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Avian Olfaction: A Review of the Recent Literature

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All birds studied to date have a functioning sense of smell, which they use for a wide range of tasks, from foraging to mate choice. However, compared with other avian senses, olfaction has received comparatively little research attention and is often overlooked when designing experiments, or interpreting data, in which birds have been used as subjects. This brief review aims to provide an overview of our understanding of avian olfaction, focusing in particular on articles published over the past 10 years. We emphasize studies, species, and concepts that may be of particular interest to those working within animal behavior or cognition, and we conclude by highlighting some directions for future research.

Keywords: *Birds*, *sense of smell*, *sensory ecology*, *semiochemical*

Background

Birds can smell. Despite early assumptions that birds had little or no sense of smell (Audubon, 1826; Hill, 1905; Stager, 1964), there is now abundant evidence that they are endowed with all the anatomical and neurobiological components necessary for a functional olfactory sense (Balthazart & Taziaux, 2009; Caro, Balthazart, & Bonadonna, 2015), and morphologically the olfactory systems of birds closely resembles those of amphibians, reptiles, and mammals (Kare & Mason, 1986; Wenzel, 1987). Most birds have paired external nares through which they breathe air, internal nasal cavities that contain olfactory epithelium, functional olfactory receptors, and a neuronal connection to the olfactory bulb in the forebrain (Jones & Roper, 1997). Moreover, they have been shown to use odor cues for tasks as diverse as foraging (e.g., Healy & Guilford, 1990; Nevitt, Loosekoot, & Weimerskirch, 2008; Potier, Duriez, Celerier, Liegeois, & Bonadonna, 2019), recognizing eggs (Leclaire, Bourret, & Bonadonna, 2017), selecting nest material (e.g., Gwinner, 2013), and avoiding predation (e.g., Amo, Galvan, Tomás, & Sanz, 2008), as well as in social contexts such as species (e.g., Krause et al., 2014), kin (e.g., Bonadonna & Sanz-Aguilar, 2012; Coffin, Watters, & Mateo, 2011; Krause et al., 2012), and mate recognition (e.g., Bonadonna & Nevitt, 2004). However, we argue that even today there is a tendency for researchers to underappreciate the possible role olfaction plays in birds' everyday lives.

Compelling evidence shows that vision and, to a lesser extent, hearing are the primary avian senses (Martin, 2017). By contrast, few bird species smell noticeably to humans (although there are notable exceptions, such as Crested auklets [*Aethia cristatella*]; Hagelin, Jones, & Rasmussen, 2003), and they do not typically engage in any overt olfactory behavior, such as sniffing. However, this should not be taken to mean that olfaction is of limited importance to them. To put birds' sense of smell in perspective, it is useful to provide a comparison with humans. In humans, as in birds, olfaction is commonly considered to be the least acute sense; despite this, it has been estimated that humans with intact olfactory systems can detect (Amoore, 1977) and discriminate (Bushdid, Magnasco, Vosshall, & Keller, 2014) virtually all volatile chemicals, and we are known to use olfactory (in association with visual and auditory) information widely in our day-to-day lives for tasks ranging from identifying palatable food to selecting mates (e.g., Milinski, Croy, Hummel, & Boehm, 2013; Stevenson, 2010). Similarly, passerine birds have traditionally been considered to have comparatively poor olfactory abilities, in a large part because of the small relative size of their olfactory bulbs (typically well below the median for birds as a whole; Avilés & Amo, 2018). However some passerine species, such as zebra finches (*Taeniopygia guttata*), have a similar number of functional olfactory receptor genes (which encode for olfactory receptors) to humans (Malnic, Godfrey, & Buck, 2004; Steiger, Kuryshev, Stensmyr, Kempenaers, & Mueller, 2009) and are known to use olfaction for tasks as subtle as discriminating between conspecifics and heterospecifics (Krause et al., 2014) and discerning kin from non-kin (Krause, Krueger, Kohlmeier, & Caspers, 2012). Moreover, although we know very little about odor detection thresholds in birds, there is evidence that for certain odorants, detection thresholds in passerines are probably comparable with those of mammals, such as rabbits, rats (Clark, Avilova, & Bean, 1993), and possibly humans (Abraham, Sanchez-Moreno, Cometto-Muniz, & Cain, 2012). Although the sense of smell undoubtedly varies considerably between bird species, there is every reason to assume that for most species olfaction plays an important role in their day-to-day lives. This alone highlights the importance we should give to avian olfaction, not only as a topic of research in its own right but as a factor to consider when designing and interpreting experiments in areas that use birds as subjects.

Several excellent reviews on the general topic of avian olfaction already exist, and readers interested in a historical perspective on the development of avian olfaction as a research topic, those interested in the role of olfaction in specific aspects of avian behavior (e.g., reproductive behavior), and those interested in specific mechanistic aspects (e.g., those relating to the neurophysiology or genetics of avian olfaction) are referred to them (in particular, see reviews in Balthazart & Taziaux, 2009; Caro et al., 2015; Hagelin, 2007; Jones & Roper, 1997; Roper, 1999; Steiger et al., 2008). Here we provide a general overview of avian olfaction, particularly as it relates to bird behavior, focusing predominantly on articles published (and, hence, themes addressed) over the past decade.

Odor Detection, Discrimination, and Identification

Foraging

Abundant evidence shows that birds can detect and discriminate odors in the lab (Roper, 1999) and in the wild. For example, when kea (*Nestor notabilis*) and kaka (*Nestor meridionalis*) were allowed to exhibit natural explorative behaviors, both species were able to distinguish between biologically relevant odors (including fruit-based odors, the odor of a herbaceous plant, and the odor of conspecific and heterospecific feathers—odors of the type they may experience in their natural environment) and controls, and were able to detect novel odors (Gsell, Hagelin, & Brunton, 2012). Similarly, a number of other bird species are known to use odors during foraging. For example, the North Island brown kiwi (*Apteryx mantelli*) may use short-range olfactory information (probably in the order of a few centimeters) to locate profitable food patches (S. J. Cunningham, Castro, & Potter, 2009), whereas various vulture species are attracted by real and synthetic odors (e.g., ethyl mercaptans) indicative of decaying animal carcasses, often from considerable distances (Graves, 1992; Stager, 1964). Recently, Potier et al. (2019) showed that both turkey vultures (*Cathartes aura*) and Southern caracaras (*Caracara plancus*) interacted more with a stainless-steel perforated ball containing the odor of putrefied meat compared with an odorless but otherwise identical control ball, suggesting that both species are able to use olfactory cues for foraging. Moreover, turkey vultures seemed to disregard associated visual information when it conflicted with the olfactory cue, which is consistent with the suggestion that olfaction is the predominant sense in turkey vultures (Potier et al., 2019).

