

- Pied Flycatcher *Ficedula hypoleuca*. *Am. Nat.* 117: 738-753.
- BREITWISCH, R., P. G. MERRITT, AND G. H. WHITESIDES. 1986a. Parental investment by the Northern Mockingbird: male and female roles in feeding nestlings. *Auk* 103:152-159.
- BREITWISCH, R., R. C. RITTER, AND J. ZAIAS. 1986b. Parental behavior of a bigamous male Northern Mockingbird. *Auk* 103:424-427.
- BRISKIE, J. V., AND S. G. SEALY. 1987. Polygyny and double-brooding in the Least Flycatcher. *Wilson Bull.* 99:492-494.
- DOWSETT-LEMAIRE, F. 1979. The sexual bond in the Marsh Warbler, *Acrocephalus palustris*. *Le Gerfaut* 69:3-12.
- DYRCZ, A. 1986. Factors affecting facultative polygyny and breeding results in the Great Reed Warbler (*Acrocephalus arundinaceus*). *J. Ornithol.* 127: 447-461.
- FORD, N. L. 1983. Variation in mate fidelity in monogamous birds, p. 329-356. *In* R. F. Johnston [ed.], *Current ornithology*. Vol. 1. Plenum Press, New York.
- FREED, L. A. 1986. Usurpatory and opportunistic bigamy in Tropical House Wrens. *Anim. Behav.* 34:1894-1896.
- HAARTMAN, L., VON. 1969. Nest-site and evolution of polygamy in European passerine birds. *Ornis Fenn.* 46:1-12.
- LASKEY, A. R. 1935. Mockingbird life history studies. *Auk* 52:370-381.
- LASKEY, A. R. 1936. Fall and winter behavior of Mockingbirds. *Wilson Bull.* 48:241-255.
- LASKEY, A. R. 1941. An instance of mockingbird bigamy. *Migrant* 12:65-67.
- LASKEY, A. R. 1962. Breeding biology of mockingbirds. *Auk* 79:596-606.
- LOGAN, C. A. 1983. Reproductively dependent song cyclicality in mated male mockingbirds (*Mimus polyglottos*). *Auk* 100:404-413.
- LOGAN, C. A., AND K. R. FULK. 1984. Differential responding to spring and fall song in mockingbirds (*Mimus polyglottos*). *J. Comp. Psychol.* 98:3-9.
- LOGAN, C. A., AND M. RULLI. 1981. Bigamy in a male mockingbird. *Auk* 98:385-386.
- MICHENER, H., AND J. R. MICHENER. 1935. Mockingbirds, their territories and individualities. *Condor* 37:97-140.
- MICHENER, J. R. 1951. Territorial behavior and age composition in a population of mockingbirds at a feeder station. *Condor* 53:276-283.
- ORIAN, G. H. 1969. On the evolution of mating systems in birds and mammals. *Am. Nat.* 103: 589-603.
- PRESCOTT, D.R.C. 1986. Polygyny in the Willow Flycatcher. *Condor* 88:385-386.
- VERNER, J. 1964. Evolution of polygyny in the Long-billed Marsh Wren. *Evolution* 18:252-261.
- VERNER, J., AND M. F. WILLSON. 1969. Mating systems, sexual dimorphism, and the role of male North American passerine birds in the nesting cycle. *Ornithol. Monogr.* No. 9. American Ornithologists' Union, Washington, DC.
- WITTENBERGER, J. F., AND R. L. TILSON. 1980. The evolution of monogamy: hypotheses and evidence. *Annu. Rev. Ecol. Syst.* 11:197-232.
- WOOLFENDEN, G. E. 1976. A case of bigamy in the Florida Scrub Jay. *Auk* 93:443-450.
- YASUKAWA, K., AND W. A. SEARCY. 1982. Aggression in female Red-winged Blackbirds: a strategy to ensure male parental investment. *Behav. Ecol. Sociobiol.* 11:13-17.
- ZAIAS, J., AND R. BREITWISCH. 1989. Intra-pair cooperation, fledgling care, and renesting by Northern Mockingbirds (*Mimus polyglottos*). *Ethology* 80:94-110.

The Condor 91:732-735

© The Cooper Ornithological Society 1989

OLFACTION IN SUBANTARCTIC SEABIRDS: ITS PHYLOGENETIC AND ECOLOGICAL SIGNIFICANCE¹

BENOÎT LEQUETTE, CHRISTOPHE VERHEYDEN, AND PIERRE JOUVENTIN
*Centre d'Etudes Biologiques des Animaux Sauvages, Centre National de la
Recherche Scientifique, 79360 Beauvoir/Niort, France*

Key words: Olfaction; seabirds; procellariiforms; feeding ecology.

