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# Odors and Chemical Signaling

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## 3.1 INTRODUCTION

Ornithologists rarely consider the role of chemosensory information in avian reproduction. Yet, every bird that has been examined has a functional olfactory system (Bang and Wenzel 1985; Roper 1999). Like other vertebrates, birds detect and respond adaptively to odors in their environment while foraging (e.g. Nevitt et al. 1995, 2004; reviewed in Roper 1999), homing over long and short distances (e.g. Bonadonna and Bretagnolle 2002; Nevitt and Bonadonna 2005a,b; Wallraff 2004, 2005), and perhaps even avoiding predators (Fluck et al. 1996). There is also evidence that some avian species monitor the chemical environment of nests (Petit et al. 2002). However, compared to other organisms, information on the production or social use of self-produced odor compounds in birds has been largely neglected (Roper 1999).

The chemosensory abilities of birds stand as a promising means of understanding avian biology, because it challenges traditional views that birds respond to their world primarily through visual and auditory signals. Like other sensory systems, studies of the chemical senses are inherently interdisciplinary, as they involve responses at the molecular, physiological, developmental and behavioral levels. In particular, studies of avian-derived odors have the potential to fundamentally alter how we interpret social behavior. Social odors have been studied in other animals for decades, but, until recently, birds appeared to be the only vertebrate group that lacked them altogether (Wingfield et al. 1994). Thus, the chemical signals of birds represent an entirely new mode of avian communication that have the potential to reveal new and interesting aspects of behavioral ecology and sensory perception. They are akin to the startling discovery that some birds respond to ultraviolet plumage ornaments which humans cannot see (see Chapter 1).

This chapter has several goals. First, I examine the ways in which breeding birds adaptively employ odors derived from the environment, such as the use of odiferous plant materials in nests. The remainder of the chapter focuses in

detail on odors that birds produce themselves, as they relate to reproduction. I consider where avian-derived odors come from and how scent functions in social breeding contexts, with particular detail paid to two avian groups (petrels [Procellariidae] and auklets [Alcidae]) for which we presently have the most information. In view of recent developments, I highlight gaps in our basic understanding of avian odors and point out research areas that have proven quite productive in understanding the reproductive behavior of other animal systems, such as mammals. Finally, I propose a conceptual framework for future studies of avian chemical signals that addresses multiple levels of bird biology. To illustrate, I examine how olfactory anatomy can inform investigations that aim to understand how avian chemosignals function.

## 3.2 ODORS DERIVED FROM THE ENVIRONMENT

### 3.2.1 Plants

The nest site of breeding birds is an inherently dirty place, as it may contain ectoparasites, fungi, viruses and bacteria (e.g. Loye and Zuk 1991; Clayton and Moore 1997). Other organisms, such as invertebrates, regularly employ the chemical compounds of plants to protect themselves against harmful parasites, pathogens or predators (e.g. Rodriguez and Wrangham 1993; Berenbaum 1995), leading several authors to propose that the incorporation of certain types of herbaceous material into nests has an adaptive, or medicinal effect on avian residents. The “nest protection hypothesis” suggests that the volatile chemicals of plants produce a repellent or let  affect on organisms harmful to birds (e.g. Wimberger 1984; Clark and Mason 1985; Clark 1991). Similarly, the “drug hypothesis” (Gwinner *et al.* 2000) suggests that, when inhaled or absorbed through the skin, plant compounds provide positive stimulation to the immune function of chicks, thereby reducing infection. Plant materials have been reported in the nests of several avian species, such as the House sparrow (*Passer domesticus*; Sengupta 1981), Wood stork (*Mycteria americana*; Rodgers *et al.* 1988), and Common buzzard (*Buteo buteo*; Roulin *et al.* 1997). However, I will focus on investigations of European starlings (*Sturnus vulgaris*) and the Corsican blue tit (*Parus caeruleus ogliastroe*), as these are the most extensive, and provide both indirect and direct support for the two hypotheses listed above.

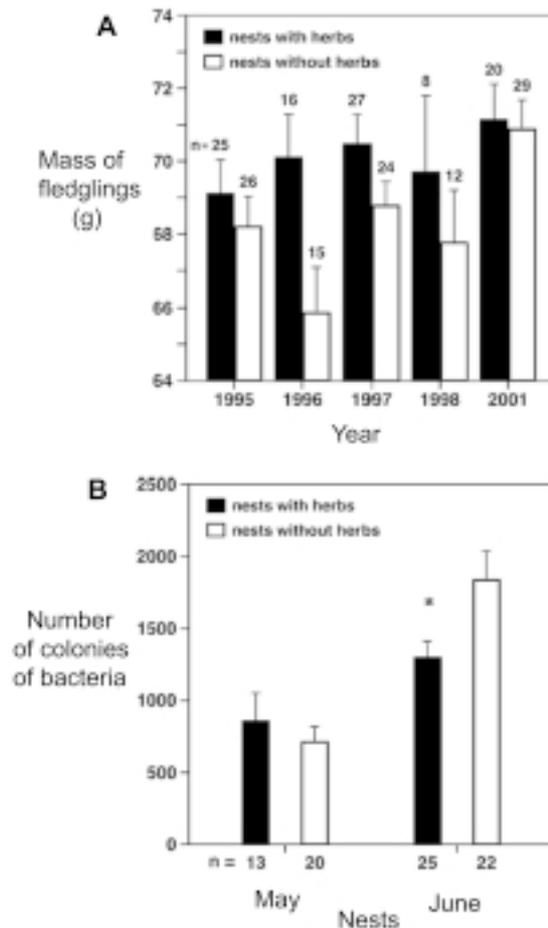
**European starlings.** *Sturnus vulgaris* and other passerines that reuse cavity nests for several seasons (and thus may suffer from higher parasite loads) are more likely to include green nesting material, compared to species that use a nest only once (Clark and Mason 1985). Despite an exceedingly small olfactory anatomy (see 3.7.1), *S. vulgaris* also responds (via cardiac conditioning) to the volatile compounds contained in the green plants that it prefers (Clark and Mason 1987a; Clark and Smeranski 1990). Herbaceous material also inhibited growth of bacteria and slowed the development of mites, a key

ectoparasite (Clark and Mason 1985, 1988). However, subsequent tests failed to measure the same effect on mites (e.g. Brouwer and Komdeur 2004; Gwinner and Berger 2005).

Interestingly, only male starlings add green plants to otherwise dry nest materials. The behavior primarily occurs during courtship and nest building, but discontinues after egg-laying (Pinxten and Eens 1990; Fauth *et al.* 1991; Gwinner 1997). Nests containing green materials are more likely to be chosen by females, indicating that the herbaceous components operate as sexually selected ornaments (Brouwer and Komdeur 2004; see also Soler *et al.* 1998). Although females respond to lower concentrations of some odor compounds than males (Clark and Mason 1987b), any olfactory cues involved in female choice (i.e. during nest building) are untested. Chemical assessment by the female of plant compounds contained in a male's decoration has been recently suggested in another avian species, however. Female Satin bower birds (*Ptilorhynchus violaceus*) nibble at a mascerated plant-saliva mixture (called "paint") that males add to walls of their complex display arenas (Bravery *et al.* 2006).

For European starlings (*Sturnus vulgaris*), ornamental green plant material has a positive effect on reproduction. Gwinner and Berger (2005) provided direct evidence for the "nest protection hypothesis" from a five-year field manipulation in which experimental nests containing herbs produced heavier fledglings than those without, and late season nests with herbs exhibited reduced bacteria loads (Fig. 3.1; Wimberger 1984; Clark and Mason 1985; Clark 1991). The authors also observed that the mass and number of herbaceous plant species that males carried to nest sites changed over the course of two nesting events within a breeding season. Specifically, males brought more green material to their second (late-season) nest. Such a response is consistent with the enhanced infestation problems that second broods often face (Fig. 3.1B), and thus provides additional, indirect support for the "nest protection" hypothesis. More green nest material at second nests may also reflect greater effort on the part of the male to attract a second female (Gwinner and Berger 2005; Gwinner 1997). Though green plant material did not reduce numbers of mites at starling nests, it may interfere with blood sucking behavior (Gross 1975 as cited in Clark 1991), or stimulate certain aspects of a nestling's immune system (consistent with the "drug hypothesis;" Gwinner *et al.* 2000), which could be particularly advantageous during challenging environmental conditions (Gwinner *et al.* 2000, 2005).

**Blue tits.** Unlike *Sturnus vulgaris*, female blue tits (*Cyanistes (=Parus) caeruleus*), rather than males, frequently incorporate aromatic plant materials into the nest throughout egg laying and chick rearing (Lambrechts and Dos Santos 2000). On the island of Corsica, *P. c. ogliastrae* selects 6-10 aromatic herbs, including yarrow (*Achillea ligustica*), lavender (*Lavandula stoechas*) and mint (*Mentha suaveolus*), from more than 200 different plants identified on study plots (Petit *et al.* 2002). Furthermore, preferred herbs contained chemical



**Fig. 3.1** **A.** Fledging mass of starling nestlings (*Sturnus vulgaris*) was greater in experimental nests containing herbs than those without. Specifically, mass was 2 g heavier in nests with herbs (General Linear Model: Nest type:  $F_{1,120} = 12.0$   $P = 0.001$ ). **B.** Though infestation of bacteria increased between May and June nests (General Linear Model: Season:  $F_{1,76} = 34.0$   $P = 0.0001$ ), the presence of herbs in experimental nests significantly reduced the bacteria load of June nests, as indicated (t-test:  $t = -2.4$ ,  $n = 45$ ,  $*P = 0.02$ ). From Gwinner, H. and Berger S. 2005. *Journal für Ornithologie*. 146: 365-371, Figs. 6 and 4, respectively.

compounds known for repellent and antiseptic properties. The particular fresh herb fragments that females preferred also tended to lose their volatile compounds over a 48-hour period (Petit *et al.* 2002).

Petit *et al.* (2002) tested whether the odor of the nest environment stimulated females to replace fresh herb material. The investigators divided 64 nests (controlled for laying date, clutch size and chick age) into two equal treatments. In both treatments, the visual cues of herbs were removed from the

nests. However, aromatic cues were maintained in one set of nests by hiding fresh plant material (*A. linguistica* and *L. stoechas*) in a plastic cache attached to each breeding site. In the unscented treatment, nests lacked both herbs and odor, as the plastic caches were empty. Birds rapidly replaced herbs when scent was missing. However, where aromatic scent was maintained, birds only added herbs after 48 hours, consistent with natural odor depletion. Consequently, *Parus caeruleus ogliastrae* monitored the scent of a nest in a manner consistent with maintaining a disinfected and/or ectoparasite-repellent environment (Petit *et al.* 2002). Like the behavior of *Sturnus vulgaris*, the results indirectly suggest that plant materials may function in “nest protection” (Wimberger 1984; Clark and Mason 1985; Clark 1991). Since the plants are highly aromatic to humans, the phenomenon has been specifically described for *P. c. ogliastrae* as the “potpourri hypothesis” (Lambrechts and Dos Santos 2000).

In contexts other than breeding, odor learning in adults of *Parus caeruleus ogliastrae* has revealed some unexpected differences in response between the sexes (Mennerat *et al.* 2005). Namely, males, which do not build nests or help maintain an aromatic nest environment, were more attracted to feeder boxes emitting lavender odor than to odorless controls. Females, however, showed little difference in response to scented and unscented feeder boxes. The result was unexpected, as only females add scented materials to the nest (Petit *et al.* 2002). Nonetheless, there appear to be inherent sexual differences in behaviors related to odor learning when birds forage. Perhaps males are socially dominant to females at feeders, or maybe females are unable to associate odor with food rewards during the breeding season, while concurrently monitoring the scented environment of nests (Petit *et al.* 2002; Mennerat *et al.* 2005). Regardless, the interesting pattern is applicable to odor learning that occurs during the breeding season, and it is clearly worthy of future testing.

