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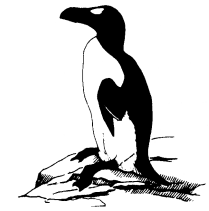

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PERSPECTIVES IN ORNITHOLOGY

BIRD ODORS AND OTHER CHEMICAL SUBSTANCES: A DEFENSE MECHANISM OR OVERLOOKED MODE OF INTRASPECIFIC COMMUNICATION?

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Birds emit many chemical compounds, though ornithologists rarely consider them. Avian odors, for example, are readily detectable to humans in at least 17 avian orders and 80 genera (Table 1; data from Weldon and Rappole 1997). Scents consist of volatile chemicals, and birds embrace a remarkable diversity of aromas, such as the musky plumage of storm-petrels (Hydrobatidae; Jacob and Zisweiler 1982); the tangerine-like perfume of Crested Auklets (*Aethia cristatella*; Humphrey and Phillips 1958); the acrid, sour odor of Hooded Pitohuis (*Pitohui dichrous*) and Variable Pitohuis (*P. kirkocephalus*; Dumbacher et al. 1992); the sweet and dusty fragrance of the Kakapo (*Strigops habroptilus*; Butler 1989, J. C. Hagelin pers. obs.); and the foul stench of the Hoatzin (*Opisthocomus hoatzin*; see Weldon and Rappole 1997). Birds also produce a variety of substances consisting of larger, less volatile compounds. Frequently odorless, these occur in various forms, such as saturated fatty acids of uropygial gland secretions (Jacob and Zisweiler 1982, Sweeney et al. 2004) or toxins sequestered in plumage or skin (e.g., Dumbacher et al. 1992).

Human detection of an avian compound clearly does not mean that it is important to a bird, unless this has been verified experimentally. Here, we focus on two major types of adaptive functions that have been proposed for a variety of odors and other chemical substances that birds either produce themselves or sequester from secondary sources. First, avian compounds may serve as a chemical defense. This includes protection against predators, ectoparasites, and microbes and can involve substances that act as an interspecific deterrent or signal (e.g., Cott 1947, Swennen 1968, Dumbacher et al. 1992, Mouritsen and Madsen 1994, Douglas et al. 2001, Shawkey et al. 2003). Alternatively, some authors posit that avian compounds function as an intraspecific chemosignal, similar to those found in other vertebrates, such as mammals (e.g., Balthazart and Schoffeniels 1979; review in Roper 1999, Hagelin 2007). Recently, birds have been shown to recognize conspecific body odor (Hagelin et al. 2003) and personal body odor or mate odor (Bonadonna and Nevitt 2004). Some chemical signatures are even individually specific (e.g., Bonadonna et al. 2003a, b, 2004, 2007).

The use of chemical signals in intraspecific communication has the potential to fundamentally alter how we interpret bird behavior. The idea is relatively new and challenges the traditional view that birds predominantly respond to their world through sight and sound. Birds readily respond to chemicals derived

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Table 1. Some avian orders considered odorous to ornithologists (adapted from Hagelin [2007]; original data collected from Weldon and Rappole [1997]).

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

from their environment during activities such as foraging, navigation, or nest building (e.g., Wenzel 1968; Hutchison and Wenzel 1980; Clark and Mason 1985; Nevitt et al. 1995; Petit et al. 2002; Wallraff 2004; Nevitt and Bonadonna 2005a, b). Birds also exhibit the three vertebrate chemosenses—olfaction, taste, and a trigeminal system, though ornithologists rarely consider them separately (Roper 1999). A fully functional olfactory system, which detects volatile chemical stimuli, has been found in every bird studied, and it is similar in design to that of other vertebrates (Bang and Wenzel 1985, Roper 1999). Avian species also have taste buds, a sense of taste (e.g., Wenzel 1973, Ganchrow and Ganchrow 1985), and a trigeminal system that processes chemical sensations, such as the burning of a chemical irritant (e.g., Clark et al. 1991, Mora et al. 2004, McKeegan et al. 2005; review in Roper 1999). Consequently, we believe that the use of avian compounds as intraspecific signals is to be expected in birds, just as chemosignals are commonly linked to the senses and behavioral repertoire of other vertebrate groups.

To introduce the topic of avian odor and chemical substances, we focus on common sources of scents, secretions, and other compounds, such as those stored in tissues. Next, we discuss the use of avian chemicals as a heterospecific defense mechanism, and then examine in detail the role of intraspecific chemical signals, a topic that is usually overlooked in studies of avian social behavior. For both hypotheses, we define terms and provide a set of testable predictions. We also highlight gaps in our knowledge of avian species, point out productive research topics from other animal systems, and call attention to discussions of birds that we find rather speculative.

Future investigations of the chemical senses and signals of birds are promising. Such studies are inherently interdisciplinary, involving responses at the molecular, physiological, developmental, and behavioral levels. Research on any aspect of avian chemosensory biology will lead to informative comparisons with other vertebrates, such as mammals, which are known in far greater detail (e.g., Ache and Young 2005, Brennan and Kendrick 2006; see also Wyatt 2003, Johansson and Jones 2007).

Sources of Avian Chemicals, Patterns, and a Null Hypothesis

Chemical substances of birds occur in many forms, such as plumage odor (e.g., Jones 1993), feces (Swennen 1968, Jones and Gentle 1985, Jones and Roper 1997), stomach oils (Swennen 1974, Jouventin 1977, Wenzel 1986), and blood (Jones and Black 1979). Birds also have a variety of glands that produce sebaceous substances, including the uropygial (preen) gland, anal gland, salt gland, salivary gland, ear (wax) glands, and even epidermal cells called sebokeratocytes (Lucas and Stettenheim 1972, Jacob and Zisweiler 1982, Menon and Menon 2000). Other specialized structures, such as powder down, may also exude lipid-like secretions (Menon and Menon 2000).

Some compounds have been linked directly to dietary sources, such as the batrachotoxins found in several species of the genus *Pitohui* and Blue-capped Ifrita (*Ifrita kowaldi*) of New Guinea, as well as in poison dart frogs (Dendrobatidae) of South America (Dumbacher et al. 1992, 2000). The poisons in both birds and frogs putatively come from those stored in melyrid beetles, because stomach contents

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contain beetle remains (Dumbacher et al. 2004). Alternatively, birds, frogs and beetles obtain toxic compounds by ingesting similar plants; however, this explanation seems unlikely, given that at least one species of *Ifrita* is considered exclusively insectivorous (Dumbacher et al. 2004). Another example of a dietary link has been noted in Procellariiformes that produce odorous stomach oils derived from the fish they consume (Clarke and Prince 1976).

