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ODOR TRANSMISSION AND OLFACTION: THE TUFT OF THE UROPYGIAL GLAND AND OLFACTORY ABILITY IN BIRDS

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Abstract. The role of olfaction in birds is poorly understood, in part because of our limited knowledge of signal-transmission mechanisms. Here we evaluate the hypothesis that the secretions of the uropygial gland serve as olfactory signals in birds by testing the prediction that size of the olfactory bulb, a proxy for olfactory ability, covaries positively with the size of the uropygial gland's tuft, a circlet of feathers whose size varies extraordinarily from species to species. The function of this tuft has remained a mystery, but mechanical or protective roles are unlikely on the basis that these feathers are downy and always saturated with gland secretion. These observations instead suggest that the tuft may be involved in trapping the compounds produced by the gland's secretions to facilitate conspecifics' perception of odor. We therefore predicted that the uropygial gland's tuft should be more developed in birds with better capacity to smell. Using a dataset of 29 species of birds of 20 families of nonpasserines, we show that the sizes of the tuft (relative to the uropygial gland) and olfactory bulb (relative to the cerebral hemisphere and body mass) are positively correlated after the confounding effects of colonial breeding and phylogeny are controlled for. This suggests that the tuft may have evolved because of the adaptive benefits of enhancing the transmission of body odors. Additionally, colonial species have tufts larger than those of solitary species, as expected because sociality increases encounter rates and the prevalence of odor-producing bacteria.

Key words: birds, coloniality, olfaction, olfactory bulb.

La Transmisión del Olor y la Olfacción: El Penacho de Plumas de la Glándula Uropigial y la Habilidad Olfativa en las Aves

Resumen. La función de la olfacción en aves es poco conocida, en parte debido a nuestro escaso conocimiento de los mecanismos de transmisión de las señales olfativas. Aquí evaluamos la hipótesis de que las secreciones de la glándula uropigial actúan como señales olfativas en aves evaluando la predicción de que el tamaño del bulbo olfatorio, un indicador de la capacidad olfatoria, covaría positivamente con el tamaño del penacho de plumas en torno a la glándula uropigial, un círculo de plumas cuyo tamaño varía extraordinariamente entre especies. La función de este penacho de plumas ha sido un misterio, pero no es probable que tenga funciones mecánicas o protectoras ya que está compuesto por plumón que siempre está saturado por la secreción de la glándula. Estas observaciones sugieren por el contrario que el penacho de plumas en torno a la glándula uropigial podría estar implicado en la captura de los compuestos producidos por las secreciones de la glándula para facilitar la percepción del olor por parte de otros individuos de la misma especie. Por lo tanto predijimos que el penacho de plumas en torno a la glándula uropigial debería estar más desarrollado en las aves con mayor capacidad para oler. Utilizando datos de 29 especies de aves pertenecientes a 20 familias de no paseriformes, mostramos que los tamaños del penacho de plumas (en relación al tamaño de la glándula uropigial) y del bulbo olfatorio (relativo al tamaño del hemisferio cerebral y al tamaño corporal) están positivamente correlacionados cuando los efectos de confusión constituídos por el tipo de colonialidad durante la reproducción y la filogenia son controlados. Esto sugiere que el penacho de plumas en torno a la glándula uropigial podría haber evolucionado debido a los beneficios adaptativos de la mejora de la transmisión de olores corporales. Además, las especies coloniales tienen penachos más grandes que las especies solitarias, como se esperaba debido a que la sociabilidad aumenta la tasa de encuentros con otros individuos y la prevalencia de bacterias productoras de olor.

INTRODUCTION

The uropygial gland of birds is a holocrine gland located dorsal to the levator muscle of the tail, secreting lipidic substances that are smeared onto the plumage during preening (Elder 1954, Jacob and Ziswiler 1982). The function of secretions produced by the uropygial gland has been subject to several studies in recent years, especially after Galván and Sanz (2006) showed that the size of this gland can be quantified in live birds. It has long been considered that uropygial

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gland secretions serve mainly to waterproof and maintain the plumage flexible and in optimal condition for flight (Jacob and Ziswiler 1982), an inference supported by comparative studies showing that species inhabiting humid environments have larger uropygial glands (Jacob and Ziswiler 1982, Galván et al. 2008, Møller et al. 2010). Moreno-Rueda (2011) has shown that individual birds with larger uropygial glands have feathers that are less damaged. A second primary function that probably promotes the evolution of the uropygial gland is the capacity of its secretions to combat bacteria and fungi (Shawkey et al. 2003, Soler et al. 2008, Martín-Vivaldi et al. 2010; but see Galván 2011). Additionally, feather mites living on the surface of feathers feed on uropygial gland secretions and may thus exert selective pressures on both the gland's size and the chemical composition of its secretions by removing micro-organisms and debris that accumulate on feathers (Haribal et al. 2005, 2011, Galván et al. 2008). Secondary functions of uropygial gland secretions that have probably evolved subsequent to the evolution of the primary functions are the secretion's capacity to prevent detection by mammalian predators (Reneerkens 2007) and to enhance plumage color properties (Galván and Sanz 2006, Delhey et al. 2007, Amat et al. 2011).