### 3.2.2 Heterospecific Animals

Common waxbills (*Estrilla estrilla*) of Africa add the odiferous products of other animals, namely carnivore scat, to their nests (Schuetz 2005). Similar to the blue tit (*Cyanistes (=Parus) caeruleus*; see 3.2.1), *E. estrilla* adds scat throughout the nestling period, though it is unknown whether birds specifically monitor the aromatic environment at the nest. Scat reduces predation risk in both natural and experimentally manipulated nests, suggesting that it acts as an olfactory deterrent and/or chemical camouflage (Schuetz 2005). The incorporation of other kinds of heterospecific animal materials into nests, such as snake skin, has also been hypothesized as providing a similar benefit (Bolles 1890 as cited in Schuetz 2005). One might expect scat (or snake skin) to be a particularly potent deterrent when it is fresh, and volatile chemical components are most noticeable. However, it is currently unknown how or whether birds use odor cues to preferentially select certain types of nest items over others.

Heterospecific compounds are also employed in other ways, and may serve a hygienic function similar to that of plant materials in nests (see 3.2.1; reviewed in Dumbacher and Pruett-Jones 1996). For example, the poisonous *Pitohou* and *Ifrita kowaldi* of New Guinea have sour-scented feathers that contain neurotoxins, which are lethal to feather lice (Dumbacher *et al.* 1992; Dumbacher 1999; Dumbacher *et al.* 2000). Toxic compounds are likely derived from beetles in the diet (Dumbacher *et al.* 2004). Other avian species engage in “anting” or “defensive anointing,” the active daubing of chemicals from other organisms (i.e. ants) into plumage, which may also reduce parasites or pathogens (e.g. Ehrich *et al.* 1986; Moyer and Clayton 2003; Weldon 2004). However, unlike birds that use plant materials in nests, it is unclear whether this type of chemical warfare plays a heightened role during breeding or mate choice (for additional discussion see 3.4.5 and 3.5).

### 3.3 ODORS DERIVED FROM BIRDS

#### 3.3.1 Odors, Chemical Signals and Pheromones

Aside from those naturally found in the environment, birds also produce a variety of odors themselves and, as we will see, some species are capable of recognizing and adaptively employing their scents. Throughout the text, I will refer broadly to the term “chemical signal” as any self-produced chemical compound or mixture that has a social or physiological effect on conspecifics (Johnston 2000). Investigators typically refer to conspecific odor as a chemical signal when intraspecific detection, recognition and/or transfer of information via odor stimuli has been demonstrated experimentally (Kavaliers *et al.* 2005).

The term “pheromone” is sometimes used interchangeably to describe any chemical signal (e.g. Wyatt 2003). However, its precise meaning has been the topic of some debate. Karlson and Luscher (1959) first defined a pheromone as a compound that, when present in minute quantities, is capable of eliciting an innate, stereotyped behavior, or other physiological or developmental process. Consequently, investigators often consider a pheromone to be a very specific kind of chemical signal, analogous to the ethological concept of a “sign stimulus” or “releasing stimulus” (Johnston 2000). Such a precise definition reduces ambiguity and lends itself to a specific set of testable predictions (e.g. Schaal *et al.* 2003). Since we are only just beginning to understand the role of odors and chemosignals in birds, it is, as yet, premature to claim that any avian odor signal functions as a pheromone (Hagelin *et al.* 2003).

#### 3.3.2 Production of Avian Odors

Birds have a variety of glands (e.g. the preen or uropygial gland, anal gland, salt gland, as well as glands throughout the epidermis) that are capable of producing odors (Lucas and Stettenheim 1972; Jacob and Zisweiler 1982; reviewed in Waldvogel 1989). Avian scent also appears to be widespread. Odors that are readily detectable to humans occur throughout the class Aves

(19 orders, 80 genera; Weldon and Rappole 1997). A sub-sample of such groups is presented in Table 3.1. Likewise, odors derived from other avian sources, such as feces (Jones and Gentle 1985; Jones and Roper 1997), saliva (Bravery *et al.* 2006), stomach oils (Jouventin 1977; Wenzel 1985) and even conspecific blood (Jones and Black 1979) appear to be reasonable sources of chemical cues.

**Table 3.1** Some avian orders considered very odorous by ornithologists. Data assembled from Weldon, P.J. and Rappole, J.H. 1997. *Journal of Chemical Ecology* 23: 2609-2632. Table 1.

<i>Order</i>	<i>Common name</i>	<i>Number of species</i>
Procellariiformes	Petrels, shearwaters, diving petrels	16
Ciconiiformes	Hérons, storks, New World vultures	12
Anseriformes	Ducks, geese, swans, screamers	49
Charadriiformes	Sandpipers, gulls, auks	23
Psittaciformes	Parrots	14
Cuculiformes	Cuckoos	16
Coraciiformes	Kingfishers, rollers, hoopoes, woodhoopoes	14
Piciformes	Woodpeckers, barbets, tucans	33
Passeriformes	Grackles, starlings, ravens, finches, honeycreepers	46

Human detection of avian scent clearly does not mean that an odor is important to a bird. However, early anatomical studies compared the uropygial gland, the primary source of secretions spread on plumage, to the scent glands of mammals and proposed that it produced odor signals (Pycraft 1910; Paris 1913 as cited in Jacob and Zisweiler 1982). Odiferous uropygial secretions of some seabirds, such as petrels and shearwaters (family Procellariidae), account for musky plumage scent, which readily rubs off onto other substrates (DeLeón *et al.* 2003; Bonadonna and Nevitt 2004). In other birds the gland size and the chemical components of uropygial secretions also vary by season (Kennedy 1971; Piersma *et al.* 1999; Reneerkens *et al.* 2002), sex (Jacob *et al.* 1979; Bhattacharyya and Chowdhury 1995), age class and diet (Sandilands *et al.* 2004a,b), suggesting that the chemical make-up and amount of secretions may differ depending on time of year or circumstance. Seasonal changes in odor have been quantified in one species (Table 3.2; Crested auklet [*Aethia cristatella*], Hagelin *et al.* 2003) and suggested in at least one other (Musk duck, *Biziura lobata*, Gamble 1966; see also 3.4.5).

Complex chemicals have been identified from the uropygial gland of numerous passerine and non-passerine species (Jacob and Zisweiler 1982; Reneerkens *et al.* 2002; Haribal *et al.* 2005) and are widely recognized as a means of chemical defense against feather parasites and pathogens (Jacob and Zisweiler 1982; Moyer *et al.* 2003; Shawkey *et al.* 2003). Long hydrocarbon chains of ester waxes are common, and substances appear to require frequent replenishment, as they degrade over time (Haribal *et al.* 2005). However, little

**Table 3.2** Some volatile compounds of crested auklet (*Aethia cristatella*) plumage odor that vary in a seasonally significant manner. Data from Hagelin, J.C., Jones, I.L. and Rasmussen, L.E.L. 2003. Proceedings of the Royal Society. Series B: 270 1323-1329. Table 1.

Compound	Median concentration ( $\mu\text{g/g}$ feathers)	
	Breeding Season <sup>1</sup>	Winter
Octanal	2.98**	0.25
Z-4-Decenal	1.10**	ND
Hexanoic acid	0.84*	0.36
Octanoic acid	0.63*	0.15
Undecanal	0.35**	0.03
Z-2-Decenal	0.30**	ND
Tridecanal	0.30***	0.03
Octanol	0.18*	ND
Heptanal	0.15*	0.35

\* P < 0.01, \*\* P < 0.005, \*\*\*P < 0.001

ND= not detectable in chemical analyses (< 0.0001  $\mu\text{g/g}$  feathers)

<sup>1</sup>Statistical significance is the result of a Wilcoxon two-sample test of scented feathers (breeding season) versus unscented (winter) feathers.

is known about the volatile compounds of uropygial secretions that make up avian-derived scent. In at least one species, the volatile fraction derived from uropygial secretions might repel predators. The cavity-roosting Green woodhoopoe (also known as the Red-billed woodhoopoe, *Phoeniculus purpureus*) turns away from a threat and produces a variety of foul-scented volatile compounds from its uropygial gland including several short-chain fatty acids, aldehydes, and dimethyl sulfide, which appear to act as a defensive secretion (Burger *et al.* 2004).

Aside from a direct connection between odor and uropygial secretions, it is important to note that some birds with striking feather scent actually produce uropygial secretions that are remarkably unscented. For example, Crested auklets (*Aethia cristatella*) emit a strong, citrusy plumage odor (Jones 1993), and a critically endangered parrot, the Kakapo of New Zealand (*Strigops habroptilus*), produces a distinctively sweet and musky odor (Hagelin 2004), but both birds produce uropygial secretions that are odorless to humans (personal observation). The volatile compounds that make-up the tangerine-like plumage odor of *A. cristatella* contain many simple hydrocarbons, including aldehydes and alcohols (Table 3.2). Though the odor source is unclear, the scent of *A. cristatella* is seasonal (Table 3.2), and does not differ strikingly between the sexes (Hagelin *et al.* 2003). Odor intensity, however, appears to vary between different captive populations (Douglas *et al.* 2001; Hagelin *et al.* 2003), suggesting that scent may be linked to diet or some other environmental factor.

Some avian scent appears to be derived from the chemical degradation of uropygial secretions. Namely, odor results from the breakdown of relatively complex and non-volatile compounds into strongly-scented acids and alcohols (Jacob and Zisweiler 1982: 306). Birds also host a diverse microbial community that may also play a role (Burt and Ichida 1999; Muza *et al.* 2000; Lucas and Heeb 2005). One Gram-positive, coccal bacterium, isolated from the uropygial gland of the green woodhoopoe, has been suggested to be involved in odor production (Laws-Brown 2001; Laws-Brown and Meyers 2003). It is also plausible that bacteria on plumage surfaces may be capable of producing odor (Hussain *et al.* 2005).

### 3.4 SOCIAL CONTEXTS OF AVIAN ODORS

#### 3.4.1 Using Avian-derived Odors to Locate Home

Anyone who has visited a thriving colony of seabirds has undoubtedly noticed that the thousands of adults, young, and high concentrations of odiferous feces, all tightly packed into a small patch of breeding habitat, results in a potent olfactory experience. Procellariiform seabirds are well-known for their large olfactory bulbs relative to brain size (see 3.7.1; Bang and Cobb 1968; Bang 1971; Bang and Wenzel 1985), and for their response to food-related odors (Nevitt and Bonadonna 2005a,b; reviewed in Roper 1999). In particular, some birds, such as petrels and prions (Procellariidae), nest in areas with high densities of underground burrows and produce a musky plumage scent (Jacob and Zisweiler 1982; De León *et al.* 2003). Most return from sea after dark and several species appear to have poor night vision (Brooke 1989; Warham 1996), making their ability to locate the colony as well as their specific nest site rather remarkable (for discussion see Bonadonna *et al.* 2001; Bonadonna 2001). Some petrels even locate their burrow without the aid of song, as predation pressure at breeding sites can be intense (Warham 1996).

Pioneering studies by Grubb (1973, 1974, 1979) suggested that olfaction plays a role in the ability of Leach's storm-petrel (*Oceanodroma leucorhoa*) to correctly locate its burrow site in a colony of thousands. Grubb (1974) originally recognized that burrow odor may be involved when he discovered that birds consistently approached nest entrances from down wind. Bonadonna and Bretagnolle (2002) extended the work by manipulating the olfactory capacity of nine petrel species via two methods (plugging nostrils with putty, and injecting zinc-sulfate to temporarily destroy olfactory mucosa). The authors demonstrated that an intact sense of smell was especially important to successfully locating burrow sites in nocturnal species, but less so in diurnal species.

