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The perfume of reproduction in birds: Chemosignalling in avian social life

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Abstract

Chemical cues were probably the first cues ever used to communicate and are still ubiquitous among living organisms. Birds have long been considered an exception: it was believed that birds were anosmic and relied on their acute visual and acoustic capabilities. Birds are however excellent smellers and use odors in various contexts including food searching, orientation, but also breeding. Successful reproduction in most vertebrates involves the exchange of complex social signals between partners. The first evidence for a role of olfaction in reproductive contexts in birds only dates back to the seventies, when ducks were shown to require a functional sense of smell to express normal sexual behaviors. Nowadays, even if the interest for olfaction in birds has largely increased, the role that bodily odors play in reproduction still remains largely understudied. The few available studies however suggest that olfaction is involved in many reproductive stages. Odors have been shown to influence the choice and synchronization of partners, the choice of nest-building material or the care for the eggs and offspring. How this chemical information is translated at the physiological level mostly remain to be described, although available evidence suggests that, as in mammals, key reproductive brain areas like the medial preoptic nucleus are activated by relevant olfactory signals. Olfaction in birds receives increasing attention and novel findings are continuously published, but many exciting discoveries are still ahead of us, and could make birds one of the animal classes with the largest panel of developed senses ever described.

Keywords

olfaction; pheromone; avian; sexual selection recognition

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1. Introduction

Animals evolve constrained by the surrounding environment that models their responses to external inputs, indirectly selecting those behaviors that benefit to fitness. In other words: animals interact with their environment. These interactions occur *via* cues and clues that the receiver interprets, learns and uses to optimize its responses, and thus to maximize its fitness. Environmental cues may come from other individuals (same or different species) or from the abiotic environment. Chemical cues have probably been the first cues ever used by organisms to assess the environment around them and, as a corollary, to communicate. It is even probable that primordial life elements had no other “receptors” than those for chemical molecules originating from both the physical environment and other primordial life elements. It is not surprising then, that among the currently living organisms, chemical signals are almost universally used. One indirect example of the old nature of chemical signaling may be the discovery that so different organisms as the Asian elephant (*Elephas maximus*) and 140 species of moths share the same female sex pheromone (Rasmussen et al., 1996).

Communication underlies all sociality, regardless of its level of complexity, and is thus a keystone of animal behavior. As a consequence, communication among individuals is fundamental to breeding; from mate choice to the fitness benefits that result from successfully recruiting offspring. Much of the information exchanged when two animals encounter each other serves two main behavioral processes: recognition and assessment. Recognition is a cognitive process based on a wide range of information such as species, sex, familiarity and so on. This information can provide simple class dichotomies (e.g. conspecific versus heterospecific, male versus female, familiar versus unfamiliar), or much finer variation such as relatedness, or individual identity (Thom and Hurst, 2004). Upon perception and discrimination of this information, animals can sort encounters and produce appropriate behavioral responses. Assessment, on the other hand, consists of the evaluation by the receiver of some of the emitter’s qualities, using qualitative or quantitative properties of the signal emitted. Yet, assessment based on communication signals is not restricted to the context of sexual selection. It can also occur in various situations such as rivals judging each other’s competitiveness, or members of a social group gauging each other’s physiological condition.

In spite of the importance of chemical cues in communication, the facts that these cues are often beyond the conscious human senses, and that the tools to study them are still underdeveloped in comparison to other cues, such as visual and acoustic cues, delayed their study. One exception is chemical communication in insects, probably because many insects are considered pests and the control and/or eradication of some species has commercial and/or public health interests (Wyatt, 2003).

Many different terms and definitions are currently used in the field of chemical ecology, sometimes with little agreement between authors. *Semiochemicals*, the broadest term, encompasses any chemical involved in animal communication. It includes signals used for either intraspecific or interspecific communication. *Pheromones*, on the other hand, are a subclass of semiochemicals used exclusively for intraspecific chemo-communication

(Wyatt, 2003). Originally, pheromones were defined as “*substances secreted to the outside by an individual and received by a second individual of the same species in which they release a specific reaction, for instance a definite behaviour or developmental process*” (Karlson and Lüscher, 1959). Arguably, some authors have subsequently broadened the original definition of pheromones to include signals of social recognition (kin, clan, individuality) even though such signals do not necessarily elicit a specific response from the receiver (Caro and Balthazart, 2010; Wyatt, 2003). We will adopt here the conservative approach of not applying the term pheromone to social signals of recognition. Instead, these signals will be referred to simply as *chemosignals* or *odors* throughout.

Chemosignals involved in animal communication (e.g. social chemosignals, scent marks, personal odors) carry information about the emitting animal, and are thus of biogenic origin. They typically contribute to relatively short-range interactions such as territoriality, attraction, recognition and mate-choice. The biogenic nature of these chemosignals implies that, in contrast to the visual or acoustic channels, they are often not suited for immediate, modulated and mutually responsive communication. Yet this is not always true, as some species such as many hymenopterans have developed a chemical language of great complexity and responsiveness (Wyatt, 2003). In most vertebrates, chemosignals are used for the prolonged and maintained broadcasting of personal characteristics. This is why some authors consider them to be state signals, i.e. signals that remain ‘on’ for a prolonged time; in contrast to event signals, which are typically very short-term manifestations (Hauser, 1996). Importantly, the biogenic origin of social chemosignals also makes them particularly appropriate for the transport of subtle physiological and genetic information. In mammals for example, chemosignals can potentially carry diverse social information such as species (Bowers and Alexander, 1967), group membership (Burgener et al., 2008; Safi and Kerth, 2003), relatedness (Ables et al., 2007), hierarchical status (Zhang et al., 2001) or individuality (Burgener et al., 2009; Hagey and MacDonald, 2003; Smith et al., 2001). As a consequence, mammalian chemosignals participate in a whole range of social behaviors (see Brennan and Kendrick, 2006; Burger, 2005 for reviews) including territorial marking (Ralls, 1971), maternal bonding (Lévy et al., 1995), young-born feeding chemotaxis (Schaal et al., 2003), mate choice (Johansson and Jones, 2007) and social structuring (Burgener et al., 2009). Known examples of social chemosignalling are much scarcer in other vertebrate species but include fish (Reusch et al., 2001), amphibians (Waldman and Bishop, 2004), reptiles (Martin and Lopez, 2006) and birds (see below).

Avian chemical communication has long been overlooked because birds were historically considered microsmatic or even anosmic (i.e. having little or no smell). This relates in part, we believe, to the fact that their beak is not flexible and thus prevents movements such as sniffing that are the hallmark of olfactory sampling of the environment. Bright colors and elaborated songs have thus monopolized the attention of ornithologists and researchers for a very long time (Wenzel, 1973). Several findings over the last 50 years have, however, progressively led biologists to reconsider the question. First, anatomical evidence emerged supporting claims of functional olfaction in most birds (Bang, 1960). Second, some avian groups were shown to possess acute olfactory capabilities, used for foraging or orientation (see Roper, 1999 for review). Nevertheless, research was restricted to the responses of a few

species (vultures, kiwis, pigeons, and procellariiform seabirds) to environmental cues only (Benham, 1906; Benvenuti et al., 1977; Grubb, 1972; Papi et al., 1974; Shallenberger, 1975; Smith and Paselk, 1986; Stager, 1967; Wenzel, 1968).

In the seventies, a few experiments drew the attention of ornithologists to the role of olfaction in avian social interactions. For example, sexual differences in the chemical composition of the uropygial secretions of domestic ducks were detected before the nesting period (Jacob et al., 1979), which may explain the alteration of sexual behaviors observed in males that were made anosmic (Balthazart and Schoffeniels, 1979). But it is only at the beginning of 2000 that this idea received a new input when individual olfactory recognition was discovered in seabirds (Bonadonna and Nevitt, 2004; De Leon et al., 2003). Recently many other studies, on different bird species, added evidence to the importance of chemical communication in birds. If we compare the number of papers found in Web-of-Science searching for [(olfaction OR smell OR odo*r) AND (bird* OR avian)] between 1960 and 1999 (i.e. timespan of 40 years), when the last comprehensive review of avian olfaction was published by T.J. Roper (1999), we find 121 papers; if we do the same between 2000 and 2014 (i.e. timespan of 15 years) we find 259 papers (Fig. 1A). This shows that the interest in avian olfaction dramatically increased in recent years, and became a significant field in avian research in general (Fig. 1B). In the light of many of these new results, chemosignals are now suspected to play a more significant role than previously assumed in the social lives, and thus reproduction, of birds (Hagelin and Jones, 2007), highlighting the need to examine these questions in a review.

In this review, we shall first present a brief overview of the data accumulated over the last 50 years or so (since the seminal paper of Bang, 1960) showing beyond any doubt that birds have a functional sense of olfaction. The core of the review will then be dedicated to the analysis of the data suggesting, and in some cases strongly supporting the idea, that olfaction indeed plays a role in the control of avian reproduction.

2. The existence of a functional sense of olfaction in birds

It has been assumed for a long time and even written in many textbooks (e.g. Grassé, 1950; Marshall, 1961; and even more recently del Hoyo et al., 1992) that birds are either anosmic or at best microsmatic and therefore could not use olfactory signals to guide their behavior. This idea was so broadly accepted until the middle of the 20th century that it is still present in the mind of many people, even if it is obviously wrong. In fact many, if not all, avian species are equipped with a functional olfaction. This conclusion is derived from various types of evidence: behavioral, morphological, neuroanatomical and physiological.

2.1. Behavioral evidence of functional olfaction

The idea that some birds could have a functional olfaction was initially suggested by the observation that the size of the olfactory bulbs relative to the rest of the brain (diameter of bulbs/diameter of hemispheres in percentage) varies enormously between avian orders from a ratio of over 25% in vultures or procellariiforms (petrels, prions, ...) to less than 5% in some passeriformes (Bang and Cobb, 1968). Attention was therefore initially directed to these species with large olfactory bulbs and carefully designed field experiments indeed

showed that these birds are able to detect and localize their food based on olfactory cues (Grubb, 1972; Houston, 1986; Stager, 1964; Wenzel, 1971, 1973).

Behavioral studies have now shown in selected species that birds use olfaction in a multitude of biologically relevant contexts, including food location in kiwis (Cunningham et al., 2009; Wenzel, 1968, 1971), turkey vultures (Graves, 1992; Houston, 1986), and petrels (Cunningham et al., 2003; Hutchison and Wenzel, 1980; Nevitt, 2000, 2008), predator detection (Amo et al., 2008; 2011a; Leclaire et al., 2009), recognition of various odors in domestic chicks (Bertin et al., 2010; 2012; Burne and Rogers, 1996; Jones and Roper, 1997; Marples and Roper, 1996; Porter et al., 1999) and navigation in many different species (reviewed by Gagliardo, 2013), including pigeons (reviewed by Papi, 1989; 1990; Wallraff, 2004; although some scientists disagree with this conclusion, see Jorge et al., 2009; 2010; and see Wallraff, 2014; Phillips and Jorge 2014 for recent discussions on the topic); swifts, *Apus apus* (Fiaschi et al., 1974); starlings, *Sturnus vulgaris* (Wallraff et al., 1995); catbirds *Dumetella carolinensis* (Holland et al., 2009) and Cory's shearwaters, *Calonectris borealis* (Gagliardo et al., 2013).