The ability of procellariform seabirds, such as shearwaters and petrels, to use odor for navigation has been established for decades (e.g., Grubb, 1972). Antarctic prions (*Pachiptila desolata*), for example, can detect and behaviorally respond to biologically relevant levels of dimethyl sulphide, a compound produced by

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phytoplankton that contributes to the natural olfactory landscape over the world's oceans and that is used as a foraging cue in the wild (Nevitt & Bonadonna 2005). Similarly, Wandering albatrosses (*Diomedea exulans*) forage over thousands of square kilometers of open ocean for patchily distributed food sources and exhibit flight patterns consistent with searching for, and then localizing, an odor plume emanating from a prey item (Nevitt et al., 2008).

There is evidence that insectivorous birds can detect odors produced by their prey. A recent study by Saavedra and Amo (2018), for instance, showed that wild birds attacked imitation plasticine caterpillars more when they were placed on trees with dispensers emitting winter moth (*Operophtera bumata*) pheromones than on trees with control dispensers, strongly suggesting that the birds were using odor cues to mediate their choice of foraging location. Many plants also release volatile compounds in response to insect herbivory, which act to attract parasitoids and insect predators, and there is good evidence that these volatiles can be used by insectivorous birds to identify insect-rich trees (Dicke, 2009; Fatouros et al., 2012; Mäntylä, Alessio, et al., 2008). For example, naïve captive adult great tits (*Parus major*) have been shown to respond to volatiles (possibly α-farnesene) emitted by trees damaged by the winter moth (Amo, Jansen, van Dam, Dicke, & Visser, 2013), a potential prey species. When given the option to choose between olfactory and visual cues, either on their own or combined, birds preferentially chose the infested trees based solely on the volatile chemical emitted rather than by visual cues, such as the presence of moth larvae or their feeding damage, or differences in leaf coloration (Amo et al., 2013). Wild birds have also been shown to respond to herbivore-induced odors in a similar way. For example, by experimentally inducing production of herbivore-induced volatiles on grey willow (*Salix cinerea*), Mrazova and Sam (2018) demonstrated that wild birds attacked plasticine caterpillars placed on treatment trees significantly more often than controls. Similarly, a study by Hiltpold and Shriver (2018) showed that imitation clay caterpillars were attacked 7 times more frequently when located close to dispensers emitting a synthetic blend of herbivore-induced volatiles than when located close to control dispensers containing only the solvent. However, Koski et al. (2015) found no evidence that great tits or blue tits (*Cyanistes caeruleus*) responded to either artificial or real trees supplemented with herbivore-induced volatiles, or toward herbivore-damaged saplings when these saplings were hidden from view.

Insectivorous birds will also feed upon insect eggs if larvae and adults are unavailable, and great tits and blue tits have been shown to be more attracted to Scots pine (*Pinus sylvestris*) branches on which pine sawflies (*Diprion pini*) had deposited eggs than to untreated controls, even when there were no larvae or adults present (Mäntylä, Kleier, Kipper, & Hilker, 2017). Treatment branches released more of the compound (E)-β-farnesene compared with control branches, which may be the olfactory cue to which the birds were responding (although the precise compound or mixture of compounds that birds were using to discriminate between infected and uninfected trees is not known). Taken together, the studies just discussed provide compelling evidence for the key role that olfaction can play in avian foraging behavior.

Mate Choice

Birds possess a preen (or uropygial) gland, which secretes waxy fluids (preen oils) that a bird picks up with its bill and spreads over its feathers when it preens. The primary function of preen oils is to provide a protective function to feathers by waterproofing the contour and flight feathers and maintaining feather flexibility. However, because any odorous compounds present in the preen oil (derived either from the preen oil itself or from bacterial degradation of preen oil constituents; Maraci, Engel, & Caspers, 2018) will be spread over much of the feather surface during preening, it has also been suggested that they may provide a source of body odor (Caro et al., 2015; J. Jacob, 1978a, 1978b). The precise composition of this preen oil varies considerably among different species, individuals, and sexes (Grieves, Bernards, & MacDougall-Shackleton, 2019b; Leclaire et al., 2011; Potier et al., 2018; Tuttle et al., 2014; Whittaker et al., 2010), at least in part because of its links to genotype (specifically variation at the major histocompatibility complex; Leclaire et al., 2014; Slade et al., 2016) and age (Grieves, Kelly, Bernards, & MacDougall-Shackleton, 2018; Shaw, Rutter, Austin, Garvin, & Whelan, 2011). Preen oil composition also varies seasonally (Bhattacharyya & Chowdhury, 1995; Fischer, Halinski, Meissner, Stepnowski, & Knitter, 2017; Grieves et al., 2019b) and is associated with a bird's diet (Thomas, Bourgault, Shipley, Perret, & Blondel, 2010), microbiome (S. Jacob et al., 2014), and parasite load (Grieves et al., 2018). For example, the chemical composition of preen oil in song sparrows (*Melospiza melodia*) differed between birds that had been inoculated with malarial parasites (*Plasmodium* sp.) and those that had been sham inoculated (Grieves et al., 2018). The secretion of the uropygial gland, therefore, has the potential to provide a rich source of information to conspecific receivers (Caro et al., 2015; Hagelin & Jones, 2007).

A number of studies have demonstrated that birds can detect and discriminate between preen oil–derived odors and use them for key ecological tasks, such as discriminating between conspecifics and heterospecifics (Krause et al., 2014), between kin and non-kin (Fracasso, Tuliozi, Hoi, & Griggio, 2019; Krause et al., 2012), and between males and females of the same species (Amo et al., 2012; Whittaker et al., 2011). For example, when zebra finches were presented with the odor of conspecifics compared with that of a closely related heterospecific with an overlapping distribution area (diamond firetails, *Stagonopleura guttata*) in a Y-maze, they showed a significant preference for the odor of conspecifics, although diamond firetails exhibited no such preference, possibly because zebra finches are a more social species than diamond firetails (Krause et al., 2014). Grieves, Bernards, and MacDougall-Shackleton (2019a) presented breeding-condition song sparrows with a choice between opposite-sex and same-sex preen oil odors in a Y-maze and demonstrated that both males and females preferred the opposite-sex odor. Fracasso et al. (2019) investigated whether house sparrow (*Passer domesticus*) females can recognize kin-related odors, and how perception of kin may be affected by familiarity, by offering them a simultaneous choice between the scents of a related familiar male, an unrelated familiar male, and an unrelated unfamiliar male. The authors found that females avoided the odor of unrelated familiar males, both in the breeding and nonbreeding seasons, and suggested that this aversion may play a role in minimizing the chances of aggressive interactions.

