# Symposium Overview

## Olfaction in Birds: A Dedication to the Pioneering Spirit of Bernice Wenzel and Betsy Bang

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When Darwin proposed his theory of sexual selection, a sense of smell in birds was widely disregarded by olfactory scientists and ornithologists alike. The reasons behind this error have been reviewed in the popular literature,[1,2] and the consensus seems to be that most of the blame falls on J.J. Audubon, a highly respected bird artist and ornithologist of the 19th century. Audubon believed that birds could not smell and he devised ways to prove it. For example, flying in the face of Aristotle's theories that turkey vultures (*Cathartes aura*) scavenged by olfaction, Audubon held that they were anosmic. Whether the peer-review process has improved since that day is the topic for a different article, but a careful read of Audubon's field experiments suggests that he was a better artist than a field biologist.[3] In any event, Audubon's opinions helped shape the way biologists thought about bird behavior, and "anosmic" worked its way into the lexicon of ornithology texts well into the next century. At the same time, birds were becoming important models for testing evolutionary theory, including sexual selection, largely failing to consider a potential function for chemical cues.

Olfactory abilities in birds were occasionally explored in the 20th century,[4] but Professor Bernice Wenzel and Betsy Bang stand out as the mavericks of their generation whose combined accomplishments eventually legitimized the field for other researchers. As one of the few female professors of physiology in the United States, Wenzel broke the mold by focusing her research on the study of olfaction in birds. Wenzel's laboratory was the first to apply a state-of-the-art, integrative approach to this problem, incorporating neuroanatomical, physiological, and behavioral techniques to study olfaction in a variety of avian species.[5,6] For example, she spearheaded investigations using electrophysiological recording and neuroanatomical methods to investigate olfactory sensitivity and neuro-architecture of pigeons (*Columba livia*).[7–9] She and co-workers meticulously developed nerve-section and bulb-ablation techniques to study effects on olfactory responsiveness.[10] Her work also extended to field behavioral experiments. For example, she was the first to show that brown kiwi birds (*Apteryx australis*) use their sense of smell to forage,[11] and she and her student, Larry Hutchison, demonstrated that various procellariiform seabirds were attracted to odors at sea.[12] She and E. Meisami went on to describe the fine structure of the olfactory bulb of one of these procellariiforms, the northern fulmar (*Fulmarus glacialis*),[13] and working with colleagues, she later produced a brain atlas of this species.[14] While these are just a few examples, Wenzel's work demonstrated, by anatomical, physiological, and behavioral measures, that the sense of smell was highly developed in a variety of avian species across a wide phylogenetic range.[15,16]

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Wenzel's contemporary, Betsy Bang, was a scholar, an amateur ornithologist, and a scientific illustrator trained at Johns Hopkins University, who produced a series of foundational works beautifully and meticulously illustrating olfactory structures across a wide phylogenetic range of birds. According to her daughter, Molly Bang, "she was deeply concerned that 'wrong' information was out there about the olfactory abilities of birds and she wanted to correct this misunderstanding." Her son, Axel Bang attests "she was full of energy, into nature and didn't mind taking on a fight, even if it meant taking on Audubon. She knew the songs of birds, their calls and habits, and even the most obscure birds, especially if they had interesting nasal passages." Her first paper on this subject was published in *Nature*[17] and provided unequivocal anatomical evidence for olfactory function in birds. In a second *Nature* paper,[18] she went on to illustrate the olfactory system of the snow petrel (*Pagodroma nivea*), which has the largest olfactory bulb of any bird. From there she produced a series of articles, which are, to this day, the cornerstone references for olfactory structures of birds. These include "The olfactory apparatus of the tubenosed birds (Procellariiformes),"[19] "The size of the olfactory bulb in 108 species of birds,"[20] and "Functional anatomy of the olfactory system in 23 orders of birds."[21] These studies documented variation in both the degree of folding in the tubercles and the relative size of olfactory bulbs, which led to increased debate about the relative olfactory abilities of the major orders of birds. Quoting Bernice Wenzel,[4] "Without Bang's early papers. . .avian olfaction as a serious research topic might have had little appeal. . . She made an essential contribution at a receptive time."

