Individual Odor Recognition in Procellariiform Chicks

Potential Role for the Major Histocompatibility Complex

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Since the groundbreaking work of Wenzel, Bang, and Grubb in the 1960s, enormous progress has been made toward elucidating the sense of smell in procellariiform seabirds. Although it is now well established that adult procellariiforms use olfaction in many behaviors, such as for foraging, nest relocation, and mate recognition, the olfactory abilities of petrel chicks are less well understood. Recent studies have shown that petrel chicks can recognize prey-related odors and odors associated with their nest before leaving their burrow for the first time. The recognition of burrow odors by petrel chicks is unlikely to be used for homing, and we have suggested that chicks may be learning personal odors associated with the nest's occupants for use later in life in the context of kin recognition or mate choice. The source of personal odors in petrels is unknown. However, in other vertebrates, the major histocompatibility complex influences body odors, which in turn influence mating preferences. It is not currently known whether this highly polymorphic gene region influences body odors and individual recognition in the procellariiforms, but this could be a fruitful area of future research.

Key words: **olfaction; individual recognition; major histocompatibility complex; mate choice**

Introduction

The pioneering research of Wenzel, Bang, and Grubb in the 1960s focused on establishing that the procellariiforms (petrels and albatrosses) had large olfactory bulbs and could detect prey-related or nest-specific odors.[1–6] In the ensuing decades, considerable headway has been made in understanding the sensory ecology of olfactory foraging and homing in these long-lived pelagic seabirds. Our report will briefly outline some of the major discoveries on the olfactory capabilities of the procellariiforms with a focus on our recent research on the development of personal odor sensitivity in petrel chicks. We will also discuss the potential role of the major histocompatibility complex (MHC) in individual odor recognition and mate choice. See Refs. 7–9 for a more detailed discussion of the use of olfaction by these charismatic seabirds.

Adult procellariiforms possess a remarkable sense of smell. Investigations in a wide range of species, encompassing all the major procellariiform groups, have demonstrated that olfaction plays an important role in activities as varied as foraging, nest relocation, and mate recognition. For example, several procellariiform species are sensitive to scents, such as dimethyl sulfide, that naturally occur in the marine environment. These odors are often associated with

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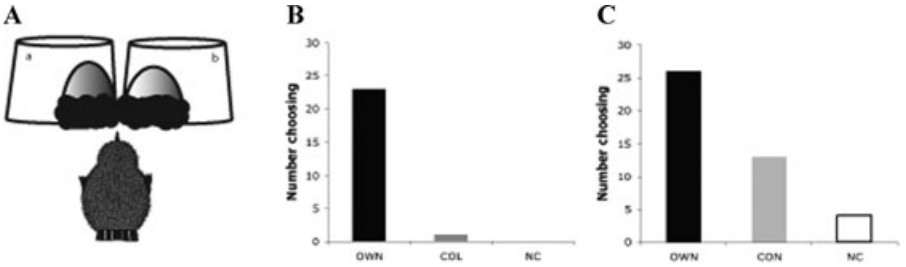

Figure 1. Odor preferences of Leach's storm-petrel (*Oceanodroma leucorhoa*) chicks. (**A**) Experimental setup for odor preference trials. (**B**) Experiment 1: own burrow material versus similar colony material ($N = 24$, binomial test, $P < 0.001$). (**C**) Experiment 2: own burrow material versus conspecific's burrow material ($N = 39$, binomial test, $P = 0.05$). OWN, own burrow material; COL, similar colony material; CON, conspecific's burrow material; NC, no choice. Adapted from O'Dwyer *et al.*, 2008.[19]

bathymetric features, such as seamounts, where food is likely to occur. It has been suggested that variation in these odors can help guide birds, which forage over vast areas of the open ocean for patchily distributed food, to these productive areas.[10] In regard to olfactory-mediated homing, nocturnal, burrow-nesting species require a functional sense of smell to relocate their burrow among hundreds of others when they return to their colony at night. Because petrels have a strong musty odor, it is suspected that birds are detecting an odor that originates from the burrow's occupants. In support of this idea, at least one species of burrow-nesting petrel, the Antarctic prion *Pachyptila desolata*, can detect, and is attracted to, the odor of its mate.[11] Furthermore, analyses of odors collected from petrel feathers suggest that they have an endogenously produced personal odor that is distinctive from other individuals.[12]

Olfactory Abilities of Procellariiform Chicks

Investigations on odor sensitivity in procellariiform chicks are limited to only a few species, all of which are burrow or crevice nesting. However, the evidence gathered to date shows that petrel chicks can detect both food-related and personal odors before they leave their nest for the first time.[13–18] In our recent studies on Leach's storm-petrels, *Oceanodroma leucorhoa*, for example, we used two-choice tests (Fig. 1) to show that 4- to 6-week-old chicks can discriminate (1) the odor of their own nest material from the odor of similar organic material collected away from any petrel nest and (2) the odor of their own nest material from the odor of material collected from the nest of a conspecific. In both experiments, chicks recognized, and they preferred to orient toward, the odor of their own burrow material (Fig. 1). European storm-petrel chicks can also recognize the odor of their burrow as well as their own personal odor.[17] It was concluded that European storm-petrel chicks were using burrow-related odors to home to their nest site. However, Leach's storm-petrel chicks, like the chicks of most burrow-nesting petrels, do not leave their burrow prior to fledging. Thus, burrow odor recognition is unlikely to be used for homing in this species. Because the odor of the occupants (i.e., the parents and the chick) is likely to contribute to the odor of the burrow, we have reasoned that chicks may be learning personal odors for use in other contexts later in life, such as kin recognition or mate choice.[19]

Although both adult and young procellariiforms can recognize personal odors, the source of these odors is unknown. In a wide range of vertebrates, individual odors are influenced by the highly polymorphic genes of the MHC.