Interestingly, some of these studies used birds with small olfactory bulbs (e.g. chicken, doves and starlings) that had been considered as lacking a functional sense of olfaction. Even passerines that have some of the smallest olfactory bulbs (Bang and Cobb, 1968) possess olfactory capacities that are similar to those of other avian species and even of mammalian species such as rats or rabbits (Clark et al., 1993). It seems therefore that olfaction should be functional in a wide range of avian species even those with the smallest olfactory bulbs

2.2 Anatomical evidence

It was pointed out quite early that the anatomical organization of the olfactory system is similar in birds and in other tetrapods including mammals: the three nasal fossae (conchae) are organized to filter, warm, moisten and chemically sample the inspired air (Bang, 1960). The mucosa of the third concha is then innervated by dense fibers that assemble to form the olfactory nerves that reach the brain at the level of the olfactory bulbs (Jones and Roper, 1997).

Thanks to progress in molecular biology techniques, it has also been possible to show in recent years that the avian olfactory epithelium contains a large number of genes that code for olfactory receptors (Steiger et al., 2008). Olfactory receptors (ORs) are seven trans-membrane G-coupled olfactory proteins that are encoded by a fairly large number of ORs genes. There are, for example, approximately 150 ORs genes in the zebra fish (*Danio rerio*) genome and over 1,000 in mammals. Birds are intermediate in this respect in that they possess between 100 and 650 ORs genes depending on the species, with nocturnal species tending to possess larger number of genes than diurnal ones (Steiger et al., 2008; 2009a; 2009b). These data contradicted earlier studies that had suggested that a very large percentage of the genes encoding for ORs were pseudogenes i.e. mutated genes that no longer encode for a functional protein in red junglefowls, *Gallus gallus* (see Steiger et al., 2008 for additional discussion and references). The number of these potentially functional ORs genes identified in this study also correlated roughly with the size of the olfactory bulbs (Steiger et al., 2008).

This functional relationship was also analyzed focusing on two nocturnal species that are known to rely on olfaction to find their food, namely the brown kiwi (*Apteryx australis*) and the kakapo (*Strigops habroptilus*). A very large number of genes could be identified in these two species (respectively 478 and 312) especially in comparison with closely related diurnal species (number of ORs ranging between 55 and 109; see Steiger et al., 2009a).

More recently the availability of drafts of the complete zebra finch and chicken genomes allowed more detailed analyses of the ORs genes in these two species. This approach is more reliable than the polymerase chain reaction (PCR) with degenerate primers that was used before and could lead to a distorted view of the reality due to primer biases. Data mining indicated the presence of respectively 479 and 553 OR gene homologs in chicken and zebra finches respectively including 111 and 221 pseudogenes (Steiger et al., 2009b). Interestingly the vast majority of these genes belong to a single class (called γ -c clade) whereas reptiles such as the green anole (*Anolis carolinensis*) possess a smaller number of genes (156 including 42 pseudogenes) but these genes belong to multiple classes (α , θ and γ clades). The large number of ORs genes thus appears to be the result of a specialization of this function in birds (Steiger et al., 2009b). Together, these molecular data suggest the presence of a fairly decent and adaptive sense of olfaction in birds.

2.3. Neuroanatomical organization of olfactory pathways

The cells of the olfactory mucosa containing these OR are directly connected to the olfactory bulbs via paired olfactory nerves. Based on the limited (and often relatively old) available evidence, it seems that these bulbs are not organized in layers in birds as they are in mammals but rather resembles olfactory bulbs of reptiles (Allison, 1953; Andres, 1970). In particular, the glomerular region where olfactory receptors inputs converge is relatively undifferentiated in birds (see Hagelin, 2007b for review). Mitral cells are, however, differentiated and their number varies widely from species to species with some species possessing up to six times as many mitral cells as mice (Nevitt, 2008; Wenzel and Meisami, 1987). There is apparently no vomeronasal organ and no accessory olfactory bulbs in birds or they are vestigial, but this topic was never investigated in great detail (Hagelin, 2007b).

The olfactory bulbs then project to multiple brain areas that are homologous to areas that process olfactory information in mammals. It should be noted that our knowledge of these putative olfactory pathways is largely based on tract-tracing techniques and therefore describes existing anatomical connections *sensu stricto*. This approach does not prove that neural activity generated by social chemosignals actually travels through all these connections. It is indeed well established in mammals that electrical activity generated by odors of sexual partners reaches the medial preoptic area (a center controlling male copulation) after transiting through various sub-nuclei of the amygdala whereas non sexual odors do not affect these regions and are handled in cortical areas (Newman, 1999; Pfaff and Pfaffmann, 1969; Wood and Newman, 1995). Only functional studies (electrophysiology, analyses of brain activation; see section 2.4 and 2.5) can determine whether a given stimulus actually influences the activity in a given brain area. This type of investigation has been carried out for some olfactory stimuli but there are only a handful of studies that approached this question for chemosignals implicated in the control of reproduction.

Projections of the olfactory nerves and bulbs were investigated by multiple tract-tracing techniques (autoradiography, retrograde transport of wheat-germ agglutinin horseradish peroxidase) in a few avian species but many gaps remain in this field. It is nevertheless established that the avian olfactory bulbs project to the piriform cortex, the mesopallium (formerly hyperstriatum ventrale), the medial septal region and medial striatum (formerly lobus parolfactorius) (Reiner and Karten, 1985; Rieke and Wenzel, 1978; see also Reiner et al., 2004 for the revision of the avian brain nomenclature).

Secondary and tertiary projections were however poorly investigated in these initial studies. A study in ducklings used injections of tracer (horse radish peroxidase) in the piriform cortex and analysis of lesion-induced degenerations to describe these secondary connections. These experiments indicated the existence of connections between the piriform cortex and limbic structures such as the hippocampus and parts of the arcopallium that are presumably homologous to the mammalian amygdala (Teuchert et al., 1986). Bingman et al. (1994) also investigated by retrograde and anterograde tracing the connections of the piriform cortex in pigeons. This work showed that large parts of the forebrain including the parahippocampus, hippocampus, the nucleus taeniae of the amygdala, the dorsal arcopallium and large parts anterior telencephalon including the olfactory bulbs and the medial striatum (previously lobus parolfactorius) send inputs to the piriform cortex. Conversely, the piriform cortex was shown to project to broad telencephalic areas mostly in its anterior portion and more importantly for the topic of the present review to brain areas that are known to play a significant role in the control of reproductive behavior such as the nucleus taeniae of the amygdala, the bed nucleus of the stria terminalis, the septal region and multiple regions of the thalamus and hypothalamus (Bingman et al., 1994). Tract-tracing studies in quail also identified a dense projection from the arcopallium (homologous to parts of the mammalian amygdala) and in particular the nucleus taeniae of the amygdala to the medial preoptic nucleus (Balthazart and Absil, 1997), a brain region that is critical for the control of male copulatory behavior (Balthazart and Ball, 2007; Panzica et al., 1996), suggesting that olfactory inputs could indeed reach this nucleus and thus possibly influence sexual behaviors.

Recently, one study re-analyzed the telencephalic organization of the olfactory pathways in homing pigeons with the use of modern and thus more effective tract-tracing techniques. This confirmed that the olfactory bulbs project bilaterally to the prepiriform cortex, the piriform cortex, the dorsolateral corticoid area and nucleus taeniae of the amygdala. Ipsilateral projections to the medial septum were also observed and the prepiriform cortex was shown to secondarily project to the piriform cortex thus providing secondary olfactory inputs to this region (Patzke et al., 2011). No evidence of lateral asymmetry in the projection from the olfactory bulbs to the piriform cortex could be detected (Patzke et al., 2011) thus suggesting that the previously reported functional lateralization of olfactory function as used in pigeon homing (Gagliardo et al., 2007; 2011; Patzke et al., 2010) is not based simply on an anatomical lateralization of this projection.

2.4. Electrophysiological evidence

2.4.1 Olfactory nerves—Electrophysiological studies showed that these anatomically-defined pathways are actually functional and respond to the presentation of olfactory stimuli as indirectly suggested by behavioral experiments. Already in the 1960s, action potentials were recorded in fibers of the olfactory nerves in response to a variety of odors in 14 avian species. This electrical activity was shown to be proportional to the concentration of the olfactory stimuli (Tucker, 1965). Similar results were subsequently obtained in response to amyl acetate with domestic pigeons, black-tailed gulls (*Larus crassirostris*) and two species of vultures (Oley et al., 1975; Shibuya and Tucker, 1967; Shibuya et al., 1970). Recording single nerve endings in the olfactory mucosa in turkey vultures (*Cathartes aura*) and black vultures (*Coragyps atratus*), Shibuya and Tucker (1967) found that olfactory receptor units fired mostly during inspiration, that some displayed responses proportional to the dose of stimuli while others responded in an all-or-none fashion.

All this work, like most other studies that will be described in section 2.4 was carried out with artificial odors coming from pure chemical compounds such as amyl acetate, pyridine or trimethylpentane. One study in starlings however showed the presence of multi-unit responses in the olfactory nerves following exposure to a variety of odorant plants that these birds incorporate in their nest, possibly to repel nest parasites (see section 4.4). Birds were also able to discriminate between volatile odors emitted by these different plants and developed conditioned avoidance when some of these plants were paired with gastrointestinal malaise (Clark and Mason, 1987). Electrophysiological activity in the olfactory nerves thus develops in response to biologically relevant olfactory stimuli.

2.4.2 Olfactory bulbs—Sieck and Wenzel (1969) implanted electrodes in the olfactory bulbs of pigeons (*Columba livia*) and recorded olfactory spindles associated with presentation of odor stimuli (the same arbitrary organic compounds described before) similar to signals previously identified in mammalian olfactory bulbs and nerves. Similar results were later obtained in several other species (Wenzel and Sieck, 1972) and more recently via single units recording (McKeegan et al., 2002; McKeegan and Lippens, 2003). Several studies also revealed that olfactory bulb neurons are spontaneously active but odor stimulation increases or decreases their firing rate (McKeegan et al., 2002; McKeegan and Lippens, 2003; Sieck and Wenzel, 1969). One study in chicken showed that single unit responses in the chicken olfactory bulb adapt to repeated presentation of the same stimulus (McKeegan and Lippens, 2003). Olfactory bulb responses were abolished by section of the olfactory but not the trigeminal nerves clearly indicating that they originate from the olfactory receptors in the nasal cavity (Sieck and Wenzel, 1969; Wenzel and Sieck, 1972).

2.4.3 Central olfactory pathways—Electrophysiology was further used to show that the electrical activity detected at the level of olfactory nerves and bulbs propagates from there to various parts of the brain. These parts include the medial striatum (formerly lobus parolfactorius), cortex prepiriformis, mesopallium (formerly hyperstriatum ventrale) as well as higher-order sites such as the apical part of the hyperpallium (formerly hyperstriatum accessorium), the densocellular part of the hyperpallium (formerly hyperstriatum dorsale), the globus pallidus (formerly paleostriatum primitivum), the lateral striatum (formerly

paleostriatum augmentatum), the nucleus septalis lateralis and the caudal nidopallium (formerly neostriatum caudale) (Macadar et al., 1980). This network thus includes multiple associative zones implicated in the decoding and integration of sensory information.

