<1 m) the surface, whereas other species approached from a direction independent of wind direction and from a greater height (>6 m). Thus, specific searching behavior is associated with olfactory foraging and we found it to be closely related to direction, height, and speed of odor diffusion by wind. Reaction to the odor test varied according to families or subfamilies, some taxa showing consistent responses (attraction or indifference) to several experiments and some taxa showing conflicting reactions. We obtained some evidence that olfactory behavior may differ before and after locating odor sources, as well as vary according to oceanic zones (coastal vs. pelagic). We discuss the hypothesis that certain species rely mainly on visual cues, recognizing and following species that are tracking food-related odors. Finally, we propose some new ideas about the evolution of olfaction in birds.
Received 3 August 1992, accepted 25 November 1992.

ALTHOUGH OLFACTORY sensitivity in birds is now documented in a growing number of species (see a review in Waldvogel 1989), olfactory foraging remains unusual. In terrestrial environments, only two species have been shown to locate their food by smell: the Kiwi (*Apteryx australis*; Wenzel 1971) and the Turkey Vulture (*Cathartes aura*; Stager 1964). Some others have shown good capacities under artificial conditions, including honeyguides (*Indicator indicator* and *I. minor*; Stager 1967) and Black-billed Magpies (*Pica pica*; Buitron and Nuechterlein 1985). In contrast, there is evidence that at least 22 procellariiform species may use olfaction when foraging (reviewed in Lequette et al. 1989). The existence of such a widespread ability and the extreme development of olfactory structures (Wood Jones 1937, Cobb 1960, Bang 1966, 1971, Bang and Cobb 1968) make this order unique among birds, and may explain its success in exploiting the pelagic environment. Very few laboratory studies have been conducted (Wenzel 1967, Wenzel and Sieck 1972, Jouventin 1977). Our present knowledge comes mainly

from a small number of field studies in the North Atlantic (Grubb 1972), the North Pacific (Hutchison and Wenzel 1980, Hutchison et al. 1984), the Antarctic (Jouventin and Robin 1983), and the South Indian Ocean (Lequette et al. 1989). These studies used a standardized method under artificial conditions (rafts) and showed that olfactory capacities are partly related to phylogeny and anatomy. Feeding ecology, particularly diet and feeding techniques, also play a role in olfactory ability (Lequette et al. 1989). Seabirds using olfaction employ search patterns that seem to depend on wind conditions (Hutchison and Wenzel 1980, Hutchison et al. 1984). Nonetheless, important questions remain unsolved. First, can we extend the results obtained under the artificial conditions of the standardized method to natural feeding situations? Second, are there specific search behaviors in those species which do rely on olfactory cues and, if so, how are they related to wind?

We report the results of field experiments designed to answer these questions, and provide new data for 15 species of procellariiforms. We

give details about the behavior of olfactory foraging, and describe the role olfaction plays in the foraging strategies of these seabirds.

STUDY AREA AND METHODS

Two series of experiments were conducted from August 1991 to March 1992 on board a 36-m yacht during a cruise from the American to the African sector of the Southern Ocean (35–64°S, 70°W–10°E). Whole cod-liver oil was used as an odor stimulus since it has been shown to be attractive in previous field studies of procellariiforms.

Fine-scale experiment.—The odor stimulus was presented for 15 min by spreading 0.5 L on the ocean surface, thereby creating isolated surface slicks. Experiments were attempted only when the yacht was anchored near the shore (500–1,000 m) of an open bay in order to allow prolonged observations, and only when the wind was blowing from land to the mouth of the bay so as to enhance the diffusion of the odor towards the open ocean. Under these conditions, the slick tended to float away from the boat (maximum distance 100 m) and closely resembled slicks frequently observed at sea (oily material originating from dead animals, excreta, krill swarms) where many birds feed. Each bird sighted within 50 m of the slick was identified to species with binoculars and followed by eye until it left the spot. Each bird was counted as a single event, including those that sometimes approached repeatedly. Directions of approach were recorded as upwind approaches if they occurred within 45° on either side of the wind source, and as indifferent approach if they did not. Flight heights were measured with graduated binoculars and assigned to one of three classes (<1 m, 1–6 m, >6 m). Special behaviors such as landing or feeding on the slick also were recorded. Control conditions consisted of a period of 15 min before spreading the oil, during which all the birds present within 50 m of the future location of the slick were identified and counted. We also took into account birds present within 500 m of the spot during the same period. Ambient conditions on the ocean surface, such as wind direction and velocity, as well as wave direction and height, were recorded at the beginning of each trial (control + odor test).

