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REVIEW

Olfaction in raptors

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Raptors from the orders Accipitriformes and Falconiformes have been considered to rely principally on vision. Historically, this assumption has led scientists to discount any possible sense of smell in these birds, until work on cathartid vultures indicated that these species at least rely on olfaction to find carrion. In this review I provide evidence that raptors in general have functional olfactory systems that they may use in a range of different contexts. Anatomical studies show that raptors have well-developed olfactory bulbs that are within the range of other bird species. Furthermore, all raptors studied have multiple functional olfactory genes, with, for instance, 283 olfactory genes in the Oriental honey buzzard, *Pernis orientalis*, of which 81.5% are functional. It has also been shown that some raptors species may functionally use olfactory cues to forage and, potentially, for communication. While further research is required, the available evidence suggests that olfaction may be a more important sensory modality in these birds than previously thought.

KEYWORDS: Accipitriformes – chemosignalling – communication – Falconiformes – foraging – olfactory bulb – sensory ecology – smell.

INTRODUCTION

The use of chemical cues is considered to be the oldest and most widespread method by which living organisms assess their surrounding environment (Wyatt, 2014). Despite the long-standing belief that birds lack any sense of smell, it is now clear that many birds do have functional olfactory systems. Indeed, olfaction may play an important role in many avian behaviours, including foraging, navigation and communication (Nevitt, 1999; Roper, 1999; Gagliardo, 2013; Caro *et al.*, 2015; Amo & Bonadonna, 2018). For instance, Cory's shearwaters, *Calonectris borealis* (Cory, 1881), use olfaction to navigate over many hundreds of kilometres in order to return to their colony (Gagliardo *et al.*, 2013). Another surprising example of avian olfaction is that European storm petrels, *Hydrobates pelagicus* (Linnaeus, 1758), are able to avoid inbreeding using smell alone (Bonadonna & Sanz-Aguilar, 2012).

While olfaction is well accepted in many avian orders, most raptors, also widely referred to as

birds of prey (from the orders Accipitriformes and Falconiformes), are still considered to depend primarily on vision. Raptor vision has been extensively studied, because most species chase highly manoeuvrable prey, sometimes spotted at long distance, which needs an accurate and long-distance sense and, therefore, they use their visual system (Martin, 2017). For instance, raptors have relatively high temporal resolution (e.g. up to 130 Hz for the peregrine falcon, *Falco peregrinus* Tunstall, 1771), allowing them to track fast and highly manoeuvrable prey (Potier *et al.*, under revision). Moreover, some raptors species have the highest spatial resolution found to date for any vertebrate, both in the achromatic [reviewed recently by Mitkus *et al.* (2018), with the wedge-tailed eagle, *Aquila audax* (Latham, 1801), having a visual acuity of 142–143 c/deg; Raymond (1985)] and the chromatic (Potier *et al.*, 2018c) channels. Therefore, some raptor species may be able to detect food (and other objects) with high achromatic or chromatic (colour difference) contrast from the background at greater distances than any other vertebrate. However, it is important to consider that not all raptors have high relative visual acuity. For instance, the chimango

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caracara, *Phalacrocorax chimango* (Vieillot, 1816), has a spatial resolution of around 30 c/deg (Potier *et al.*, 2016a), which is considerably lower than that of humans (maximum acuity: 72 c/deg; Land & Nilsson, 2012). These differences in visual abilities reflect the broad ecological diversity found in raptors (Ferguson-Lees & Christie, 2001; Potier *et al.*, 2016b, 2017, 2018a). For example, while a number of raptors are predators (e.g. hawks, falcons, eagles), others, such as vultures, caracaras and some kites, are mostly scavengers, which may rely on different sensory abilities when foraging (Ferguson-Lees & Christie, 2001). Raptors also differ in their sociality, with some species considered to be solitary [including most predatory species, such as falcons, hawks and eagles, although Harris's hawk, *Parabuteo unicinctus* (Temminck, 1824) and Eleonora's falcon, *Falco eleonorae* (Géné, 1839), are examples of social predatory species], while others are gregarious or social, such as vultures, kites and some fish eagles (Ferguson-Lees & Christie, 2001). Therefore, we should expect that different species of raptors will have different sensory abilities, depending on their specific ecological demands.