Predator Odor

Certain bird species have been shown to detect and respond behaviorally to the scent of predator odor, particular that of putative mammalian predators (e.g., Amo et al., 2008; Amo, Visser, & van Oers, 2011; Fluck, Hogg, Mabbutt, & File, 1996; Hagelin et al., 2003; Leclaire, Mulard, Wagner, Hatch, & Danchin, 2009; T. C. Roth, Cox, & Lima, 2008), although not in all situations (Amo, Caro, & Visser, 2011a; Godard, Bowers, & Wilson, 2007): Amo, Caro, and Visser (2011), for example, found that great tits were unable to detect predator chemical cues while sleeping. Zidar and Løvlie (2012) exposed naïve captive red junglefowl (*Gallus gallus gallus*) to fecal samples from two of their natural predators, tigers (*Panthera tigris*) and dholes (*Cuon alpinus*), as well as to nonpredator fecal odors. The birds were found to spend the least time foraging, and the most time engaged in vigilance behavior, when exposed to predator fecal odor. More recently, Mahr and Hoi (2018) have shown that red-legged partridge (*Alectoris rufa*) preferentially avoided the odor of both a mammalian predator (ferret [*Mustela putorius furo*] faeces) and an avian alarm signal (the alarm secretion of the European hoopoe [*Upupa epops*]) compared with a control odor. Avilés, Parejo, and Exposito-Granados (2019) looked at whether exposing various Mediterranean hole-nesting birds, including little owls (*Athene noctua*), scops owls (*Otus scops*), Eurasian rollers (*Coracias garrulus*), European hoopoes, great tits, spotless starlings (*Sturnus unicolor*), rock sparrows (*Petronia petronia*), and jackdaws (*Corvus monedula*), to predator odors affected their settlement patterns in nest boxes. Among other things, they found that control nest boxes were occupied more rapidly and in higher numbers than nest boxes with the odor of a mammalian predator, the ferret. Because olfactory cues may be used by these species to assess habitat quality, this may have considerable implications for population management and conservation strategies, both of which require a detailed understanding of the target species' perceptual capabilities.

Choice of Nest Material

Several bird species incorporate herbaceous plant material into their nests, which tend to be rich in volatile compounds (in many cases the same chemical compounds humans use to make aromatic house cleaners and herbal medicines; Petit, Hossaert-McKey, Perret, Blondel, & Lambrechts, 2002) and produce noticeable odors (Dubiec, Gozdz, & Mazgajski, 2013). For example, male European starlings (*Sturnus vulgaris*) incorporate herbs such as yarrow (*Achillea millefolium*) into their nests; this is sparsely distributed in the environment, and so its inclusion does not appear to be random, suggesting that birds must be actively selecting them as nesting materials (Ruiz-Castellano, Tomás, Ruiz-Rodríguez, & Soler, 2018). They might engage in this particular behavior for a number of reasons (Tomás et al., 2013), including to attract a mate or signal condition or paternal quality, to act as olfactory repellents or toxins by decreasing nest parasites and pathogens, or to stimulate nestling immune systems. Some species, such as blue tits, seem to be able to use odor cues to determine how often they need to replenish the nest with fresh herbaceous material (Petit et al., 2002). In their study, Petit et al. (2002) added leaves of the herbs southern yarrow (*Achillea ligustica*) and lavender (*Lavandula stoechas*) to nests in which all herbaceous material had been removed, in such a way that birds could smell but not see them. They found that a significantly greater percentage of experimental nests were replenished with herb fragments compared with control nests.

There is evidence that starlings' ability to detect biologically relevant odors, such as that of yarrow, is seasonal (Clark & Smeraski, 1990), as cardiac-conditioned responses were most evident when birds were in breeding condition and all but ceased once birds were in nonbreeding condition. Building on this work, De Groof, Gwinner, Steiger, Kempenaers, and Van der Linden (2010) used repeated in vivo manganese-enhanced magnetic resonance imaging (MRI) to quantify the seasonal changes in the activity of the olfactory bulb. This work has demonstrated that the olfactory bulb was able to discriminate yarrow odor from background odors only during the reproductive period.

Odor-Based Navigation

Considerable literature exists on birds' ability to navigate their environment using olfactory information, and this topic is discussed in depth elsewhere (e.g., Bingman, 2018; Gagliardo, 2013; Wallraff, 2004). Although there is some controversy regarding the extent to which pigeons (*Columba livia*) rely on olfaction for navigation (Bingman, 2018), there is little doubt that, under some circumstances, environmental odors allow homing pigeons to determine where they are relative to home from unfamiliar locations (Gagliardo, 2013; Wallraff, 2005, 2014). Specifically, it is thought that homing pigeons are able to generate an odor-based navigational map by associating wind-borne odors at their home location with the direction in which the winds are traveling. On a homeward flight, they can then determine the most appropriate direction of displacement by making use of local odor information (Papi, 1989). In a recent study by Gagliardo, Pollonara, and Wikelski (2016), for instance, homing pigeons were rendered temporarily anosmic (i.e., lacking a sense of smell) just prior to their release, and their homeward flights were tracked using GPS. When pigeons had been able to sample environmental odors both during their transportation and on arrival at their release site, they were able to orientate correctly toward their destination but showed impaired homing performance (i.e., they knew which direction to fly in initially but were less good at navigating along the way). By contrast, pigeons that were transported and kept at the release site in purified air were unable to orient toward home and were impaired during homing. These results are consistent with the notion that local odors at the release site are essential for pigeons to develop an olfactory navigational map.

Although much of the work in this area has focused on pigeons, it is notable that experimental evidence for olfactory navigation has also been found in several wild bird species, including swifts (*Apus apus*; Fiaschi, Farina, & Ioalé, 1974), starlings (Wallraff, Kiepenheuer, Newmann, & Streng, 1995), catbirds (*Dumetella carolinensis*; Holland et al., 2009), Cory's shearwaters (*Calonectris borealis*; Gagliardo et al., 2013), and lesser black-backed gulls (*Larus fuscus*; Wikelski et al., 2015).

Odor Learning

We know very little about the acquisition of odor preferences, although there is evidence that the odors an embryo is exposed to inside the egg can affect its behavior after hatching (Burne & Rogers, 1999; Jones, Facchin, & McCorquodale, 2002; Mabayo et al., 1996). For example, chicken hatchlings typically find strawberry odor highly aversive. However, Sneddon, Hadden, and Hepper (1998) found that this aversion could be completely overcome by exposing embryos to strawberry odor during incubation (by presenting the odor in the air around the egg, rubbing it onto the shell, or injecting it into the air space). After hatching, chicks were given binary choices between strawberry-flavored drinking water and plain water, and between strawberry-smelling wood shavings and unscented shavings; in each case they significantly preferred the strawberry-smelling option. More recently, research has demonstrated that chicks can also use olfactory information gained from within the egg to guide their feeding behavior, although the behavioral response varied depending on the concentration of the odor to which they were exposed (in this case, a blend of orange essential oil and vanillin; Bertin et al., 2010). Specifically, chicks that had previously been exposed to a relatively low concentration of the odor spent significantly more time eating scented food than control chicks; conversely, scented foods were completely avoided by chicks previously exposed to a high odor concentration.