One more recent study showed that exposure of anesthetized chicken to a range of odors (amyl acetate, methyl anthranilic acid, limonene, geraniol, ionone) induces changes in the electroencephalographic (EEG) signals recorded on the vertex and the occipital protuberance of the head. EEG signals displayed a decrease in slow waves and an increase in rapid waves in response to geraniol (Oosawa et al., 2000). The olfactory stimuli thus affect in a broad manner brain electrical activity.

Taken together, these studies clearly indicate that a wide variety of avian species detect olfactory stimuli, some of them at very low concentration, and transfer corresponding signals to the brain. These action potentials reach telencephalic sites that are likely to be able to decode the information and then transmit it through mono- or poly-synaptic connections to multiple brain areas where they could play a role in the control of a variety of physiological or behavioral reactions.

3. Why is chemical communication important in avian reproduction?

Chemical substances produced by birds have been studied in various contexts, including taxonomy (Jacob, 1978), phylogeny (Sweeney et al., 2004), physiology (Sandilands et al., 2004), ectoparasite repellence (Hagelin, 2008), organic pollutants biomonitoring (Jaspers et al., 2007), purely descriptive (Montalti et al., 2005), or general exploration of the functions of such substances (Bolliger and Varga, 1961; Burger et al., 2004; Piersma et al., 1999; Reneerkens et al., 2002). Relatively few, however, have done so from the perspective of chemical communication by investigating the existence of potential semiochemicals (chemical substance produced by the organism that carries a message for purpose of communication).

In birds, the odors produced by the body mostly originate from uropygial secretions or feathers lipids. The uropygial gland, located at the dorsal base of the tail, is indeed the only sebaceous gland of birds and as such, is often considered as the key source of avian chemical signals (Jacob, 1978). It produces large amounts of waxy fluids that are spread on feathers as part of the plumage maintenance (Jacob and Ziswiler, 1982; Stettenheim, 2000), which is critical for the bird's survival. In the rest of this review, bodily odors (and thus semiochemicals) will be considered as originating from the uropygial gland only, although we currently do not know whether these secretions truly reflect what conspecifics may perceive as a chemosignal.

Successful reproduction requires that males and females from the same species meet and copulate (in warm-blooded vertebrates at least) at a time when both are sexually mature and when the young that will be produced have a high chance of surviving. This implies that subjects must be able to recognize members of their own species, recognize their sex and also detect whether the potential partner is sexually receptive (reacting to sexual approaches with sexual rather than escape or, even worse, aggressive behaviors) and able to release sperm or ova.

It is well established that, in mammals, these different features of an individual are mediated by multisensory inputs and include visual, acoustic but also olfactory signals (see Balthazart and Young, 2014 for review). As already stated before, it was long believed that birds almost exclusively rely on visual and acoustic signals in their social life, so that olfactory input was either negligible or completely absent in reproductive contexts.

3.1 Species recognition

One important challenge during breeding is having mechanisms that maintain reproductive isolation. Such species-recognition systems reduce or preclude heterospecific mating (Noor, 1995; Ritchie, 2007). This is particularly important for species that have spatial and temporal overlap, because hybrid pairs often result in offspring that are nonviable, infertile or have reduced fitness (Butlin, 1989; Hobel and Gerhardt, 2003). Thus, the strongest selection for, and the most rapid evolution of, effective species-recognition systems is experienced by closely related sympatric species (Coyne and Orr, 1989, 1997; Seddon, 2005; Via, 2001). Species recognition does however not always request specific signals, and signaling used for sexual selection, like mating displays, are generally only recognized by the receiver if it is of the same species (Coyne and Orr, 2004; Panhuis et al., 2001; Ritchie, 2007; Ryan and Rand, 1993). Divergence in these signals therefore favors reproductive isolation (Balakrishnan and Sorenson, 2006; Detto et al., 2006). Chemical stimuli can be powerful mechanisms for interspecific recognition and speciation in birds and many other animals (reviewed in Smadja and Butlin, 2009). Examples include sympatric sea snake species (Shine et al., 2002), populations of red-sided garter snakes (*Thamnophis sirtalis parietalis*) (Lemaster and Mason, 2003) and closely related species or populations of lizards (Barbosa et al., 2005; Cooper and Vitt, 1986; Martin and Lopez, 2006), where chemical signals (often primarily involved in mating displays) are efficient in keeping species apart.

Isolation mechanisms based on chemical cues have been identified in mammals (Smadja and Ganem, 2008), reptiles (Barbosa et al., 2006), amphibians (Houck and Arnold, 2003) and invertebrates (Wyatt, 2003), but to date birds have not been investigated, probably owing to the fact that visual and acoustic cues were considered sufficiently adequate. Nevertheless, in some species visual and acoustic cues might not be sufficient, and olfactory cues might be a supplemental mechanism to fine-tune species recognition. For example in petrel seabirds, the use of visual cues is often hampered by underground nesting habits and nocturnality at the colony. These same species are often similar in colors (Warham, 1996) and do not seem to distinguish completely among vocalizations of different species (Bolton, 2007; Bretagnolle, 2009). As a consequence, divergence in the chemical profiles of species may provide a good mechanism for species recognition, and therefore a good mechanism to avoid hybridization (Bonadonna and Mardon, 2010; Soini et al., 2013; Zhang et al., 2013).

3.2 Selection of an optimal partner

Birds, like any other animals, should also be able to identify mating partners that will optimize the survival of their offspring and therefore, maximize their inclusive fitness. Failing to meet these criteria would obviously have a high cost for the concerned individuals in particular, and the species survival in general. Selecting the “wrong” partner is indeed

associated to two types of costs. The direct costs refer to the fact that a poor partner will provide little help in raising the young and protecting them from predators, which will decrease their survival. The indirect costs relate to the fact that a poor partner is likely to transmit to his/her descendants' genetic traits (genes) that will decrease their survival and reproduction. Individuals might indeed choose a mate with "good" or "compatible genes", such as those with specific alleles or allele combinations increasing fitness or with high heterozygosity (Eizaguirre et al., 2011; Ekblom et al., 2004; Freeman-Gallant et al., 2003; Neff and Pitcher, 2005; Olsson et al., 2003; Schwensow et al., 2008; Tregenza and Wedell, 2000). *In fine*, many species exhibit non-random mating. Using chemical cues to select a partner in this context can be quite advantageous because these signals can provide information about the genetic make-up of an individual.

Of particular interest are situations in which a signal can be used for both recognition (e.g. individuals previously encountered or related) and quality assessment of potential partners. This is the case, for example, for genetically-based individuality signals such as the ones associated with the highly polymorphic genes of the Major Histocompatibility Complex (MHC). The MHC plays a central role in disease resistance and immune defence through self/non-self recognition mechanisms (Milinski 2006). MHC molecules, i.e. glycoproteins encoded in the large cluster of genes known as the MHC, display peptides derived from foreign proteins to T lymphocytes, whose function is to tell whether such peptides are derived from foreign or self-proteins, and eventually to kill infected and foreign cells. There are two different classes of MHC molecules that deliver peptides to T lymphocytes. MHC class I molecules pick up within the cell virus-derived peptides and take them to the cell surface. MHC class II molecules bind peptides from extracellular bacteria and larger parasites. As stated above, these MHC genes are highly polymorphic, meaning that they greatly vary among individuals. By identifying and choosing a mate with dissimilar MHC genes a given individual can increase MHC polymorphism in offspring, and relative heterozygosity in MHC genes can increase offspring viability through enhanced immunocompetence and avoidance of costs of inbreeding (Penn and Potts 1999). Research on laboratory mice has for instance shown that genes of the MHC complex influence their urinary odours, and that mate choice can be based on these "odortypes". Indeed, mice are able to discriminate between the smell of urines coming from strains that only differ in some of their MHC loci (Yamaguchi et al., 1981).

The strong genetic determinism of these chemosignals provides therefore an opportunity for the receiver, not only to uniquely identify the emitter, but also to assess its genetic make-up (Brown and Eklund, 1994; Penn, 2002). By then comparing this information to a reference (itself for instance), an individual may obtain a proxy of the genetic distance between itself and the emitter. This notion of genetic distance, or genetic dissimilarity, is crucial in mate choice systems based on genetic compatibility. In such systems, individuals typically try to avoid partners with genomes overly similar to their own, such as kin for the particular case of inbreeding avoidance (Tregenza and Wedell, 2000). In this way, breeding pairs increase the allelic diversity of their offspring and avoid potential effects of deleterious familial mutations.

Signals associated with MHC polymorphism could also be used to assess the quality of the immune system of potential partners (Olsson et al., 2003; Wedekind et al., 1995; Yamazaki et al., 1979). The MHC indeed encodes antigen-presenting molecules. It therefore plays a critical role in the activation of adaptive immune response and in disease resistance. MHC heterozygotes have been shown to have stronger immune capacities and to resist to a wider range of pathogens than homozygotes (Bonneaud et al., 2004; Juola and Dearborn, 2012; Strandh et al., 2011; 2012; Thoss et al., 2011; Wedekind et al., 2004; Westerdahl et al., 2005). MHC alleles are however not directly assessable and they need to be expressed in the phenotype to influence mate choice.

Genetically-based recognition/assessment systems require the ability to contrast one's own genetic makeup with that of a conspecific; a complex task that appears, based on current evidence, to be achieved primarily through the use of chemical communication, and thus olfaction (Penn and Potts, 1999; Schaefer et al., 2002; Tregenza and Wedell, 2000). Association between genetic distance, MHC characteristics, olfactory cues and/or mating preferences have been strongly suggested or showed in vertebrates including fish, reptiles, mammals, and, not surprisingly, birds. Odor, for instance, has been shown to correlate with overall heterozygosity in ring-tailed lemurs (*Lemur catta*) (Charpentier et al., 2008) but also in kittiwakes (*Rissa tridactyla*) (Leclaire et al., 2012). The preference for odors of genetically MHC dissimilar males has been shown in rodents (Radwan et al., 2008; Yamazaki et al., 1979), and reptiles (Olsson et al., 2003); MHC-heterozygous conspecifics' odor is preferred by women and men, independently from the gender (Thornhill et al., 2003; Wedekind and Furi, 1997; Wedekind and Penn, 2000), and in sticklebacks (*Gasterosteus aculeatus*), females prefer the odor of males that have a higher number of MHC alleles (Reusch et al., 2001). MHC dependent mate choice has also been highlighted in birds (Bonneaud et al., 2006; Juola and Dearborn, 2012; Strandh et al., 2012), but mechanisms leading the choice are still unknown. However, evidence on olfactory kin recognition in birds (Bonadonna and Sanz-Aguilar, 2012; Caspers et al., 2013; Krause et al., 2012), and individual odors broadcasting individual qualities (Amo et al., 2012b; Whittaker et al., 2013) strongly suggest that olfactory-based genetic assessment may be achieved by olfactory cues.