Uropygial secretions are frequently posited as a key source of avian chemical substances, because the gland produces large amounts of volatile and nonvolatile compounds in the form of waxy fluids that are spread on feathers as part of plumage maintenance (Jacob and Zisweiler 1982). These fluids are believed to deter feather wear and waterproof plumage, though the exact function is still debated (cf. Sweeney et al. 2004). Avian uropygial glands can vary seasonally in size and secretory chemistry (Kennedy 1971, Bohnet et al. 1991, Piersma et al. 1999, Reneerkens et al. 2002, Soini et al. 2007). Secretions can also differ by sex (Jacob et al. 1979, Bhattacharyya and Chowdhury 1995) and by age and diet (Sandilands et al. 2004a, b), which indicates that they could reveal important patterns of information relevant to social interactions.

Aside from studies of the uropygial gland, intraspecific patterns of avian compounds are rarely noted in the literature. Important exceptions include adult Crested Auklets, pitohuis, and Antarctic Prions (*Pachyptila desolata*), which exhibit individual variation in the chemical substances they produce—in the rate of odor emissions (Douglas 2006a), concentration of feather toxins (Dumbacher et al. 2000), and volatile compounds extracted from plumage (Bonadonna et al. 2007), respectively. No striking chemical differences are evident between the sexes (Dumbacher et al. 2000, Hagelin et al. 2003, Bonadonna et al. 2007). Data for Crested Auklets and pitohuis also reveal some evidence for age patterns. Young Crested Auklets are far less odorous than adults (Sealy 2006), and a juvenile pitohui from at least one species (*P. kirhocephalus*) had almost no feather toxins, compared with an adult from the same site (Dumbacher et al. 2000). Furthermore, compounds that make up Crested Auklet odor are elevated during the breeding season (Hagelin et al. 2003), and qualitative observations indicate that odor production begins in late spring and wanes by the end of summer (Sealy 2006, Hagelin 2007). Variable toxin levels and chemical profiles of several pitohui species have also been suggested to reflect seasonal or geographic differences (Dumbacher et al. 2000).

Volatile chemicals identified from uropygial secretions have been linked to avian odor, such as the noxious scent of Green Woodhoopoes (*Phoeniculus purpureus*; Burger et al. 2004) and Eurasian Hoopoes (*Upupa epops*; Kristin 2001). Females and young of the latter species reportedly exhibit alterations in the color and scent of uropygial substances, which become dark during the nestling period and smell similar to rotten meat (Kristin 2001). Uropygial secretions are also hypothesized to account for the musky plumage scent of some procellariiforms (De León et al. 2003, Bonadona et al. 2007).

The uropygial gland, however, is not the only source of avian body odor. Several bird groups lack the gland altogether (see Moyer et al. 2003). Two in particular, parrots (Psittacidae) and woodpeckers (Picidae), are noted in a survey of malodorous birds (Weldon and Rappole 1997). Other strongly scented species have fully functional uropygial glands but produce secretions that are notably unscented. Both the citrusy Crested Auklet (Humphrey and Phillips 1958, Jones 1993) and the sweet-smelling Kakapo (Hagelin 2004) emit uropygial secretions that are odorless to humans, compared with the strong scent of fresh feathers (J. C. Hagelin pers. obs.).

The data above suggest that volatile compounds in avian odor may be derived from very different mechanisms. Powder down is one plausible source of substances in parrot odor. Birds also host a diversity of avian microbes on feathers and skin (Burtt and Ichida 1999, Muza et al. 2000, Lucas and Heeb 2005, Shawkey et al. 2005), which may be involved in the production or degradation of chemical substances. Jacob and Zisweiler (1982:306) hypothesized that natural degradation of uropygial secretions from large, nonvolatile (unscented) compounds into smaller, strongly scented acids and alcohols contributed to the musky plumage-odor of seabirds. Birds may also synthesize substances *de novo*. Douglas (2006b) speculated that compounds in Crested Auklet odor are similar to those expected during fatty-acid synthesis. Unfortunately, no experimental evidence exists to support such odor-producing mechanisms in parrots or seabirds.

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Before considering two major functions of avian compounds (chemical defense and intraspecific chemosignal), below, it is important to clarify a null hypothesis. Specifically, the chemical substances of birds may simply be the byproduct of physiological processes, such as feather growth and maintenance or other bodily functions. An analogy for this is wet paint, the odor of which has no function *per se* but is related to the paint's functional properties, such as its ability to dry quickly and its color, texture, and durability. Studies positing a function for avian chemical substances should accept the null hypothesis if experimental or comparative evidence does not support the alternative.

Defensive Properties of Avian Chemicals

Pioneering tests by Cott (1947) were among the first to experimentally suggest that predators respond to chemical substances contained in birds. Cott noted that the carcasses of some birds were less palatable than those of others when presented to potential mammalian predators (i.e., humans, domestic cats) or invertebrate scavengers (hornets). Other avian species are reported to produce noxious or unpalatable substances, apparently during defensive situations; examples include Northern Fulmars (*Fulmaris glacialis*), which spit stomach oils at intruders (Swennen 1974), and the malodorous "nest feces" of Northern Shovelers (*Anas acuta*) and Common Eiders (*Somateria mollisima*), which are sprayed over eggs when an agitated adult is flushed from the nest (Swennen 1968). More recent studies discuss another kind of avian chemical protection. A common defensive function attributed to uropygial secretions is to keep feathers and skin free of parasites and microbes (Jacob and Zisweiler 1982, Sweeney et al. 2004, Haribal et al. 2005). Uropygial compounds combat a wide range of organisms, including lice, bacteria, yeast, molds, and fungi (e.g., Jacob et al. 1997, Bandyopadhyay and Bhattacharyya 1999, Law-Brown 2001, Moyer et al. 2003, Shawkey et al. 2003, Martín-Platero 2006), or have been hypothesized to present a physical barrier that blocks harmful microbes such as feather-degrading bacteria (*Bacillus lichenoformis*; Reneerkens et al. 2008). Heterospecific substances that birds apply via specialized behaviors may also facilitate a similar form of defense, as in "anting" or self-anointing (review in Weldon 2004) or adding plants with antiseptic properties to nests (e.g., Wimberger 1984, Clark and Mason 1985, Lambrechts and Dos Santos 2000, Lambrechts and Hossaert-McKey 2006).

Dumbacher and Pruett-Jones (1996:139) offered the following definition: "Chemical defense occurs when an individual contains or uses behaviorally one or more chemical substances that deter predators or parasites." The authors described avian defensive substances as being either toxic or unpalatable. These categories generally reflect those defined in Brower (1984). Toxic compounds cause physiological or physical damage when a heterospecific is exposed to them at levels normally encountered in nature. Unpalatable compounds are innocuous substances that result in an aversive response, given the way in which the chemicals stimulate the chemosensory receptors of a target animal. The distinction between the two types of compounds is not always clear-cut. For example, low concentrations of toxic compounds can also elicit an unpalatable or aversive reaction in a predator (Dumbacher and Pruett-Jones 1996).