We conducted 16 experiments in several locations: Cape Horn and Diego Ramirez Islands (3 tests); South-Shetlands (6 tests); and Western Antarctic Peninsula (7 tests). These locations were chosen for the presence of procellariiform and nonprocellariiform species that we had already tested in previous work using the standard method (Lequette et al. 1989).

Large-scale experiment.—The odor stimulus (0.2 L) was kept in an airtight metal box (diameter 12 cm, height 19 cm) fixed on the back of the yacht and was released in the air for 50 min after opening the box. Trials were conducted in pelagic waters because they

represent the main feeding area of most procellariiforms, unlike coastal waters where most previous studies have been conducted. This choice also permitted the exclusion of larids that may attract other seabirds (including procellariiforms) to the yacht (Haney et al. 1992). We operated only when the boat was sailing close ($\pm 40^\circ$) to the wind at speeds varying from 5.3 to 9.7 knots in order to create a linear odor trail behind us. Immediately after closing the box, birds flying within a radius of 300 m around the yacht were identified to species and counted for 10 min. Each period was divided into five circular counts of 2 min each to reduce the risk of counting the same bird several times. The highest count for each species in a unit period was retained to compensate for potential underestimates. We separated birds flying upwind in our wake (within 45° on either side of the vessel axis) from those flying in other directions. Control conditions were based on a 10-min count prior to opening the box, and another count (also for 10 min) 50 min after the closing of the box. We conducted a total of 26 trials, including 10 around the Scotia Sea and Drake Passage, and 16 during a cruise in the South Atlantic from Tierra del Fuego to Cape Town.

Comparisons.—In both experiments, we compared groups of birds (e.g. having vs. not having olfactory capacities), experimental conditions (control vs. test), and bird distributions (observed vs. expected) using chi-square statistics (when $n \geq 5$ in all classes) or G-test (when $n < 5$ at least in one class). Contingency tests (chi-square with Yate's correction or G-test) were applied to 2×2 tables. Our basic null hypothesis was that birds were distributed in proportion to the number of classes that were compared.

RESULTS

Fine-scale experiment.—When confronted with a simulated feeding situation (oil slick), the four species that had previously been shown to respond positively with the standard method (Giant Petrel [*Macronectes giganteus*], Antarctic Fulmar [*Fulmarus glacialis*], Cape Pigeon [*Daption capense*] and Wilson's Storm-Petrel [*Oceanites oceanicus*]) also showed a positive response; their frequency of occurrence (32.8%) and total numbers ($n = 65$) around slicks were, respectively, 5 and 13 times those recorded in the same place free from oil (frequency = 6.2%, $n = 5$). This distribution is significantly different ($X^2 = 29.4$, $P < 0.001$) from that expected if birds were not attracted to the slick.

Three species known as indifferent to odors (Kelp Gull [*Larus dominicanus*], Antarctic Tern [*Sterna vittata*] and Imperial Shag [*Phalacrocorax atriceps*]) showed no interest in oil slicks. Their

frequencies of occurrence (25%) and numbers ($n = 22$) around slicks were close to those observed under control conditions (frequency = 20.8%, $n = 16$). This distribution does not differ from that expected by chance ($X^2 = 0.21$, $P = 0.64$). Opposite reactions of the two groups of species ($X^2 = 41.8$, $P < 0.001$) in a simulated feeding context are not only due to phylogenetic divergences between procellariiforms and other seabirds: two large procellariiforms, the Grey-headed Albatross (*Diomedea chrysostoma*) and the Black-browed Albatross (*D. melanophris*) also showed no reaction to odor stimulus (14 compared to 38 for control).

Proportions of birds approaching the slicks against the wind and from the other three directions in group 1 (species with olfactory capacities) tended to reverse in group 2 ($G = 82.01$, $P < 0.001$), the former approaching exclusively upwind, whereas the latter approached more often from other directions (Table 1). In both groups, observed proportions differed significantly from those expected if bird arrivals were uniform with respect to wind direction ($G = 91.96$, $P < 0.001$, and $G = 6.63$, $P = 0.001$, respectively).