The mechanism by which MHC genes influence odor is still unclear, but several hypotheses have been suggested (Penn, 2002). MHC genes may influence odor directly through odorant MHC proteins themselves or odorant peptides that bind to MHC-molecules (Milinski et al., 2005; Milinski, 2006; Penn and Potts, 1998; Penn, 2002). Non-exclusively, MHC genes may influence odor indirectly by shaping an individual's particular microbial composition, through antigen-mediated elimination of some bacterial species (Penn, 2002).

4. Importance of chemosignals in successive reproductive stages

As summarized above, olfactory signals from the environment are playing a role in the control of many types of behaviors in birds. Comparatively, research on the production and social use of bodily odors in the context of avian reproduction has been largely neglected as compared to other vertebrate classes. Available data nevertheless suggest and sometimes clearly show that species-specific odors play an important role in the control of social interactions in birds. This information is reviewed in this section.

4.1. Territoriality

For many bird species, defending a territory is a significant activity during reproduction. Territories vary greatly in size, from the square miles patrolled by a falcon to the tiny area around the nests of cliff-nesting kittiwake (Askins, 1987). They have in common that they are defended against other individuals of the same species, but they strongly differ in their purpose: food resource defense for the falcon, nest defense for the kittiwake. Nearly a century has passed since Howard (1920) published one of the first books on territoriality in birds. Since then, territory defense has generally been assumed to be advertised by means of acoustic and visual signals, which contrasts with the situation in mammals, where territory defense would mostly occur by means of chemical signaling (Gosling and Roberts, 2001). Scent marking behaviors have, to our knowledge, never been formally identified in birds, but several observations in emblematic species for the study of avian chemical communication, suggest that olfaction could play a role in territory defense. Scent-marking has been suggested in kiwis (*Apteryx mantelli*), a species that defends large territories (Taborsky and Taborsky, 1992). Kiwis' reaction to self and conspecific fecal odors was described to range from attraction to escaping behaviors, which according to the authors suggests scent-marking territory defense (Castro et al., 2010). Petrels often breed in a burrow, and several species have been shown to be able to locate its entrance by smell. This breeding burrow could be considered as a territory. Snow petrels (*Pagodroma nivea*) have been suggested to scent-mark their burrow by regurgitating strong-smelling stomach oil at its entrance, and this behavior would be enhanced during territorial disputes (Jouventin, 1977). Whether kiwis and petrels 1) purposefully mark their territories with odors, and whether 2) conspecifics prospecting for potential territories would use these cues to decide whether or not to penetrate an area, deserves further study.

4.2. Mate choice: species, sex and individual olfactory recognition

Mate choice is a key life-history decision that impacts an individual's current reproductive success and fitness (Andersson, 1994). Both direct and indirect benefits, such as parental care, gene quality for the offspring or access to a high quality territory, can be derived from selecting an appropriate partner (Davies et al., 2012). As mate choice is a crucial prerequisite for breeding, one can predict that mate-choosing individuals will try to collect as much information as possible on the identity and quality of available mate candidates.

The first step in a mate-choice decisional process is to identify conspecifics and their sex, to avoid pairing with individuals from another species and/or the same sex, in which case successful breeding is virtually impossible (see above). Chemical cues have been shown to play a role in both species and sex recognitions in birds. The comparisons of the chromatographic profiles of chemical compounds coming from different bird species, populations and sexes have shown that all these levels of organization can be reliably identified (Bonadonna et al., 2007; Jacob et al., 1979; Leclaire et al., 2011; Mardon et al., 2010; 2011b; Whittaker et al., 2010; Zhang et al., 2013). For example, two subspecies of shearwaters, the Atlantic and the Mediterranean Cory's shearwaters, have recently been shown to differ in their chemical profiles (Gabirot M., Raux L., Dell'Arciccia G., Bried J., Gonzales-Solis J., Buatois B., Crochet P.A., Bonadonna, F., unpublished data). Interestingly, a recent study has failed to phylogenetically classify the preen oil volatile compounds of 18

(mostly) songbird species. The main reason for this lack of phylogenetic organization is that closely related species tend to have very divergent chemical profiles, presumably to avoid hybridization (Soini et al., 2013) (see Figure 2).

This hypothesis recently received support from a study showing that body odors strongly differ between zebra finches (*Taeniopygia guttata*) and diamond firetails (*Stagonopleura guttata*), two Estrildinae finches that have an overlapping distribution area and are thus exposed to risks of hybridization (Krause E.T. Brummel C., Kohlwey S., Baier M.C., Müller C., Bonadonna F., Caspers B.A., unpublished data).

Whether these statistical differences in compound compositions have a biological meaning, and are similarly discriminated by birds, requests behavioral experiments. A few studies have addressed this question, and even if the behavioral responses are much less consistent than the chemical profiles described, there is growing evidence that many bird species are able to discriminate between species and/or sexes. Crested auklets (*Aethia cristatella*) and blue petrels (*Halobaena caerulea*) placed in a Y-maze, are attracted to conspecific feather odor when tested versus the odor of other species, even if closely related (Bonadonna and Mardon, 2010; Hagelin et al., 2003) (Fig. 3A). Similar behavioral species-recognitions, based on chemical cues, have been suggested in dark-eyed juncos (*Junco hyemalis*) (Whittaker et al., 2011), waxwings (*Bombycilla sp.*) (Zhang et al., 2013), zebra finches (Krause et al, unpublished data), and in budgerigars (*Melopsittacus undulatus*) (Zhang et al., 2010; but see Mardon et al., 2011a; Zhang, 2011). However, while species recognition seems quite unequivocal, sex recognition seems much less widespread. Petrels, prions and juncos indeed do not discriminate between odors from males and females (Bonadonna et al., 2009; Mardon et al., 2010; Whittaker et al., 2011). To our knowledge, the only species that has so far been shown to recognize the sex of conspecifics is the spotless starlings (*Sturnus unicolor*) (Amo et al., 2012a) (Fig. 3B).

Chemical signals emitted by birds have also been suggested to encompass information specific to individuals, such as genetic make-up (Celerier et al., 2011; Leclaire et al., 2011) and reproductive success (Amo et al., 2012a; Whittaker et al., 2013). Identification and interpretation of individual odor signatures by conspecifics would be highly interesting in a mate-choice context, as it would open the door to recognition mechanisms of indices of individual quality, and of potential relatedness (kin recognition), that are of primary interest when choosing a mate. The first evidence for personal scent recognition in birds occurred about one decade ago, when two studies showed that it was possible for birds to gather information from individual conspecifics through odor cues only. Firstly, De Leon and colleagues (2003) noted that chicks of European storm petrel (*Hydrobates pelagicus*) preferentially oriented to a maze arm in which they had walked before, as compared to an arm in which another chick had walked before. The authors argued that the maze arms become impregnated with the body scent of the chicks, which then formed the basis of the discrimination (De Leon et al., 2003). This study was closely followed by another experiment from Bonadonna and Nevitt (2004) who showed that Antarctic prions (*Pachyptila desolata*) were preferentially attracted to their mate's odor when tested against the odor of another conspecific (Bonadonna and Nevitt, 2004) (Fig. 3C). Similar findings were subsequently described in other Procellariiforms, namely the Wilson's storm petrel

(*Oceanites oceanicus*) (Jouventin et al., 2007) and the blue petrel (Mardon and Bonadonna, 2009). Quite unexpectedly, the studies on blue petrels and Antarctic prions also discovered a pattern of scent discrimination that is well documented in mammals. Antarctic prions and blue petrels avoided their own odor when presented against the scent of another conspecific (Bonadonna and Nevitt, 2004; Mardon and Bonadonna, 2009) (Fig. 3D). Such behavior was first reported in mice and was related to MHC genes, kin recognition and inbreeding avoidance (Manning et al., 1992). The self-odor avoidance of petrels might serve the same functions as in mice, since these seabirds are highly phylopatric, which exposes them to the risk of inbreeding and should select for mechanisms allowing discrimination of kin. Recent work showing MHC-based pair bonds in blue petrels reinforced this hypothesis (Strandh et al., 2011; 2012).

Mice have been used in experiments where they were asked to discriminate between odors sampled on birds (Celerier et al., 2011; Karlsson et al., 2010). The conclusion of these studies was that mice can discriminate olfactory and kin signatures in birds. In the first experiment, Karlsson and colleagues (2010) used an operant conditioning paradigm in which water-deprived mice had to lick a steel tube if they perceived the odor of a specific individual junglefowl (*Gallus gallus*) to which they had been previously habituated. The results showed that mice were clearly able to discriminate between individual fowls, and therefore that junglefowls possess an olfactory signature (Karlsson et al., 2010). Celerier and colleagues (2011) habituated mice to the odor of blue petrel individuals. Mice were then simultaneously presented with the odors of two unrelated individuals, one being the individual to which they had been habituated, and the numbers of sniff bouts to each of the odor sources were recorded (see Figure 4).

Results show that mice were exploring the unknown odor significantly more often than expected by chance (Celerier et al., 2011), confirming that blue petrels have an individual odor (Mardon et al., 2010; 2011b), and showing that mice were able to perceive and discriminate this perfumed individuality. But mice also seemed able to identify kin-related individual birds. If mice were presented with a choice of two odors, but in which the familiar odor did not come from the individual to which they had been habituated (a fledging chick), but from kin-related individuals (that chick's parents), mice again spent more time exploring the unrelated unknown odor (Celerier et al., 2011). Alternatively, one could argue that the odors of chicks and parents could be extremely similar only because rubbing each other in the nest. In that respect, a recent study in dark-eyed juncos showed that mothers were transferring their own preen oil to their chick during brooding (Slowinski et al., 2013), and therefore in petrels too, the chicks' odor could be identical to their parents if the scent was transferred to the chick during brooding. It must be noted however that in the study of Celerier and colleagues (2011) mice discriminated between chick and parent odors only if the chicks were close to fledge (with a functional uropygial gland and thus with all definitive feathers preened), and not if the odors came from younger chicks (with down feathers that have not been preened yet). This suggests that in petrels (1) chicks' odors do not originate from the brooding made by the parents (2) the olfactory signature is acquired shortly before fledging.

Kin recognition through olfactory signals has also been recently investigated in other species including Humboldt penguins (*Spheniscus humboldti*) (Coffin et al., 2011), zebra finches (Caspers et al., 2013; Krause et al., 2012), and European storm petrels (Bonadonna and Sanz-Aguilar, 2012). In these experiments, the birds themselves were asked to discriminate between odors coming from related and non-related individuals, and while all were able to discriminate between kin and non-kin individuals, the behavior was dissimilar according to the species. In seabirds, both storm petrels and Humboldt penguins avoided kin-related odors, like previously shown in blue petrels and Antarctic prions (see above). Zebra finches however were attracted to kin-related odors. Nevertheless, in a recent experiment, it was found that female zebra finches skipped reproduction when kept in a cage with both a related and a non-related males. This lack of breeding disappeared if females were made anosmic, in which case they randomly mated with any of the two males (Caspers B.A., Gagliardo A., Krause E.T., unpublished data). The mechanisms hypothesized by authors both in seabirds and passerines are self-referent phenotype matching, or olfactory imprinting (Hudson, 1993): young petrels in the nest may learn through the parents' odors a kind of 'family odor template' that they use subsequently to recognize kin-related individuals. Whatever the mechanisms involved, these experiments suggest that birds are equally skilled in discriminating subtle odor variation as mice (Steiger et al., 2008; Wenzel and Meisami, 1987) and that kin-recognition through olfactory cues might be common among avian taxa.