In the brain, neural structures compete for space (Zelenitsky *et al.*, 2011), and vision may have extra neural demands that may have led scientists to think that neural space for other senses, such as olfaction, may have been reduced in raptors. Indeed, raptors have large eyes that may require a larger brain, or a greater proportion of brain space dedicated to vision, to process the extra information captured by those large eyes (Brooke *et al.*, 1999). However, olfactory bulbs, considered as the primary neural structures of the vertebrate forebrain involved in olfaction, appear to be freer to vary in size irrespective of the size of other sensory structures (Yopak *et al.*, 2010; Corfield *et al.*, 2015; Yopak *et al.*, 2015). Consequently, olfaction should not be considered poor in raptors because of their high visual abilities.

Like other birds, raptors may use their sense of smell for a diverse range of tasks, such as foraging or communicating. For communication, olfaction may be an appropriate sense, because this does not necessarily require access by an accurate and long-distance sense (such as vision). Here, I present a review of the literature on the sense of smell in raptorial birds, first exploring anatomical evidence, followed by a review of the use of smell in raptors in the contexts of foraging and its potential for communication and navigation.

ANATOMICAL EVIDENCE OF A SENSE OF SMELL

The functional anatomy of the olfactory system in birds follows the typical vertebrate Bauplan, except

that birds lack a vomeronasal organ and probably a terminal nerve (Wenzel, 1987). The nostrils, through which air enters, are always open and positioned toward the base and above the bill in the majority of birds, including raptors (Fig. 1). In all species, inhaled air passes from the nostrils and then successively through three chambers called conchae (Roper, 1999). The first chamber probably serves to filter out small debris, and also to warm and moisten the air. The second chamber also filters the air, together with allowing some air to pass directly to the lungs for respiration. The third concha is lined with the olfactory epithelium that contains the olfactory receptor neurons. The olfactory receptors (OR) are seven-transmembrane domain G protein-coupled receptors located in the cell membranes of the olfactory receptor neurons and are responsible for the detection of odorous compounds (odorants).

Olfactory receptors can be assigned to subfamilies on the basis of sequence relationships, with members of the same subfamily having related sequences and thus being likely to recognize structurally related odorants (Malnic *et al.*, 2004). The number of olfactory receptor genes can be a good indicator of a functional sense of smell in vertebrates (Steiger *et al.*, 2008), because it is related to olfactory acuity and to the diversity of scents being detected and distinguished in mammals (Niimura & Nei, 2006, 2007). In birds, the number of OR genes varies among species [from 107 in the galah, *Eolophus roseicapilla* (Vieillot, 1817), to 667 in the kakapo, *Strigops habroptila* (Gray, 1845)]. While these numbers are often less than those in mammals – for example, from 60 in the minke whale, *Balaenoptera acutorostrata* (Lacépède, 1804) or *B. bonaerensis* Burmeister, 1867 (Yim *et al.*, 2014), to 2129 in cows, *Bos taurus* (Linnaeus, 1758) (Niimura & Nei, 2007) – the percentage of potentially functional OR genes in birds is actually high (approximately 84%) (Steiger *et al.*, 2008). To date, evidence for a functional sense of smell based on OR genes has been found in a few different raptor species, listed hereafter. A small number of OR genes (63) has been found in two species of falcons, the peregrine falcon and the saker falcon, *Falco cherrug* (Gray, 1834), but only 44.4% of these genes were considered to be functional (Zhan *et al.*, 2013). The golden eagle, *Aquila chrysaetos* (Linnaeus, 1758), has a similar total number of OR genes (Doyle *et al.*, 2014), but the number of functional OR genes in this species is unknown. In contrast, the Oriental honey buzzard, *Pernis ptilorhynchus* (Temminck, 1821), has a much higher number of OR genes (283), 81.5% of which are functional (Yang *et al.*, 2015).