Early studies of olfaction in birds concentrated on the anatomy of olfactory structures (Bang 1966, 1971; Bang and Cobb 1968; Cobb 1960). More recently, authors

have emphasized physiological aspects of olfaction (Smith and Paselk 1986, Clark and Mason 1987). Nevertheless, our field knowledge of the role of seabird olfaction remains poor (Grubb 1972, 1974; Hutchinson and Wenzel 1980; Wenzel 1980; Hutchinson et al. 1984; Bang and Wenzel 1985).

The aim of this paper is firstly to use a well-established method to test the olfactory capacities of several species belonging to different seabird families. Olfactory guidance to a source of food-related odor has never

¹ Received 23 November 1988, Final acceptance 30 March 1989.

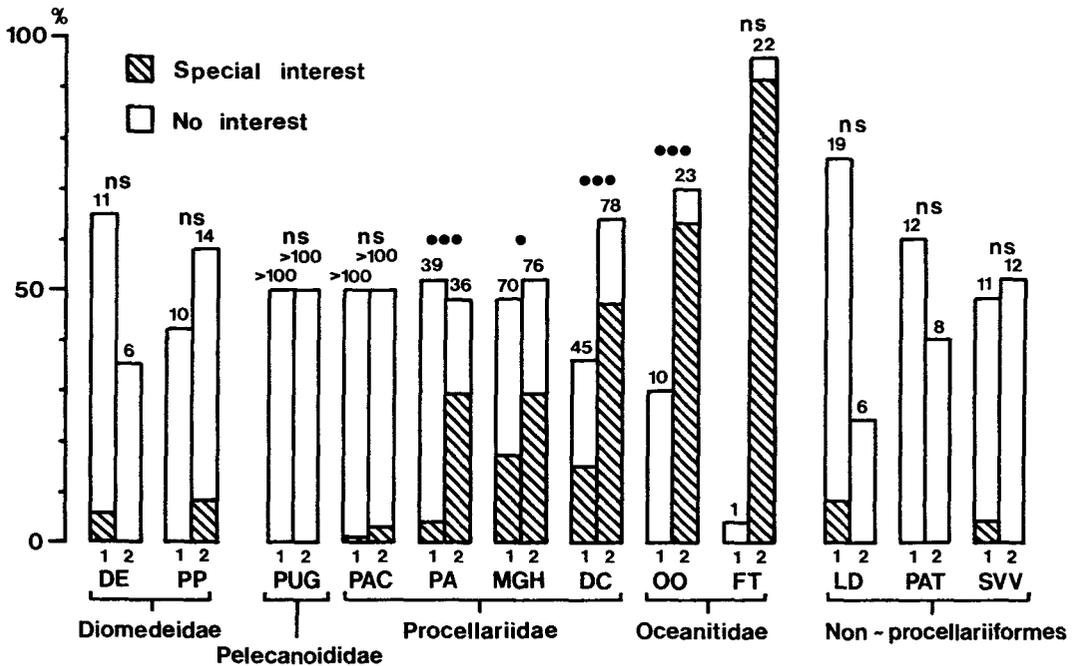


FIGURE 1. Reaction of seabirds to odor tests (observed numbers over each column). 1 = seawater control, 2 = cod-liver oil. Fisher's exact method; ● = $P < 0.05$, ●●● = $P < 0.001$.

been studied in Subantarctic seabird species; we therefore compare our results with similar studies on Antarctic (Jouventin and Robin 1983) and North Pacific or Atlantic seabirds (Grubb 1972, Hutchison and Wenzel 1980, Hutchison et al. 1984). Secondly, we relate these olfactory capacities to the systematic position of these species, the anatomy of their olfactory bulbs and their feeding ecology.