So far, studies investigating olfactory discrimination of individuals in birds have mostly focused on partner and kin recognition. Whether birds also use olfactory signals as a way to gather information about genetic or phenotypic qualities of conspecifics (and in the context that interests us here: of potential mates), has rarely been investigated. The existence of such olfactory signature of quality was first suggested in crested auklets (Hagelin, 2007a). This socially monogamous seabird species has a seasonally elevated citrusy scent associated with a display behavior called "ruff-sniff" involving a bird rubbing its face multiple times in the scented nape of a display partner (Jones, 1993). The citrusy odor, which would not be associated with the uropygial secretions but with wick feathers in the interscapular region, has been intensively studied as a parasite chemical repellent (Douglas et al., 2001, 2004; 2005; Douglas, 2006, 2013; Douglas III et al., 2001), and the associated "ruff-sniff" behavior suggested as a mean to exchange chemical deterrents between conspecifics by alloanoointing (Douglas, 2008). Nevertheless, it cannot be excluded that during this unusual parade the two potential mates also acquire information on respective health status: a bird with high level of citrusy odor would be well protected against parasites, and thus may represent a good mate. In this case, the odors would acquire the status of ornament and be involved in social behaviors and mate choice (Hagelin, 2007a). This crested auklet example suggests that avian personal odors could evolve as chemical ornaments (i.e. sexually selected phenotypic traits) and could be involved in social behaviors in general.

In dark-eyed juncos, personal odors correlate with reproductive success (Whittaker et al., 2013). Junco females with a more 'female-like' volatile profile produced more offspring. Males with a more 'male-like' profile had more offspring and more surviving nestlings, whilst males with 'female-like' profile suffered from a higher rate of paternity loss (Whittaker et al., 2013) (Fig. 5). This study, however, somehow contradicts the results of a

previous experiment on a different junco subspecies (*J. h. thurberi*) where females seemed to be more attracted by the odor of males that have small wing length and lower body mass/tarsus length ratio. This result was somewhat surprising as short wings are generally associated with smaller body size and low mass/tarsus ratios with poorer body condition. Nevertheless, these results in juncos again suggest an association between odor signatures and sexually selected phenotypic traits.

In another passerine, the house finch (*Carpodacus mexicanus*), phenotypic information broadcasted through personal odors seems to be assessed during male-male competition. While males do not seem to distinguish between male and female odors in binary choice tests, they avoided the scent of males that were in better condition than themselves and preferably moved towards the scent of lower quality males (Amo et al., 2012b). Such attraction of males for other male rather than female odors is surprising but might be widespread. In fact, no study so far ever found that males were attracted to female odors, hence male dark-eyed juncos, spotless starlings and crested auklets all showed attraction to scents of other individual males (Amo et al., 2012b). This suggests that males might use olfactory cues, not for assessing potential mates, but exclusively for gauging potential rivals.

Odors might not only broadcast indices of phenotypic qualities, but also signals of genetic qualities. In birds, this is still debated although recent years have seen an upsurge of interest for genetically-determined olfactory signals in general, and MHC-related signals in particular. In black-legged kittiwake (*Rissa tridactyla*) for example, male and female semiochemical profiles are correlated with heterozygosity, and male semiochemical distance is correlated with genetic distance (Leclaire et al., 2012). MHC on the other hand has often been viewed as a way to allow the identification of different degrees of genetic relatedness (kin recognition) and by extension, as a potential mechanism to avoid inbreeding (Brown and Eklund, 1994; Eggert et al., 1998). But MHC-related traits may also broadcast other information such as resistance to pathogens or genetic compatibility. Many bird species are known to mate according to MHC traits (Bonneaud et al., 2006; Ekblom et al., 2004; Freeman-Gallant et al., 2003; Griggio et al., 2011), and in junglefowl males allocate more sperm to females that are MHC-dissimilar (Gillingham et al., 2009). The phenotypic cues used in the assessment of genetic relatedness in birds have not yet been determined, but odors might play a critical role. Petrels and penguins that are known for their acute sense of smell, were also shown to mate disassortatively according to MHC (Knafler et al., 2012; Strandh et al., 2011; Strandh et al., 2012). Whether these two characteristics are causally linked remains to be investigated, but the hypothesis that MHC-based mate choice is achieved through personal odor profiles has been emphasized on several occasions (e.g. Zelano and Edwards, 2002). This link between personal odor and MHC might involve bacterial communities in feathers or uropygial gland (Strandh et al., 2012).

4.3. Mate synchronization

Once a suitable partner has been identified, it is still critical to make sure that he/she is in an adequate physiological state in order to reproduce. More specifically, the partner should be able to produce in the near future mature gametes (sperm or ova) and correlatively should be

hormonally prepared to mate. This synchronization of mating partners is largely based in birds on visual and auditory signals and has been studied already a long time ago in great detail in at least two species, the ring dove, *Streptopelia risoria* (Lehrman, 1965) and the canari, *Serinus canaria* (Hinde, 1965). There is however indirect evidence that semiochemicals could also be implicated in this synchronization.

Initial suggestion that this might be the case came from work on semi-domesticated duck, *Anas platyrhynchos*. The secretion of the uropygial gland was collected and its composition was analyzed monthly during the reproductive season between December and June in male and female ducks. Gas chromatography showed that the secretion contains large amounts of fatty acids belonging to three categories: ramified ester waxes, non-ramified ester waxes and diesters waxes (Jacob et al., 1979). In December, the secretion in both sexes was relatively similar: all birds had branched and unbranched ester waxes and none of them had diesters. This chemical composition remained stable in males during the next 6 months but, in contrast, females completely stopped producing branched and unbranched ester waxes during the breeding season from January to April and only started secreting these compounds again after the period of active copulation (i.e., in May and June). In addition, the uropygial gland secretion of females contained diester waxes throughout the reproductive season (but not before in December) that were never present in male secretions (Jacob et al., 1979).

It is also interesting to note that a more recent study confirmed this sex difference in composition of the secretions and showed that the seasonal variation in the composition of the uropygial gland secretion in female mallards is controlled by estrogens and thyroxine thus adding credence to the idea that this secretion reflects the reproductive status of the female (Bohnet et al., 1991). Injection of estrogens to males also induced the secretion of these female typical compounds that they normally never produce (Bohnet et al., 1991). These studies also identified some of the enzymatic mechanisms that mediate these seasonal changes in secretion composition.

The uropygial gland secretions or products of their degradation that are widely spread on the female plumage could thus provide males with information on the reproductive status of females although this idea was never specifically tested to our knowledge. It has however been shown that the uropygial gland plays a role in the control of chicken copulation. Male chicken preferred to mate with intact female chicken as opposed to females who had their gland surgically removed. In addition, this difference was no longer seen in males that had been made anosmic by surgical removal of the olfactory bulbs, which strongly suggests that the differential reaction relates to the perception of olfactory stimuli (Hirao et al., 2009). This work however does not identify the specific features of the female that are the basis of male choice: the uropygial gland signals could in this experiment indicate the species, the sex or the reproductive status of the female.

4.4. Parental care/fitness optimization

In a breeding context, olfaction is not only important between (potential) partners, but also in the relationships between parents and their progeny. Over the past few years, there has been an upsurge of interest for the role that chemical cues play in all phases of birds'

parental life, from the nest building to the chick feeding stages. Chemical cues have been shown to be involved in most of these stages, illustrating how ubiquitous olfactory signals are for birds.

During nest building, birds often do not choose material at random, but specifically select some items over others (e.g. Bailey et al., 2014). Some species like ovenbirds use a complex mixture of clay, straw, hair and other materials to build a complex domed structured nest; other species incorporate odorant items to their nest and, it has been suggested on several occasions that the odor of these items play a role in repelling predators or parasites. Black larks (*Melanocorypha yeltoniensis*) or common waxbills (*Estrilda astrild*) pile up relatively large amounts of dung in and around their nest. While the reason for this behavior is still debated, one hypothesis is that the odor emitted by the dung acts as an olfactory deterrent or camouflage and therefore repulses or distracts potential predators (Fijen et al., 2013; Schuetz, 2005). Other species, like tits or starlings incorporate aromatic plants to their nests, which creates a pleasant odorous environment. In this case, aromatic herbs have often been suggested to repel ectoparasites and hence, their addition to the nest would enhance the growth and survival of the offspring, thereby the fitness of the parents (the “nest protection hypothesis”, Clark and Mason, 1988; Wimberger, 1984). Starlings apparently use their olfactory capabilities to select the plants to add to the nest (Gwinner, 2013), and experiments in tits have shown that parents use odor cues to determine the frequency with which to replenish the nest with fresh aromatic herbs (Petit et al., 2002)(Fig. 6).

Odors can also be used by birds to identify and locate their nest. This has been shown in nocturnal Procellariiforms that have poor night vision (Brooke, 1989; Martin and Brooke, 1991). Pioneering work on nest-site olfactory recognition was conducted in the Leach’s storm petrel (*Oceanodroma leucorhoa*) a species that breeds in burrows like most other petrel species (Nevitt, 2008; Warham, 1990). Petrels’ nests are characterized by a strong, musky odor that permeates the area around the burrow and is perceptible to the human nose at quite a distance (Grubb, 1973). In the 1970s, Grubb conducted several observational studies and showed that Leach’s storm petrels flying at night over the breeding colony were significantly more attracted by the scent of nest material collected in the colony than by forest leaf litter (Grubb, 1973). Subsequent experiments in mazes have validated these observations and have indicated that petrels were indeed able to identify their own burrow only by smell (Benvenuti et al., 1993; Bonadonna et al., 2001; Bonadonna and Bretagnolle, 2002; Bonadonna et al., 2003b; Bonadonna et al., 2003a; Dell’Ariccia and Bonadonna, 2013; Grubb, 1974).

Olfaction has also been shown to be critical in subsequent nesting stages involving parental care to eggs and nestlings. Dark-eyed juncos were shown to spend less time incubating their eggs right after some preen oil solution from male northern mockingbirds (*Mimus polyglottos*) was added to the nest and eggs (Whittaker et al., 2009). This effect of foreign odor was temporary and females quickly resumed normal incubation behavior thereafter, with no apparent negative impact on hatching success. More extreme results were described in ring doves (*Streptopelia risoria*), for which treating offspring with a highly artificial citrus odor resulted in parents rejecting nestlings. Interestingly, parents continued to care for

their odor-treated nestlings if bilateral olfactory nerve sections had been performed in the parents (Cohen, 1981).