Use of air layers when approaching the odor source was different in the two groups (Table 1), as shown by reversed proportions in the three height classes ($G = 96.10$, $P < 0.001$). Species using olfactory cues (group 1) almost always approached very close to the ocean surface (<1 m), whereas the others (group 2) tended to fly above 6 m, in proportions that differ from those expected by chance ($G = 75.04$, $P < 0.001$, and $G = 16.71$, $P < 0.001$, respectively). The different flight behaviors observed in the two groups are not only a consequence of phylogenetic differences since two albatrosses (see above) approached the slicks exactly as did non-procellariiforms of the group 2.

Species that use olfactory cues arrived first on the slicks slightly more often than others (56.2 vs. 43.7%, $n = 16$ trials), although the difference was not statistically significant ($P > 0.05$). A possible influence of wind speed on bird response is hinted at (although not statistically significant) by an increasing number of birds on the slicks and a reduction in delay of arrival with increasing wind speed (Pearson's $r = 0.34$, $P = 0.20$, and $r = -0.30$, $P = 0.20$, respectively).

Large-scale experiment.—Around the yacht (except downwind), the total number of species, mean number of species, birds per count, and

TABLE 1. Flight features (percent) of two groups of seabird species differing in their olfactory capacities and way of approaching an oil slick: (group 1) attracted by odor (*Daption capense*, *Fulmarus glacialis*, *Macronectes giganteus*, *Oceanites oceanicus*); (group 2) indifferent to odor (*Larus dominicanus*, *Phalacrocorax atriceps*, *Sterna vittata*).

	Attracted group (4 species, $n = 65$)	Indifferent group (3 species, $n = 23$)
Direction		
Upwind	100.0	4.4
Other	0.0	95.4
Height		
<1 m	98.4	0.0
1-6 m	1.6	17.4
>6 m	0.0	82.6

proportion of positive counts remained unchanged under control and test conditions (Table 2). Downwind, however, the total number and mean number of species per count increased twofold, the mean number of birds per count increased threefold, and the proportion of positive counts increased by 44% when an odor plume was diffused in the wake (Table 2).

Responses to odor tests varied according to families and groups (Table 3). Taken collectively, members of the family Diomedidae (*Diomedea chlororhynchos*, *D. chrysostoma*, *D. epomophora*, *D. exulans*, *D. melanophris*) tended to be more frequent and more numerous in the wake when the odor was presented, but this must be interpreted with caution, since 83% of all individuals were of a single species (*D. melanophris*). The same tendency was observed for members of the Oceanitidae, where five species (*Fregatta grallaria*, *F. tropica*, *Garrodia nereis*, *Oceanites oceanicus*, *Pelagodroma marina*) dis-

TABLE 2. Distribution of 24 procellariiform species flying in wake (downwind) and around (other directions) a sailing yacht, depending on presence (test) or absence (control) of an odor plume in the wake ($n = 26$ trials).

	Downwind		Other directions	
	Control	Test	Control	Test
Total species	9	19	21	21
Mean species/count	1.0	2.1	2.3	2.4
Mean birds/count	3.5	11.3	6.3	5.7
Percent counts with birds	52	96	88	96

TABLE 3. Number and frequency of occurrence (percent in parentheses) of 24 procellariiform species flying around versus behind a sailing yacht that was (test) or was not (control) diffusing an odor stimulus in its wake (26 trials). Distributions compared using chi-square test (when $n \geq 5$ in all classes) or G -test (when $n < 5$ at least in one class).

Taxon (no. species)	Birds around		Birds behind		P
	Control	Test	Control	Test	
Diomedidae (5)	14 (32)	17 (28)	4 (12)	14 (36)	0.04
Fulmarines (3)	8 (20)	16 (16)	16 (24)	39 (28)	>0.05
Prions (4)	45 (28)	15 (28)	1 (4)	4 (12)	0.03
Others (7)	61 (48)	57 (52)	19 (24)	43 (40)	0.01
Oceanitidae (5)	34 (44)	28 (40)	8 (20)	19 (40)	0.05

played a similar reaction. Members of the family Procellariidae comprised about 60% of the species tested and showed more varied reactions than other families; fulmarine petrels (*Macronectes giganteus*, *Fulmarus glacialis*, *Daption capense*) typically were ship followers and were more numerous both around and in the

wake of the vessel when odor was presented. Prions and allies (*Halobaena caerulea*, *Pachyptila belcheri*, *P. desolata*, *P. vittata*), however, clearly avoided the wake, but less so when the odor was present. Members of the "other" group (*Procellaria aequinoctialis*, *P. cinerea*, *Pterodroma incerta*, *P. mollis*, *Puffinus gravis*, *P. griseus*, *Calonectris diomedea*) were the most commonly observed around the yacht (out of the wake) under control and test conditions and, clearly, began following when the odor began to spread. This was mainly due to a single species (*P. gravis*), which accounted for 60% of total numbers, whereas two species (*Procellaria cinerea* and *C. diomedea*) showed no reaction.