Two key predictions emerge for the defense hypothesis: (1) Avian compounds should exhibit evidence of a toxic or simply unpalatable, aversive effect on predators, parasites, or microbes at the concentration naturally exhibited by an individual; and (2) individuals with less protection should experience reduced fitness, because they cannot protect themselves adequately, compared with individuals that produce more (Dumbacher and Pruett-Jones 1996). Controlled experiments are required to assess these predictions, with the compounds manipulated at levels that are ecologically realistic.

We now consider three cases of chemicals acting in avian defense. The examples illustrate common themes and issues in the literature, for which experimental data are often lacking. Dumbacher and Pruett-Jones (1996) provide many more detailed accounts of species that produce compounds that have been characterized as toxic, unpalatable, malodorous, or aversive to heterospecifics. Although there are a great many hypothesized cases and anecdotal accounts, few species have been investigated thoroughly.

Pitohuis and ifritas.—The genera *Pitohui* and *Ifrita* of New Guinea contain species that harbor toxic compounds (Dumbacher et al. 1992, 2000).

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Batrachotoxins are among the most potent poisons known to occur in vertebrates and invertebrates. The compounds are >250× more powerful, by mass, than strychnine (Dumbacher and Pruett-Jones 1996, Dumbacher et al. 2004). Hooded and Variable pitohuis sequester particularly high concentrations in feathers and skin; extracts injected into lab mice cause convulsions and death (Dumbacher et al. 1992). Batrachotoxins target voltage-gated sodium channels of animal cells that are highly conserved in vertebrate predators (Dumbacher et al. 1992, 2004), and can thereby cause harm to a target animal.

Hunters in New Guinea avoid eating the more toxic species, and close contact with a bird can cause nausea or chemosensory reactions indicative of the trigeminal system, such as burning, irritated mucus membranes, sneezing, and watery eyes (Majnep and Bulmer 1977, Dumbacher and Pruett-Jones 1996). Some native predators, such as the green tree python (*Chondropython* [= *Morelia*] *viridis*) and brown tree snake (*Boiga irregularis*) also react to natural concentrations of the toxin (Dumbacher 1999, J. P. Dumbacher unpubl. data). Such observations suggest that low-level exposure to batrachotoxins, possibly transmitted via feathers or skin dander, can cause an unpalatable or aversive reaction in at least some vertebrates, which could function as an interspecific repellent signal. The two most toxic species, Hooded and Variable pitohuis, also emit an acrid or sour odor (Dumbacher et al. 1992), though the chemical identity and any signaling function are unknown. Odor may result from degradation of batrachotoxins (large, nonvolatile compounds) into smaller, volatile components or arise from other sources altogether (J. P. Dumbacher pers. comm.).

Dumbacher and Fleischer (2001) used a molecular phylogeny of races of *Pitohui* to gather comparative evidence for chemical defense and warning coloration as a signal against vertebrate predators. The two most toxic pitohuis exhibited convergent evolution in bright, orange and black plumage patterns, which supports the idea that aposomatic coloration of plumage may deter certain visual predators (Götmark 1994, Marples et al. 2005). These authors also suggest a pattern of Müllerian mimicry in which two prey species containing chemical defenses visually resemble each other.

Dumbacher (1999) experimentally tested the effectiveness of pitohui feathers on ectoparasitic chewing lice (Order Phthiraptera). A realistic level of toxin was presented to lice, in that treatments involved fresh feathers. Lice experienced significantly shortened lifespans on feathers of Hooded Pitohui, which is consistent with avian compounds producing a toxic effect. Furthermore, when given a choice, lice more frequently avoided toxic feathers than nontoxic control feathers, though the sensory means by which lice detected toxins is unclear.

Crested Auklets.—The Crested Auklet is a highly social, monogamous seabird that emits an unusual tangerine-like scent consisting of simple hydrocarbons, including aldehydes and alcohols, during summer breeding months (Table 2; Douglas et al. 2001, Hagelin et al. 2003). One function proposed for the volatile compounds present in Crested Auklet odor is that they repel ectoparasites, because the substances are similar to other invertebrate repellents found in nature (Douglas et al. 2001). The seabird tick (*Ixodes uriae*) is a common ectoparasite with levels of infestation varying from 2% to 100% of birds attending breeding colonies (I. L. Jones pers. obs.; see also Douglas 2006a). The tick transmits disease, including the spirochete *Borrelia* and viruses (Muzaffar and Jones 2004).

TABLE 2. Some volatile compounds of Crested Auklet plumage odor that exhibit significant seasonal variation. Compounds in bold were used in field tests (Jones et al. 2004); the data are from table 1 in Hagelin et al. (2003).

	Median concentration ($\mu g\ g^{-1}$ feathers)	
Compound	Breeding season[a]	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 $\mu g\ g^{-1}$ feathers).

[a]Statistical significance is the result of a Wilcoxon two-sample test of scented feathers (breeding season) versus unscented (winter) feathers.

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It has also been implicated in Cassin's Auklet (*Ptychoramphus aleuticus*) chick mortality (e.g., Morbey 1996).

Evidence supporting the repellent properties of Crested Auklet compounds against ticks or other ectoparasites is mixed. Partial support comes from tests of synthetic compounds and chemical blends against both seabird ticks and a generalized mammalian tick (*Amblyomma americanum*). Douglas et al. (2004) used a moving-object bioassay, which mimics the heat and movement of a host (Dautel et al. 1999), to test the attachment times of ticks to small pieces of filter paper treated with compounds found in Crested Auklet odor. In a series of different concentrations, the attachment time of ticks was reduced in a dose-dependent fashion (Douglas et al. 2004), which indicates an aversive or repellent effect. Compounds also had a toxic effect on two genera of auklet feather lice (*Quadraceps* and *Austromenopon*; Douglas et al. 2004), which became moribund within seconds when placed on feathers treated with synthetic chemicals found in Crested Auklet odor.

However, Hagelin (2007) used data on the natural concentration of Crested Auklet plumage scent (from Hagelin et al. 2003) to estimate whether the experiments on ticks and lice, described above, simulated ecologically relevant doses of auklet compounds. Some dilute chemical treatments during tick experiments were up to 5× more concentrated than levels measured on wild birds, whereas tests of lice occurred at concentrations 6.8×10^4 to 9.6×10^5 times greater than that of natural plumage (Hagelin 2007). Aversive responses and lethal damage to ectoparasites are practical considerations for the repellent-manufacturing industry (see Douglas et al. 2005a), but we question whether such tests replicated the chemical experience of most ticks or lice on wild Crested Auklets.

Two other field investigations further call into question the defensive properties of Crested Auklet compounds. First, fresh plumage of adults did not repel or reduce mortality of feather lice (Douglas et al. 2005b). Second, auklet ticks exposed to fresh piles of scented and unscented feathers in a petri dish were not repelled by scented plumage (Hagelin 2007). Crested Auklet odor is quite volatile, and fresh feathers can lose scent in a few days (Hagelin et al. 2003). The experiments described above took place over a period of hours, but it is plausible that natural odor loss of plumage could have partly contributed to the negative results.