Could the MHC also play a role in individual recognition and mate choice in the Procellariiformes?

MHC, Personal Odors, and Mating Preferences

The MHC is a multigene family that plays a central role in immune function and self/nonself recognition. The main role of MHC-encoded molecules is to bind both self- and pathogen-derived protein fragments and display them on cell surfaces to T cells for a suitable immune response.[20] The MHC, with hundreds of alleles occurring at some loci in humans,[21] is the most polymorphic of any gene region studied to date. An individual's MHC genotype influences his or her susceptibility to infectious diseases, and the high degree of polymorphism found at MHC loci is generally thought to be driven by pathogen- or reproduction-mediated evolutionary forces.[22]

In addition to its primary role in immune function, the MHC also influences individual odors.[23] Moreover, MHC-associated odors are involved in individual recognition and mate choice in a wide range of vertebrates, including humans, mice, fish, and reptiles. In mice, for example, both males and females exhibit mating preferences for MHC-dissimilar partners.[24,25] Mice can also learn the MHC identity of family members during early development and will avoid mating with individuals with familial MHC genes.[26] In humans, women prefer the odor of men with MHC genes different from their own. In a study by Wedekind *et al.*,[27] women judged the odor of t-shirts worn by men who were dissimilar to themselves with respect to MHC to be more pleasant than those worn by MHC-similar men. In fish, female Atlantic salmon, *Salmo salar*, also prefer to mate with MHC-dissimilar males,[28] and in sticklebacks, *Gasterosteus aculeatus*, females prefer the odor of males with many MHC alleles over those with fewer alleles.[29] An odor-based MHC component to mate choice has also been found in reptiles, where female sand lizards, *Lacerta agilis*, prefer the odor of males who are MHC dissimilar over those with MHCs that are similar to their own.[30]

Mating preferences based on the MHC are thought to be adaptive for several reasons.[31] First, a preference for mates with certain MHC alleles will produce offspring with either increased heterozygosity or a particular combination of alleles, both of which will influence their resistance to infectious diseases. Second, an MHC component to mating preferences provides a moving target to rapidly evolving parasites. Third, MHC-based mating preferences may be involved in the avoidance of inbreeding,[32] which can lead to a decrease in offspring fitness by increasing homozygosity and uncovering deleterious alleles.[33–36] A mechanism to recognize kin is likely to be important in species where the probability of encountering close relatives is high, such as petrels that are natally philopatric to isolated islands.

Although results have sometimes been ambiguous, there is also evidence for MHC-associated mating preferences in birds. For example, female savannah sparrows, *Passerculus sandwichensis*, avoid pairing with MHC-similar males.[37] Also, females who are paired with MHC-similar males are more likely to be unfaithful to their partners if more dissimilar males are available. Similarly, MHC diversity in house sparrows, *Passer domesticus*, is positively correlated in breeding pairs, suggesting that mating is not random with respect to MHC in this species.[38] In contrast, Westerdahl[39] found no evidence that female great reed warblers, *Acrocephalus arundinaceus*, were choosing mates on the basis of predictions for MHC heterozygosity or incompatibility.

How birds differentiate between potential mates on the basis of their MHC genotypes is currently not known. Perhaps disease will influence the display of condition-dependent traits, including body condition or secondary sexual characteristics. Thus, those in better health would show the most favorable condition-dependent traits and differences in these traits

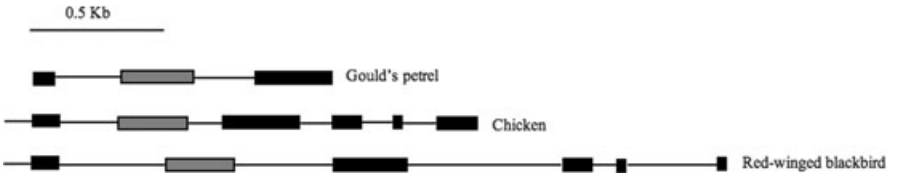

Figure 2. Partially characterized MHC class II *B* gene in the Gould's petrel. Bars represent introns; boxes represent exons. The polymorphic exon 2 is represented by the gray boxes. Structure of MHC class II genes in the chicken[42] and the red-winged blackbird[43] are shown for comparison.

may provide visual cues to the chooser.[40] In support of this idea, in ring-necked pheasants, *Phasianus colchicus*, there is an association between MHC genotype and tarsal spur length, a secondary sexual characteristic.[41] However, in other avian studies that found MHC-associated mating preferences, there was no correlation between MHC genotype and condition-dependent traits,[37,38] suggesting that some other cues must be involved.

Whether personal odor can convey MHC genotype in birds, as it does in other vertebrates, is not known, but it presents an intriguing possibility. To this end, we have recently partially characterized an MHC class II *B* gene in a hole-nesting procellariiform, the Gould's petrel *Pterodroma leucoptera*, with the aim of examining the role of the MHC in individual recognition in this species (Fig. 2). Our preliminary results indicate that there is both intra- and interindividual variation in the coding region for the peptide-binding site, exon 2 (O'Dwyer *et al.*, unpublished), which suggests that positive selection is acting on this gene, perhaps through MHC-based disassortative mating.

In conclusion, the Procellariiformes have an excellent sense of smell, including an ability to recognize the personal odor of their breeding partner. The genes of the highly polymorphic MHC influence body odors and mate choice in a wide range of vertebrates. Although there is evidence that the MHC also influences mate choice in birds, whether they use odor to assess the MHC genotype of potential mates is unknown. If MHC-related odors are involved in individual recognition in birds, the procellariiforms, with their excellent sense of smell, are an excellent group in which to begin such an investigation.

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Conflicts of Interest

The authors declare no conflicts of interest.

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