The environment in which petrels and other seabirds live can be visually featureless (open ocean) and inherently "noisy" when wind and waves obscure sight and sound. Consequently, avian-derived scent may not only function in locating a burrow, but perhaps also in navigation over longer

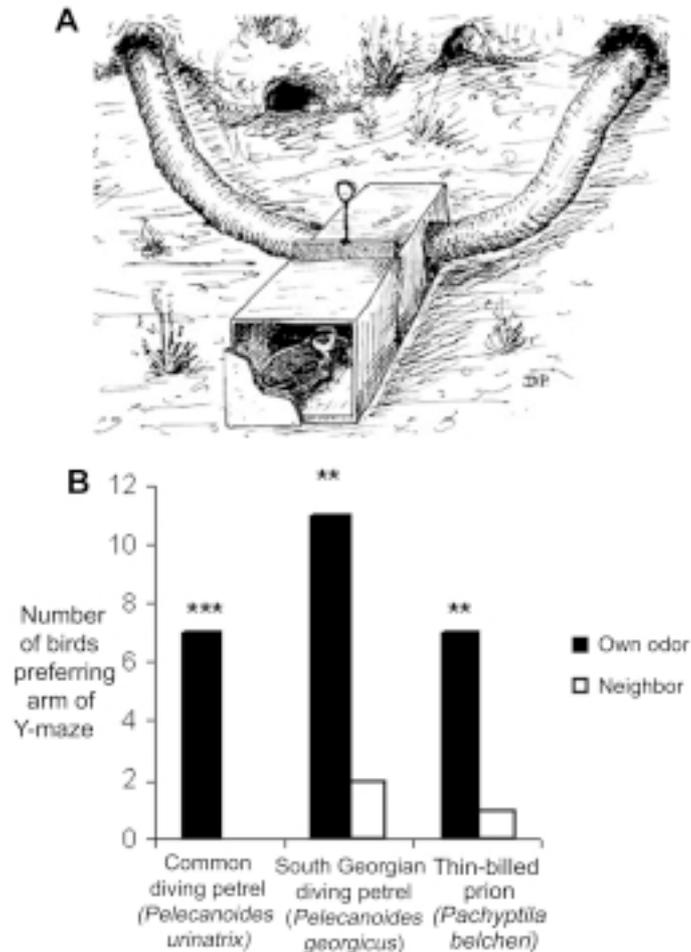
distances, such as returning to a colony, or locating large flocks of foraging conspecifics at dense patches of food. Both situations would appear to implicate homing to avian-derived scent in a manner similar to situations that involve prey-related odors (Nevitt and Bonadonna 2005b). On the foggy Bering Sea, for example, one can smell the citrusy scent of feeding Crested auklets (*Aethia cristatella*) long before birds are visible (Sealy 2006; personal observation).

### 3.4.2 Discrimination of Own-Nest Odor

There is now ample evidence that several petrel species actively discriminate between the odor signatures of their own nest site relative to those of neighboring conspecifics (European storm-petrel, *Hydrobates pelagicus*; De León *et al.* 2003; Mínguez 1997; two prions, *Pachyptila* spp.; Bonadonna *et al.* 2003a,b; Blue petrels, *Halobaena caerulea*; Bonadonna *et al.* 2004; and two Diving petrels, *Pelacanooides* spp.; Bonadonna *et al.* 2003a). Even empty burrows are likely to emit the specific scent of inhabitants, as they contain feathers, feces (Bonadonna *et al.* 2003a,b) as well as body odor, which readily rubs off of a bird and onto other substrates (De León *et al.* 2003; Bonadonna and Nevitt 2004). Tests of burrow odor signatures have typically employed a Y-maze apparatus, which can simultaneously examine, for example, whether birds distinguish between the scents of two different burrow sites (Fig. 3.2A). To prove that birds located their own nests by scent alone, investigators ruled out other, potentially confounding factors associated with burrow location by: (1) removing scented materials from burrows and placing them in an artificial setting (a metal box) attached to arms of the Y-maze (Bonadonna *et al.* 2003a), (2) creating artificially displaced burrow entrances (Bonadonna *et al.* 2004), (3) positioning the arms of the maze into the original burrow entrances but blocking air (and thereby odor) movement (Bonadonna *et al.* 2003b, 2004), and (4) blocking a bird's own sense of smell (Mínguez 1997; Bonadonna *et al.* 2003b). In the first two cases, above, birds correctly located their own nest odor, but in the latter two they did not. It is important to note that the ability to recognize burrow scent extends to species with relatively unremarkable olfactory bulb sizes, such as diving petrels (Fig. 3.2B; Bonadonna *et al.* 2003a; see also 3.7.1), which also do not respond to food-related odors at sea (Lequette *et al.* 1989; Nevitt *et al.* 1995).

### 3.4.3 Discrimination of Self, Conspecific and Mate Odor

Burrows containing resident petrels have a noticeably strong scent, which is detectable to humans (Bonadonna and Bretagnolle 2002). Given a bird's ability to correctly locate its nest site using nest-odor cues alone, the next logical step was to test whether petrels distinguished between their own body odor, conspecific, or mate odor. Previous work suggested that Wedged-tailed shearwaters (*Puffinus pacificus*) experienced elevated heart rates when exposed to mate odor (Shallenberger 1975), although results were not particularly clear cut.



**Fig. 3.2** Several species of petrels readily recognize the scent of their own burrow from that of a neighboring conspecific. **A.** Example of a Y-maze test apparatus with arms that lead to two different burrows. Especially convincing results came from tests in which a maze was not connected to burrows, but contained nest materials only at the end of maze arms. **B.** Individual recognition of burrow odor has been demonstrated in diving petrels, which do not respond to food-related odors while foraging, as well as species that do, such as the thin billed prion. Significance indicates the preferences for home burrow odor in each species. \*\*\* $P = 0.008$ , \*\* $P = 0.01$ , \* $P = 0.03$ . From Bonadonna, F., Cunningham, G.B., Jouventin, P., Hesters, F. and Nevitt, G.A. 2003a. *Journal of Experimental Biology* 206: 3719-3722, Fig. 1; data from Table 1 were used to create 3.2B.

Using a Y-maze, Bonadonna and Nevitt (2004) discovered partner-specific odor recognition in Antarctic prions (*Pachyptila desolata*), a species that is philopatric to the same burrow and monogamous for life (Warham 1996). The

musky plumage odor used in the experiment was cleverly obtained by allowing scent to absorb into the cotton fabric bags in which birds were held. The results are striking (Fig. 3.3). Compared to the odor of a conspecific, resident birds were more attracted to the scent of mates, the odor of which is most likely to be in a burrow when a partner returns from sea (Fig. 3.3A; Bonadonna and Nevitt 2004). Birds also clearly recognized, and were attracted to, their own odor over a cloth bag control (Fig. 3.3B).

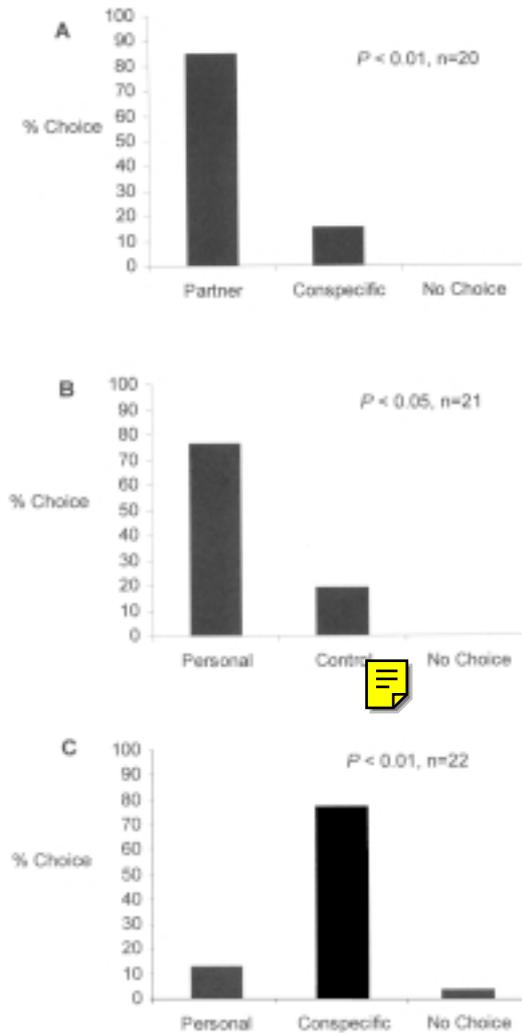
However, quite unexpectedly, and perhaps most importantly, Bonadonna and Nevitt (2004) discovered a pattern of scent recognition that is well-known in mammals. Namely, Antarctic prions *avoided* self-odor, when presented with the scent of a conspecific non-mate (Fig. 3.3C). The ability to recognize the scent of individuals, as well as distinguish self from non-self is a fundamental feature of behavioral organization (e.g. Thom and Hurst 2004; Tsutsui 2004). In particular, aversion to self-odor is a key component of complex social behaviors, such as inbreeding avoidance, and kin recognition which are well-known in mammals, particularly rodents (e.g. Mateo and Johnston 2000 but see Hare et al. 2003; Penn 2002; Kavaliers *et al.* 2005).

Inbreeding avoidance during mate choice may be especially important for species like *Pachyptila desolata*, which are philopatric and monogamous for life (see 3.5; Zelano and Edwards 2002, Bonadonna and Nevitt 2004). Self-referential phenotype matching (Mateo and Johnston 2000) would also appear to be a relevant mechanism for distinguishing kin from non-kin (Bonadonna and Nevitt 2004), as birds are long-lived and produce only one chick per season. Consequently, individuals may encounter potential mates later on in life that are unknown siblings (Mateo and Johnston 2000).

Further study is necessary to determine how body odor functions in breeding contexts and whether it is capable of providing other information, such as the sex of an individual (Bonadonna and Nevitt 2004). Behavioral data on individual or conspecific odor recognition in adults of other avian species are few, but worthy of future testing (see 3.5). Female domestic chickens, for example, appear to be unable to distinguish between familiar and unfamiliar conspecifics when visual cues are absent (Hauser and Huber-Eicher 2004).

#### 3.4.4 Chicks, Parenting and Odor Learning

Similar to adult Antarctic prions (*Pachyptila desolata*), the chicks of European storm petrels (*Hydrobates pelagicus*) recognize their own body odor from that of a conspecific chick (De León *et al.* 2003). The ability to orient back to the nest is important to survival, as nests provide shelter and are the only location where chicks are fed. Evidence indicates that nest-specific odor cues assist chicks on their return (Mínguez 1997; De León *et al.* 2003). The general capacity of young birds to recognize a familiar body odor, however, does not appear to be restricted to petrels. For example, the behavior of juvenile geese exposed to parental scent versus control odors is indicative of an odor preference (Würdinger 1982). Domestic chicks (*Gallus domesticus*) also



**Fig. 3.3** Antarctic prions (*Pachyptila desolata*) show evidence of personal odor recognition and distinguish between odors of their mate (partner) and another conspecific. The figures above illustrate the results of three experiments. Each histogram indicates the proportion of birds that sought out a particular odor in Y-maze tests (or exhibited no choice). **A.** Birds preferred the scent of their partner over that of another conspecific. **B.** They also preferred their own personal scent over an unscented cloth bag control. **C.** Aversion to personal scent (and attraction to conspecific scent) is consistent with personal odor recognition and analogous to choice patterns of other vertebrates, such as mammals. From Bonadonna, F. and Nevitt, G.A. 2004. *Science* 306: 835-835. Data used in this figure came from Fig.1b-d.

preferentially orient toward the familiar scent of soiled bedding (Jones and Gentle 1985; Burne and Rogers 1995).

Studies of embryonic olfactory development in domestic chickens (e.g. Drapkin and Silverman 1999; Okano 1981), combined with tests involving artificial odor (e.g. Jones *et al.* 2002; Porter *et al.* 1999), are informative with regard to how chemical cues may function during development. For example, measurable differences in heart rate occur in embryos exposed to artificial odors (Tolhurst and Vince 1976). Furthermore, exposure to odors between embryonic day (ED) 15 through 20 (which includes the time period during which an embryo begins to breathe air), can result in post-hatching preferences for familiar scents (Sneddon *et al.* 1998; Porter and Picard 1998). Although it is currently unclear whether odor preferences can develop *in ovo* prior to ED 15, olfactory receptor neurons of chicks are functional at ED 13 (Lalloue *et al.* 2003).