In light of current data, it is difficult to assign a defensive role to natural levels of compounds produced by a single Crested Auklet. Similarly complex results were obtained in studies of uropygial secretions in Rock Pigeons (*Columba livia*; Moyer et al. 2003). If the compounds in Crested Auklet scent defend against ectoparasites, the result is not as toxic, nor is the aversion as marked as in *Pitohui* (Dumbacher 1999). Sublethal or physiological effects on auklet ectoparasites (e.g., impaired development) have been implied (Douglas et al. 2005b, Douglas 2006a), but currently require supporting data. Natural vertebrate predators (foxes, gulls) have not been tested, though Crested Auklets are traditionally hunted and eaten by local residents (Sealy 2006).

Green Woodhoopoes.—When disturbed, cavity-roosting Green Woodhoopoes turn their tails toward the threat and excrete a foul-scented secretion from their uropygial glands (Ligon and Ligon 1978). Compounds in the secretion include dimethyl-sulfide (scent of rotten eggs), and the rank odor persists on any surface it touches (Burger et al. 2004). The interesting behavioral presentation of a liquid stench suggests a putative chemical defense against vertebrate predators (Ligon and Ligon 1978, du Plessis and Williams 1994), as does the behavior of young birds, which release large quantities of foul-scented, liquid feces when disturbed (Ligon 2001). Both responses could presumably evoke unpalatable or aversive reactions in predators, such as snakes, genets and rats, which frequently attack woodhoopoes in their cavities (Ligon and Ligon 1978). No experiments have been conducted on natural predators, though pilot data described in Burger et al. (2004) suggest that some Green Woodhoopoe compounds deterred predatory cats and lizards. Interestingly, the related Eurasian Hoopoe also produces rank uropygial secretions, and young can dramatically spray fecal-like fluids ≤60 cm (Kristin 2001), which indicates that the two avian groups may exhibit similar forms of chemical protection.

Law-Brown (2001) reported 17 uropygial compounds detected in Green Woodhoopoes that were effective against several microbes, including feather-degrading bacteria (Burtt and

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Ichida 1999) and several common avian pathogens (e.g., *Salmonella gallinarum*, *Streptococcus faecalis*, *Staphyloccocus aureus*). It is unclear, however, whether lab treatments mimicked concentrations of chemical substances naturally found on plumage or skin of wild birds. A bacterium (*Enterococci phoeniculicola*) isolated from the uropygial gland (Law-Brown and Meyers 2003) may be responsible for the antimicrobial compounds. In the related Eurasian Hoopoe, another bacterium (*E. faecalis*), isolated from a nestling uropygial gland, also produces substances with antimicrobial properties (Martin-Platero et al. 2006).

An Assessment of Chemical Defense

Experimental studies of compounds involved in chemical defense primarily address Dumbacher and Pruett-Jones's (1996) first prediction, namely, that defensive substances have a toxic or unpalatable effect on predators, ectoparasites, or microbes. Multiple lines of evidence support batrachotoxins acting as a chemical defense in pitohuis: (1) the toxin is extremely potent and targets highly conserved cells of predatory animals, (2) limited exposure causes sensory irritation and aversive reactions in some vertebrates, (3) comparative evidence revealed a correlation between toxicity and the visual signal of bright plumage patterns, and (4) toxins in fresh plumage can negatively affect feather lice. The data for Crested Auklets and Green Woodhoopoes are less clear-cut but provide promising information for future study.

A rigorous assessment of the first prediction of chemical defense requires that ecologically relevant predators, parasites, or microbes be tested with levels of chemical compounds that occur naturally on an individual. The second prediction requires evidence of individual fitness benefits, experiments that are admittedly difficult to design and are presently lacking for birds. Details of the interplay between species involved and the different forces driving the evolution of avian chemical defense are also scarce.

Dumbacher and Pruett-Jones (1996) noted that defensive chemicals, particularly those of insects, correlate with gregarious or social behavior. Interestingly, in birds, gregarious behavior in the form of cooperative breeding occurs in both the toxic Hooded Pitohui and in the foul-smelling Green Woodhoopoe and Eurasian Hoopoe (Ligon and Ligon 1978, du Plessis 1992, Legge and Heinsohn 1996, Kristin 2001). From an evolutionary standpoint, kin selection could favor chemical defense and a high degree of sociality among relatives, if predators learn to avoid groups of related, aversive prey faster than solitary prey (Fisher 1930, Gagliardo and Guilford 1993; review in Dumbacher and Pruett-Jones 1996). An alternative hypothesis is that chemical defense reduces the need for a solitary or cryptic lifestyle and individuals congregate socially for other reasons (see Dumbacher and Pruett-Jones 1996).

Avian Chemicals as Intraspecific Signals

Roper (1999) considered avian odors and other chemical substances involved in intraspecific contexts to be one of the most promising topics in bird biology that has been overlooked by ornithologists. It is perhaps not surprising that intraspecific chemosignals are largely unstudied, because, until recently, birds were believed to lack them altogether (Wingfield et al. 1994). Birds commonly allopreen, which potentially exposes individuals to the chemical compounds of a mate or other conspecifics (Roper 1999). The seabird literature contains a particularly large number of anecdotal observations that assign a putative role to chemical substances involved in both intra- and intersexual contexts. For example, Bulwer's Petrel (*Bulweria bulwerii*) produces an odor during the breeding season that is hypothesized to function as a mating signal (Thibault and Holyoak 1978), whereas Snow Petrels (*Pagodroma nivea*) regurgitate unpleasant-smelling stomach oils during aggressive and defensive disputes (Jouventin 1977). Unfortunately, none of these observations has been tested experimentally.

Similar to Kavaliers et al. (2005), we broadly define chemical communication as the intraspecific detection, recognition, or transfer of information via a chemical stimulus. The stimulus is referred to as a "chemical signal" and is considered to be any self-produced chemical compound or mixture that has a social or physiological effect on conspecifics (Johnston 2000). Two key predictions accompany the use of social chemosignals: (1) individuals recognize and respond (overtly, physiologically or developmentally) to the chemical information produced

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by a conspecific, and (2) the response increases an individual's fitness.

It is important to note that the term "pheromone" is sometimes used to describe any chemical signal (e.g., Wyatt 2003, Johansson and Jones 2007). However, Karlson and Luscher (1959) originally described a pheromone as a specific kind of cue, capable of eliciting stereotyped behaviors when present in minute quantities, which is similar to the ethological concept of a "sign" or "releasing" stimulus (Johnston 2000). The exact definition has been debated, but we prefer the original definition, because it lends itself to specific, testable predictions (e.g., Schaal et al. 2003). Given that ornithologists are only just beginning to understand the roles of chemical substances in birds, it seems premature to label any avian chemosignal as a pheromone (Hagelin et al. 2003).

Below, we consider the experimental evidence for several functions of avian compounds involved in the intraspecific interactions of birds, including behaviors related to nest and mate identification, courtship signals, and sexual displays (see also Hagelin [2007] for a detailed discussion of this topic). Recent examples primarily address a bird's response to body odor, which is mediated through olfaction via the perception of volatile chemical stimuli. Birds may also obtain chemical information via the two other chemosenses, taste or trigeminal responses (review in Roper 1999), but the extent to which this occurs is unknown.