The olfactory receptor neurons are bipolar neurons and their axons project to the olfactory bulbs via the olfactory nerves (cranial nerve I). In turn, neurons projection from the olfactory bulbs transmit

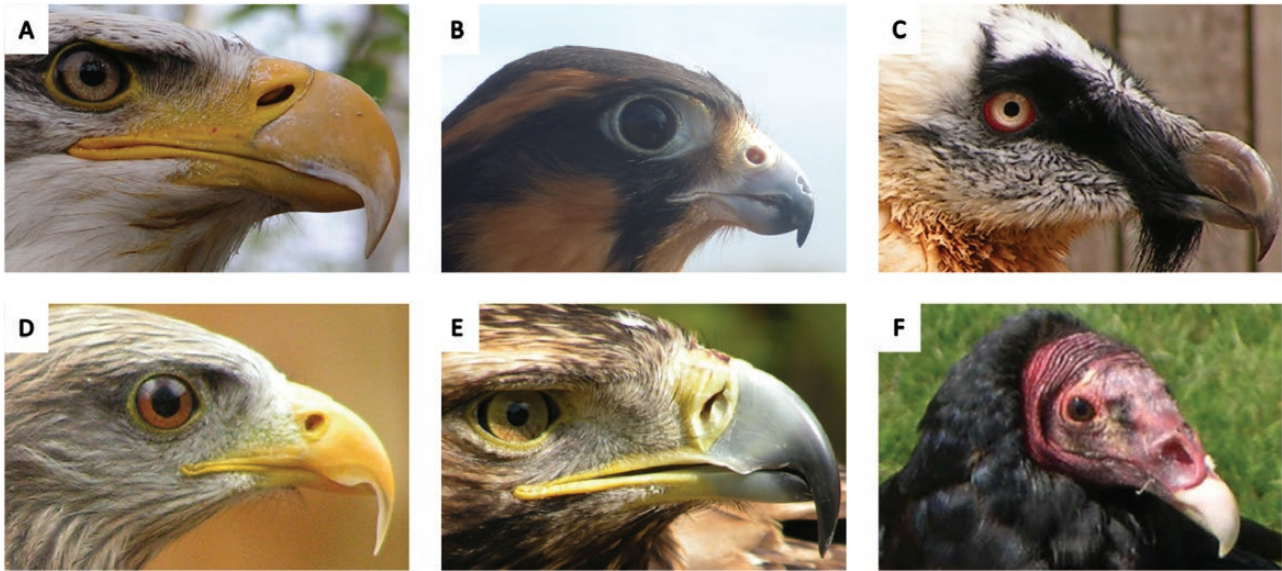


Figure 1. Pictures of the nostrils of six raptors species. A, bald eagle, *Haliaeetus leucocephalus*. B, aplomado falcon, *Falco femoralis*. C, bearded vulture, *Gypaetus barbatus* (note that the nostrils are covered by typical feathers). D, yellow billed kite, *Milvus aegyptius*. E, eastern imperial eagle, *Aquila heliaca*. F, turkey vulture, *Cathartes aura* (note that the nostrils are not divided by a septum).

information to the piriform cortex (a region of the brain involved in the discrimination and memorization of odour stimuli). The size of olfactory bulbs in birds is positively correlated to the number (but not the functionality) of olfactory receptors (Steiger *et al.*, 2008), as well as olfactory acuity (Clark *et al.*, 1993). Therefore, it appears to be a good proxy of olfactory abilities in birds. The olfactory bulbs have been described in a number of bird species (Bang & Cobb, 1968; Corfield *et al.*, 2015) and a large variation in the relative size of these structures has been found among species. Bang & Cobb (1968) used an OB ratio (olfactory bulb diameter/telencephalic hemisphere diameter) as a measure of the relative size of the olfactory bulbs. They found that the ratio varied from 37% in snow petrels, *Pagodroma nivea* (Forster, 1777), to 3% in the black-capped chickadee, *Poecile atricapillus* (Linnaeus, 1766). The OB ratio is measured from the greater diameter of one olfactory bulb and the greater diameter of the corresponding cerebral hemisphere, no matter in what axis for both (Bang & Cobb, 1968; Zelenitsky *et al.*, 2011). Variation in OB size has been correlated to bird ecology, such as habitat (Corfield *et al.*, 2015) or activity pattern (Healy & Guilford, 1990). For instance, species living in semi-aquatic habitats have larger OB than species living in aquatic or terrestrial habitats (Corfield *et al.*, 2015). Nocturnal and crepuscular species have larger OB than diurnal species (Healy & Guilford, 1990). OB size varies also among orders, but the OB of raptors (approximately 17.5% on average) is similar to the average OB in birds