TABLE 4. Review of olfactory capacities of 43 procellariiform species tested in field: (yes) attracted by odors; (no) not attracted by odors; (?) insufficient data or opposite reactions in different tests. Numbers in parentheses refer to: (1) Crossin in Wenzel 1980; (2) Grubb 1972; (3) Hutchison and Wenzel 1980; (4) Jouventin and Robin 1983; (5) Hutchison et al. 1984; (6) Miller 1942; (7) Lequette et al. 1989, and (8) this study.

Diomedidae

Diomedea chlororhynchus, no (8); *D. chrysostoma*, no (8); *D. epomophora*, no (8); *D. exulans*, no (7, 8); *D. melanophris*, yes ? (8); *D. nigripes*, yes (3, 6); *Phoebastria palpebrata*, no (7).

Procellariidae

Macronectes giganteus, yes (7, 8); *M. halli*, yes (7); *Fulmarus glacialis*, yes (3, 5); *F. glacialis*, yes (4, 7, 8); *Daption capense*, yes (4, 7, 8); *Pagodroma nivea*, yes (4); *Pterodroma incerta*, yes ? (8); *P. mollis*, yes ? (8); *Halobaena caerulea*, no (8); *Pachyptila belcheri*, no (8); *P. desolata*, no ? (8); *P. salvini*, no (7); *P. turtur*, no (7); *P. vittata*, no ? (8); *Procellaria aequinoctialis*, yes (7, 8); *P. cinerea*, no (8); *Calonectris diomedea*, no (8); *Puffinus bulleri*, yes (3); *P. creatopus*, yes (3); *P. gravis*, yes (2, 8); *P. griseus*, yes (3, 8); *P. puffinus*, yes (3); *P. tenuirostris*, yes (3).

Oceanitidae

Fregetta grallaria, yes ? (8); *F. tropica*, yes (7, 8); *Gardia nereis*, yes ? (8); *Halocyptena microsoma*, yes (3); *Oceanites oceanicus*, yes (2, 4, 7, 8); *Oceanodroma furcata*, yes (3); *O. homochroa*, yes (3); *O. leucorroa*, yes (3); *O. melania*, yes (3); *O. tethys*, yes (7); *Pelagodroma marina*, yes (8).

Pelecanoididae

Pelecanoides georgicus, no (7); *P. urinator*, no (7).

When pooled together irrespective of family or group, the eight species known to use olfaction when foraging (*Macronectes giganteus*, *Fulmarus glacialis*, *Daption capense*, *Procellaria aequinoctialis*, *Puffinus gravis*, *P. griseus*, *Fregetta tropica*, *Oceanites oceanicus*) were more frequent in the wake of the boat under test conditions than expected by chance (45.2 vs. 25%, $n = 73$), and to a lesser extent under control conditions (35.7 vs. 25%, $n = 56$). The remaining 16 species (see Table 4 for species names) were uniformly distributed around the vessel under control conditions (18 vs. 25% in the wake, $n = 34$). They tended to cluster in the wake when the odor was presented (35 vs. 25% in the wake, $n = 57$), but less so than species listed above. Moreover, at least 4 (*Diomedea chrysostoma*, *D. exulans*, *Pachyptila desolata*, and *P. vittata*) of 10 species that followed only in the odor plume belong to genera that are insensitive to odors.

The number of birds in the wake was significantly correlated with the wind speed when the odor was present (Pearson's $r = 0.42$, $n = 25$, $P < 0.05$), but the correlation was not significant when the odor was absent ($r = 0.32$, $n = 25$, $P > 0.10$). This suggests that the influences

of wind alone, and probably of the vessel itself, on these followers can be excluded.