Petrels and prions.—Members of the Procellariidae have been central to studies of individually specific chemical signatures, because many species produce a musky plumage scent. These birds also frequently use olfaction while foraging to detect prey-related odors (e.g., Nevitt and Bonadonna 2005a, b). The literature that investigates the function of seabird odor can be divided into two types of studies: (1) responses to a bird's own nest odor and (2) odor recognition of mates, self, and conspecifics.

Odors of petrels and prions putatively arise from the uropygial gland, and secretions rub off on other substrates, causing occupied burrows in high-density colonies to produce a noticeable scent (Jacob and Zisweiler 1982, De León et al. 2003). Active nests without occupants also retain odor, apparently from the presence of fresh feathers (Bonadonna et al. 2003a, b). Predation pressure can be intense, and birds often return to burrows at night without calling to mates (Warham 1996), which suggests that they rely on chemical cues. Grubb (1974) noticed that Leach's Storm-Petrels (*Oceanodroma leucorhoa*) approached their nest entrances from downwind. His pioneering studies led to the discovery that individuals use olfaction to locate their nest site (Grubb 1973, 1974, 1979). Grubb's work has since been expanded to include several other species (Bonadonna and Bretagnolle 2002).

Behavioral studies have recently revealed that adults of several procellariids distinguish between the odor signatures of their own nests and their neighbors' nests (two prions [*Pachyptila* spp.], Bonadonna et al. 2003a, b; Blue Petrels [*Halobaena caerulea*], Bonadonna et al. 2004; two diving petrels [*Pelacanoides* spp.], Bonadonna et al. 2003a). Such investigations frequently involved a T-maze apparatus. When the arms of the maze were placed into two different burrow entrances, birds preferred the arm associated with the scent of their home burrow. Preferences persisted (1) when odorous material, removed from different burrows, was placed at the end of each arm of the maze (Bonadonna et al. 2003a) and (2) when investigators created new burrow openings from which to acquire nest scent (Bonadonna et al. 2004). Such experiments ensured that individuals responded only to volatile compounds emanating from the nest, rather than to confounding factors associated with the location of the nest entrance.

Mobile chicks of the European Storm-Petrel (*Hydrobates pelagicus*) also require volatile chemical stimuli for orientation (Mínguez 1997, De León et al. 2003). Blocking a chick's nares inhibits homing to the proper burrow (Mínguez 1997). Moreover, chicks can discriminate their own scent from that of other individuals (De León et al. 2003), which suggests that chicks home to the burrow that contains their own (familiar) odor signature. Home burrows are critical to chick survival, because they provide protection and are the only place where young are fed (Mínguez 1997, De León et al. 2003).

The first tests of whether tube-noses detected the chemical signatures of mates produced interesting but not particularly clear-cut results. Shallenberger (1975) determined that heart rates of Wedge-tailed Shearwaters (*Puffinus pacificus*) increased when exposed to their partners' scent. Work on another seabird has yielded

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a much more definitive pattern. Bonadonna and Nevitt (2004) discovered partner-specific odor recognition in Antarctic Prions using a Y-maze apparatus. The investigators cleverly obtained a natural bioassay of individual scent to use in the Y-maze by holding each bird for a short period in its own cotton bag and allowing plumage odor to absorb into the fabric. Bonadonna and Nevitt (2004) reported three interesting results. First, when presented with the choice of mate odor and that of an unknown conspecific, Antarctic Prions were attracted to their mates' scent. Second, Antarctic Prions preferred self-odor over a "no-odor" cloth-bag control, which is consistent with the use of body scent to orient back to a burrow site. Third, and perhaps most importantly, Antarctic Prions actively avoided self-odor when given the alternative choice of conspecific scent from an unknown individual.

Avoidance of self-odor is well known in vertebrates. Some chemical profiles of mammals, for example, are mediated by the major histocompatibility complex (MHC; alleles associated with immune function), which correlates with an individual's genetic make-up. MHC-related chemosignals facilitate inbreeding avoidance, individual and kin recognition, and nesting patterns and selectively block pregnancy in mice (Beauchamp and Yamazaki 2003, Ziegler et al. 2005; review in Penn 2002, Brennan and Kendrick 2006). MHC alleles also occur in birds (review in Zelano and Edwards 2002), though data supporting MHC-related patterns in avian reproduction are mixed (e.g., Freeman-Gallant et al. 2003, Richardson et al. 2004, Smith et al. 2005, Tarvin et al. 2005). Given that Antarctic Prions are long-lived, philopatric, and genetically monogamous and produce one egg per season, birds could return to their natal site to breed with siblings they have never met. Analyses of compounds present on Antarctic Prion feathers suggest that individuals exhibit unique chemical signatures that are stable over years (Bonadonna et al. 2007). Soini et al. (2007) recently suggested that seasonal or individual variation in the uropygial secretions of Dark-eyed Juncos (*Junco hyemalis*) could also act as an indicator trait for birds in small populations where the potential for inbreeding is high.

The chemical signature of kin has implications for cooperative breeders, such as the Green Woodhoopoe, in which family groups defend tree cavities used for nesting and roosting (Ligon and Ligon 1978, du Plessis 1992). If individuals or groups have unique chemical profiles, such information could influence interactions between relatives or different family units, or possibly mark active tree cavities within a territory. Hypotheses related to avian chemosignals, MHC and kin selection require investigation.

Mallard.—The first experimental test yielding indirect evidence of an avian chemosignal linked to a courtship display involved male Mallards (*Anas platyrynchos*; Balthazart and Schoffeniels 1979). Males whose olfactory nerves were severed exhibited significantly fewer sexual and social behaviors toward females than sham-operated (control) males (Balthazart and Schoffeniels 1979). Differences in responses were correlated with seasonal changes in the uropygial secretions of females (Jacob et al. 1979, Bohnet et al. 1991), which suggests that an intact sense of smell is required for males to detect female chemicals and exhibit appropriate behaviors. However, the general mechanism by which chemical compounds are transmitted between individuals of this species remains unclear.

Crested Auklet.—The highly social Crested Auklet produces a citrusy plumage odor. Scent is conspicuously associated with a seasonal display, termed the "ruff-sniff" (Jones 1993), in which birds place their bills within the nape feathers of a display partner repeatedly during courtship (Fig. 1). The behavior and odor are notably elevated during summer months, in what appears to be a self-evident means of acquiring chemosensory information, or possibly of scent-marking other individuals (Jones 1993, Jones and Hunter 1993, Hagelin et al. 2003, Sealy 2006).