Odors experienced by developing embryos can also influence their subsequent olfactory search behavior. G. B. Cunningham and Nevitt (2011), for example, painted the eggs of wild thin-billed prions (*Pachyptila belcheri*) with a novel floral odor (an aqueous solution of phenyl ethyl alcohol [PEA]) or a control (water) in the days running up to hatching. They then tested whether chicks could detect the presence or absence of PEA in a wind tunnel by recording the number of times they performed head sweeps (a distinctive behavior associated with olfactory search that involves wagging the head from side to side in broad sweeping motions around the body). PEA-exposed chicks performed significantly more head sweeps in the presence of PEA odor than in response to plain water, whereas control chicks swept their heads at the same rate in response to both stimuli. Parents may therefore be able to indirectly shape olfactory-based behaviors by exposing chicks to relevant environmental odors during embryonic development (Burne & Rogers, 1999; G. B. Cunningham & Nevitt, 2011).

Finally, certain evidence suggests that embryos may be able to acquire social olfactory information from inside the egg. Hagelin, Simonet, and Lyson (2013) incubated chicken eggs either in air containing Z-4-decenal and octanal—two key components of the citrusy-smelling social odor of crested auklets (Hagelin et al., 2003)—or in nonscented air. Although unhatched embryos in both the treatment and control conditions could subsequently detect auklet odor, odor-treated embryos showed a reduced behavioral response (e.g., less kicking and body shifting), which is consistent with odor familiarity. More recently, Caspers et al. (2017) showed that the ability to make social odor discriminations is present at hatching in zebra finch chicks, even after cross-fostering, suggesting that at least some birds have the ability to acquire chemosensory knowledge of their parents before hatching (Sneddon et al. 1998).

Adult birds also have the ability to learn olfactory information. For instance, there is good evidence that pairing an olfactory warning odor (e.g., pyrazine) with a visual signal can increase the rate of learned avoidance to an unpalatable prey item and that the odor can improve the memory of this learned avoidance, as demonstrated in domestic chicks (Siddall & Marples, 2008) and wild robins (*Erithacus rubecula*; Siddall & Marples, 2011), for example. Studies have also shown that various avian species, including great tits and blue tits (Anisimov, Barsova, & Popovkina, 2004) and yellow-backed chattering lories (*Lorius garrulus flavopalliatus*; Roper, 2003), are able to learn to associate an odor with the location of a food reward. For example, using plant-derived odor cues, Roper (2003) successfully trained lories to distinguish a scented dispenser containing an artificial nectar solution from an unscented control dispenser containing water. More recently, Slater and Hauber (2017) found that several species of captive birds of prey can learn to associate a novel scent cue with the presence of food. Specifically, birds were trained to associate wrapped bundles of food (designed to allow natural ripping and tearing behavior) with the smell of peppermint oil. During tests they were then presented with two sets of sham packages (i.e., containing no food), one of which was scented with peppermint oil: Individuals more frequently and more extensively handled scented versus unscented packages. Finally, it is noteworthy that learning may play a role in birds' use of herbivore-induced olfactory cues, which they use to identify locations in which insects are feeding (see earlier). Amo, Dicke, and Visser (2016) demonstrated that naïve great tits were not attracted to insect-infested trees when they could not see the larvae or their feeding damage, and so where birds do respond to these odors (e.g., Amo et al., 2013,) this is most likely to have been acquired through learning.

Future Directions

Our understanding of avian olfaction has increased considerably over recent years, primarily driven by interest in the role that olfaction plays in birds' behavioral ecology (e.g., Caro et al., 2015). However, compared with vision and hearing, our current understanding is still patchy at best. In particular, although we have a fairly good grasp on the function that olfaction plays in birds' day-to-day lives, we know relatively little about things such as olfactory detection thresholds (the minimum concentration of an odorant that can be reliably detected and differentiated from a blank sample), how sensitive birds are to different compounds (or different classes of compound), how (readily) odors are learned and memorized, how olfaction interacts with (to either influence or enhance) other senses, or how birds use odor stimuli in cognitive tasks.

Initial studies put a lot of weight on olfactory bulb size when categorizing birds' olfactory abilities, primarily considering them to be "essentially anosmic" (e.g., most passerines) or having a functioning sense of smell (e.g., seabirds). However, just because a species has a relatively less well-developed olfactory sense (as may be reasonably deduced from its relative olfactory bulb size; Bang & Cobb, 1968), this doesn't mean that it has a poor sense of smell or that odors do not form a rich (and possibly essential) source of information (Corfield et al., 2015). In fact, to the best of our knowledge, every bird species that has been assessed for olfactory ability has been found (regardless of their relative or absolute olfactory bulb size) to be able to smell, and in the overwhelming majority of cases this ability has been linked directly to an ecological function. The number of such species in the literature now exceeds 50, and studies contain examples from approximately half of the avian orders (see the references herein). Birds exhibit enormous ecological and life-history variation, as well as marked interspecific variation in olfactory bulb sizes and in the number of functional olfactory receptor genes they possess (e.g., Steiger, Fidler, Valcu, & Kempenaers, 2008). Therefore, there is considerable potential for comparative studies, comparing olfactory abilities, mechanisms, and function between different bird species (e.g., Avilés & Amo, 2018). Given that techniques are now available for studying birds' behavioral responses to odor in both captive (lab and zoo) and wild birds (see earlier citations), we see this as a particularly fruitful direction for future research.

References

Abraham, M. H., Sanchez-Moreno, R., Cometto-Muniz, J. E., & Cain, W. S. (2012). An algorithm for 353 odor detection thresholds in humans. *Chemical Senses, 37*(3), 207–218. doi:10.1093/chemse/bjr094

Amo, L., Avilés, J. M., Parejo, D., Pena, A., Rodriguez, J., & Tomás, G. (2012). Sex recognition by odour and variation in the uropygial gland secretion in starlings. *Journal of Animal Ecology, 81*(3), 605–613. doi:10.1111/j.1365-2656.2011.01940.x

Amo, L., Caro, S. P., & Visser, M. E. (2011). Sleeping birds do not respond to predator odour. *PLOS One, 6*(11), e27576. doi:10.1371/journal.pone.0027576

Amo, L., Dicke, M., & Visser, M. E. (2016). Are naive birds attracted to herbivore-induced plant defences? *Behaviour, 153*(3), 353–366. doi:10.1163/1568539x-00003345

Amo, L., Galvan, I., Tomás, G., & Sanz, J. J. (2008). Predator odour recognition and avoidance in a songbird. *Functional Ecology, 22*(2), 289–293. doi:10.1111/j.1365-2435.2007.01361.x

Amo, L., Jansen, J. J., van Dam, N. M., Dicke, M., & Visser, M. E. (2013). Birds exploit herbivore-induced plant volatiles to locate herbivorous prey. *Ecology Letters, 16*(11), 1348–1355. doi:10.1111/ele.12177

Amo, L., Visser, M. E., & van Oers, K. (2011). Smelling out predators is innate in birds. *Ardea, 99*(2), 177–184. doi:10.5253/078.099.0207

Amoore, J. E. (1977). Specific anosmia and the concept of primary odors. *Chemical Senses, 2*, 267–281. doi:10.1093/chemse/2.3.267

Anisimov, V. D., Barsova, L. I., & Popovkina, A. B. (2004). Olfactory reception in food search in tits of the genus *Parus* (Passeriformes, Paridae). *Zoologichesky Zhurnal, 83*(9), 1138–1147.