DISCUSSION

Confirmation of previous studies.—The seven species tested previously (Lequette et al. 1989) showed exactly the same response to oil slicks as to test rafts. Those for which olfaction has been demonstrated were attracted, whereas the other species were indifferent to the olfactory stimulus. This confirms that identical odor stimuli induce the same effects when presented, even in a different manner, to members of the same species. However, under control conditions birds tended to respond more to rafts than to a seawater area alone. This suggests that rafts may cause a visual bias that does not exist with slicks. Moreover, rafts do not resemble any potential prey and do not allow any food intake by birds. However, the oil slicks we spread on the surface had the same appearance as natural slicks and provided feeding opportunities; at least one species, the Wilson's Storm-Petrel, repeatedly fed at slicks (27 of 35 trials) by pecking oily drops from the surface (one bird was observed pecking 246 times within 8 min).

A special flight for localizing odor sources.—Field studies (Grubb 1972, Hutchison and Wenzel 1980, Jouventin and Robin 1983, Hutchison et al. 1984, Lequette et al. 1989) have shown species that rely on olfaction when searching for food to approach the odor source from downwind. Our experiments corroborate this result for both coastal and pelagic waters. We even found this pattern to be exclusive in the first experiment, probably because there was no visual cue (as with rafts) that could have attracted birds from all directions. Species that were guided by olfaction toward oil slicks behaved as described by Hutchison and Wenzel (1980) for procellariiforms approaching a raft, with zig-zag crosswind excursions becoming narrower as birds came closer to the source of the stimulus. The same strategy for localizing an odor source is seen in insects responding to airborne pheromone cues (Kennedy and Marsh 1974). However, our tests also revealed a new feature of approach flights; species known to use olfaction approached exclusively in the air layer just above the surface, whereas other species flew higher. This style of flight is actually a special feature of species searching for odors

but not of procellariiforms generally. Two albatrosses reacted similarly to nonprocellariiforms, showing no response to odor and approaching with a high flight unrelated to wind direction. Similar specific olfactory behavior, independent of phylogeny, is also observed in American forest vultures (Houston 1984). The Turkey Vulture, a species that has proven olfactory ability when foraging, flies exclusively at low heights just above the canopy (<100 m), whereas a species insensitive to odors, the King Vulture (*Sarcorhamphus papa*), always flies much higher (>300 m). In vultures, as well as in procellariiforms, the species that use olfaction converge in their flight pattern. They fly in the layer of air where odorous molecules are likely to diffuse the most. This may represent the most efficient strategy for localizing food by smell. This particular flight pattern does not seem to depend on anatomical constraints. Procellariiform species as different in their body size and flight style as Giant Petrels and storm-petrels are capable of adopting the same flight pattern when searching for an odor source. Species that use olfaction also were more strongly attracted when wind speed increased, probably because odorous molecules diffused farther (Sutton 1953) and, thus, were likely to be detected by more birds. In previous work (Lequette et al. 1989), we saw some procellariiforms, particularly storm-petrels, appearing around a test raft, although they had been totally absent over a great distance (radius >1 km) before the odor was released. From the present study, we estimate a maximum recruitment distance of about 8 km for a storm-petrel flying at a speed of 30 km/h (Pennycuick 1989) and arriving in the wake of the vessel just after the 50 min of odor presentation (for a mean boat speed of 7.8 knots and a mean wind speed of 14.8 knots). This estimate, although ignoring some important factors related to the diffusion and degradation of odor molecules in this environment, increases the effective distance of odor detection by birds previously estimated (several hundreds of meters) by Waldvogel (1989) on a chemical basis.

These results lead to the conclusion that a specific searching behavior exists in those procellariiforms that use olfactory cues when foraging. This behavior is closely related to the direction, height, and speed of odor diffusion by wind.

Olfactory capacities and systematics.—Responses to odor tests differ among families,

groups, and species for a given experiment, but they also can differ between experiments for a given family, group, or species. All members of the Oceanitidae showed positive reactions to odors, whereas prions showed no or very little interest in odors, whatever the experiment. Thus, we confirm the existence of well-developed olfactory capacities in the former family and its absence in the latter group. Conclusions are less firm in those taxa where differences appear between experiments. The fulmarines, for example, usually orient toward odor sources (Hutchison and Wenzel 1980, Jouventin and Robin 1983, Hutchison et al. 1984, Lequette et al. 1989, this study), but this was not obvious in our second experiment where their numbers increased twofold all around the vessel when the odor was presented. We think this can be explained by birds attracted by odors being counted both in and out of the wake because of the tendency observed in fulmarines to circle many times around a food source once it has been located. This suggests that flight patterns may be different before and after locating the odor source. If so, this should be considered in interpreting the results of experiments like ours.