Using a T-maze, Hagelin et al. (2003) demonstrated that Crested Auklets orient preferentially toward the scent of natural plumage and a synthetic mixture of key compounds identified from feather odor. Adults also distinguished between these and other scents. Individuals were repelled by mammalian musk and did not respond significantly to banana (amyl-acetate), a novel scent. Hagelin et al. (2003) demonstrated a general attraction to Crested Auklet odor, but the results did not elucidate the odor's social function.

Jones et al. (2004) tested for odor function using a field protocol similar to that used to examine the function of facial crests (Jones and Hunter 1993, 1999). Crested Auklets exhibit mutual mate

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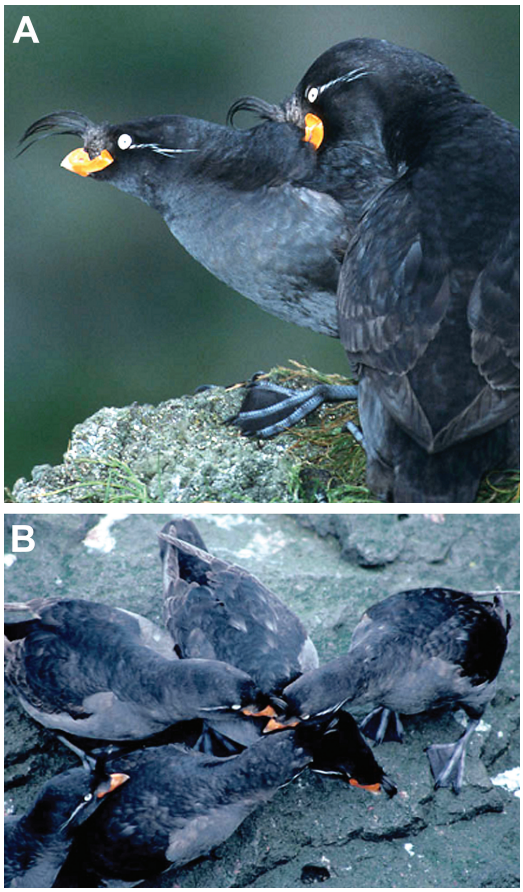

FIG. 1. The frequently repeated "ruff-sniff" display of Crested Auklets involves (A) two individuals or (B) more. Birds place their bills within the nape feathers of a display partner. The plumage of this species has a striking citrus-like scent. (Adapted from Hagelin [2007]; photographs by I. L. Jones and J. C. Hagelin.)

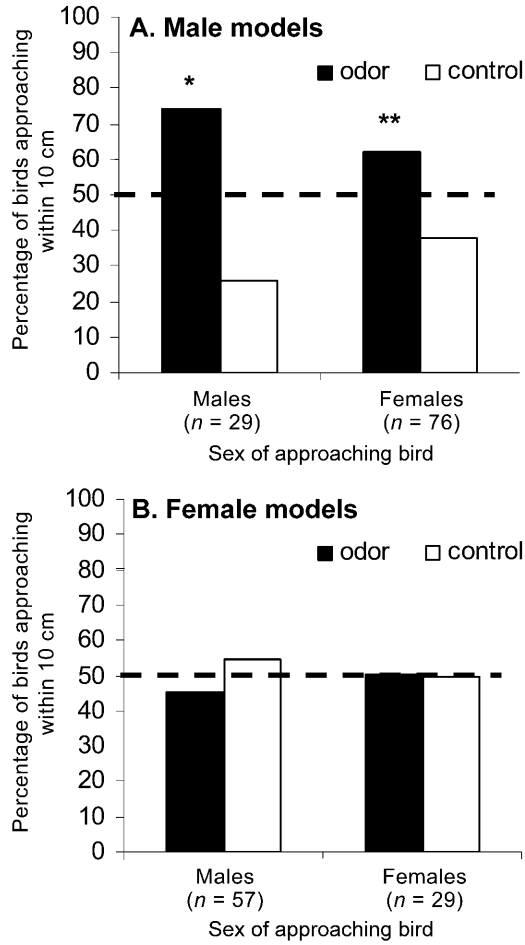

FIG. 2. In a field manipulation of the Crested Auklet's citrusy odor, (A) male models treated with two key compounds found in plumage scent were approached significantly more often by birds of both sexes than unscented male models. (B) No such pattern, however, was detected for scented female models. Dashed line indicates the null expectation. (Adapted from Hagelin [2007]; data from table 1 in Jones et al. [2004]; $^{**}P = 0.02$, $^{*}P = 0.04$.)

choice for their ornamental crests (Jones and Hunter 1993), leading several authors to suggest that odor may also serve as an olfactory "ornament" (e.g., Jones 1993, Douglas et al. 2001, Hagelin et al. 2003, Jones et al. 2004). Realistic Crested Auklet models were treated with a synthetic mixture of two seasonally elevated odor compounds (Z-4-decenal and octanal). Two patterns were evident. First, both sexes approached scented models of males more frequently than controls, but no such pattern was evident with female models (Fig. 2). Second, scent did not increase the rate of ruff-sniff displays or any other sexual behavior. The results indicated at least a general social function for Crested Auklet odor in which both sexes respond relatively more to scented males (Jones et al. 2004). Recent observations of captive birds also suggest that the concentration of some odor compounds correlates positively with male social status (J. C. Hagelin unpubl. data).

A lack of elevated ruff-sniff or sexual displays in the Crested Auklet model experiment

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raised some doubt about the odor's role in mate choice (Jones et al. 2004). The simplified chemical mixture clearly did not act as a releasing stimulus for any stereotyped sexual display. By comparison, increasing crest length (a visual cue) of models greatly increased displays of approaching birds (Jones and Hunter 1993, 1999). Odor may act as a secondary trait in relation to visual ornaments, or function in conjunction with display behaviors, which static models could not produce. Alternatively, odor may not function in displays. Visual and chemical cues, however, can operate at different scales. Birds engaged in a ruff-sniff display actively touch a partner's scented nape-plumage at close range. Close-range assessment differs from responses that occur at distances of several centimeters on the tops of windy rocks, such as those recorded by Jones et al. (2004). Currently, odor compounds are extremely difficult to manipulate in wild birds, a situation for which new techniques are badly needed. Tests conducted in locations where both wind and vision are limited, such as dark nesting crevices, could provide new insight into odor function.

A General Role for Reliable Chemical Signals?

If body odor or other chemical substances function as a signal during intraspecific interactions of birds, what information might be conveyed? Mouritsen and Madsen (1994) were the first to link the functions of avian chemical defense with intraspecific communication. They likened batrachotoxin levels of toxic pitohuis to an "honest" ornament indicative of a bird's parasite resistance. Given the diet-dependency of chemical protection in pitohuis (Dumbacher et al. 2004), chemical ornaments could operate in a manner similar to carotenoid-based plumage traits (e.g., Hill 2002). Mouritsen and Madsen (1994) further hypothesized that the signal indicative of parasite-resistance in pitohuis could be transmitted via an individual's distinctive sour odor. The volatile (scented) components of uropygial secretions in other avian species, such as *n*-alcohols and methylketones, have also been attributed to broad-spectrum antimicrobial defense of plumage and skin (Soini et al. 2007). If the compounds a bird produces correlate positively with the intensity of chemical defense, one would predict that individuals producing higher concentrations will be chosen as mates over those with lower concentrations.