(Fig. 2), suggesting a relatively high capacity to rely on olfaction. Indeed, following the principle of proper mass (Jerison, 2012), a large olfactory bulb should reflect high olfactory sensitivity and/or acuity. For instance, the turkey vulture, *Cathartes aura* (Linnaeus, 1758), is thought to depend highly on its sense of smell, because its olfactory bulb (OB ratio = 28.7%; Bang & Cobb, 1968) is four times larger than that of its close relative, the American black vulture *Coragyps atratus* (Bechstein, 1783) (Grigg *et al.*, 2017). Therefore, based on this anatomical evidence, it appears that raptors likely have a functional sense of smell that can be used for diverse behaviours.

FINDING FOOD WITH THE SENSE OF SMELL

Olfaction plays a key role in foraging in birds (Nevitt, 1999). For instance, the nocturnal brown kiwi, *Apteryx mantelli* (Bartlett, 1851), is more efficient at finding prey using olfaction than using touch or audition (Cunningham *et al.*, 2009). Olfaction also plays a particularly important role in foraging in procellariiform seabirds. For example, the wandering albatross, *Diomedea exulans* (Linnaeus, 1758), can find food by sight or smell alone, with a higher success when both senses are used in combination (Mardon *et al.*, 2010a). Furthermore, albatrosses may use olfaction to find food almost 50% of the time (Nevitt *et al.*, 2008).

There are some indications that raptors use their sense of smell to forage. The best-known example is