Caring for the offspring involves finding food to feed them. Olfaction has also been shown to be used during these foraging activities. The best known examples come again from the procellariiforms that have repeatedly been shown to be strongly attracted by the odor of fish debris and/or dimethyl sulfide (DMS), an odor produced by phytoplankton when grazed by zooplankton, and that is eventually associated with areas of high primary productivity where prey are likely to be found (Bonadonna et al., 2006; Dell'Arciccia et al., 2014; Grubb, 1972; Hutchison and Wenzel, 1980; Nevitt et al., 1995; Nevitt, 2000; Nevitt and Bonadonna, 2005). Other examples of the use of smell during foraging activities come from several passerine species. Herbivorous insect larvae, like caterpillars, often represent a significant portion of the food items brought by parents to their offspring. The annual peak of caterpillars in spring, which coincides with the occurrence of new leaves on trees, has been shown to be a major selection factor (e.g. Thomas et al., 2001). Several passerine species are strongly attracted to trees that suffer damages from herbivorous insects (Mantyla et al., 2004; 2008). While this attraction could be mediated by visual or olfactory cues, a recent study in great tits (*Parus major*) has shown that olfaction was playing a decisive role in this process, with birds being able to detect volatile compounds released by trees infested by caterpillars (Amo et al., 2013). Captive great tits were tested in large Y-maze aviaries in which apple trees that were, or had been (no remaining visual indication of insects) infested by caterpillars were placed in one arm, while the other arm contained control, undamaged trees. It was shown that birds visited the previously infested trees significantly more often than the control trees (Amo et al., 2013). In a separate experiment, birds were offered chemical or visual cues alone or in combination, and bird attraction to the infested trees was exclusively mediated by the volatile emissions of the trees (Amo et al., 2013). Birds can thus be attracted by the stress-related chemosignals emitted by plants, which has also recently been suggested in the DMS-petrel system (Savoca and Nevitt, 2014). The mechanisms by which birds learn to use odors to find food is not elucidated yet, but it might involve a simple association between food presence and odors. For example, blue tits (*Cyanistes caeruleus*) and chicken can learn to associate the perception of a non-food-related odor with the presence of food, and this sometimes occur very early in life, i.e. at the embryonic stage (Bertin et al., 2010; 2012; Mennerat et al., 2005). This shows how plastic the olfactory learning of birds is.

While birds can detect their prey by smell, they can also be preys for other species, and smell still plays a role in the relationship with their predators. Dung-piling larks and waxbills might try to protect their nest from predators using olfactory signals, but great and blue tits have also been shown to be able to detect the predator itself by smell. If the odor of a mustelid is added to the nestbox in which they breed or roost, great and blue tits delay or even avoid entering the nestbox (Amo et al., 2008; 2011b). Blue tits also spent significantly less time in the nestbox, although this did not seem to affect the condition of the chicks (Amo et al., 2008). On the other hand, this capacity to detect predators by smell seems to be limited to birds that are awake. Exposing great tits to mustelid odor while they are roosting at night does not result in more arousal, as indicated by measures of oxygen consumption

and body temperature (Amo et al., 2011a). Similar effects of odors of potential predators on bird behavior have been described in house finches (*Carpodacus mexicanus*) (Roth et al., 2008), crested auklets (*Aethia cristatella*) (Hagelin et al., 2003) and domestic fowls (*Gallus gallus*) (Zidar and Lovlie, 2012), but no such effects were found in Eastern bluebirds (*Sialia sialis*) (Godard et al., 2007) or house wrens (*Troglodytes aedon*) (Johnson et al., 2011).

5. Brain activation by social semiosignals

In mammals, there is a substantial body of information describing how perception of social semiosignals affects brain activity. Multiple brain regions are activated as evidenced by increases in the expression of immediate early genes such as *c-fos* or *egr-1* (Coolen et al., 1996; Pfaus et al., 1992; Robertson et al., 1991), enhanced phosphorylation of key molecules in intracellular signaling pathways such as the MAP kinase (Taziaux et al., 2011) or even, in humans, by imaging techniques such as positron emission tomography (PET) or functional magnetic resonance imaging (fMRI) (Burke et al., 2012; Savic et al., 2001). The gonadotropin releasing hormone (GnRH) neurons often play a key role in translating the effects of these olfactory stimuli into changes in reproductive physiology.

This type of information is in general not yet available for birds. We know that interactions with a partner of the other sex affects the functioning of the hypothalamo-pituitary-gonadal axis (see Ball and Balthazart, 2002; Dawson et al., 2001 for reviews) and that multiple brain regions are activated as evidenced by an increased *c-fos* expression (Meddle et al., 1997; Taziaux et al., 2006). However, the specific role of olfactory stimuli in these brain changes has not been investigated to our knowledge, with only one exception.

One study in Japanese quail (*Coturnix japonica*) indeed strongly suggests that olfactory inputs coming from the female modulate the metabolic activity of the medial preoptic nucleus (POM), a key brain region in the control of male sexual behavior (Taziaux et al., 2008). In this experiment, the nares of male quail were mechanically occluded (blocked with a layer of rapid-drying dental cement) and it was confirmed that they could no longer detect prominent olfactory stimuli such as the odor of acetic acid. These males were then exposed in standardized test conditions to a sexually receptive female and their sexual behavior was recorded for 10 min. Their sexual behaviors were not obviously affected: the frequency of mount attempts and of cloacal contact movements were similar in control subjects and subjects with the occluded nares (Taziaux et al., 2008). Brains of experimental and control males were collected 90 min later and processed for immunohistochemical visualization of the *Fos* protein. In control birds that copulated with a female, an increased expression of this immediate early gene was observed in brain regions associated with the control of sexual behavior such as the medial preoptic area (POA) and the medial part of the bed nucleus of the stria terminalis (BSTM) as compared to birds maintained in their home cage. Quite surprisingly, however, the number of *Fos*-immunoreactive cells in these two nuclei was significantly reduced in birds that had copulated with their nostrils plugged (Taziaux et al., 2008) (Fig. 7). For currently unidentified reasons, we did not observe a reliable expression of the *Fos* protein in the olfactory bulbs of subjects in any of the experimental groups. However, another immediate early gene called *zenk* (also known as *egr-1* or *zif-268* in mammals; Mello et al., 1992) that is also induced by sexual stimulations in male quail (Ball

et al., 1997; Charlier et al., 2005), was expressed in a larger number of cells in subjects allowed to copulate freely as compared to birds who copulated with their nares occluded or stayed in their home cage.

This experiment thus indicates that brain activity can be modulated by olfactory signals, but it also raises a number of questions concerning the interpretation of these data, namely 1) why was copulatory behavior not affected by the nares occlusion? and 2) why is the effect of olfactory deprivation specifically observed in these two brain areas?

The absence of changes in behavior following nares occlusion could relate to the fact that males were sexually experienced and potentially relied exclusively on visual/acoustic cues to control their behavior while olfactory signals might be required in naïve subjects (see Pfeiffer and Johnston, 1994; Winans and Powers, 1977 for similar data in hamsters). This leaves open the question of the nature of the neural activation inhibited in birds copulating with plugged nostrils. Their copulatory behavior was expressed at normal rates so that the decrease in brain *c-fos* expression cannot be ascribed to a decrease in motor output. It is thus likely that the decrease in brain activation reflects the removal of olfactory inputs to the POA and BSTM, which would suggest that these inputs normally reach these brain nuclei during sexual behavior (Balthazart et al., 1998). This interpretation is also supported by the observed increase in *Zenk* protein in the olfactory bulbs of birds that copulated and its inhibition following blockade of the nostrils.

In mammals, sexual behavior-related olfactory information reaches the POA through a pathway that includes the cortico-medial amygdala and the bed nucleus of the stria terminalis (BSTM) (Brennan and Zufall, 2006; Keverne, 2004; Sachs and Meisel, 1988). In quail, tract-tracing has identified an important projection from the arcopallium (homologous to parts of the mammalian amygdala) and in particular the nucleus taeniae of the amygdala to the medial preoptic nucleus (Balthazart and Absil, 1997), suggesting that olfactory inputs could indeed reach the medial preoptic nucleus through a similar route (see section 2.3 and 2.4). Surprisingly, however, olfactory deprivation did not affect *c-fos* expression induced by male sexual behavior in the nucleus taeniae nor in other nuclei such as the medial and lateral striatum, the medial septum or the piriform cortex that are also presumably part of the olfactory pathway (Bingman et al., 1994; Patzke et al., 2011; Reiner and Karten, 1985; Rieke and Wenzel, 1978). Additional work is thus needed to identify the reasons of this apparent discrepancy (olfactory information reaching the POA and BSTM of quail by another route: female olfactory signals not intense enough to induce *c-fos* expression in the first relays of olfactory pathway; olfactory signals activating other aspects of the functioning of these pathways that are not reflected in an increased *c-fos* expression).

This type of experiment should also be replicated in other avian model systems. Quail have relatively small olfactory bulbs and are usually considered to have a limited sense of smell even if they are able to discriminate between various chemical compounds and diets based on smell only (see Mills et al., 1997 for review). It is thus likely that such brain activations should be detected in other avian species that appear to have a similar or more developed sense of olfaction.

6. Conclusions

Contrary to common belief, that is still widespread despite rapidly accumulating experimental evidence, birds definitely have a functional sense of smell (olfaction), but we still poorly understand what avian olfaction is used for, in which situations it becomes a critical sense and which functions the most common chemical compounds have. Thus, although olfaction in birds is currently becoming a forefront topic in biology (Fig. 1), the way ahead of us is still long, with many avenues of research that remain to be explored.

Recent evidence suggests that even birds with small olfactory bulbs are sensitive to odors (e.g. Amo et al., 2013). This can partly be explained by the fact that olfactory capabilities of one species are still evaluated with respect to the ratio olfactory bulb/brain published by Betsy Bang and Stanley Cobb at the end of the sixties (Bang and Cobb, 1968). Without in any way diminishing their seminal work, at that time Bang and Cobb assumed that, regardless of species, the design of birds' brain was similar. This is not completely true, and modern 3-D imaging shows that this design may vary. For example the brain of the kiwi is elongated and the olfactory "lobe" is mostly a flat sheet of tissue covering the foremost part of the brain (Corfield et al., 2008). The ratio obtained by Bang and Cobb only reflected the reality in kiwis because of the unusually elongated brain, but measuring the diameter of the "bulb" may not always reflect the amount of olfactory neurons actually present in the brain. This is the case of other species, including pigeons, whose olfactory bulbs are larger than described before (Corfield J. R. unpublished data in Birkhead, 2012). More studies with modern tools are consequently needed. This example highlights one of the biggest challenges for the field of olfaction in birds for the next years: understanding the mechanisms through which chemical signals are perceived and transduced in the avian brain, and how this neural activity is translated into hormonal fluctuations that eventually modulate the behaviors and life-histories of birds. Besides one study in quail (Fig. 7), there have been so far very few attempts to link odors, their perception at the brain level and the physiological and behavioral outputs that they elicit. Although this review largely focused on the link between odors and reproduction, we are for example still unable to tell which components of the reproductive axis are modulated by odors.