Avian chemical compounds have the potential to signal other kinds of reliable information. Odors and other substances of birds, as discussed earlier, exhibit seasonal, sexual, age, and individual variation. Such correlations suggest that compounds could provide conspecifics with cues regarding an individual's health or quality, such as an infirm or contagious condition, hormonal state, social status, or genotype, as in mammals (e.g., Penn and Potts 1998, Penn 2002, Brennan and Kendrick 2006; review in Hagelin 2007). Johansson and Jones's (2007) recent review of a variety of animal species provides an interesting starting point for investigations of avian chemical indicator traits, particularly those related to mate choice.

Finally, substances that reliably connote alarm, such as the odor of avian blood or feces, have been implicated in intraspecific aversion (Jones and Gentle 1985, Jones and Roper 1997, Jones et al. 2005). In other vertebrates, compounds associated with alarm can be exploited by members of the same species, because such cues indicate immediate danger, such as a predator actively foraging on conspecifics (Kats and Dill 1998, review in Wyatt 2003). In birds, for example, the noxious odors or liquid feces of disturbed Eurasian Hoopoes or Green Woodhoopoes might act not only as an interspecific defense but as an intraspecific cue that correlates with danger. Evidence supporting any adaptive significance of chemical substances in birds acting as reliable signals of individual condition or alarm awaits further experimental study.

Chemosensory Learning

Studies of captive domestic chickens (*Gallus domesticus*) give us insight into responses to volatile chemicals and other substances that young encounter during development. Chicks, for example, recognized and responded preferentially to the familiar odor of soiled bedding (Jones and Gentle 1985, Burne and Rogers 1995). This is similar to the response of European Storm-Petrels to the scent of their home burrow or body odor (Mínguez 1997, De León et al. 2003), or to juvenile geese (*Anser* spp., *Branta* spp.) preferring parental odor over a control treatment (Würdinger 1982).

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Even unhatched chicken embryos can detect, recognize, and develop a chemical memory (reviews in Roper 1999, Hagelin 2007). Though studies often involve novel chemical substances, they raise the question of whether embryos can also recognize natural compounds present at the nest. Chicks exposed to a mixture of artificial strawberry compounds several days before hatching preferred (or were less averse to) strawberry-treated bedding and water than control chicks (Sneddon et al. 1998).

Domestic chicks also develop chemical memories posthatching. Most young birds have a neophobic response to unfamiliar scents or tastes (review in Roper 1999). However, chicks exposed regularly to vanillin were less fearful than controls, exhibiting enhanced dispersal and feeding readiness when placed in new surroundings containing vanilla scent (Jones et al. 2002). The familiarity of this volatile compound, therefore, calmed chicks in a novel environment (Jones et al. 2002). Similar responses might be expected if the compounds produced by an incubating parent or nest site are transmitted to developing embryos or newly hatched chicks.

Mechanisms of avian chemosensory learning are unstudied. However, the process and function(s) of chemical imprinting are well known in other vertebrates (e.g., Semke et al. 1995, Dittman et al. 1996; review in Brennan and Kendrick 2006). If chemical imprinting also occurs in birds, it may affect how young learn about chemical information, such as odors or other substances associated with prey (Cunningham et al. 2003), parents and sibs, natal nesting sites, or, possibly, future mates (review in Hagelin 2007).

An Assessment of Avian Chemicals as Intraspecific Signals

Studies of avian compounds have primarily addressed the first prediction of the intraspecific signaling hypothesis. Namely, body odor or other chemical substances produced by birds are expected to elicit a response in conspecifics. Recent investigations have revealed strong experimental support in multiple bird groups, indicating that adults and chicks react to and recognize conspecific scent compared with other kinds of volatile chemical stimuli. Substances produced during interspecific chemical defense, such as malodorous fluids or feces, may also function during intraspecific interactions but have not been investigated. Any fitness benefits of avian chemical compounds are unknown, and comparative data that identify evolutionary patterns of chemical compounds or their uses are scarce.

Conspecific chemical cues have produced striking behavioral reactions in some petrels and prions, but more subtle reactions in other species. Given that most birds are highly visual and auditory, we suggest that it is incorrect to assume that intraspecific compounds alone will necessarily trump all other sensory information. Avian behavior is complex and usually relies on multiple modes of perception. For example, it is difficult to understand odor function in Crested Auklets through scent manipulations only. A bird's response may require or interact with other kinds of sensory input, such as displays, visual ornaments, and vocalizations (see Partan and Marler 2005). Body odor and other chemical substances should be viewed simply as another means by which birds acquire information about their immediate environment and other conspecifics.

Experimental Design and Promising Future Studies

Ornithologists currently lack a general framework for studies of avian odor and other chemical substances. Like any signaling system, compounds involved in interspecific contexts, such as chemical defense, or those used as intraspecific signals represent an exchange of information between a sender and a receiver. The exchange may involve two or more heterospecifics, such as predator and prey, or simply relate to members of the same species. Figure 3 offers a generalized conceptual model on which to base future studies. Avian chemicals used for defense or as an intraspecific signal span multiple biological levels, such as (1) the chemical properties of the sender's signal itself (how it is produced, advertised, etc.), (2) the mechanisms and anatomical structures involved in a receiver perceiving the signal, and (3) resulting behavioral or physiological responses of the receiver to the signal. All parts of Figure 3 are potentially subject to natural or sexual selection in the form of fitness benefits to either sender or receiver. The constraints of evolutionary history also play a role.

Few details are known about the components or underlying relationships outlined in Figure 3.

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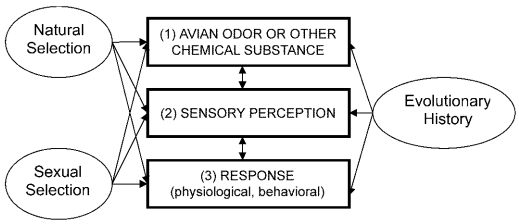

FIG. 3. A conceptual model for the interdisciplinary study of avian odors and other chemical substances (adapted from Hagelin 2007). The model can apply to interspecific signals, such as those involved in chemical defense, or to intraspecific signals. It also spans multiple levels of biology (molecular through to whole-animal responses). An exchange of chemical information, like any signaling system, can be divided into three basic components: (1) the chemistry of the signal itself (produced by a sender), (2) sensory perception of the signal by the receiver (e.g., olfactory anatomy and receptors, brain processes), and (3) any resulting response of the receiver to the signal (behavioral, physiological, etc.). Each component of the diagram interacts with the others, and all are subject to natural selection, sexual selection, and the evolutionary history of the species involved.