Results obtained with albatrosses raise further questions since two species (the Black-browed Albatross and Grey-headed Albatross) were not attracted by odors when they are tested near their colonies (first experiment), but showed positive reactions in pelagic waters (second experiment). The same occurs with a true olfactory forager, the Antarctic Fulmar, which does not react to odors near its breeding cliffs (Jouventin and Robin 1983), but shows a strong attraction in other situations with the same (Lequette et al. 1989) or with different methods (this study). Such differential responses in pelagic species do not occur in olfactorily foraging species that feed both in coastal and pelagic waters, such as Wilson's Storm-Petrel and Giant Petrels. Perhaps a mechanism exists, comparable to echolocation in bats, which mainly uses this sensory capacity in feeding context.

Direct or indirect use of odors.—In pelagic waters, albatrosses react to odors in the same way as species that are indifferent to odors; they are more numerous in the odor trail despite their apparent lack of olfactory capacities. This suggests that something other than olfaction may be involved in recruitment of birds within the diffusion range of the odorant. The low proportion (14.7%) of followers when visibility is

poor (<400 m, $n = 27$) compared to that (37.6%) observed with good visibility (>10 km, $n = 30$; $X^2 = 21.8$, $P < 0.001$) indicate that recruitment is based partly on visual cues. Some species, like albatrosses, may be attracted by flocks of birds flying over a food source or in the wake of a boat, as happens with other seabirds (Haney et al. 1992). These flocks are likely to be initiated by and composed of species that use olfaction, since these latter tend to arrive first at food-related odors (first experiment). It is also likely that visual foragers recognize birds that are actively searching for odors, since they display specific flight patterns. This idea is strongly supported by observations on King Vultures (Houston 1984), which have no functional sense of smell, but are able to locate carcasses by watching the flight behavior of sympatric Turkey Vultures, which possess well-developed olfactory capacities. In this case, the visually oriented species usually arrives after the species guided by odors, and becomes dominant in feeding interactions because of its larger size (Koster and Koster-Stoewesand 1978).

Olfactory foraging and evolution.—In procellariiforms, smaller species show more obvious olfactory capacities (e.g. storm-petrels), arrive first at odor sources, and are dominated in feeding interactions. The largest species (e.g. albatrosses) tend to arrive later, are dominant, and appear to be mostly visual foragers. Olfactory foraging in both vultures and procellariiforms seems to be restricted to small species that compensate for their low resource holding potential by detecting food from a great distance, and by moving only to those food sources that are certainly available. Arriving first on a food source is a great advantage for small species when the risk of displacement by larger species is high. Selection of olfactory capacity in small species as a response to competition has not been suggested previously. Several studies have tried to identify the forces selecting for large olfactory bulbs in birds, but Healy and Guilford (1990) stated that their conclusions must be taken with caution. They examined the relationship between the size of olfactory bulbs in 124 species of 17 orders and a number of ecological variables cited in other studies. After removing the effect of body and brain size, and controlling for the effect of taxonomy, only the timing of activity (nocturnal or diurnal) was found to have a significant influence. Healy and Guilford (1990) concluded that this validated their basic hypothesis that olfaction in birds has been se-

lected as a generalized response to compensate for reduced effectiveness of vision under low-light conditions. However, when examined at the family level, their results were not significant in procellariids. Several species of this group, such as the Snow Petrel (*Pagodroma nivea*), have both large olfactory bulbs (Bang 1966) and a diurnal activity (Bretagnolle 1988). We suggest that olfaction in procellariiforms, as well as in several other taxa (Cathartidae, Indicatoridae), may have evolved as a response to environments where food is patchily distributed and provides no visual cues that could be used for detection, whatever the light conditions.

ACKNOWLEDGMENTS

We are grateful to J. L. Etienne for organizing the expedition and providing the opportunity to conduct these experiments onboard his yacht *Antarctica*. We thank V. Bretagnolle, P. Duncan and H. Weimerskirch for helpful suggestions on an earlier draft of the manuscript. K. E. Stager, J. A. Waldvogel and an anonymous referee gave comments that greatly improved the paper. French National Television (Channel FR3), the Elf Foundation, and French Ministry of Education gave financial support to this project.