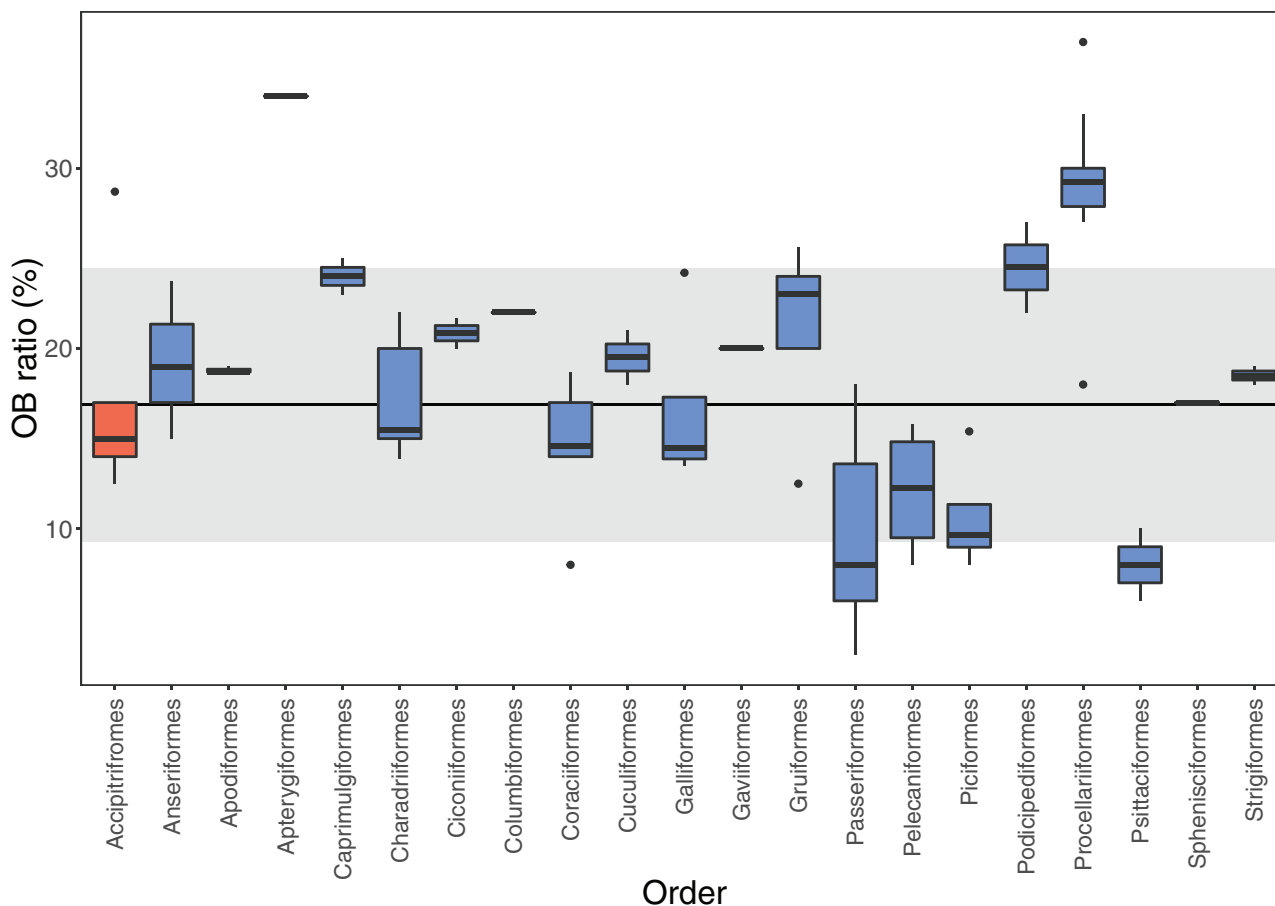


Figure 2. Olfactory bulb ratio of raptors (in red) compare to other bird orders (in blue). Horizontal black line represents the average of OB ratio of all order except Accipitriformes, grey shade represents the standard deviation. Data from [Bang & Cobb \(1968\)](#). Difference in OB ratio between raptorial and non-raptorial species was tested using phylogenetic generalized least squares (PGLS) to account for phylogenetic relatedness. Data were analysed on R 3.5.1 using [ggplot2 \(Wickham & Chang, 2015\)](#), [ape \(Paradis et al., 2004\)](#), [phytools \(Revell, 2012\)](#) and [nlme \(Pinheiro et al., 2018\)](#) packages. Phylogeny was obtained for 98 out of 108 species using a consensus tree based on 1000 randomly selected trees from [www.BirdTree.org \(Jetz et al., 2012\)](#). Edge lengths were obtained by computing the mean edge length for each edge in the consensus tree. The OB ratio of Accipitriformes was not different from the average ratio of all other species (Accipitriformes: 17.44 ± 6.50 (mean \pm SD); Other: 16.89 ± 7.58 (mean \pm SD); $t = -7.75e^{-3}$, $P = 0.99$).

that of the turkey vulture. This species is efficient at finding carcasses under the canopy (within less than a day), whether they are visible or not, suggesting that the sense of smell plays an important role in foraging ([Houston, 1986](#)). [Stager \(1964\)](#) found that turkey vultures respond to ethanethiol (a carrion-associated odorant) at approximately 61 m altitude and 183 m downwind from the odorant source. However, [Smith & Paselk \(1986\)](#) found that at such altitude, the concentration should have been 10^{-12} to 10^{-13} mol/L air, while based on heart-rate response, turkey vultures can smell ethanethiol at 'only' 10^{-6} mol/L air. These contradictory results have cast some doubt on the hypothesis that olfaction is important for food location in this species.

However, a recent experimental study has shown that olfaction does appear to play a crucial role in foraging for turkey vultures. In a series of experiments, [Potier et al. \(2019\)](#) have shown that turkey vultures can find food only by olfaction (i.e. discrimination by other cues was not possible) and, moreover, this species appears to rely more on olfaction than on sight when both cues gave contradictory information. Therefore, it seems highly likely that at least turkey vultures forage mainly using their sense of smell.

Evidence for the use of olfaction during foraging in other raptorial species is scarce, but it nonetheless appears that species other than turkey vultures rely on olfaction to some extent when finding food. A