STUDY AREA AND METHODS

Twelve experiments were performed throughout the year on the coast of Possession Island ($46^{\circ}25'S$, $51^{\circ}45'E$) in the Crozet Archipelago, Southern Indian Ocean. The diversity of breeding procellariiforms on this archipelago is the highest in the world (26 species: Jouventin et al. 1984, Jouventin, in press). The efficiency of cod-liver oil as an attractant has been demonstrated in previous studies (Grubb 1972, Jouventin and Robin 1983, Hutchison et al. 1984). For each test we used a new natural sponge, soaked either in cod-liver oil (about 50 ml) or a seawater control, and placed in an open box on a raft in the manner described by Hutchison et al. (1984). The box prevented dispersion of cod-liver oil into the sea which could otherwise constitute a visual attraction by virtue of its iridescence. Each experiment comprised three sequences (1) placing the raft with a seawater control at about 70 m from the shoreline; (2) withdrawal of the raft, followed by a pause of 5 min to avoid interference with the next launching; (3) placing the raft with a cod-liver oil sponge at a similar distance from the shoreline. The durations of two successive trials of the same experiment (control and test)

were equal but were variable in different experiments owing to changing weather conditions (range = 15–45 min). An observer with binoculars ($\times 10$) categorized each bird that approached to within approximately 50 m of the raft. A "special interest" category was given to birds making a characteristic approach downwind (described in Hutchison and Wenzel 1980) or changing their flight direction to the raft, and to birds that flew particularly close to, or over, the raft and eventually landed near it. Birds that did not show these patterns were categorized as showing "no interest." The prior species involved were probably *Pachyptila salvini* and *P. turtur*, the two predominant breeders on Crozet (Jouventin et al. 1984).

The dependency of interest on odor type was identified from Fisher's exact tests, taking into account both the number of birds attracted and their interest. The binomial test was used for two-way comparisons of frequencies.

RESULTS

Nonprocellariiform species (Kelp Gull, *Larus dominicanus*: LD; Imperial Shag, *Phalacrocorax atriceps*: PA; Kerguelen and Antarctic terns, respectively, *Sterna virgata* and *S. vittata*: SVV) showed no interest in the cod-liver oil tests (Fig. 1, right side), the only special interests occurring for control rafts. LDs were significantly more numerous during control tests than during cod-liver oil tests ($P = 0.015$).

All species (or genera for sibling species) showing special interest to the odor tests were procellariiforms. Four of these: Wilson Storm-Petrel (*Oceanites ocean-*

icus: OO), White-chinned Petrel (*Procellaria aequinoctialis*: PA), Cape Petrel (*Daption capensis*: DC), and giant-petrels (*Macronectes* spp.: MGH) were more strongly attracted by test rafts than by control rafts (Fig. 1). Only one Black-bellied Storm-Petrel (*Fregetta tropica*: FT) was observed during seawater control tests (hence $P=0.09$), however, a significant majority showed special interest during cod-liver oil tests ($P < 0.001$). Similarly, OO, DC, and FT were significantly more frequent during cod-liver oil tests than during controls ($P < 0.04$, $P < 0.004$, and $P < 0.001$, respectively). Four other species (or genera) were not attracted by tests: the Wandering Albatross (*Diomedea exulans*: DE), the Light-mantled Sooty-Albatross (*Phoebastria palpebrata*: PP), the prions (*Pachyptila* spp.: PAC), and the diving petrels (*Pelecanoides* sp.: PUG). Finally, the Antarctic Fulmar (*Fulmarus glacialis*: FGL), an Antarctic species, was frequently seen but suggested a significant interest (five special interest for six observations during cod-liver oil tests and two no interest during control, $P = 0.11$).

DISCUSSION

COMPARISON OF OLFACTORY ABILITIES BETWEEN PROCELLARIIFORM AND NONPROCELLARIIFORM SEABIRDS

Our results extend the number of seabirds tested and corroborate previous results obtained for DC and OO by Grubb (1972) and by Jouventin and Robin (1983). These results highlight variations in the intensity of response among species. The two storm-petrels, especially FT, were seen most frequently during cod-liver oil tests, because they were attracted from far away by its odor (which would explain why FT was seen only once during seawater control tests and thus gave a non-significant result). On the other hand, about the same number of PA and MGH were seen in each test, suggesting that they both use visual and olfactory cues. DC appears to take an intermediate position, although it was observed more frequently during cod-liver oil tests than during control tests. Thus, storm-petrels seem to be more reliant on odor than other procellariiforms tested. In their study on Adélie Land, Jouventin and Robin (1983) found that Antarctic Fulmars were not attracted by cod-liver sponges. In our study, this species shows similar olfactory capacities to the Northern Fulmar, *F. glacialis* (Hutchison and Wenzel 1980). Contrasting responses could be due, as Jouventin and Robin (1983) suggest, to the fact that experiments on Adélie Land were not conducted in the feeding range of the species. With regard to nonprocellariiforms, none revealed an olfactory capacity and some even showed more interest in the control raft (LD). The tests were made near a breeding site, and LD, a local species, was probably attracted to the control simply because it was the first to be launched. Aversion to the odor of the cod-liver oil is improbable since this species has been seen at oil spills after the experiments were completed.