Today the sense of smell in birds is a recognized discipline, and this symposium is presented to honor the accomplishments of these two scientists who helped make this happen. Our invited speakers were chosen to represent different nationalities, disciplines, and techniques, ranging from *in vivo* electrophysiological olfactory bulb recordings in domesticated fowl to field studies of self/non-self recognition in wild petrels nesting on remote islands. Our first contribution is from Dr. Dorothy McKeegan[22] from the University of Glasgow, Scotland. Dr. McKeegan has performed the most detailed electrophysiological studies to date on olfactory and trigeminal perception in the domesticated chicken (*Gallus domesticus*). Chickens are behaviorally sensitive to a variety of odors, and as Dr. McKeegan's work demonstrates, they are good models for electrophysiological investigation. Using single-unit recording techniques at the level of the olfactory bulb, McKeegan shows that the activity of olfactory bulb neurons closely resembles that of mammals. These cells exhibit temporal variability in their patterns of spontaneous activity, with firing rates that fall between mammals and reptiles. She shows that neurons respond to single odorants applied to the epithelium in a concentration-dependent manner that is generally similar to activity recorded in mammalian olfactory bulbs. These neurons display clear stimulus–response relationships when single odors are applied to the epithelium, but interestingly, they can discriminate unusually small step changes in odor concentration. She also has examined trigeminal sensitivity by recording from single mucosal receptors in the nasal cavity and palate, and her work is the first attempt to quantify single trigeminal receptors to a concentration range of noxious airborne chemicals.

Our next contribution is from Dr. Anna Gagliardo[23] of the University of Pisa, Italy. Dr. Gagliardo works in the area of pigeon navigation, which has been a hotly debated research topic for the last 40 years or so. Pigeons released hundreds of kilometers from their home loft are able to accurately return home, even from unfamiliar territory. A raging debate has centered on the sensory mechanisms birds use to guide them home, and specifically, the roles played by olfactory and magnetodetection. Compounding the problem, the ophthalmic branch of the trigeminal nerve (VI) has recently been shown to innervate putative magnetoreceptors located in the upper beak, and because it is difficult to section the olfactory nerve without also damaging or cutting this branch, most olfactory occlusion experiments have involved cutting both nerves. The controversy is that both senses may be knocked out by this technique, confounding results. To answer this criticism, Gagliardo has painstakingly demonstrated in an elegant set of experiments that sectioning VI has no effect on homing ability. Her symposium paper extends this methodology to investigate the effects of different developmental sensory experiences on homing performance, and concludes that olfactory cues are needed for the development of the navigational map.

Our final two contributions come from Dr. Francesco Bonadonna,[24] CNRS–Centre d'Ecologie Fonctionnelle et Evolutive, Montpellier, France, and Drs. Terry O'Dwyer and Gabrielle Nevitt,[25] from the University of California at Davis, USA. These two papers investigate the role olfaction plays in homing and individual recognition in burrow-nesting procellariiform seabirds. Procellariiforms have among the largest olfactory bulbs of any avian species and make useful field models for the study of avian olfaction in ecological or evolutionary contexts. They are pelagic seabirds, meaning they spend nearly all their time at sea and are tied to the terrestrial environment only for a few months each year or every other year to breed and rear a single offspring. Adults mate for life and are phylopatric to a nesting burrow. Upon returning from foraging trips at sea, they must relocate this nesting burrow, often at night and in dense colonies, to relieve their mates or provision offspring. Recent work has shown that burrow-nesting petrels can use olfactory cues to home and even to tell each other apart. Dr. Bonadonna's paper reviews foundational studies that he and collaborators have performed that establish the olfactory basis for homing and individual recognition in burrow-nesting procellariiforms. O'Dwyer and Nevitt's paper extends this theme to examine the development of individual recognition and a potential role for the major histocompatability complex in this behavior. These and other molecular approaches[26] will advance our understanding of whether individual-specific odor signatures are contributing factors to mate choice.

### Conflicts of Interest

The authors declare no conflicts of interest.

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