The preference of domestic chicks (*Gallus domesticus*) for artificial odors that they experienced as embryos provides strong experimental support for odor learning. For example, after experiencing a novel scent (strawberry) in one of three ways (in the air, applied to the surface of the egg shell, or injected into the airspace of the egg), *G. domesticus* exhibited a greater affinity for (or weaker aversion to) wood shavings and water scented with strawberry, compared to control treatments (Sneddon *et al.* 1998). Chemosensory learning that occurs post-hatching can also enhance dispersal and readiness to feed, while reducing fear-related responses, indicating a calming or reassuring effect (Jones and Gentle 1985; Jones *et al.* 2002). In contrast, unfamiliar chemical cues can produce neophobic responses (Porter and Picard 1998; Burne and Rogers 1999; Jones *et al.* 2002; reviewed in Roper 1999). Both the embryos and newly-hatched chicks of *G. domesticus* are thus clearly capable of developing an odor familiarity or memory, which affects behavior later in life. Although the mechanistic details are presently unclear for birds, odor learning of embryos occurs in other animals (e.g. Semke *et al.* 1995), including humans (Schaal *et al.* 2000).

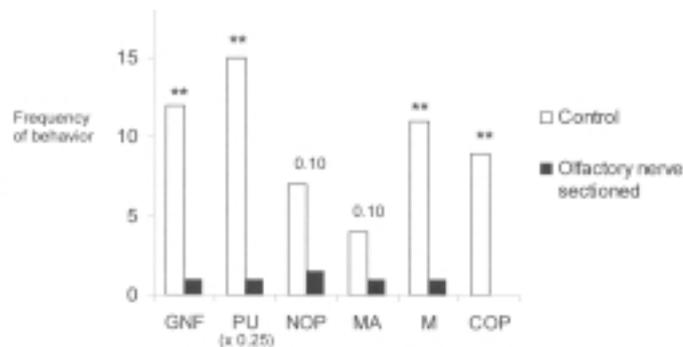
Combined, the data suggest that the ability of chicks to respond to, and possibly distinguish between, familiar nest or plumage odors occurs in at least two avian Orders. A preference for familiar odors may keep domestic chicks (*Gallus domesticus*) in close proximity to nests, or parents (Burne and Rogers 1995); a similar pattern is indicated above for petrel chicks (Minguez 1997). The propensity for odor learning *in ovo* and post-hatching, combined with partner-specific odor recognition in adult prions (*Pachyptila desolata*; see 3.4.3), further suggests that birds may be capable of imprinting to odors associated with their natal site, as in some other vertebrates (e.g. Dittman *et al.* 1996; see also 3.7.3). Likewise, chicks may be capable of learning parental scent, or recognizing other siblings by scent in broods of multiple offspring (see 3.5.2; Zelano and Edwards 2002; Nakagawa and Waas 2004).

Conversely, the odors of chicks could also affect the responses of parents. Artificial odor added to offspring has been implicated in allocation of parental

care in the Rock dove (*Columba livia*; Cohen 1981). Though the role of bird-derived odors in chick rearing and chick development is not clearly understood, there is evidence for interspecific variation in response to food-related odors, which is both consistent with early odor learning in chicks, and the foraging responses of adults (Cunningham *et al.* 2003).

### 3.4.5 Odors Linked with Courtship or Other Displays

Balthazart and Schoffeniels (1979) reported the first evidence for the existence of an avian chemosignal during courtship, based on the differential responses of experimental and sham-operated male Mallards (*Anas platyrhynchos*). Experimental males had their olfactory nerves cut, rendering them unable to smell (anosmic). Anosmic males exhibited significant deficiencies in certain sexual and social behaviors relative to controls (Fig. 3.4). Furthermore, these males did not bathe or stand in water as frequently, which suggests that other, non-breeding behaviors may also be mediated by an intact sense of smell.



**Fig. 3.4** Male mallard ducks (*Anas platyrhynchos*) exhibit responses consistent with olfactory detection of female chemosignals. Sexual displays of experimental males (olfactory nerve sectioned) were significantly inhibited compared to sham operated controls (n=10 of each). Data represent four hours of observation (16 sessions  $\times$  15 min ea.) taken in January. Significance of Mann-Whitney U-tests for each display behavior is indicated (\*\* $P < 0.01$ , and  $P = 0.10$ ). GNF: grasping neck feathers; PU: pumping toward female (difference in scale indicated); NOP: non-oriented pumping; MA: mounting attempt; M: mount; COP: copulation. Data adapted from Balthazart, J. and Schoffeniels, E. 1979. *Naturwissenschaften* 66: 55-56, Fig. 1.

The behavioral differences between anosmic and control males correlated with seasonal changes in the oil-gland chemistry of females, namely, the elevation of diester waxes (Jacob *et al.* 1979, Bohnet *et al.* 1991). The results therefore suggest that male mallards detect important chemosignals in the scent of the opposite sex. Despite intriguing evidence, the process of odor transmission during mallard courtship (or that of other species) is generally unclear, making changes in a male's behavioral repertoire somewhat difficult to interpret.

**Displays of crested auklets.** The Crested auklet (*Aethia cristatella*), a highly social, planktivorous seabird of the western arctic, produces an unusual, tangerine-like or citrusy plumage odor during the breeding season that is associated with a striking, seasonal behavior. Individuals engage in a frequently repeated “ruffsniff” display, in which birds place their bills within the nape feathers of a display partner, a region that appears to be strongly scented (Fig. 3.5; Jones 1993; Jones and Hunter 1993; Hagelin *et al.* 2003). The ruffsniff suggests a behavioral means of acquiring chemosensory information via odor assessment and/or scent marking others (Hagelin *et al.* 2003). During the breeding season *A. cristatella* display on rocks and nest in crevices of talus slopes; adults rear a single, semiprecocial chick that is provisioned by both parents (Jones 1993).

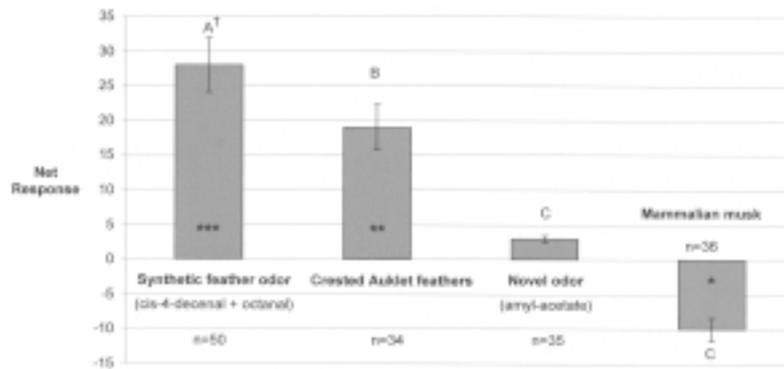
Though no striking chemical differences exist between males and females (Hagelin *et al.* 2003), the odor of *Aethia cristatella* exhibits several features consistent with a social chemosignal. First, scent is produced seasonally by both sexes (Table 3.2). Second, scent is associated with the striking ruffsniff display behavior (described above) that appears to be a self-evident means of odor assessment. Third, experimental manipulation of odors in T-maze experiments and on realistic taxidermy models revealed that individuals distinguish between, and respond preferentially to, the odor of natural plumage, and a synthetic mixture of key, seasonally-elevated odor compounds (Figs. 3.6-3.7; Hagelin *et al.* 2003; Jones *et al.* 2004).

Though Hagelin *et al.* (2003) reported a difference in scent between summer and winter birds (Table 3.2), more recent observations indicate that odor varies within the summer breeding season. Weeks before arriving at a colony, birds are noticeably unscented (Sealy 2006). In both wild and captive populations, concentrations of key odor compounds (octanal, Z-4-decenal) were greatest early in the season (June), but dropped two to six fold by the end of the season (August; unpublished data). Odor loss coincided with the loss of secondary sexual ornaments (crests, orange beak plates; personal observation), suggesting that seasonal variation in odor production is related to hormonal changes. Within-season odor loss, combined with the proclivity for *Aethia cristatella* to engage in mutual sexual selection for other plumage traits (i.e. crests; Jones and Hunter 1993, 1999), indicates that scent may function as an olfactory ornament (Jones 1993; Hagelin *et al.* 2003; Douglas *et al.* 2005a).

**Social function of crested auklet odor.** Field tests of a synthetic odor mixture (cis-4-decenal and octanal) added to the plumage surfaces of realistic taxidermy models revealed insight into the social function of *Aethia cristatella* odor (Jones *et al.* 2004). Scent had the greatest social effect in the context of the male sex. Both male and females approached scented male models more closely than controls; no such pattern was evident for scented female models (Fig. 3.7; Jones *et al.* 2004). Furthermore, synthetic scent applied to male models evoked enhanced interest from approaching males only. Males more frequently stayed



**Fig. 3.5** During the “ruffsniff” display of Crested auklets (*Aethia cristatella*), individuals place their bills within a display partner’s nape feathers, a region of the body that is strongly scented. Displays can be intersexual or intrasexual, involving two birds (**A**), or more (**B**). Photographs: I.L. Jones and J.C. Hagelin. Fig. 3.5A from Hagelin, J. C., Jones, I. L. and Rasmussen, L. E. L. 2003. *Proceedings of the Royal Society Series B* 270: 1323-1329, Fig. 1.

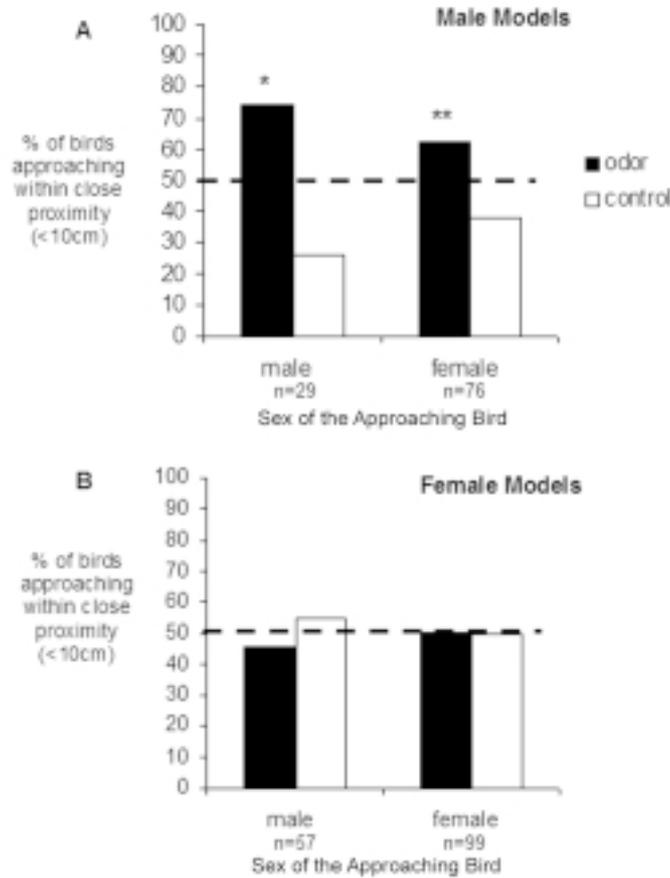


**Fig. 3.6** In T-maze experiments, crested auklets (*Aethia cristatella*) were attracted to synthetic plumage odor and to natural plumage scent, but were repelled by mammalian musk. Net response indicates the percent time a bird spent in the odored arm of the T-maze minus the control arm. Data represent means  $\pm$  standard error. Asterisks within each bar indicate the results of a paired t-test that examined whether the net response (odor minus control) was significantly different from zero. There was no significant response to banana scent (amyl-acetate). \* $P$ (two-tailed) = 0.02, \*\* $P$  = 0.006, \*\*\* $P$  = 0.0004. Different letters above bars indicate significant differences in net response between odor treatments:  $0.006 < P$ (two-tailed) < 0.02. Data adapted from Hagelin, J.C., Jones, I.L. and Rasmussen, L.E.L. 2003. Proceedings of the Royal Society Series B 270: 1323-1329, Fig. 2.