Several previous studies have compared the olfactory capacities of procellariiform and nonprocellariiform seabirds by anatomy (Bang 1971, Cobb 1960, Bang and Cobb 1968), and by experimentation (Grubb 1972, Jouventin 1977, Hutchison and Wenzel 1980, Jouventin and Robin 1983, Hutchison et al. 1984).

Our results corroborate the general conclusion that procellariiforms use olfaction and nonprocellariiforms use vision alone when searching for food.

OLFACTORY CAPACITIES OF PROCELLARIIFORMS IN RELATION TO PHYLOGENY

Olfactory capacities vary according to phylogeny. Information is scarce on albatrosses for which positive results have been reported only in the Black-footed Albatross, *D. nigripes* (Miller 1942, Hutchison and Wenzel 1980). In our tests, the Light-mantled Sooty-Albatross, *P. palpebrata*, seemed to be interested occasionally by odor baits. The negative responses of other species could be due to the fact that experiments were not performed in their feeding areas. Taken as a whole, Procellariidae showed positive reactions to olfactory tests (Table 1) although we have no information on five genera: *Thelassoica*, *Pterodroma*, *Bulweria*, *Halobaena*, and *Calonectris*. Only one genus, *Pachyptila*, was not attracted by odors. All *Oceanitidae* involved seemed to use olfaction. In contrast, the family of Pelecanoididae was homogeneous in its lack of response to olfactory tests.

OLFACTORY CAPACITIES OF PROCELLARIIFORMS IN RELATION TO ANATOMY AND ITS ROLE IN THEIR FEEDING ECOLOGY

The well-developed olfactory capacity of storm-petrels in contrast to Diving Petrels is correlated with the relative size of their olfactory bulbs (Bang 1966). On the other hand, the Cape Petrel is considerably more strongly attracted during odor experiments than the prions despite an apparent lack of difference in their bulb-to-hemisphere ratios (Bang 1966). A similar result has been obtained among landbirds, where European Starlings *Sturnus vulgaris* (Clark and Mason 1987) and House Sparrows *Passer domesticus* (Tucker 1965) have better developed olfactory capacities than would be expected from their anatomy. Correlation between the dimensions of olfactory structures and olfactory capacity may be poor if the olfactory capacity is determined primarily by ecological or behavioral factors.

All the species attracted by cod-liver oil tests frequently feed near the coast, on floating refuse and carrion (Harper et al. 1985; Harper 1987; Jouventin et al. 1988; Ridoux and Offredo, in press). Two species, OO and FT, feed in flight by pattering or dipping (Harper et al. 1985). Most of the albatrosses, however, feed far offshore and further experiments will be necessary to establish the precise role of olfaction in their foraging strategies. PUG and PAC feed principally on crustaceans near the coast (and not on refuse) by plunging and surface seizing, respectively (Jouventin et al. 1988). A possible link, therefore, appears between the feeding ecology (fishing methods and diet) and the olfactory capacities of seabirds. Species taking their prey under water probably do not need, and thus do not show, olfactory capacities. On the other hand, olfaction is related to the feeding ecology of seabirds searching on the wing for odorants floating at the surface.

This study was supported by the Administration Terres Australes et Antarctiques Françaises and GDR

TABLE 1. Olfactive capacities compared in procellariiforms.

Family, species and references	Re- sponse
Procellariidae	
<i>Macronectes</i> sp. (7)	+
<i>Fulmarus glacialis</i> (4) (6)	+
<i>Fulmarus glacialis</i> (7)	(+)
<i>Fulmarus glacialis</i> (5)	-
<i>Daption capensis</i> (5) (7)	+
<i>Pagodroma nivea</i> (5)	+
<i>Pachyptila</i> sp. (7)	-
<i>Procellaria aequinoctialis</i> (7)	+
<i>Puffinus gravis</i> (2)	+
<i>Puffinus griseus, creatopus & bulleri</i> (4)	+
<i>Puffinus puffinus & tenuirostris</i> (4)	+
Oceanitidae	
<i>Oceanites oceanicus</i> (2) (5) (7)	+
<i>Fregetta tropica</i> (7)	+
<i>Halocyptena microsoma</i> (4)	+
<i>Oceanodroma leucorhoa</i> (3) (4)	+
<i>Oceanodroma homochroa, melania & furcata</i> (4)	+
<i>Oceanodroma tethys</i> (1)	+
Pelecanoididae	
<i>Pelecanoides urinatrix & georgicus</i> (7)	-

(1) R. Crossin in Wenzel 1980, (2) Grubb 1972, (3) Grubb 1974, (4) Hutchison and Wenzel 1980, (5) Jouventin and Robin 1983, (6) Hutchison et al. 1984, (7) this study.