A more in-depth understanding will enable common physiological, behavioral, ecological, or evolutionary patterns to emerge, as they relate to the function of avian chemical compounds. An interdisciplinary approach that takes advantage of the detailed data available from other vertebrate groups (e.g., Wyatt 2003, Ache and Young 2005, Brennan and Kendrick 2006, Johansson and Jones 2007) will also provide valuable insights for future studies of birds.

There are many promising topics to investigate. Aside from studies of Crested Auklets, no study has tested whether avian compounds can both act as an interspecific means of defense against parasites and serve as a relevant intraspecific signal or indicator trait as proposed by Mouritsen and Madsen (1994). We also know that chemical secretions of some birds vary seasonally, but we have yet to find a species that is only seasonally protected from predators, parasites, or microbes. It may be more informative to test whether chemical alterations provide an added or different means of protection at particular times of the year. For example, seasonal changes in uropygial secretions have been suggested as a means of chemical camouflage against predation in ground-nesting sandpipers (Reneerkens et al. 2002, 2005). Compounds produced by incubating birds may also apply a form of microbial defense to the surfaces of egg shells (Cook et al. 2005) or young during the breeding season.

The prospects for avian chemical substances acting as reliable signals or as a recognition mechanism between kin are particularly exciting, given evidence for odor recognition and individual-specific chemical signatures. Good species to begin studying are those that have a notable chemosensory ability or produce particular odors or secretions linked with particular behaviors. Regarding avian chemosignals as ornaments, studies have not yet examined systems in which females primarily select males for indirect benefits or "good genes" (see Zelano and Edwards 2002). The Musk Duck (*Biziura lobata*), for example, is a lek-breeding species from Australia in which only males produce a seasonally elevated plumage scent (Gamble 1966, McCracken et al. 2000). Johansson and Jones (2007) reviewed a wide variety of animal studies that could help guide investigations of avian chemosignals related to mate choice, such as those involved in species recognition, mate recognition, and individual assessment of prospective mates.

Odors and other chemical substances may also be applicable to more common avian behaviors, such as territorial interactions, chicks recognizing parents, parents allocating care by assessing chick health, or conspecific alarm. Chemical communication may also occur over relatively long distances where standard avian senses (sight and hearing) are obscured by fog, wind, or waves. Humans undoubtedly cannot sense all chemical compounds that birds produce, and obtaining the exact chemical composition of complex mixtures can be difficult. However, it is still possible to understand variation in and function of chemosignals through elegant behavioral tests, similar to those used to study ants and other insects (e.g., Wilson 1959, Jackson et al. 2007; reviews in Hölldobler and Wilson 1990, Ayasse et al. 2001, Johansson and Jones 2007).

Currently, plumage odor and other avian chemical substances are viewed as an unusual aspect of bird biology that serves a unique or

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unusual adaptive function. Chemical defense and intraspecific communication have received attention in recent literature, though it is naïve to assume that these are the only key ways in which birds use chemical compounds. We agree with Berenbaum (1995) that it is perhaps unrealistic to develop a single, unifying theory for all cases in which avian chemical compounds are important. However, research that focuses on mechanisms (genetic, biochemical, behavioral) and evolutionary patterns, both within and across taxa, appears quite promising. For example, given the growing literature on bird body odor, comparative work could help us predict patterns of odor use. We already know that nocturnal birds have larger olfactory bulbs, the region of the brain involved in processing volatile chemical stimuli (Healy and Guilford 1990), but it is unclear whether such species are more likely to employ odor signals. It is also plausible that island birds that have evolved in the absence of mammalian predators may be more likely to emit odorous substances (I. Castro pers. comm.). Almost all Hawaiian honeycreepers (Drepanidinae), for example, produce plumage odor (Weldon and Rappole 1997).

Studies of avian chemosensory anatomy, physiology, and development are also needed. Ornithologists rarely distinguish between the three vertebrate chemosenses: olfaction, taste, and the trigeminal system. Olfaction has received the most attention, but data on the other two are scarce. Hagelin (2007) also pointed out that few details on the microstructure of avian chemosensory anatomy are known. Different cell types in the olfactory bulb, for example, have been quantified only in two Rock Pigeons and one Northern Fulmar (Wenzel and Meisami 1987, 1990). Seasonal shifts in sensitivity to volatile chemical stimuli occur in adults of at least one avian species (European Starling [*Sturnus vulgaris*]; Clark and Smeraski 1990), but the underlying anatomical changes, if any, are unstudied. Changes in chemosensory microstructure of developing birds or embryos exposed to avian compounds are also unknown, even though the process of chemical imprinting in other vertebrates can involve dramatic morphological and behavioral alterations (e.g., Semke et al. 1995, Dittman et al. 1996).

Finally, recent investigations have uncovered intriguing neuroanatomical and molecular patterns in birds and humans. Like humans, birds apparently lack a functional vomeronasal system (Rieke and Wenzel 1975, 1978), which is considered one important pathway for processing sex pheromones in mammals and other vertebrates (e.g., Baxi et al. 2006). Both birds and humans, however, retain the terminal nerve, which has been suggested to transmit pheromonal cues to parts of the brain that control reproductive behavior (e.g., Wirsig 1987, Fields 2007). Understanding the terminal nerve's function in birds could provide evidence for the first avian pheromone. Sequencing of the chicken genome has also revealed that birds exhibit a large expansion of olfactory receptor genes, some of which are orthologous to those in humans (e.g., International Chicken Genome Sequencing Consortium 2004, Furlong 2005). Soini et al. (2007) pointed out that CD1 genes, which are evolutionary precursors to MHC genes (Penn 2002, Zelano and Edwards 2002), occur in both humans and birds. In humans, CD1 is involved in fatty acid and glycolipid synthesis, but in birds it may regulate production of oils in preen glands and thereby affect avian odor or other secretions (Soini et al. 2007). Birds and people rely heavily on visual and auditory cues, but chemosignals and the mechanisms that control them are clearly emerging as an overlooked aspect of our shared biology.

Conclusions

Studies of chemical defense and intraspecific chemosignals in birds have the potential to reshape our understanding of avian biology by altering fundamental assumptions. Just as startling as the link between pitohui toxins and poison dart frogs (Dumbacher et al. 1992), the existence of avian chemosignals is akin to birds responding to ultraviolet plumage ornaments that humans cannot see (i.e., Bennett et al. 1997).

The evidence we have presented indicates the following conclusions. (1) Scents, secretions, and other chemical substances are widespread in birds and potentially derived from a number of different sources. (2) Data for avian chemical defense is particularly strong for pitohuis, but our understanding of these and other species will benefit from studies that consider interspecific as well as intraspecific roles for how chemical substances function. (3) Avian body odors and olfaction have been linked to numerous social circumstances involving conspecific

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communication, including courtship, mate recognition, homing to nest sites, development, odor learning, and scent aversions, all of which potentially involve adaptive behavioral responses. (4) Studies of sensory systems are inherently interdisciplinary, and the future is promising for investigations that focus on odors or chemical substances at every level of avian biology, particularly those that take advantage of detailed chemosensory information available for other animal groups.

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