†Net response to synthetic feather odor (a more concentrated scent than plumage odor) was greater than the net response to natural plumage odor  $P$ (one-tailed) = 0.042. A one-tailed test was used, as the authors made the directional prediction that birds would be more attracted to stronger auklet scent.

for durations greater than 10 seconds in front of scented male models than unscented controls, but females did not (Jones *et al.* 2004).

Intrasexual aggression between males is emphasized in *Aethia cristatella*, as males jockey for position at prime display locations (Jones 1993; Gaston and Jones 1998; Jones and Hunter 1998). Though both sexes engage in territorial disputes (Jones *et al.* 2004), males usually retain the nest site from year to year (e.g. Zubakin and Zubakina 1994) and actively defend it during laying (personal observation). In *A. cristatella*'s dark, underground nesting environment, odor could therefore serve as a reliable cue of an approaching aggressor, as males can displace residents from crevices (personal observation). The chemical concentration of at least one odor compound correlated positively with the social status of captive males, further indicating a link between odor and male behavior (unpublished data). At present, the data suggest that odor serves at least a general social function in *Aethia cristatella* (Jones *et al.* 2004). Further tests are required to clarify the role of odor in the context of male-male competition.



**Fig. 3.7** **A.** Male models treated with synthetic citrus odor were approached significantly more often than unscented models by both male and female crested auklets (*Aethia cristatella*). **B.** No differences were detected for birds approaching scented female models. Dashed line indicates the null expectation of equal approach frequency. \*\* $P = 0.02$ , \* $P = 0.04$ . Figure created from data in Jones, I.L., Hagelin, J.C., Major, H.L. and Rasmussen, L.E.L. 2004. Condor 106: 71-78, Table 1.

**Synthetic odor does not elicit ruffsniff displays on approach.** Interestingly, field tests of synthetic scent applied to *Aethia cristatella* models failed to increase the frequency of ruffsniff displays (or any other sexual behavior) of approaching birds (Jones *et al.* 2004). Such results indicate that odor may be employed in a more complex, or multi-modal fashion, in which a combination of olfactory, visual and/or auditory cues evokes a response, or, perhaps, odor is not involved in displays. Unlike synthetic odor, experimental manipulation of crest size on models increased the rates of sexual display behavior of wild birds by two to fourfold (Jones and Hunter 1993; Jones and Hunter 1998).

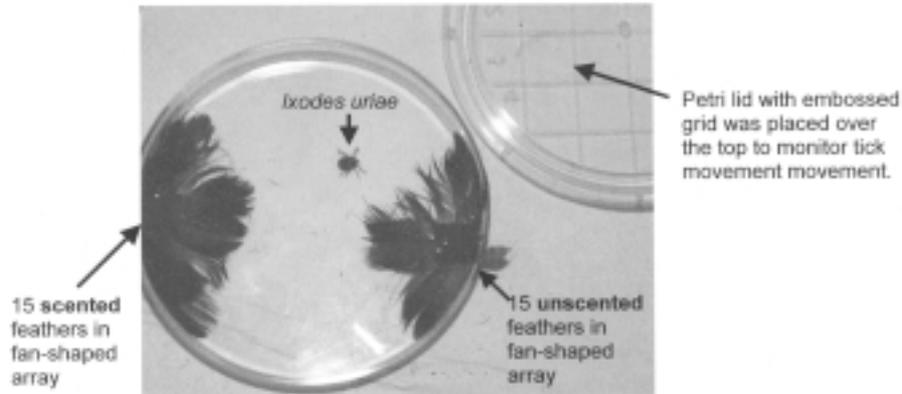
Combined, the data suggest that approaching birds respond more readily to visual than to odor cues (Jones *et al.* 2004).

As one bird approaches another, the crest, rather than odor, would appear to be a more reliable signal, given that both wind speed and direction on top of display rocks are quite variable, and could thereby reduce detection of an olfactory signal. Instead, scent may be assessed at much closer range (i.e. on contact), when birds engage in ruffsniff and neck-twist displays (Jones *et al.* 2004). Future tests of captive birds that use more complex odor mixtures and examine interactions between visual and odor cues (e.g. Osterbauer *et al.* 2005), may prove more successful than inanimate models treated with only two synthetic odor compounds (Jones *et al.* 2004).

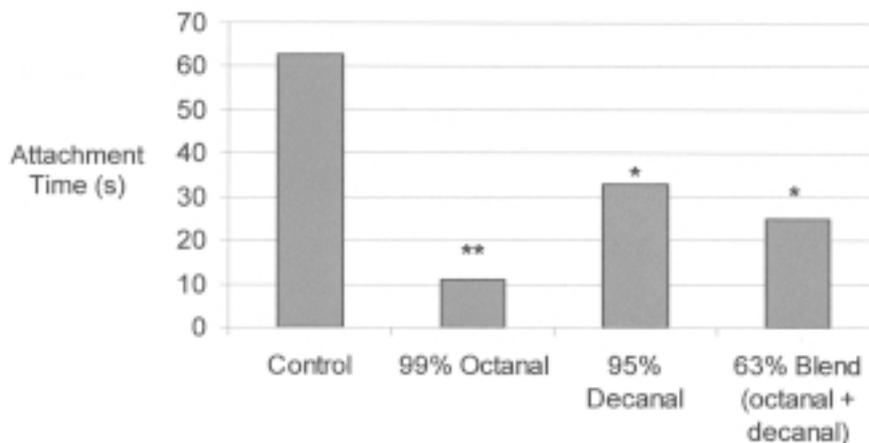
**Repellent properties of crested auklet odor.** Douglas *et al.* (2001) proposed that crested auklet odor may serve as an honest indicator trait during sexual displays (see Chapters 2, 4 and 5), because the odor contains aldehydes that are chemically similar to some invertebrate repellents. Thus, a more strongly scented individual may be advertising its ability to combat parasites or possibly pathogens on itself or perhaps the chicks it broods. This idea is analogous to the hygienic properties of plants or other heterospecific toxins (see 3.2.1 and 3.2.2).

Ectoparasites on feathers and skin do not appear to be problematic to most adult *Aethia cristatella* (Douglas *et al.* 2004). However, young birds, which are noticeably unscented (Sealy 2006), are occasionally infested with lice and ticks (Douglas *et al.* 2005a; personal observation). Experimental tests examining the defensive properties of plumage odor on ectoparasites have produced mixed results. Volatiles from freshly plucked feathers failed to reduce the survivorship of feather lice (Douglas *et al.* 2005a). Ticks, collected at an auklet breeding colony (*Ixodes uriae*) and subjected to 24 hour dyadic choice test in petri dishes, were also just as likely to prefer scented as unscented feathers (Fig. 3.8). Auklet odor is highly volatile (Douglas *et al.* 2004), and fresh plumage can lose its potency in a matter of days (Hagelin *et al.* 2003), which might explain the lack of repellency for tests involving natural feathers. Although the source of odor is unclear, live birds presumably re-apply scent through frequent preening.

Unlike tests of natural feather odor, those involving synthetic odor compounds (e.g. octanal, Z-4-decenal) have repelled two species of ticks (including *Ixodes uriae*; Fig. 3.9; Douglas *et al.* 2004), mosquitoes (Douglas *et al.* 2005b), and greatly increased mortality in two genera of auklet feather lice (Quadriceps, Austromenopon; Douglas *et al.* 2004). Though the results are consistent with scent acting as an honest indicator trait with regard to chemical defense, some chemical treatments exceeded the natural odor concentration of fresh plumage. For example, Douglas *et al.* (2004) placed 1  $\mu$ l of Z-4-decenal on a single auklet feather, which caused feather lice to become moribund within seconds. This amount of odor is over 7,200 times that estimated from natural plumage, as a single nape feather weighs approximately 0.0008 g



**Fig. 3.8** Ticks (*Ixodes uriae*) collected at a crested auklet colony (*Aethia cristatella*) were placed in the center of a petri dish and given a 24 hour “choice” to climb into fresh, scented feathers of (*A. cristatella*) or unscented feathers (of parakeet auklets [*A. psittacula*; n = 45 trials] or least auklets [*A. pusilla*; n = 45 trials]). Plumage odor did not appear to act as a repellent, as 49 ticks chose scented feathers, and 41 chose unscented feathers ( $\chi^2 = 0.71$ ,  $df = 1$ ,  $P = 0.40$ ). Plumage from each unscented species lacked chemical compounds found in *A. cristatella* odor (*A. psittacula*, Hagelin *et al.* 2003; *A. pusilla*, unpublished data).



**Fig. 3.9** Ticks (*Ixodes uriae*) that parasitize crested auklets (*Aethia cristatella*) were repelled more readily from a paper substrate treated with synthetic odor than an ethanol control. Mean attachment time is given for four treatments, each of which tested 30 ticks in a moving object bioassay (Dautel *et al.* 1999). Significant differences between each treatment and the control are indicated. Odor treatments consisted of synthetic compounds dissolved in ethanol. Adapted from Douglas III, H.D. Co, J.E., Jones, T.H. and Conner, W.E. 2004. *Journal of Chemical Ecology* 30 (10): 1921-1935. Fig. 5. \* $P < 0.05$  \*\* $P < 0.01$ .

(n=10) and the concentration of volatiles in the nape region is approximately 1.1  $\mu\text{l}$  per gram of feather weight (Table 3.2; Hagelin *et al.* 2003).

A similar argument can be made for the repellent effect of synthetic odor on ticks. Douglas *et al.* (2004) used a moving object bioassay (Dautel *et al.* 1999) to assess the attachment time of ticks to a filter paper treated with synthetic compounds and odor blends. The authors reported a pattern consistent with dose-dependent repellency, namely, reduced attachment times with increasing odor concentration. However, I estimate that concentrated odor treatments (e.g. 99% octanal; Fig. 3.9), applied to a relatively small surface area of paper (7.6 cm  $\times$  3.2 cm), in some cases hourly, were equivalent to the scent of the entire plumage of 5 to 14 adults. My calculations are based on: (1) the concentration of natural plumage odor (2.98  $\mu\text{g}$  octanal/g of feathers; Table 3.2; Hagelin *et al.* 2003), (2) the density of octanal (0.843 g/ml), (3) the volume of the solution tested (0.008-0.025 ml/cm<sup>2</sup> of filter paper; Douglas *et al.* 2004), and (4) the average dry weight of adult plumage (11.93 g; n=5 adult *Aethia cristatella*, unpublished data).

However, it is equally important to note that less-concentrated solutions, such as a 63% synthetic blend (Fig. 3.9) and a 1% dilution (see Douglas *et al.* 2004) also repelled ticks. These tests simulated more reasonable odor concentrations, equivalent to the plumage odor of 0.1 to five adults. Thus, there is some support for dilute, synthetic odor compounds, acting as a chemical defense.

If *Aethia cristatella* odor acts as a chemical defense, either as an honest indicator trait in adults and/or a means of protecting unscented chicks, it does not have an immediate, lethal impact like toxic *Pitohou* feathers (Dumbacher 1999). Natural concentrations could have repellent or sublethal effects, but it is unknown how odor may interfere with or impair the physiology of parasites (Douglas *et al.* 2005a). Preliminary tests indicate that some synthetic compounds of *A. cristatella* odor inhibit the growth of bacteria (such as *Salmonella*; unpublished data), consistent with other avian secretions (Shawkey *et al.* 2003).

**Other species and observations.** The role of scent during courtship or territorial displays had been suggested, but untested, in other birds, such as the Musk duck (*Biziura lobata*) of Australia, in which adult males produce a musky scent during the breeding season only (Gamble 1966). Likewise, Bulwer's petrel (*Bulweria bulwerii*) emits an unusual odor during pre-laying that could act as a mating signal (Thibault and Holyoak 1978). Snow petrels (*Pagodroma nivea*) also regurgitate odiferous stomach oils at nest entrances during territorial disputes (Jouventin 1977). Many birds regularly engage in social behaviors, such as mutual preening, which potentially exposes them to odors of mates or other conspecifics (Roper 1999). Greater shearwaters (*Puffinus gravis*), in particular, nibble at the uropygial gland during allopreening (Hagen 1952 as cited in Roper 1999).