species closely related to turkey vultures, the greater yellow-headed vulture, *Cathartes melambrotus* (Wetmore, 1964), is also able to find visually hidden carcasses (e.g. covered by leaves), suggesting a role for olfaction (Graves, 1992). Gilbert & Chansocheat (2006) observed several Old World vulture species [white-rumped vultures, *Gyps bengalensis* (Gmelin, 1788), red-headed vultures, *Sarcogyps calvus* (Scopoli, 1786) and slender-billed vultures, *Gyps tenuirostris* (Gray, 1844)] excavating and feeding on the carcass of a cow buried at a depth of 30 cm. From their observations, the most likely explanation for how these birds were able to rapidly (within three days) and accurately localize hidden food, is that they used of their sense of smell. However, it was not possible to know which species may have used its sense of smell (if so) and which species may have used local enhancement. More recently, Röder *et al.* (2014) showed that the foul-smelling secretion of the great spotted cuckoo, *Clamator glandarius* (Linnaeus, 1758), may act as an olfactory repellent for different species of falcons. Indeed, when a synthetic mixture of juvenile cuckoo secretions was sprayed on chicken meat, falcons always refused to eat it. However, Röder *et al.* (2014) acknowledged that spraying the mixture directly on to the meat may have modified its visual and gustative properties and, therefore, they could not have concluded with certainty that falcons refused to eat the sprayed meat because of olfactory cues alone, even if it is highly probable. Yang *et al.* (2015) explored the functional sense of smell for foraging in the Oriental honey buzzard. While this species consumes honeycombs and larvae, they also eat pollen dough, a mixture of pollen, soybeans and sugar used as supplementary food for bees by beekeepers, which has a special odour used by other organisms, such as pollen beetles *Brassicogethes aeneus* (Fabricius, 1775) (Cook *et al.*, 2002). Yang *et al.* (2015) showed that Oriental honey buzzards strongly preferred pollen-containing dough to dough made only of soybeans and sugar, suggesting that they use olfaction to differentiate between these two, even though the authors could not exclude the possibility that different compositions of dough may have led to differences in visual cues as perceived by the buzzards.

Two recent studies have shown experimentally that different raptor species may use olfaction to find food. Slater & Hauber (2017) found that vultures and eagles have learned to associated a non-biologically relevant odour (peppermint oil) to food reward. Thus, olfactory ability can also be applied to biologically relevant odours in a foraging context. Potier *et al.* (2019) have shown that, using the same experimental setup as used for the turkey vulture experiments mentioned earlier, southern caracara, *Caracara plancus* (Miller, 1777), may find food only using smell when no other sensory cues are available. However, contrary to the turkey vulture, olfactory cues

did not seem to be prevalent compared to visual cues when both cues gave contradictory information.

In conclusion, a review of the recent literature reveals that there is growing evidence that raptors, according to their ecology, may be able to use their sense of smell to forage. For foraging, olfaction may be useless for species that hunt at high altitude. However, some species may rely heavily on olfaction while foraging. Indeed, as illustrated by the examples listed above, carrion-eating raptors may have an advantage in using olfaction for foraging. Furthermore, the palm-nut vulture, *Gypohierax angolensis* (Gmelin, 1788), which eats mostly palm-fruits, could use fruit-associated odours to find food, similar to primates (Dominy, 2004). While further studies on the role of olfaction by foraging raptors are needed, we will see that there is almost no information on chemical communication or the use of olfactory cues for navigation in raptors.

CHEMOSIGNALLING IN RAPTORS

Avian chemical communication is now well accepted (for a review see: Caro *et al.*, 2015). The main source of avian odour is probably the secretions of the preen/uropygial gland (Campagna *et al.*, 2012), even if microbiota play a key role too (Maraci *et al.*, 2018). In birds, the chemical composition of preen oil encodes information such as sex, age, individuality, seasonal variation, species affiliation or genotype (Hagelin, 2007; Mardon *et al.*, 2010b; Wyatt, 2014; Caro *et al.*, 2015; Gabirot *et al.*, 2016). Most of these odour cues can be recognized by birds. For instance, individual Antarctic prions, *Pachyptila desolata* (Gmelin, 1789), can recognize their partners by smell only (Bonadonna & Nevitt, 2004). Furthermore, European storm petrels (Bonadonna & Sanz-Aguilar, 2012), zebra finches, *Taeniopygia guttata* (Vieillot, 1817) (Krause *et al.*, 2012) and house sparrows, *Passer domesticus* (Linnaeus, 1758) (Fracasso *et al.*, 2019) can recognize their kin based on olfactory cues alone.