Audubon, J. J. (1826). Account of the habits of the turkey vulture, *Vulture aurea*, particularly with the view of exploding the opinion generally entertained of its extraordinary power of smelling. *Edinburgh New Philosophical Journal, 2*, 172–184.

Avilés, J. M., & Amo, L. (2018). The evolution of olfactory capabilities in wild birds: A comparative study. *Evolutionary Biology, 45*(1), 27–36. doi:10.1007/s11692-017-9427-6

Avilés, J. M., Parejo, D., & Exposito-Granados, M. (2019). Avian and rodent responses to the olfactory landscape in a Mediterranean cavity community. *Oecologia, 191*(1), 73–81. doi:10.1007/s00442-019-04487-w

Balthazart, J., & Taziaux, M. (2009). The underestimated role of olfaction in avian reproduction? *Behavioural Brain Research, 200*(2), 248–259. doi:10.1016/j.bbr.2008.08.036

Bang, B.G., & Cobb, S. (1968) The size of the olfactory bulb in 108 species of birds. *Auk*, *85*(1), 55–61. doi:10.2307/4083624

Bertin, A., Calandreau, L., Arnould, C., Nowak, R., Levy, F., Noirot, V., … Leterrier, C. (2010). In ovo olfactory experience influences post-hatch feeding behaviour in young chickens. *Ethology, 116*(11), 1027–1037. doi:10.1111/j.1439-0310.2010.01820.x

Bhattacharyya, S. P., & Chowdhury, S. R. (1995). Seasonal-variation in the secretory lipids of the uropygial gland of a subtropical wild passerine bird, *Pycnonotus cafer*, in relation to the testicular cycle. *Biological Rhythm Research, 26*(1), 79–87. doi:10.1080/09291019509360326

Bingman, V. P. (2018). Requiem for a heavyweight—Can anything more be learned from homing pigeons about the sensory and spatial-representational basis of avian navigation? *Journal of Experimental Biology, 221*(20). doi:10.1242/jeb.163089

Bonadonna, F., & Nevitt, G. A. (2004). Partner-specific odor recognition in an Antarctic seabird. *Science, 306*(5697), 835–835. doi:10.1126/science.1103001

Bonadonna, F., & Sanz-Aguilar, A. (2012). Kin recognition and inbreeding avoidance in wild birds: the first evidence for individual kin-related odour recognition. *Animal Behaviour, 84*(3), 509–513. doi:10.1016/j.anbehav.2012.06.014

Burne, T. H. J., & Rogers, L. J. (1999). Changes in olfactory responsiveness by the domestic chick after early exposure to odorants. *Animal Behaviour, 58*, 329–336. doi:10.1006/anbe.1999.1151

Bushdid, C., Magnasco, M. O., Vosshall, L. B., & Keller, A. (2014). Humans can discriminate more than 1 trillion olfactory stimuli. *Science, 343*(6177), 1370–1372. doi:10.1126/science.1249168

Caro, S. P., Balthazart, J., & Bonadonna, F. (2015). The perfume of reproduction in birds: Chemosignaling in avian social life. *Hormones and Behavior, 68*, 25–42. doi:10.1016/j.yhbeh.2014.06.001

Caspers, B. A., Hagelin, J. C., Paul, M., Bock, S., Willeke, S., & Krause, E. T. (2017). Zebra Finch chicks recognise parental scent, and retain chemosensory knowledge of their genetic mother, even after egg cross-fostering. *Scientific Reports, 7,* Article 12859. doi:10.1038/s41598-017-13110-y

Clark, L., Avilova, K. V., & Bean, N. J. (1993). Odor thresholds in passerines. *Comparative Biochemistry and Physiology A–Physiology, 104*(2), 305–312. doi:10.1016/0300-9629(93)90322-u

Clark, L., & Smeraski, C. A. (1990). Seasonal shifts in odor acuity by starlings. *Journal of Experimental Zoology, 255*(1), 22–29. doi:10.1002/jez.1402550105

Coffin, H. R., Watters, J. V., & Mateo, J. M. (2011). Odor-Based Recognition of Familiar and Related Conspecifics: A First Test Conducted on Captive Humboldt Penguins (*Spheniscus humboldti*). *PLoS One, 6*(9), e25002. doi:10.1371/journal.pone.0025002

Corfield, J. R., Price, K., Iwaniuk, A. N., Gutierrez-Ibañez, C., Birkhead, T., & Wylie, D. R. (2015). Diversity in olfactory bulb size in birds reflects allometry, ecology, and phylogeny. *Frontiers in Neuroanatomy*, *9*, Article 102. doi:10.3389/fnana.2015.00102

Cunningham, G. B., & Nevitt, G. A. (2011). Evidence for olfactory learning in procellariiform seabird chicks. *Journal of Avian Biology, 42*(1), 85–88. doi:10.1111/j.1600-048X.2010.05184.x

Cunningham, S. J., Castro, I., & Potter, M. A. (2009). The relative importance of olfaction and remote touch in prey detection by North Island brown kiwis. *Animal Behaviour, 78*(4), 899–905. doi:10.1016/j.anbehav.2009.07.015

De Groof, G., Gwinner, H., Steiger, S., Kempenaers, B., & Van der Linden, A. (2010). Neural correlates of behavioural olfactory sensitivity changes seasonally in European starlings. *PLOS One, 5*(12), e14337. doi:10.1371/journal.pone.0014337

Dicke, M. (2009). Behavioural and community ecology of plants that cry for help. *Plant Cell and Environment, 32*(6), 654–665. doi:10.1111/j.1365-3040.2008.01913.x

Dubiec, A., Gozdz, I., & Mazgajski, T. D. (2013). Green plant material in avian nests. *Avian Biology Research, 6*(2), 133–146. doi:10.3184/175815513x13615363233558

Fatouros, N. E., Lucas-Barbosa, D., Weldegergis, B. T., Pashalidou, F. G., van Loon, J. J. A., Dicke, M., . . . Huigens, M. E. (2012). Plant volatiles induced by herbivore egg deposition affect insects of different trophic levels. *PLOS One, 7*(8), e43607. doi:10.1371/journal.pone.0043607

Fiaschi, V., Farina, M., & Ioalé, P. (1974). Homing experiments on swifts *Apus apus* (L.) deprived of olfactory perception. *Monitore Zoologico Italiano*, *8*, 235–244.