Further increasing our knowledge of the functions and mechanisms of olfaction in birds might require a reconsideration of the model species that we use. Commonly studied species like Procellariiform seabirds (petrels and shearwaters) or kiwis will still contribute to our knowledge on the importance of olfaction in birds, but other models may be more appropriate for neuroanatomical, genetic, as well as behavioral studies, especially when they require laboratory-controlled conditions, and detailed knowledge of their biology/ecology/behavior. In our opinion passerine species like juncos, tits, canaries or zebra finches are extremely promising models (e.g. Amo et al., 2011a; Caspers and Krause, 2011; Caspers et al., 2013; Whittaker et al., 2013). Even if the last two are largely domesticated, which means that they were exposed to different selection pressures than their wild-counterparts (Caro, 2012; Tschirren et al., 2009), they still offer many advantages for deciphering the interconnections between the various senses, their ontogeny and genetic make-up. The zebra finch for example has its genome sequenced (Warren et al., 2010), it is extremely easy to raise in captivity, with strains presenting various phenotypic characteristics, and at the same

time, wild Australian populations can still be accessed to validate finding on domestic strains (Zann, 1996). Studies on this species largely took into account many aspects of their behavior, from acoustic and visual communication to mechanisms leading to mate choice, inbreeding avoidance, and imprinting. The wide knowledge about zebra finches, and other commonly studied avian species, will be critical in the future for characterizing the actual importance of chemosignals in reproduction.

Another area of research that requires further development concerns the chemosignals (i.e. active compounds in a chemical profile) effectively used by birds. Besides a few exceptions (e.g. Hagelin et al., 2003), we know virtually nothing about their exact nature, how they are produced (e.g. maybe bacterial degradation of uropygial products: Bonadonna and Mardon, 2013) and what message they carry for individual birds. In particular, we do not know whether the putative olfactory signals that are described in chemical profiles and that seem to encode information about the species, sex, and kin of a given individual (Mardon et al., 2010; 2011b; Whittaker et al., 2010), are actually used by birds in their social interactions. Similarly, olfaction seems to advertise on genetic qualities of potential mates (Whittaker et al., 2013) or competitors (Amo et al., 2012b), but we do not know whether a chemosignal reflects the physiological status, or the overall fitness. A same chemical compound or group of compounds could indeed simultaneously transfer information about all these features, but specific compounds might also be required to encode the different types of information. We are thus far from the deep knowledge on the visual and acoustic signal properties in use among birds, and the tools available to study them still need further development. We are far from the knowledge accumulated on the chemical ecology of insects for example, which has been boosted in the past by pest control needs.

In the people's mind, the widely acknowledged senses of hearing and sight of birds are probably about to be joined by their excellent sense of smell. This capacity to detect what appears to be very subtle odors, might even explain large trends in avian life-histories and phylogeny. Semiochemicals might for instance be widespread and powerful species-recognition signals in birds (Bonadonna and Mardon, 2010; Soini et al., 2013; Zhang et al., 2013). Speciation in birds is considered to result from precopulatory isolation mechanisms (Price, 2007). Thus, if birds develop a simple preference for their own "group" odors, probably originally shaped by different ecologies and/or environmental conditions (e.g. foraging), this might isolate groups of phylogenetically-close subjects and lead to speciation, even when those groups live in sympatry. Such efficient olfactory mechanisms might help explaining the large number of avian species, with respect to other vertebrate species (more than 10500 birds versus 5400 mammal species, 7200 amphibians, 9700 reptiles) in addition to the obviously easier dispersion of subjects related to avian flight. This is just an example and pure speculation at this point, but it illustrates the potential impact of future discoveries about avian chemical sensitivity.

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Highlights

- Research on avian olfaction has increased markedly during the last two decades
- Secretions of the uropygial gland provide specific recognition signals
- Birds recognize the species and sex of congeners and their partner based on odors
- Olfactory signals affect avian behavior at all stages of reproduction
- Olfactory signals reach brain areas controlling reproductive behaviors in birds

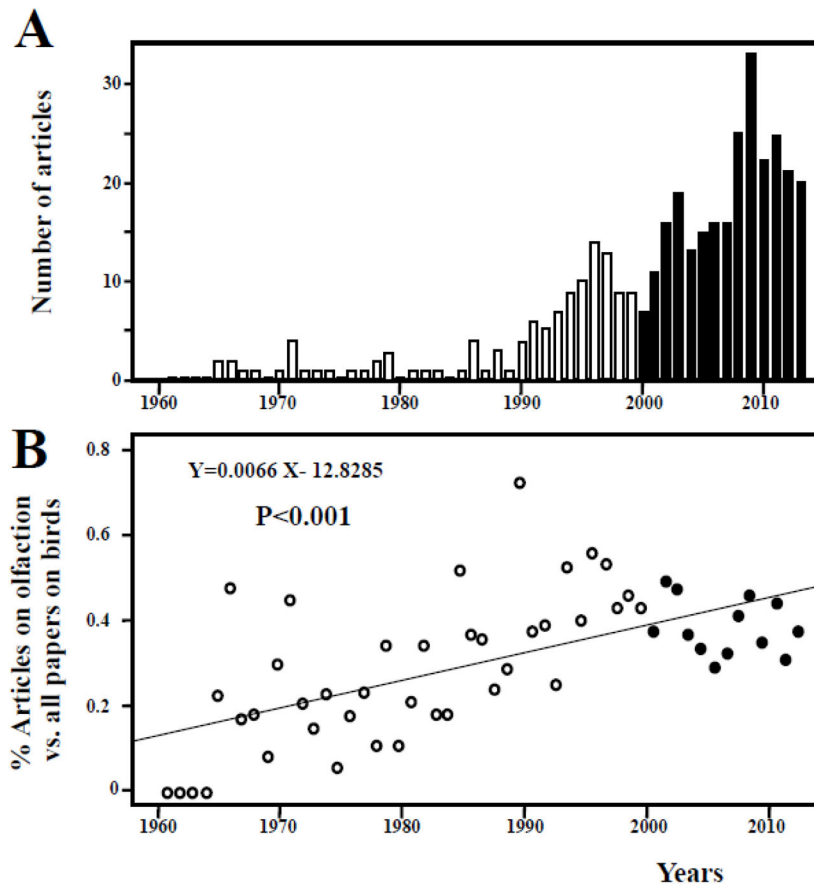


Figure 1. Number of papers on avian olfaction after the seminal Bang 1960 paper published in Nature, based on ISI Web of Science [search term: (olfaction OR smell OR odo*r) AND (bird* OR avian)]. Panel A presents the absolute number of papers per year, panel B these papers expressed as a percentage of all papers on birds for the given year. This figure illustrates the tremendous increase of scientific research on the topic of avian olfaction, especially within the last 5 years. Open bars (panel A) and open circles (panel B) highlight the 121 papers published before 1999, black bars and circles refer to the 259 papers that were published over the past 15 years.

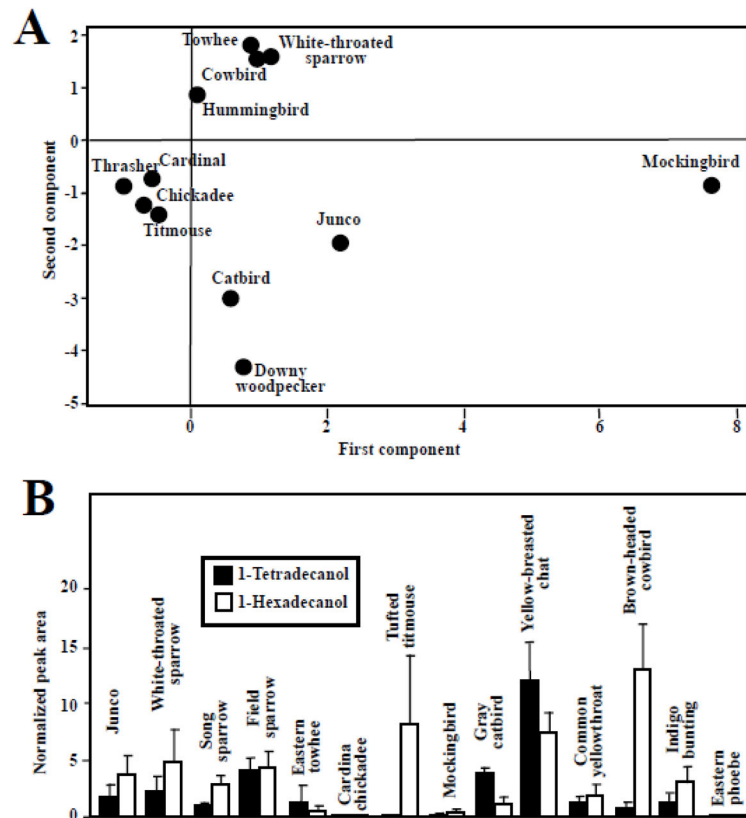


Figure 2. Differences and similarities in chemical nature of volatile organic compounds present in the secretion of the uropygial (preen) gland in various species of birds as analyzed by gas chromatography–mass spectrometry. A. The first two factors extracted by a principal component analysis of data (presence or absence of 172 tentatively identified chemical compounds) collected in 12 different species ($n=1/\text{species}$) provide a classification of species based on similarities in preen gland oil composition that diverges completely from the species phylogenetic distance (e.g. the 3 mimidae species northern mockingbird, brown thrasher and gray catbird are quite distant). The divergent oil composition of closely related species is consistent with the notion that the oil volatile compounds may play a role in avoiding hybridization between species. B. The relative abundance of two specific alkanols (1-tetradecanol and 1-hexadecanol) represents a species characteristic that is also not directly related to their phylogenetic relatedness. Redrawn from data in Soini et al. (2013)

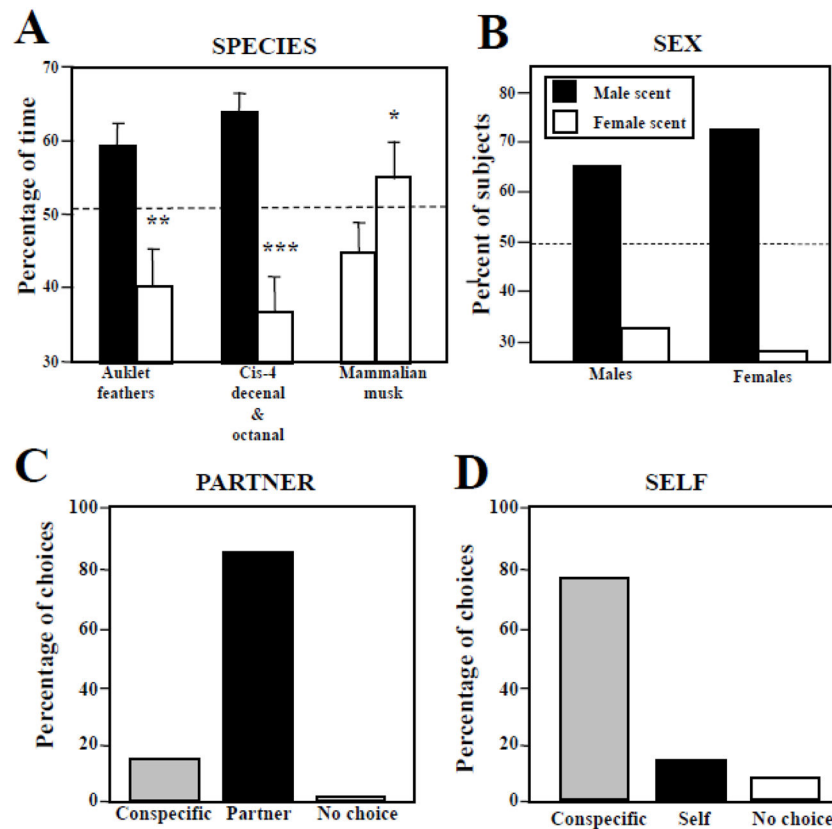


Figure 3.