LITERATURE CITED

- BANG, B. G. 1966. The olfactory apparatus of tubenosed birds (procellariiforms). *Acta Anat.* 65:391-415.
- BANG, B. G. 1971. Functional anatomy of the olfactory system in 23 orders of birds. *Acta Anat.* 158: 1-76.
- BANG, B. G., AND S. COBB. 1968. The size of the olfactory bulb in 108 species of birds. *Auk* 85:55-61.
- BRETAGNOLLE, V. 1988. Cycles de présence et rythme d'activité chez cinq espèces de pétrels antarctiques. *L'oiseau et la R.F.O.* 58:44-58.
- BUITRON, D., AND G. L. NUECHTERLEIN. 1985. Experiments on olfactory detection of food caches by Black-billed Magpies. *Condor* 87:92-95.
- COBB, S. 1960. Observations on the comparative anatomy of the avian brain. *Perspect. Biol. Med.* 3:383-408.
- GRUBB, T. C. 1972. Smell and foraging in shearwaters and petrels. *Nature* 237:404-405.
- HANEY, J. C., K. M. FRISTRUP, AND D. S. LEE. 1992. Geometry of visual recruitment by seabirds to ephemeral foraging flocks. *Ornis Scand.* 23:49-62.
- HEALY, S., AND T. GUILFORD. 1990. Olfactory-bulb size and nocturnality in birds. *Evolution* 44:339-346.
- HOUSTON, D. C. 1984. Does the King Vulture *Sarcorhamphus papa* use a sense of smell to locate food? *Ibis* 126:67-69.
- HUTCHISON, L. V., AND B. H. WENZEL. 1980. Olfactory guidance in foraging by procellariiforms. *Condor* 82:314-319.
- HUTCHISON, L. V., B. H. WENZEL, K. E. STAGER, AND B. L. TEDFORD. 1984. Further evidence for olfactory foraging by Sooty Shearwaters and Northern Fulmars. Pages 78-89 in *Marine birds: Their feeding ecology and commercial fisheries relationships* (D. N. Nettleship, G. A. Sanger, and P. F. Springer, Eds.). Canadian Wildlife Service Special Publication, Ottawa.
- JOUVENTIN, P. 1977. Olfaction in Snow Petrels. *Condor* 79:498-499.
- JOUVENTIN, P., AND P. ROBIN. 1983. Olfactory experiments on some Antarctic seabirds. *Emu* 84:46-48.
- KENNEDY, J. S., AND D. MARSH. 1974. Pheromone-regulated anemotaxis in flying moths. *Science* 184:999-1001.
- KOSTER, F., AND H. KOSTER-STOEWESAND. 1978. Königsgaier Beobachtungen im Tayrona-Nationalpark im Norden Kolumbiens, Sudamerika. *Z. Koeln. Zoo* 21:35-41.
- LEQUETTE, B., C. VERHEYDEN, AND P. JOUVENTIN. 1989. Olfaction in subantarctic seabirds: Its phylogenetic and ecological significance. *Condor* 91:732-735.
- MILLER, L. 1942. Some tagging experiments with Black-footed Albatrosses. *Condor* 44:3-9.
- PENNYCUICK, C. J. 1989. *Bird flight performance: A practical calculation manual*. Oxford Univ. Press, New York.
- STAGER, K. E. 1964. The role of olfaction in food location by the Turkey Vulture (*Cathartes aura*). *Los Angeles Co. Mus. Contrib. Sci.* 81:1-63.
- STAGER, K. E. 1967. Avian olfaction. *Am. Zool.* 7:415-420.
- SUTTON, O. G. 1953. *Micrometeorology*. McGraw-Hill, New York.
- WALDVOGEL, J. A. 1989. Olfactory orientation by birds. *Curr. Ornithol.* 6:269-321.
- WENZEL, B. M. 1967. Olfactory perception in birds. Pages 203-217 in *Olfaction and taste 2* (T. Hayashi, Ed.). Pergamon Press, Oxford.
- 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 seabirds. Pages 41-67 in *Behavior of marine animals: Current perspectives in research*. Vol. 4, *Marine birds* (J. Burger, B. L. Olla, and H. E. Winn, Eds.). Plenum Press, New York.
- WENZEL, B. M., AND M. SIECK. 1972. Olfactory perception and bulbar electrical activity in several avian species. *Physiol. Behav.* 9:287-300.
- WOOD JONES, F. 1937. The olfactory organ of the Tubinares. I. *Emu* 36:281-286.