001 of the CNRS. We thank H. Weimerskirch for starting the project, G. Sibaud for constructing the rafts, P. Doncaster for comments and helpful changes to the English, V. Bretagnolle and H. Weimerskirch for their constructive comments on the manuscript, and L. Ruchon for drawing the figure.

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.* (Suppl.) 1 58:1-76.
- BANG, B. G., AND S. COBB. 1968. The size of the olfactory bulb in 108 species of birds. *Auk* 85:55-61.
- BANG, B. G., AND B. M. WENZEL. 1985. Nasal cavity and olfactory system, p. ??-??. In A. S. King and J. McLelland [eds.], *Form and function in birds*. Vol. 3. London.
- CLARK, L., AND R. MASON. 1987. Olfactory discrimination of plant volatiles by the European starling. *Anim. Behav.* 35:227-235.
- 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.
- GRUBB, T. C. 1974. Olfactory navigation to the nesting burrow in Leach's Petrel (*Oceanodroma leucorhoa*). *Behaviour* 22:192-202.
- HARPER, P. C. 1987. Feeding behaviour and other notes on 20 species of procellariiforms at sea. *Notornis* 34:169-192.
- HARPER, P. C., J.-P. CROXALL, AND J. COOPER. 1985. A guide to foraging methods used by birds in Antarctic and Subantarctic seas. *Biomass Handbook* No. 24.
- HUTCHISON, L. V., AND B. H. WENZEL. 1980. Olfactory guidance in foraging by procellariiforms. *Condor* 82:314-319.
- HUTCHINSON, L. V. [sic, FOR HUTCHISON, L. V.], B. H. WENZEL, K. E. STAGER, AND B. L. TEDFORD. 1984. Further evidence for olfactory foraging by Sooty Shearwater and Northern Fulmars, p. 78-89. In D. N. Nettleship, G. A. Sanger, and P. F. Springer [eds.], *Marine birds: their feeding ecology and commercial fisheries relationships*. Canadian Wildlife Service Special Publication, Ottawa.
- JOUVENTIN, P. 1977. Olfaction in Snow Petrels. *Condor* 79:498-499.
- JOUVENTIN, P. In press. Salvin Albatross *Diomedea cauta salvini* breeding on Penguin Island, Crozet Archipelago, Indian Ocean. *Ibis*.
- JOUVENTIN, P., V. RIDOUX, J. C. STAHL, AND H. WEIMERSKIRCH. 1988. La ségrégation écologique entre les pétrels des îles Crozet. *Terre et Vie* 43:29-38.
- JOUVENTIN, P., AND P. ROBIN. 1983. Olfactory experiments on some Antarctic seabirds. *Emu* 84:46-48.
- JOUVENTIN, P., J. C. STAHL, H. WEIMERSKIRCH, AND J.-L. MOUGIN. 1984. The seabirds of the French Subantarctic Islands and Adélie land, their status and conservation, p. 609-625. In J.-P. Croxall, P.G.H. Ewans, and R. W. Schreiber [eds.], *Status and conservation of the world's seabirds*. I.C.B.P. Technical Publications No. 2.
- MILLER, L. 1942. Some tagging experiments with Black-footed Albatrosses. *Condor* 44:3-9.
- RIDOUX, V., AND C. OFFREDO. In press. The diets of five summer breeding birds in Adélie land, Antarctica. *Polar Biol.*
- SMITH, S. A., AND R. A. PASELK. 1986. Olfactory sensitivity of the Turkey Vulture (*Cathartes aura*) to three carrion-associated odorants. *Auk* 103:586-592.
- TUCKER, D. 1965. Electrophysiological evidence for olfactory function in birds. *Nature* 207:34-36.
- WENZEL, B. M. 1980. Chemoreception in sea birds, p. 41-67. In J. Burger, B. L. Olla, and H. E. Winn [eds.], *Behavior of marine animals: current perspectives in research*. Vol. 4. Marine birds. Plenum Press, New York.