To date, it appears that only one study has explored the possible role of olfaction for communication in a raptorial species, the black kite, *Milvus migrans* (Boddaert, 1783), (Potier *et al.*, 2018b). While the functionality of the chemical communication has to be tested in this species, the chemical compounds of the preen gland secretion do encode important information for communication in this species. First, each individual has its own olfactory signature, i.e. the chemical profile of an individual is more similar across seasons than that of other individuals. Therefore, black kites might recognize their partner, for example, only using olfactory cues. Second, while the individual signature is maintained across seasons, its chemical profile varies between the non-breeding and breeding season. This

means that, as found in the domestic chicken, *Gallus gallus domesticus* (Linnaeus, 1758) (Hirao *et al.*, 2009), black kites may be synchronized for reproduction as preen oil compounds may convey information about the reproductive status of an individual. Finally, during the breeding season, the chemical profile reflects genetic relatedness, that may allow these birds to avoid inbreeding by choosing non-kin mates.

While the process of communication is essential to understand how species interact with their biotic environment, there is a lack of knowledge regarding what role olfaction plays in raptor communication, and further studies are thus essential. In particular, it may be advantageous for species that are gregarious or that live with some degree of social organization to use olfaction for intra- or interspecific communication. For example, dominance status is expressed through olfactory signals in the ring-tailed lemur, *Lemur catta* (Linnaeus, 1758) (Scordato & Drea, 2007), and this may also be the case in some bird species. Indeed, because Harris's hawks are reported to breed regularly in cooperative units with social organization and dominance status (Dawson & Mannan, 1991), olfaction could be essential to recognize and behave adequately with other group members in this species.

CAN RAPTORS NAVIGATE AND ORIENTATE USING OLFACTORY CUES?

Olfactory navigation has been relatively well studied in two groups of birds: pigeons and seabirds (for a review see: Gagliardo, 2013). For instance, the lesser black-backed gull, *Larus fuscus fuscus* (Linnaeus, 1758) can use olfactory information to correct for displacement in their migratory route and, therefore, navigate successfully (Wikelski *et al.*, 2015). However, as mentioned by Gagliardo (2013) in her review, '... the investigation of a possible role of olfactory cues in wild bird navigation is still at an early stage'. Indeed, apart from pigeons and seabirds, only a small number of studies have shown olfactory navigation in other birds, e.g. in swifts, *Apus apus* (Linnaeus, 1758) (Fiaschi *et al.*, 1974), starlings, *Sturnus vulgaris* (Linnaeus, 1758) (Wallraff *et al.*, 1995) and catbirds, *Dumetella carolinensis* (Linnaeus, 1766) (Holland *et al.*, 2009). In the latter, olfaction appears to play a dominant role in migration. While some raptor species navigate over long distances (Ferguson-Lees & Christie, 2001), with home-range sizes up to 122 550 ha for the peregrine falcon (Peery, 2000), to my knowledge, no studies have explicitly explored the role of olfactory cues for navigation in these birds. For example, ospreys, *Pandion haliaetus* (Linnaeus, 1758), show a high degree of repeatability in their migration routes (Vardanis *et al.*, 2016), but it is still unclear which sensory modalities they use to orientate correctly. The role of olfaction

has been shown to be essential for orientation during migration in song birds (Holland *et al.*, 2009) and, therefore, the importance of olfaction while migrating in ospreys should be studied. The role of olfaction in bird navigation is an important issue that needs further investigation (Gagliardo, 2013), especially in raptorial species.

CONCLUSION AND PERSPECTIVES

While it is well accepted that raptors rely heavily on vision, there is growing evidence that olfaction also plays a key role in many behaviours, such as foraging and, potentially, communication. However, information about this sensory modality in raptors remains extremely scarce. Increasing our understanding of raptor sensory systems is essential to better protect them from collisions with man-made objects and/or from poisoning (Martin, 2017) and to improve conservation programmes (Campbell-Palmer & Rosell, 2011). Understanding the olfactory abilities of animals is essential for conservation programmes, particularly, to increase animal welfare in captivity, encourage captive breeding, influence habitat selection for reintroduction, etc. (for detailed key areas in which understanding animal chemical communication aids conservation see: Campbell-Palmer & Rosell, 2011). Moreover, raptors are more threatened than birds in general, with 52% of species having declining global populations (McClure *et al.*, 2018). Consequently, understanding the olfactory abilities of raptors is not only essential to understand more deeply how they interact with their anthropomorphic and non-anthropomorphic environment, but also for improving conservation and management strategies for these magnificent birds.

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