Fischer, I., Halinski, L. P., Meissner, W., Stepnowski, P., & Knitter, M. (2017). Seasonal changes in the preen wax composition of the Herring gull *Larus argentatus*. *Chemoecology, 27*(4), 127–139. doi:10.1007/s00049-017-0239-z

Fluck, E., Hogg, S., Mabbutt, P. S., & File, S. E. (1996). Behavioural and neurochemical responses of male and female chicks to cat odour. *Pharmacology Biochemistry and Behavior, 54*(1), 85–91. doi:10.1016/0091-3057(95)02170-1

Fracasso, G., Tuliozi, B., Hoi, H., & Griggio, M. (2019). Can house sparrows recognize familiar or kin-related individuals by scent? *Current Zoology, 65*(1), 53–59. doi:10.1093/cz/zoy018

Gagliardo, A. (2013). Forty years of olfactory navigation in birds. *Journal of Experimental Biology, 216*(12), 2165–2171. doi:10.1242/jeb.070250

Gagliardo, A., Bried, J., Lambardi, P., Luschi, P., Wikelski, M., & Bonadonna, F. (2013). Oceanic navigation in Cory's shearwaters: Evidence for a crucial role of olfactory cues for homing after displacement. *Journal of Experimental Biology*, *216*, 2798–2805. doi:10.1242/jeb.085738

Gagliardo, A., Pollonara, E., & Wikelski, M. (2016). Pigeon navigation: exposure to environmental odours prior to release is sufficient for homeward orientation, but not for homing. *Journal of Experimental Biology, 219*(16), 2475–2480. doi:10.1242/jeb.140889

Godard, R. D., Bowers, B. B., & Wilson, C. M. (2007). Eastern bluebirds *Sialia sialis* do not avoid nest boxes with chemical cues from two common nest predators. *Journal of Avian Biology, 38*(1), 128–131. doi:10.1111/j.2007.0908-8857.03788.x

Graves, G. R. (1992). Greater yellow-headed vulture (*Cathartes melambrotus*) locates food by olfaction. *Journal of Raptor Research, 26*(1), 38–39.

Grieves, L. A., Bernards, M. A., & MacDougall-Shackleton, E. A. (2019a). Behavioural responses of songbirds to preen oil odour cues of sex and species. *Animal Behaviour, 156*, 57–65. doi:10.1016/j.anbehav.2019.06.035

Grieves, L. A., Bernards, M. A., & MacDougall-Shackleton, E. A. (2019b). Wax ester composition of songbird preen oil varies seasonally and differs between sexes, ages, and populations. *Journal of Chemical Ecology, 45*(1), 37–45. doi:10.1007/s10886-018-1033-2

Grieves, L. A., Kelly, T. R., Bernards, M. A., & Macdougall-Shackleton, E. A. (2018). Sick birds don't smell: Assessing the impact of haematozoan infection on avian preen oil chemical composition. *Integrative and Comparative Biology, 58*, E82.

Grubb, T. C. J. (1972). Smell and foraging in shearwaters and petrels. *Nature, 237*, 404–405. doi:10.1038/237404a0

Gsell, A. C., Hagelin, J. C., & Brunton, D. H. (2012). Olfactory sensitivity in Kea and Kaka. *Emu, 112*(1), 60–66. doi:10.1071/mu11052

Gwinner, H. (2013). Male European starlings use odorous herbs as nest material to attract females and benefit nestlings. In M. L. East & M. Dehnhard (Eds.), *Chemical signals in vertebrates* (Vol. 12, pp. 353–362). New York, NY: Springer. doi:10.1007/978-1-4614-5927-9_28

Hagelin, J. C. (2007). The citrus-like scent of crested auklets: reviewing the evidence for an avian olfactory ornament. *Journal of Ornithology, 148*, S195–S201. doi:10.1007/s10336-007-0185-6

Hagelin, J. C., & Jones, I. L. (2007). Bird odors and other chemical substances: A defense mechanism or overlooked mode of intraspecific communication? *Auk, 124*(3), 741–761. doi:10.1642/0004-8038

Hagelin, J. C., Jones, I. L., & Rasmussen, L. E. L. (2003). A tangerine-scented social odour in a monogamous seabird. *Proceedings of the Royal Society B–Biological Sciences, 270*(1522), 1323–1329. doi:10.1098/rspb.2003.2379

Hagelin, J. C., Simonet, J. C., & Lyson, T. R. (2013). Embryonic domestic chickens can detect compounds in an avian chemosignal before breathing air. In M. L. East & M. Dehnhard (Eds.), *Chemical signals in vertebrates* (Vol. 12, pp. 363–377). New York, NY: Springer. doi:10.1007/978-1-4614-5927-9_29

Healy, S., & Guilford, T. (1990). Olfactory-bulb size and nocturnality in birds. *Evolution, 44*(2), 339–346. doi:10.2307/2409412

Hill, A. (1905). Can birds smell? *Nature, 71*, 318–319. doi:10.1038/071318b0

Hiltpold, I., & Shriver, W. G. (2018). Birds bug on indirect plant defenses to locate insect prey. *Journal of Chemical Ecology, 44*(6), 576–579. doi:10.1007/s10886-018-0962-0

Holland, R. A., Thorup, K., Gagliardo, A., Bisson, I.-A., Knecht, E., Mizrahi, D., & Wikelski, M. (2009). Testing the role of sensory systems in the migratory heading of a songbird. *Journal of Experimental Biology*, *212*, 4065–4071. doi:10.1242/jeb.034504

Jacob, J. (1978a). Chemical composition of preen gland secretions from some ciconiiform birds. *Lipids, 13*(4), 274–282. doi:10.1007/bf02533670

Jacob, J. (1978b). Hydrocarbon and multibranched ester waxes from uropygial gland secretion of grebes (Podicipediformes). *Journal of Lipid Research, 19*(2), 148–153.

Jacob, S., Immer, A., Leclaire, S., Parthuisot, N., Ducamp, C., Espinasse, G., & Heeb, P. (2014). Uropygial gland size and composition varies according to experimentally modified microbiome in great tits. *BMC Evolutionary Biology, 14,* Article 134. doi:10.1186/1471-2148-14-134

Jones, R. B., Facchin, L., & McCorquodale, C. (2002). Social dispersal by domestic chicks in a novel environment: reassuring properties of a familiar odourant. *Animal Behaviour, 63*, 659–666. doi:10.1006/anbe.2001.1943

Jones, R. B., & Roper, T. J. (1997). Olfaction in the domestic fowl: A critical review. *Physiology & Behavior, 62*(5), 1009–1018. doi:10.1016/s0031-9384(97)00207-2

Kare, M. R., & Mason, J. R. (1986). The chemical senses in birds. In P. D. Sturkie (Ed.), *Avian physiology* (4th ed., pp. 59–73). New York, NY: Springer-Verlag.