Careful observations of the olfactory system of European starlings (*Sturnus vulgaris*) indicated an elevated sensitivity to odors during the breeding season

(Clark and Smeranski 1990), which also correlated with changes in beak color (Clark and Mason 1987b). Thus, chemical cues may be especially important during breeding months and appear to reflect changes in sex hormones. Such a pattern is consistent with the seasonality of scent and display behaviors in crested auklets (*Aethia cristatella*; see **Displays of Crested Auklets**), Mallards (*Anas platyrhynchos*; Balthazart and Schoffeniels 1979; Jacob *et al.* 1979, Bohnet *et al.* 1991), and the chemical changes in odor and glandular secretions of other species (see 3.3.2).

### 3.5 IMPLICATIONS OF AVIAN ODOR AS A SIGNAL

The links between genes, odor, and complex social behavior are well-documented in animals, especially in rodents (reviewed in Penn and Potts 1998; Beauchamp and Yamazaki 2003; Hurst and Benyon 2004; Kavaliers *et al.* 2005; Ziegler *et al.* 2005). For example, volatile chemosignals mediated by alleles of the major histocompatibility complex (*Mhc*) play a key role in sexual and social behaviors of mammals and fish (Reuch *et al.* 2001; Penn 2002; Aeschlimann *et al.* 2003; Beauchamp and Yamazaki 2003; Kavaliers *et al.* 2005), but have been largely overlooked in birds (Zelano and Edwards 2002). Odors mediated by *Mhc* can be pathogen-driven, and thus indicative of infection, or they may relate to non-pathogenic mechanisms, such as selection for inbreeding avoidance (reviewed in Zelano and Edwards 2002). Such signals are applicable to both “good genes” models of sexual selection (see Chapter 6) and those that emphasize genetic compatibility (Mays and Hill 2004; Neff and Pitcher 2005). However, any odor cues that may drive such behaviors in birds are unknown.

#### 3.5.1 A General Role for Honest Odor Signals in Birds?

Just as rodents use odor to detect parasitized or infected conspecifics, assess age, sex, social status or kinship, avian scent (or other chemical secretions) may also act as an “honest indicator” trait (reviewed in Andersson 1994; Penn and Potts 1998, 1999; Penn 2002; Beauchamp and Yamazaki 2003; Zala *et al.* 2004; Kavaliers 2005). Consequently, bird-derived odor could form the basis of secondary sexual traits (Hagelin *et al.* 2003), similar to the way in which bright plumage, complex song, or ornamental green nesting material correlates with reduced pathogens, parasites, or enhanced offspring survival (e.g. Zuk 1993; Gwinner and Berger 2005; Spencer *et al.* 2005; see 3.2.1, 3.2.3 and Chapters 5 and 6 for additional discussion). Furthermore, links between visual stimuli (colors) and scent perception (e.g. Cooper *et al.* 1994; Osterbauer *et al.* 2005) have interesting implications for complex or multimodal signals involving avian odor, as birds show a heavy reliance on visual cues. With regard to patterns of odor and choice, one might expect positive or negative responses, depending on circumstance.

**Positive relationships between odor and choice.** Compounds used as chemical defenses in some birds appear to be derived from the diet

(Dumbacher *et al.* 2004; see also 3.2.2), similar to visually-mediated plumage ornaments like carotenoid pigments (Hill 2002; and Chapter 2). The magnitude of direct or indirect benefits associated with such compounds may therefore correlate positively with odor concentration. This would be especially true if odiferous compounds have antiseptic or anti-parasitic properties, as suggested for some toxic species in the genus *Pitohou* (Dumbacher 1999) as well as the citrusy scent of crested auklets (*Aethia cristatella*; Douglas *et al.* 2001, 2005a,b; Hagelin *et al.* 2003). Feather lipid concentration may act as an honest signal, as it is related to age in domestic chickens (*Gallus domesticus*); age and bird growth are also related to the development of the uropygial gland, which provides secretions that birds spread over feather surfaces (see 3.3.2; Sandilands *et al.* 2004a,b).

**Negative relationships between odor and choice.** Aversive odors in birds have been linked to the scent of blood and feces (Jones and Gentle 1985; Jones and Roper 1997; Jones *et al.* 2005). In rodents, however, chemical aversion can be pathogen driven, as odors correlate with parasitized individuals, or they can be indicative of genetic incompatibility (reviewed in Penn and Potts 1998, 1999; Penn 2002; Beauchamp and Yamazaki 2003; Kavaliers *et al.* 2005).

One of several general functions attributed to non-volatile secretions of the avian uropygial or preen gland is an ability to combat bacteria (or other ectoparasites, such as lice) and to keep feathers clean (Jacob and Zisweiler 1982; Shawkey *et al.* 2003; Haribal *et al.* 2005). Clean and well-preened feathers clearly look different than dirty feathers. However, evidence from domestic chickens (*Gallus domesticus*) also suggests that odor cues may be involved. For example, birds responded differentially to feathers that contain oils from the uropygial gland (McKeegan and Savory 2001). Furthermore, feather lipid concentrations were greatly affected by the presence or absence of a dustbathing substrate (Sandilands *et al.* 2004b), suggesting that compounds spread onto feathers may also correlate reliably with hygiene.

The production of avian odor has been hypothesized to result from the breakdown of non-volatile preening compounds (Jacob and Zisweiler 1982), either via natural degradation or in combination with ectosymbionts, such as bacteria or feather lice (Haribal *et al.* 2005). Hence, low-levels of plumage scent (or the lack of a particular compound that is associated with pathogenic infection), may reflect the ability of a bird to successfully clean its feathers via frequently re-application of non-volatile secretions. Reduced feather scent could be particularly adaptive for a breeder that must remain chemically “inconspicuous” in the face of mammalian predation (Reneerkens *et al.* 2002). An aversion to certain odors, such as the scent of self in Antarctic prions (*Pachyptila desolata*), also has implications for studies of genetic compatibility (see 3.4.3, 3.5.2; Bonadonna and Nevitt 2004).

The potential for hypothesis testing of avian odors, as they relate to honest signaling, pathogens, sex, status, age and/or genetic compatibility is rather extraordinary. Future studies will require an understanding of: (1) odor-mediated choice as it relates to parasites, infection and genetic compatibility,

(2) conspecific variation in odor signatures relative to sex, age and social status, (3) the ecology of plumage ectosymbionts and their role, if any, in odor production, and (4) a detailed chemical understanding of volatile and non-volatile compounds in avian odor that may result from the diet, natural chemical degradation and/or the glandular secretions themselves.

### 3.5.2 Prospects for Odors Related to Kin Selection and Mating System

**Kin selection.** Aside from pathogen-mediated scent, the odor of rodents has profound ties to kin recognition. For example, *Mhc*-mediated odor profiles of mice can influence mate choice (via disassortative mating and inbreeding avoidance), individual recognition, nesting patterns, and selective block of pregnancy (reviewed in Penn 2002; Beauchamp and Yamazaki 2003; Ziegler *et al.* 2005). The interesting discovery that adults and chicks of some petrels species distinguish between odors of self and other conspecifics (see 3.4.3, 3.4.4), paves the way for more in-depth studies (Bonadonna and Nevitt 2004; Nevitt and Bonadonna 2005a). Given the marked odor of some species that are well-known for cooperative breeding, such as the green woodhoopoe (*Phoeniculus purpureus*; du Plessis 1992; Ligon and Ligon 1978; Burger *et al.* 2004), the prospects of odor affecting the social interactions between kin would also appear fruitful.

**Mating system.** Zelano and Edwards (2002) suggested a number of mating situations in which *Mhc*-mediated responses of birds are likely to occur. Such environments appear to be generally good places to search for avian-derived odor signals, given the links between odor and mate choice in other vertebrate groups (see 3.5). The authors highlighted long-lived species, such as seabirds and raptors, which may be subject to inbreeding or exhibit lifetime monogamy. Both characteristics have enhanced consequences for mate choice based on good genes and/or genetic compatibility. Evidence for discrimination between the plumage odor of self, mate and other conspecifics has already been discovered in one avian species (see 3.4.3; Bonadonna and Nevitt 2004).

Likewise, lek mating is expected to be linked to females that focus on the indirect (genetic) benefits of males that typically provide no parental care. One notable lek breeder with seasonally elevated scent in males only is the musk duck (*Biziura lobata*; Gamble 1966; McCracken *et al.* 2000; Guay and Mulder 2005). Another species, the critically endangered kakapo of New Zealand (*Strigops habroptilus*) might also employ odors in its unusual lekking system (see 3.5.3; Eason *et al.* 2006). Odor function in any lek breeding system, however, is unstudied.

Finally, Zelano and Edwards (2002) suggested that *Mhc*-mediated responses are applicable to situations in which birds may choose from many prospective mates or engage in extra-pair fertilizations. Genetic patterns attributable to *Mhc* have been implicated in avian sexual selection and reproductive behavior (e.g. von Schantz *et al.* 1996; Freeman-Gallant *et al.*

2003). Though the role, if any, of odor is unknown, some data suggest that females may select extra pair mates in a manner consistent with inbreeding avoidance and selection for genetically dissimilar mates (e.g. Richardson *et al.* 2005; Tarvin *et al.* 2005, but see Smith *et al.* 2005). More studies are necessary to examine whether avian scent correlates with extra pair mate choice and exhibits odor-mechanisms similar to those of mammals.

### 3.5.3 Applied Problems and Species Recovery

Bird responses to odors have already provided useful information applicable to situations involving animal welfare and captive breeding, such as the poultry industry (reviewed in Jones and Roper 1997, Jones T. A. *et al.* 2005). For example, exposure to concentrated ammonia from feces, can reduce egg laying capacity and growth rates of domestic chickens (*Gallus domesticus*; Reese *et al.* 1980; Hester 2005; Jones E. K. M. *et al.* 2005). Familiar odorants, however, can reassure or attract birds (see 3.4.4; Burne and Rogers 1995; Jones *et al.* 2002). One extreme example involving an aberrant attraction to plumage, chronic feather pecking, has been linked to uropygial secretions on feather surfaces (McKeegan and Savory 2001). Avian scent is also related to reproductive contexts, such as courtship and nesting (see 3.4, 3.5.2; Hagelin *et al.* 2003; Bonadonna and Nevitt; 2004). Consequently, it may be feasible to apply our knowledge to species recovery, particularly in management situations that aim to increase the breeding success of captive or endangered populations.

Avian-derived odors or unusual chemical substances have been implicated in at least two critically endangered species: (1) the Kakapo, a parrot endemic to New Zealand (*Strigops habroptilus*; Hagelin 2004) and (2) the Toki, or Japanese crested ibis (*Nipponia nippon*; Wingfield *et al.* 2000). *S. habroptilus* is nocturnal, solitary and unusually scented; plumage odor is detectable (to humans) from a distance of 6 m (Hagelin 2004). Birds also have a large olfactory anatomy, respond to olfactory cues while foraging (Hagelin 2004). Furthermore, *S. habroptilus* exhibits an unusual lek breeding system (Merton *et al.* 1984), in which odor could provide a means for *Mhc*-mediated mate choice (see 3.5.2; Zelano and Edwards 2002; Eason *et al.* 2006). If birds detect feather scent, the data suggest they may be capable of employing it to sense and/or assess conspecifics in their vicinity. Scent would appear to be particularly applicable to facilitating the successful management of infrequent breeding events, which occur every two to seven years (Hagelin 2004; Eason *et al.* 2006).