Results of choice test experiments showing that various avian species are able to recognize, based on odors only, their own species (A), the sex of a conspecific (B), their sexual partner (C) and their own odor (D). A. Crested auklet preferentially orient in a Y maze towards the odor of conspecific feathers or of two of its major components, cis-4-decenal and octanal but avoid the musky odor of a mammalian predator. B. Both male and female spotless starlings prefer to approach male scent over female scent in a two way choice test. C–D. Antarctic prions preferentially approach, in a Y maze, the odor of their partner as opposed to another conspecific (C) but avoid their own odor as compared to the conspecific odor (D). In panels A and B the horizontal dotted line indicates the null hypothesis (50% choice of each stimulus). Redrawn from data in Hagelin et al. 2003 (A), Amo et al. 2012a (B) or Bonadona and Nevitt 2004 (C–D)

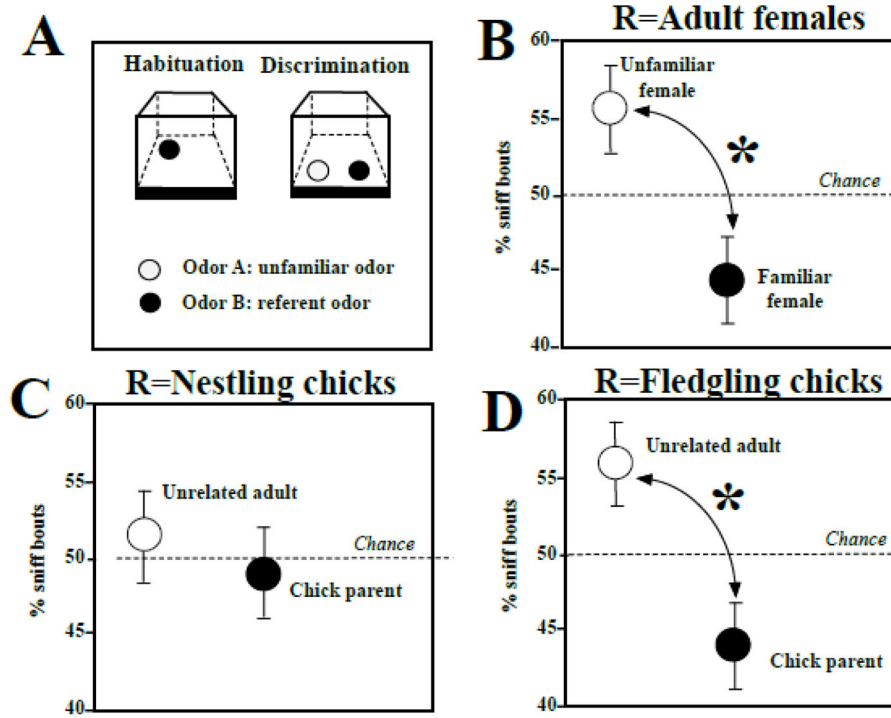


Figure 4.

Mice are able to discriminate individual odors of blue petrels. A. Schematic presentation of the experimental design in which mice were first habituated to the odor of either an adult female, a nestling chick in downy plumage or a fully feathered chick near fledging (the Referent [R] odor; left drawing). After they habituated to this stimulus as evidenced by a decrease in olfactory exploration, they were then exposed to pairs of odors, one of which was related to the referent odor while the other was not (right drawing). Mice were able to discriminate between the odors of a familiar vs. unfamiliar female (B) and between the odors of the parent of referent fledgling chick and of an unrelated adult (D) but not between the odors of the parent of a downy chick and an unrelated adult (C). These data indicate that blue petrels have individual odors and that odors of fledgling chicks match those of the parents but not in the downy chick whose uropygial gland is still poorly or not developed. Data are means \pm SEM of percentages sniffing bouts. * = $p < 0.05$. Redrawn from data in C  lerier et al. (2011).

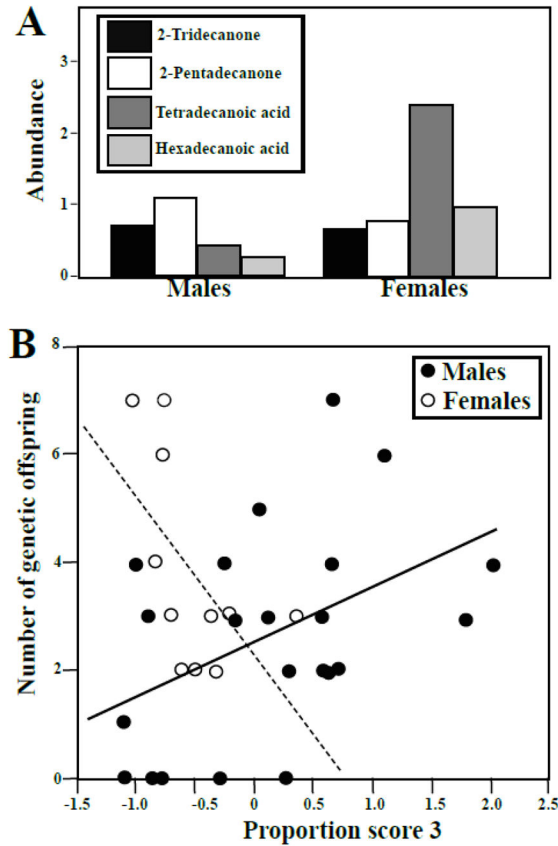


Figure 5.

The proportions of volatile compounds in the uropygial gland secretion of dark-eyed juncos differ between males and females and predict reproductive success. A. Comparison of the relative abundance of four volatile compounds in the secretions of males and females. Both tetradecanoic and hexadecanoic acids are present in higher concentration in females than in males. B. Relationships between the number of genetic offspring produced (sum of within- and extra-pair offspring) with the relative proportion of diverse volatile compounds present in uropygial gland secretion as represented by the proportion score 3 derived from a principal component analysis. Proportion score 3 largely reflects the abundance of 2-tridecanone, 2-tetradecanone and 2-pentadecanone that are particularly abundant in males. These two variables are positively correlated in males (black regression line) but negatively correlated in females (dotted regression line). Therefore females with a more female-like and males with a more male-like secretion (odor?) have a higher reproductive success. Redrawn from data in Whittaker et al. 2013

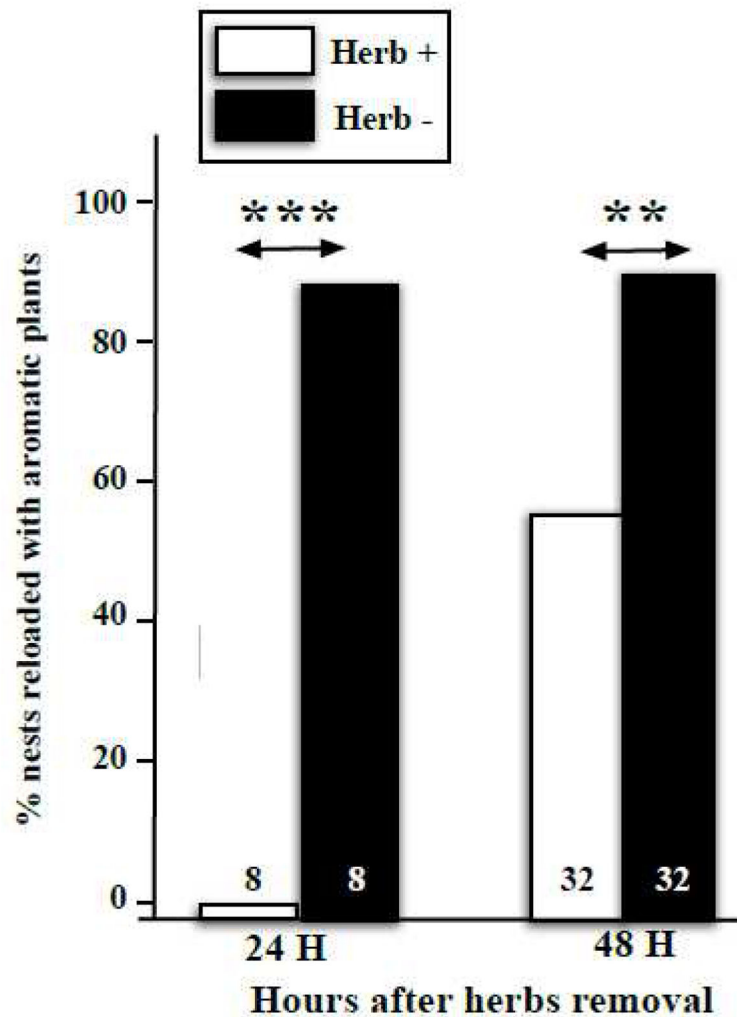


Figure 6. Effect of the (hidden) presence or absence of aromatic herbs on the addition of fresh aromatic plants in the nests of blue tits. The figure shows the percentages of nests in which tits added aromatic plant fragments within 24 or 48 hours, according to whether these nests contained hidden aromatic plants (Herb +) or did not contain such material (Herb -). The numbers of nests in each category are indicated at the base of the bars. **= $p < 0.01$, ***= $p < 0.001$. Drawn from data in Petit et al. (2002)

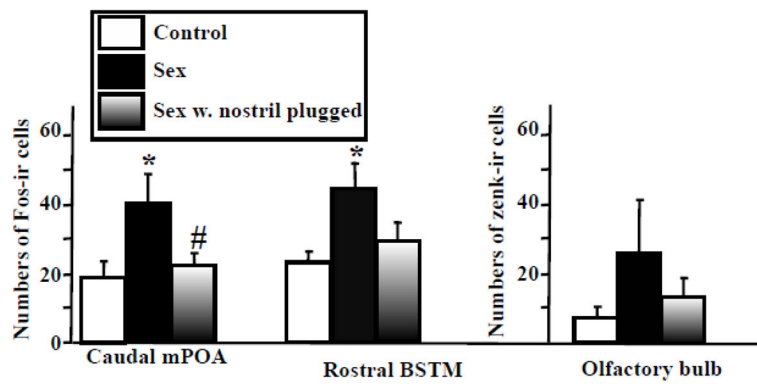


Figure 7.

Occlusion of the nostrils in male Japanese quail markedly decreases the induction of *c-fos* expression in the medial preoptic area (mPOA) and in the rostral bed nucleus of the stria terminalis (BSTM) as well as the induction of *zenk* expression in the olfactory bulbs following sexual interactions with a female and performance of copulatory behavior. Cells immunoreactive for the Fos or the Zenk protein (Fos-ir and Zenk-ir) were counted in these three brain regions in males who had copulated with a female (Sex), had copulated with a female with their nostril occluded (Sex w. nostril plugged) or males who stayed in their home cage as a control. *= $p < 0.05$ vs Control; #= $p < 0.05$ vs. Sex. Redrawn from data in Taziaux et al. 2008.