Koski, T.-M., Laaksonen, T., Mantyla, E., Ruuskanen, S., Li, T., Giron-Calva, P. S., … Klemola, T. (2015). Do Insectivorous Birds use Volatile Organic Compounds from Plants as Olfactory Foraging Cues? Three Experimental Tests. *Ethology, 121*(12), 1131-1144. doi:10.1111/eth.12426

Krause, E. T., Brummel, C., Kohlwey, S., Baier, M. C., Mueller, C., Bonadonna, F., & Caspers, B. A. (2014). Differences in olfactory species recognition in the females of two Australian songbird species. *Behavioral Ecology and Sociobiology, 68*(11), 1819–1827. doi:10.1007/s00265-014-1791-y

Krause, E. T., Krueger, O., Kohlmeier, P., & Caspers, B. A. (2012). Olfactory kin recognition in a songbird. *Biology Letters, 8*(3), 327–329. doi:10.1098/rsbl.2011.1093

Leclaire, S., Bourret, V., & Bonadonna, F. (2017). Blue petrels recognize the odor of their egg. *Journal of Experimental Biology, 220*, 3022–3025. doi:10.1242/jeb.163899

Leclaire, S., Merkling, T., Raynaud, C., Giacinti, G., Bessiere, J. M., Hatch, S. A., & Danchin, E. (2011). An individual and a sex odor signature in kittiwakes? Study of the semiochemical composition of preen secretion and preen down feathers. *Naturwissenschaften, 98*(7), 615–624. doi:10.1007/s00114-011-0809-9

Leclaire, S., Mulard, H., Wagner, R. H., Hatch, S. A., & Danchin, E. (2009). Can Kittiwakes smell? Experimental evidence in a Larid species. *Ibis, 151*(3), 584–587. doi:10.1111/j.1474-919X.2009.00935.x

Leclaire, S., van Dongen, W. F. D., Voccia, S., Merkling, T., Ducamp, C., Hatch, S. A., … Wagner, R. H. (2014). Preen secretions encode information on MHC similarity in certain sex-dyads in a monogamous seabird. *Scientific Reports, 4*, Article 6920. doi:10.1038/srep06920

Mabayo, R. T., Okumura, J., Hirao, A., Sugita, S., Sugahara, K., & Furuse, M. (1996). The role of olfaction in oil preference in the chicken. *Physiology & Behavior, 59*(6), 1185–1188. doi:10.1016/0031-9384(95)02152-3

Mahr, K., & Hoi, H. (2018). Red-legged partridges perceive the scent of predators and alarm scents of an avian heterospecific. *Animal Behaviour, 144*, 109–114. doi:10.1016/j.anbehav.2018.08.008

Malnic, B., Godfrey, P. A., & Buck, L. B. (2004). The human olfactory receptor gene family. *Proceedings of the National Academy of Sciences of the United States of America, 101*(8), 2584–2589. doi:10.1073/pnas.0307882100

Mäntylä, E., Alessio, G. A., Blande, J. D., Heijari, J., Holopainen, J. K., Laaksonen, T., … Klemola, T. (2008). From plants to birds: Higher avian predation rates in trees responding to insect herbivory. *PLOS One, 3*(7), Article 2832. doi:10.1371/journal.pone.0002832

Mäntylä, E., Kleier, S., Kipper, S., & Hilker, M. (2017). The attraction of insectivorous tit species to herbivore-damaged Scots pines. *Journal of Ornithology, 158*(2), 479–491. doi:10.1007/s10336-016-1412-9

Maraci, O., Engel, K., & Caspers, B. A. (2018). Olfactory communication via microbiota: What is known in birds? *Genes, 9*(8), e387. doi:10.3390/genes9080387

Martin, G. (2017). *The sensory ecology of birds*. Oxford, England: Oxford University Press. doi:10.1093/oso/9780199694532.001.0001

Milinski, M., Croy, I., Hummel, T., & Boehm, T. (2013). Major histocompatibility complex peptide ligands as olfactory cues in human body odour assessment. *Proceedings of the Royal Society B–Biological Sciences, 280*(1755). doi:10.1098/rspb.2012.2889

Mrazova, A., & Sam, K. (2018). Application of methyl jasmonate to grey willow (*Salix cinerea*) attracts insectivorous birds in nature. *Arthropod-Plant Interactions, 12*(1), 1–8. doi:10.1007/s11829-017-9558-9

Nevitt, G. A., & Bonadonna, F. (2005). Sensitivity to dimethyl sulphide suggests a mechanism for olfactory navigation by seabirds. *Biology Letters*, *1*(3), 303–305. doi:10.1098/rsbl.2005.0350

Nevitt, G. A., Losekoot, M., & Weimerskirch, H. (2008). Evidence for olfactory search in wandering albatross, *Diomedea exulans*. *Proceedings of the National Academy of Sciences of the United States of America, 105*(12), 4576–4581. doi:10.1073/pnas.0709047105

Papi, F. (1989). Pigeons use olfactory cues to navigate. *Ethology Ecology and Evolution*, *1*, 219–231. doi:10.1080/08927014.1989.9525511

Petit, C., Hossaert-McKey, M., Perret, P., Blondel, J., & Lambrechts, M. M. (2002). Blue tits use selected plants and olfaction to maintain an aromatic environment for nestlings. *Ecology Letters, 5*(4), 585. doi:10.1046/j.1461-0248.2002.00361.x

Potier, S., Besnard, M. M., Schikorski, D., Buatois, B., Duriez, O., Gabirot, M., … Bonadonna, F. (2018). Preen oil chemical composition encodes individuality, seasonal variation and kinship in black kites *Milvus migrans*. *Journal of Avian Biology, 49*(7), e0728. doi:10.1111/jav.01728

Potier, S., Duriez, O., Celerier, A., Liegeois, J.-L., & Bonadonna, F. (2019). Sight or smell: which senses do scavenging raptors use to find food? *Animal Cognition, 22*(1), 49–59. doi:10.1007/s10071-018-1220-0

Roper, T. J. (1999). Olfaction in birds. In P. J. B. Slater, J. S. Rosenblat, C. T. Snowden, & T. J. Roper (Eds.), *Advances in the study of behavior* (Vol. 28, pp. 247–332). New York, NY: Academic Press. doi:10.1016/S0065-3454(08)60219-3