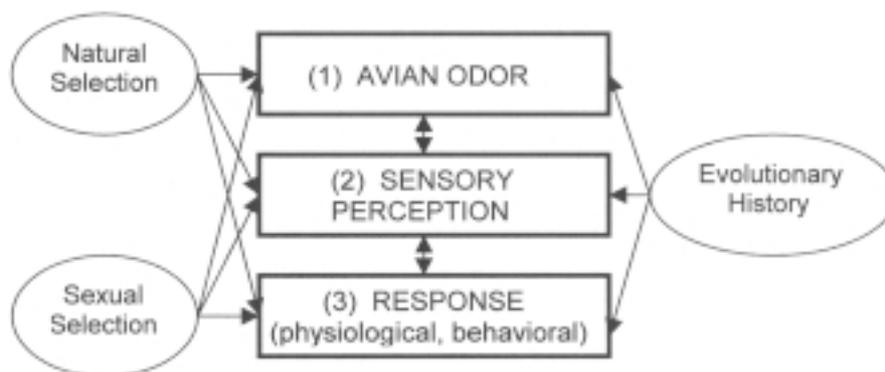
The Toki (*Nipponia nippon*) secretes a tar-like substance from a discrete patch of skin in the neck and throat region. The substance is actively spread on the head, neck and torso, resulting in specialized nuptial plumage (Wingfield *et al.* 2000). Such ornamentation probably provides visual as well as chemical information to prospective mates or competitors (J. Wingfield, personal communication). The tar-like secretion is only found in adults, and successful breeding is related to hormone levels (Wingfield *et al.* 2000). Hormone therapy applied to failed breeders, which could facilitate gonadal

development, egg-laying, and presumably the acquisition of nuptial plumage, has been suggested as a means of promoting reproduction in this species (Wingfield *et al.* 2000).

### 3.6 CALL FOR A MULTIDISCIPLINARY APPROACH

Despite a number of interesting studies and intriguing prospects, biologists currently lack a basic framework for studies of avian chemosignals. The problem exists, because we know relatively little about the context(s) in which odors are actually used in birds, the structures and mechanisms of the anatomy that perceives odors, and the details of odor chemistry. Studies that integrate multiple disciplines have proven extremely useful in other vertebrate groups (e.g. Sorenson 1996), because the chemosensory signaling process involves an interrelated series of three components: (1) the chemical signal itself, (2) the anatomy involved in perception, and (3) any behavioral or physiological response (Fig. 3.10). Each component can impact the next or previous step, and each is subject to evolutionary history as well as natural and/or sexual selection.

The conceptual model in Fig. 3.10 provides a general framework that is applicable to most any signaling system and has helped guide my own research on the Crested auklet (*Aethia cristatella*). Earlier in this chapter I discussed information related to the production and chemistry of odor signals (see 3.3) as well as behavioral responses to odor signals (see 3.4). I will now examine the remaining component of the model, avian olfactory anatomy, because an understanding of chemoreception is central to studies of odor signals in birds.

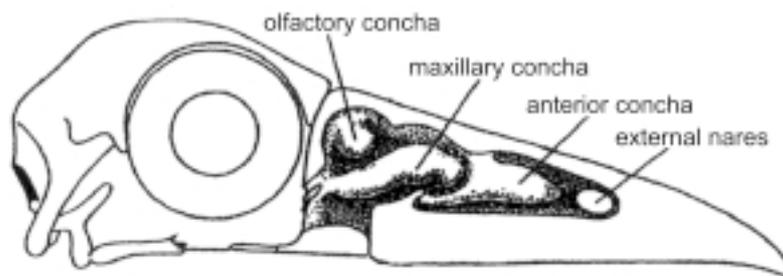


**Fig. 3.10** A conceptual model for the study of avian odors. Chemical communication, like any signaling system, is divided into three basic components: (1) odor chemistry of the signal itself, (2) anatomy involved in perceiving the signal, and (3) the resulting behavioral or physiological response. Each component is subject to natural and sexual selection as well as evolutionary history. Original.

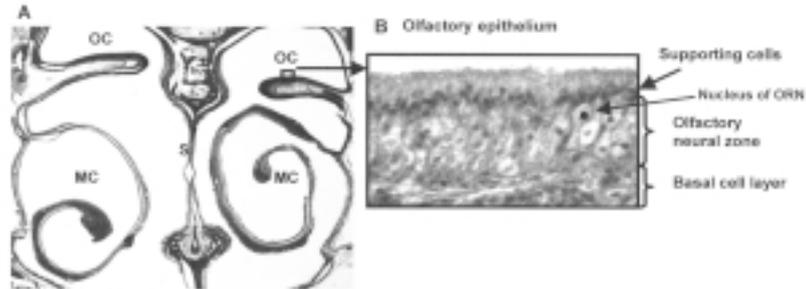
### 3.7 AVIAN OLFACTION: STRUCTURE AND FUNCTION

Though I provide a brief overview of anatomy, readers are encouraged to refer to more detailed material (Bang 1971; Bang and Wenzel 1985; Roper 1999). Chemical perception of vertebrates is divided into three senses: (1) the olfactory system, in which volatile chemical information is detected by olfactory receptors, (2) taste or gustation, in which compounds are detected by receptors in the buccal cavity, and (3) the trigeminal system, which perceives nociceptive stimuli, such as the burning sensation of a chemical irritant (Roper 1999). Most studies of birds do not distinguish between the three systems, although birds exhibit tastebuds and a sense of taste (e.g. Wenzel 1973, Ganchrow and Ganchrow 1985) as well as trigeminal responses (e.g. Mora *et al.* 2004; McKeegan *et al.* 2005; reviewed in Roper 1999). However, birds appear to lack a vomeronasal organ and an accessory olfactory bulb, features associated with the detection and processing of some types of chemical signals in other organisms (Riecke and Wenzel 1975, 1978). For simplicity, like Roper (1999), I consider “olfaction” to include any means by which volatile chemosensory information is obtained by a bird. It may involve one or more of the systems mentioned above.

Once air enters a bird’s nares, it passes through a series of three chambers, arranged in sequence, which contain mucous-covered invaginations of cartilage and/or thin bone called conchae (Fig. 3.11). As air flows caudally through each chamber, it is probably cleaned, warmed and moistened by the anterior and maxillary conchae. Odors are detected upon reaching the olfactory concha in the third chamber. Olfactory conchae are covered in a layer of sensory cells called the olfactory epithelium (Fig. 3.12). The epithelium is similar to that of other vertebrates, as it is densely packed with olfactory

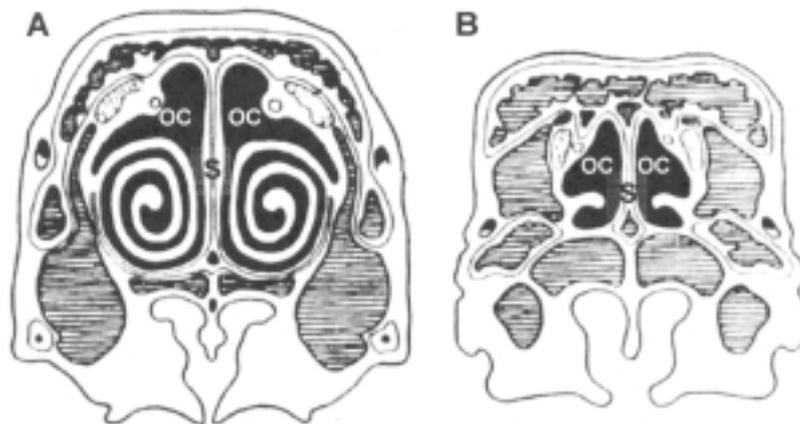


**Fig. 3.11** A longitudinal section through a generalized bird beak illustrating the conchae (invaginated or convoluted structures) found in the three chambers of the nasal cavity. Air enters through the external naris, then passes over the anterior concha in the first chamber, and the maxillary concha in the second chamber. Odors are detected in the olfactory concha (OC) in the third chamber. Generalized drawing adapted from Roper, T. J. 1999. Pp. 247–332. In P. J. B. Slater, J. S. Rosenblat, C. T. Snowden and T. J. Roper (eds), *Advances in the Study of Behavior*, Vol. 28. Academic Press, Boston, Fig. 1.



**Fig. 3.12** **A.** Transverse section through the nasal cavity of an adult crested auklet (*Aethia cristatella*). The olfactory conchae (OC) of this species are fairly small, finger-like structures. This photo was taken in an anterior region of the third nasal chamber where the OC project dorsally to maxillary conchae (MC). The septum (S) is also shown. **B.** Close-up (40 × objective) of cell layers in the olfactory epithelium. Nucleii of olfactory receptor neurons (ORN) are visible within the olfactory neural zone. Other cell layers of the epithelium are also indicated. Original.

receptor neurons (that contain chemoreceptors) and other specialized cells (Fig. 3.12; Wenzel 1973, 1987). Olfactory receptor neurons transmit information via the olfactory nerve to the olfactory bulb, a discrete structure in the anterior region of the brain, for further processing (Pearson 1972; Wenzel 1987).



**Fig. 3.13** Transverse section of the olfactory conchae of **(A)** the turkey vulture (*Cathartes aura*), a species well-known for its olfactory abilities, and **(B)** the black vulture (*Coragyps atratus*), a species that emphasizes visual cues, rather than olfaction. Drawing shows striking differences in surface area (scrolling) of the olfactory conchae (OC), which are covered in olfactory receptor epithelium. S=septum. (Unlike Fig. 3.13, this drawing was made in the caudal end of the third nasal chamber where maxillary conchae are not visible). Adapted from Bang, B. G. 1971. *Acta Anatomica Supplementum* 58 (79): 1-71, Fig. 16.

### 3.7.1 Form and Function of Olfactory Anatomy

The gross olfactory anatomy of birds is quite variable and has been described for close to 200 species from 23 Orders (Bang and Cobb 1968; Bang 1971). Form can be predictive of function in several ways. First, extensive surface area (scrolling) of olfactory conchae occurs in birds that are known to rely on smell during foraging (Fig. 3.13), such as the Turkey vulture (*Cathartes aura*; Stager 1964; Bang 1971), the Brown kiwi (*Apteryx australis*; Wenzel 1968), and the Northern fulmar (*Fulmaris glacialis*; Wenzel and Meisami 1990). Second, across avian orders, increased size of the olfactory bulb relative to brain size, a measure known as the “olfactory bulb ratio,” correlates with greater olfactory acuity (Table 3.3; Clark *et al.* 1993). Third, within families, larger bulbs correlate with nocturnal behavior, a habit that likely emphasizes olfactory adaptation (Healy and Guilford 1990). Larger olfactory bulb size may indicate greater functional capacity, because it probably reflects an increase in the number of cells and neural circuits contained within (Table 3.3; Meisami 1991).