Roper, T. J. (2003). Olfactory discrimination in Yellow-backed Chattering *Lories Lorius* garrulus flavopalliatus: First demonstration of olfaction in Psittaciformes. *Ibis, 145*(4), 689–691. doi:10.1046/j.1474-919X.2003.00195.x

Roth, T. C., II, Cox, J. G., & Lima, S. L. (2008). Can foraging birds assess predation risk by scent? *Animal Behaviour, 76*, 2021–2027. doi:10.1016/j.anbehav.2008.08.022

Ruiz-Castellano, C., Tomás, G., Ruiz-Rodríguez, M., & Soler, J. J. (2018). Nest material preferences by spotless starlings. *Behavioral Ecology, 29*(1), 137–144. doi:10.1093/beheco/arx139

Saavedra, I., & Amo, L. (2018). Insectivorous birds eavesdrop on the pheromones of their prey. *PLOS One, 13*(2), Article 190415. doi:10.1371/journal.pone.0190415

Shaw, C. L., Rutter, J. E., Austin, A. L., Garvin, M. C., & Whelan, R. J. (2011). Volatile and semivolatile compounds in gray catbird uropygial secretions vary with age and between breeding and wintering grounds. *Journal of Chemical Ecology, 37*(4), 329–339. doi:10.1007/s10886-011-9931-6

Siddall, E. C., & Marples, N. M. (2008). Better to be bimodal: the interaction of color and odor on learning and memory. *Behavioral Ecology, 19*(2), 425–432. doi:10.1093/beheco/arm155

Siddall, E. C., & Marples, N. M. (2011). The effect of pyrazine odor on avoidance learning and memory in wild robins *Erithacus rubecula*. *Current Zoology, 57*(2), 208–214. doi:10.1093/czoolo/57.2.208

Slade, J. W. G., Watson, M. J., Kelly, T. R., Gloor, G. B., Bernards, M. A., & MacDougall-Shackleton, E. A. (2016). Chemical composition of preen wax reflects major histocompatibility complex similarity in songbirds. *Proceedings of the Royal Society B–Biological Sciences, 283*(1842). doi:10.1098/rspb.2016.1966

Slater, M. N., & Hauber, M. E. (2017). Olfactory enrichment and scent cue associative learning in captive birds of prey. *Zoo Biology, 36*(2), 120–126. doi:10.1002/zoo.21353

Sneddon, H., Hadden, R., & Hepper, P. G. (1998). Chemosensory learning in the chicken embryo. *Physiology & Behavior, 64*(2), 133–139. doi:10.1016/s0031-9384(98)00037-7

Stager, K. E. (1964). The role of olfaction in food location by the Turkey vulture (*Cathartes aura*). *Contributions in Science: Los Angeles County Museum of Natural History, 81*, 3–63.

Steiger, S. S., Fidler, A. E., Valcu, M., & Kempenaers, B. (2008). Avian olfactory receptor gene repertoires: evidence for a well-developed sense of smell in birds? *Proceedings of the Royal Society B–Biological Sciences, 275*(1649), 2309–2317. doi:10.1098/rspb.2008.0607

Steiger, S. S., Kuryshev, V. Y., Stensmyr, M. C., Kempenaers, B., & Mueller, J. C. (2009). A comparison of reptilian and avian olfactory receptor gene repertoires: Species-specific expansion of group gamma genes in birds. *BMC Genomics, 10,* Article 446. doi:10.1186/1471-2164-10-446

Stevenson, R. J. (2010). An initial evaluation of the functions of human olfaction. *Chemical Senses, 35*(1), 3–20. doi:10.1093/chemse/bjp083

Thomas, D. W., Bourgault, P., Shipley, B., Perret, P., & Blondel, J. (2010). Context-dependent changes in the weighting of environmental cues that initiate breeding in a temperate passerine, the corsican blue tit (*Cyanistes caeruleus*). *Auk, 127*(1), 129–139. doi:10.1525/auk.2009.09141

Tomás, G., Merino, S., Martinez-de la Puente, J., Moreno, J., Morales, J., & Rivero-de Aguilar, J. (2013). Nest size and aromatic plants in the nest as sexually selected female traits in blue tits. *Behavioral Ecology, 24*(4), 926–934. doi:10.1093/beheco/art015

Tuttle, E. M., Sebastian, P. J., Posto, A. L., Soini, H. A., Novotny, M. V., & Gonser, R. A. (2014). Variation in preen oil composition pertaining to season, sex, and genotype in the polymorphic white-throated sparrow. *Journal of Chemical Ecology, 40*(9), 1025–1038. doi:10.1007/s10886-014-0493-2

Wallraff, H. G. (2004). Avian olfactory navigation: its empirical foundation and conceptual state. *Animal Behaviour, 67*, 189–204. doi:10.1016/j.anbehav.2003.06.007

Wallraff, H. G. (2005). Beyond familiar landmarks and integrated routes: goal-oriented navigation by birds. *Connection Science, 17*(1–2), 91–106. doi:10.1080/09540090500138218

Wallraff, H. G. (2014). Do olfactory stimuli provide positional information for home-oriented avian navigation? *Animal Behaviour, 90*, E1–E6. doi:10.1016/j.anbehav.2014.01.012

Wallraff, H. G., Kiepenheuer, J., Neumann, M. F., & Streng, A. (1995). Homing experiments with starlings deprived of the sense of smell. *Condor*, *97*, 20–26. doi:10.2307/1368979

Wenzel, B. M. (1987). The olfactory and related systems in birds. *Annals of the New York Academy of Sciences, 519*, 137–149. doi:10.1111/j.1749-6632.1987.tb36293.x

Whittaker, D. J., Soini, H. A., Atwell, J. W., Hollars, C., Novotny, M. V., & Ketterson, E. D. (2010). Songbird chemosignals: Volatile compounds in preen gland secretions vary among individuals, sexes, and populations. *Behavioral Ecology, 21*(3), 608–614. doi:10.1093/beheco/arq033

Whittaker, D. J., Soini, H. A., Gerlach, N. M., Posto, A. L., Novotny, M. V., & Ketterson, E. D. (2011). Role of testosterone in stimulating seasonal changes in a potential avian chemosignal. *Journal of Chemical Ecology, 37*(12), 1349–1357. doi:10.1007/s10886-011-0050-1

Wikelski, M., Arriero, E., Gagliardo, A., Holland, R. A., Huttunen, M. J., … Wistbacka, R. (2015). True navigation in migrating gulls requires intact olfactory nerves. *Scientific Reports*, *5*, Article 17061. doi:10.1038/srep17061

Zidar, J., & Løvlie, H. (2012). Scent of the enemy: Behavioural responses to predator faecal odour in the fowl. *Animal Behaviour, 84*(3), 547–554. doi:10.1016/j.anbehav.2012.06.006