**Table 3.3** Olfactory bulb, brain hemisphere size and olfactory bulb ratio (OBR) for four birds with large olfactory anatomy (highlighted in bold), a diving petrel, non-passerines and passerines (mean  $\pm$  sd), and the European starling

Common name	Species	Bulb diameter (mm)	Hemisphere diameter (mm)	Olfactory bulb ratio (%)
Snow Petrel <sup>a,b</sup>	<i>Pagodroma nivea</i>	6.7	18.0	37.0
Brown Kiwi <sup>a,c</sup>	<i>Apteryx australis</i>	12.0	35.0	34.0
Kakapo <sup>d</sup>	<i>Strigops habroptilus</i>	10.2	33.8	30.2
Turkey Vulture <sup>a,e</sup>	<i>Cathartes aura</i>	6.0	24.0	28.7
Diving Petrel <sup>f</sup>	<i>Pelecanoides georgicus</i>	2.0	11.3	18.0
Non-passerines <sup>f</sup>	<i>n</i> = 81 species	3.4 $\pm$ 1.9	17.1 $\pm$ 5.9	19.6 $\pm$ 6.5
Passerines <sup>a</sup>	<i>n</i> = 25 species	1.5 $\pm$ 0.5	13.6 $\pm$ 0.2	9.7 $\pm$ 4.9
European Starling <sup>a</sup>	<i>Sturnus vulgaris</i>	1.4	14.5	9.7

<sup>a</sup> From Bang and Cobb (1968)

<sup>b</sup> Largest olfactory bulb ratio reported for any bird (Bang and Wenzel 1985)

<sup>c</sup> For olfactory behavior, see Wenzel (1968)

<sup>d</sup> From Hagelin (2004)

<sup>e</sup> For olfactory behavior, see Stager (1964)

<sup>f</sup> For olfactory behavior, see Bonadonna *et al.* (2003a)

<sup>g</sup> Values calculated 80 non-passerines from Bang and Cobb (1968), plus the Kakapo (Hagelin 2004)

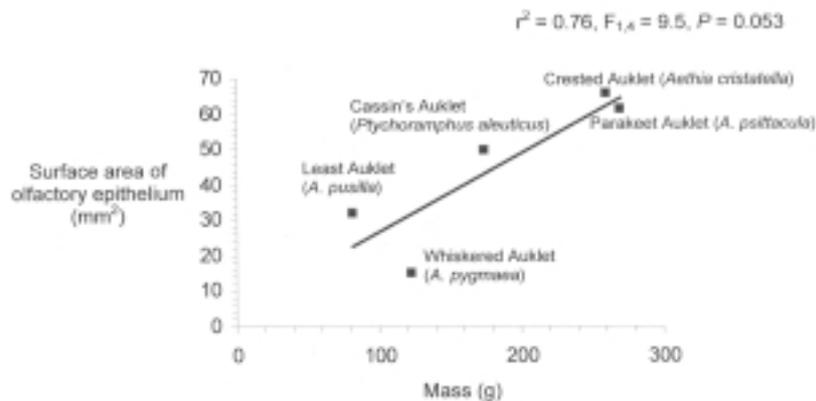
While larger olfactory anatomy in birds appears to correlate positively with function in some species, the reverse is not necessarily true. For example, European starlings (*Sturnus vulgaris*), Crested auklets (*Aethia cristatella*) and Diving petrels (*Pelecanoides* spp.) are all capable of employing odors during the breeding season (Clark and Mason 1985; Bonadonna *et al.* 2003a; Hagelin

*et al.* 2003). Yet, each has fairly small olfactory anatomy (Table 3.3 for *S. vulgaris* and *Pelecanoides*; Fig. 3.12 for olfactory conchae of *A. cristatella*). Consequently, even small anatomical structures are quite capable of detecting certain odors. The larger olfactory anatomy of some birds (Table 3.3) may reflect an ability to detect a greater variety of odors (Adrian 1951 as cited in Bang and Wenzel 1985), but this idea remains untested.

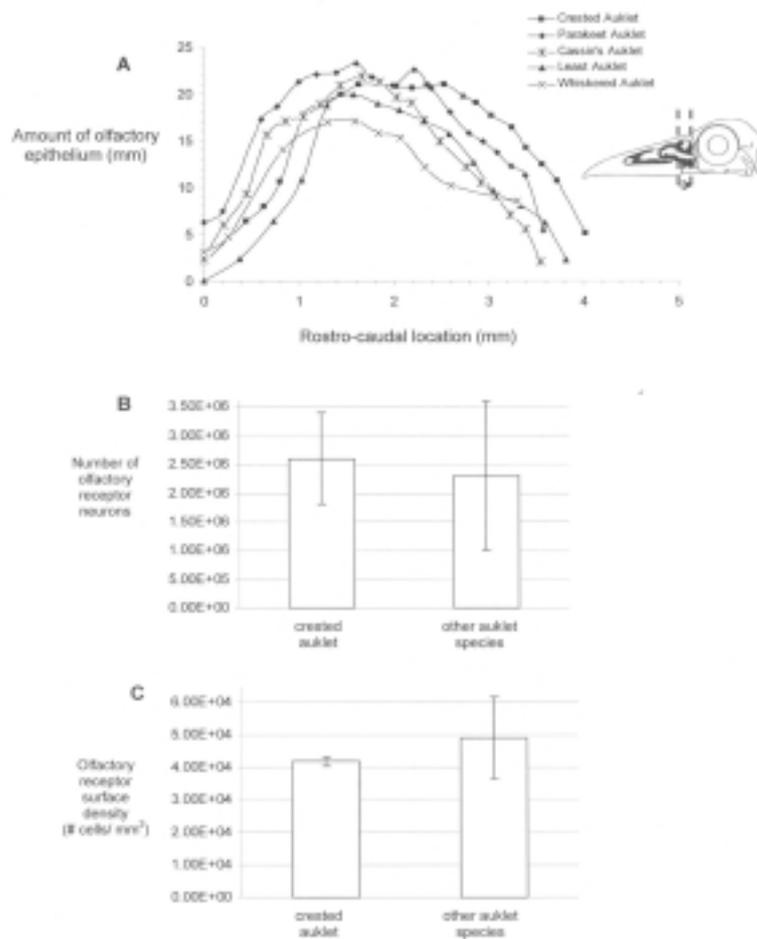
### 3.7.2 Olfactory Microstructure

Data on the microstructure of the avian olfactory system are scarce. Our laboratory examined how the microstructure of the tangerine-scented Crested auklet (*Aethia cristatella*) compared to four other auklet species (all but one of which lacked plumage odor and the unique nape-sniffing display behavior; see 3.4.5, Displays of crested auklets). Contrary to expectation, *A. cristatella* did not exhibit more olfactory epithelium than expected for its body size (Fig. 3.14). In fact, *A. cristatella* did not differ dramatically from any auklet species with regard to any aspect of olfactory anatomy that we measured (Fig. 3.15). We obtained a similar pattern for the whiskered auklet (*Aethia pygmaea*; Figs. 3.14, 3.15A), the only other species that produces both an unusual plumage odor (Douglas *et al.* 2005a) and exhibits a nape-sniffing display identical to *A. cristatella* (I. L. Jones, personal communication). If *A. cristatella* (and possibly *A. pygmaea*) employ social chemosignals with relatively *unremarkable* olfactory microstructure, the pattern may apply more broadly to other birds.

**Olfactory bulb.** Descriptive accounts of the laminar layers of cells within the olfactory bulb of the brain suggest that birds are similar to reptiles, in that they lack some of the distinctive layering patterns found in mammals (Allison



**Fig. 3.14** The amount of olfactory epithelium scales positively with body size across five auklet species. Interestingly, the Crested auklet (*Aethia cristatella*) does not appear to exhibit more olfactory epithelium than expected for its body size. Data represent mean values ( $n=3$  [*A. cristatella*] and 2 of each other species). Serial sections of olfactory tissue were measured according to methods in Meisami (1989).



**Fig. 3.15** The distribution of olfactory receptor tissue along a longitudinal transect of the olfactory conchae was quite similar between auklet species (**A**)<sup>†,‡</sup>. Likewise, the total number of olfactory receptor neurons (**B**)<sup>†</sup> and the density of receptor neurons per mm<sup>2</sup> of olfactory epithelium (**C**)<sup>†</sup> did not differ between the Crested auklet (*Aethia cristatella*) and four other auklet species. Methods followed Meisami (1989) and Paternostro and Meisami (1993).

<sup>†</sup>Data represent means and standard deviations of the specimens presented in Fig. 3.14.

<sup>†</sup>Drawing in **A**. indicates the region of the transect. Data were collected from transverse serial sections (10 μm) that began at the first dashed line and proceeded caudally, through the olfactory conchae, to the second dashed line.

<sup>‡</sup>The longitudinal transects provide a relative comparison of different auklet species. The first data point of each line represents the point at which olfactory receptor tissue was first noted in a 10 μm section. Serial sections were quantified approximately every 0.4 mm thereafter.

1953; Andres 1970). In particular, the glomerular layer, the region where the axons of olfactory receptor neurons converge into the brain, appears to be relatively undifferentiated in birds (Wenzel and Meisami 1990). Yet, we know very little else. The cells of the olfactory bulb have been quantified in two Rock doves (*Columba livia*) and one Northern fulmar (*Fulmar glacialis*; Wenzel and Meisami 1987, 1990). In both species, mitral cells, structures that process olfactory signals, were counted. In *F. glacialis* only, two other cell types were also measured; glomeruli, sites where the axons of chemoreceptors converge, and granular cells, the innermost relay cells to the brain. While the number of cells in both species compared favorably to mammals, interspecific comparison indicated the relationship between bulb size and mitral cell number was more complex than expected (Wenzel and Meisami 1987), possibly because the specimens belonged to very different avian orders. Electrophysiological recordings have been made in numerous avian species from multiple structures in the olfactory system (reviewed in Roper 1999). Those from single olfactory bulb neurons in the Domestic chicken (*Gallus domesticus*) verify that cells exhibit adaptation in response to prolonged odor exposure (McKeegan and Lippens 2003).

### 3.7.3 Gaps in Anatomical Studies

Studies that quantify the microstructure of the avian olfactory system are few. Such data are key to understanding how chemosensory adaptations evolve in birds, their relevant ecological contexts, and any structural or seasonal changes associated with taxa that employ odor cues. Investigations that consider phylogeny are also rare, with the exception of Healy and Guilford (1990). Most studies examine only 1-3 individuals per species, making it difficult to interpret among-taxa comparisons with confidence.

Studies that focus on seasonal change could yield predictive tools for identifying promising species for future behavioral studies of odor use. For example, seasonal shifts in olfactory acuity occur in European starlings (*Sturnus vulgaris*; Clark and Smeranski 1990) and have been implicated in the selection of nest materials (see 3.2.1). However, any underlying structural changes that may occur, like those of other vertebrates (e.g. Dawley *et al.* 2000), are not well understood.

**Development.** Studies of the domestic chicken (*Gallus domesticus*) have provided interesting insight into the development of the avian olfactory system (e.g. Drapkin and Silverman 1999; reviewed in Ayer-LeLievre *et al.* 1995; Roper 1999). Details of developmental and functional properties of the olfactory receptor epithelium have also been examined (Fornaro *et al.* 2001; Lalloue *et al.* 2003; Comte *et al.* 2004; Jung *et al.* 2005). However, to the best of my knowledge, studies quantifying the macro- and microstructure of the nasal cavity and olfactory bulb of a developing chick are needed. Wenzel and Meisami (1990), for example, reported that the surface area of olfactory epithelium from one fulmar chick (*Fulmar glacialis*) was considerably less than

that of an adult. The olfactory bulb ratio (see 3.7.1) of Blue petrel chicks (*Halobaena caerulea*) is also smaller than that of an adult, but by the time a chick fledges, it is similar to adult-sized (G. Cunningham, pers. comm.). Yet, we know little else about developmental changes in the extent of olfactory epithelium, receptor cell density, or odor processing capacity of the brain, like we do in mammals (e.g. Meisami 1989; Rosselli-Austin and Williams 1990; Apfelbach *et al.* 1991). Changes in the olfactory structure of vertebrates usually coincide with changes in function, such as modifications that occur during odor “imprinting” (e.g. Rehn *et al.* 1986; Jarrard, 1997). Consequently, our understanding of birds would greatly benefit from a detailed study of olfactory structure in a developmental series of an avian model species, such as *G. domesticus*. Such data would serve as a useful comparison for other avian groups, such as seabirds, in which adaptive responses to body or environmental odors are emphasized (see 3.4).

### 3.8 CONCLUSIONS

Odors and chemical perception provide a unique and largely overlooked modality, which, in addition to sight and sound, apply to studies of avian reproductive behavior. Combined, the evidence indicates: (1) Both the production of scent and the response to environmental odors is widespread in birds. (2) Odors are linked to a variety of social situations during reproduction, all of which involve adaptive behavioral responses, such as: (a) nest building, (b) homing to nest sites or breeding areas, (c) discrimination between mates and conspecifics, (d) courtship and sexual selection, and (e) development, odor learning, and parental care. (3) Given the broad range of circumstances that implicate avian-derived odors, scent has the potential to alter how we interpret reproductive and social behavior in a wide variety of bird species, and may even be applicable to situations involving species recovery. (4) Research thus far has tended to focus on arbitrary situations and isolated cases; we have yet to obtain a general understanding of how odors impact avian breeding behavior or reproduction. (5) Future, interdisciplinary studies that explore avian odor chemistry, anatomy and behavioral responses hold great promise, particularly those that compare avian scent to well-documented chemosensory mechanisms that function in the reproduction and development of other vertebrate systems, such as mammals and fish.

### 3.9 ACKNOWLEDGEMENTS

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