Uropygial gland secretions also seem to be involved in mating behavior through the odor they produce, as first proposed by Balthazart and Schoffeniels (1979) and Jacob et al. (1979) and more recently by Hirao et al. (2009). Various authors (Jacob et al. 1979, Leclaire et al. 2011, Whittaker et al. 2010, Amo et al. 2012) have identified sexual differences in the chemical composition of uropygial gland secretions in various species of birds, and attempts to experimentally test for an association between uropygial gland secretions and olfactory communication of birds have recently been made. Zhang et al. (2010) reported a preference of female Budgerigars (*Melopsittacus undulatus*) for certain volatile compounds present in the uropygial gland secretion of males, and in the Dark-eyed Junco (*Junco hyemalis*) Whittaker et al. (2011) found a preference of both males and females for odor from uropygial gland secretions of males. Indeed, the importance of olfaction has increased during the evolution of birds (Zelenitsky et al. 2011), and a growing number of studies shows that birds are neither anosmic nor microsmatic and actually use perceived odors in a variety of behaviors associated with both inter- and intraspecific communication (e.g., Amo et al. 2008, Balthazart and Taziaux 2009, Caro and Balthazart 2010, Cunningham and Nevitt 2011, Krause et al. 2012). Thus the uropygial gland may also function as an odor-producing organ, representing one of the most likely sources of odor in birds (Mardon et al. 2011, Hagelin and Jones 2007).

In many groups of birds, the external surface of the uropygial gland has a circlet of feathers (*circulus uropygialis*) surrounding the orifices through which the secretion comes out, forming a tuft (Jacob and Ziswiler 1982). These feathers are downy (i.e., they do not have barbules that maintain the cohesion between barbs) and are saturated with gland secretions (Jacob and Ziswiler 1982). Interspecific variation in the length, density, and conformation of the tuft feathers is extraordinary (Jacob and Ziswiler 1982, Johnston 1988), suggesting that the importance of this structure might differ among birds. However, the adaptive function that has led to the evolution of this conspicuous structure remains unknown. Given the downy nature of these feathers (i.e., it is not likely that they have a mechanical or protective role) and the fact that they are always saturated with gland secretions, we propose that the uropygial gland tuft may be involved in trapping and transmitting the volatile compounds of secretions and thus allow conspecifics a better perception of the odor, in parallel to the function of certain patches of body hair in humans and other animals (Kohl and Francoeur 2002). During preening, the beak and face of birds probably contact the uropygial gland tuft, so this structure may also act as a "brush" to spread uropygial gland secretions onto the plumage. Thus the uropygial gland tuft may provide a large surface over which uropygial gland secretions can spread, facilitate trapping of volatiles, and also mechanically facilitate spreading of secretion when a bird's head is rubbed into the tuft feathers.

If the uropygial gland tuft has a function in trapping and spreading the volatile odors of secretions, it should be expected that the tuft is more developed in species in which olfaction plays a more prominent role and thus have a greater sense of smell. This olfactory ability can be quantified by the size (relative to the size of the cerebral hemisphere) of the olfactory bulb, a structure of the forebrain of vertebrates that is responsible for odor perception (for birds, see Bang and Wenzel 1985; for mammals, see Jacobs 2012), as the bulb's relative size is positively related to the number and size of its mitral cells and the number of glomeruli and receptor genes (Bang and Wenzel 1985, Zelenitsky et al. 2011 and references therein). Therefore, we predicted a positive relationship between the size of the uropygial gland tuft and the relative size of the olfactory bulb. We tested this prediction in 29 species of birds of 20 families of non-oscine birds, controlling for the potentially confounding effect of colonial breeding. The rationale for controlling for coloniality is that olfactory ability in birds is increasingly being shown to be associated with intraspecific communication (see reviews in Balthazart and Taziaux 2009, Caro and Balthazart 2010), and species that breed in colonies have more encounters with conspecifics than do those that breed solitarily. Furthermore, the prevalence of bacteria increases with colony size in birds (Møller et al. 2009), and at least in some species bacteria are responsible for the volatile compounds that create the odor of uropygial gland secretions (Martín-Vivaldi et al. 2010). These two facts suggest that coloniality may affect the olfactory ability of birds (an association between size of the olfactory bulb and colonial nesting has been reported by Bang and Wenzel 1985) and

also the size of the uropygial gland tuft, if this structure actually acts in trapping the odor of uropygial gland secretions. Therefore, we also predicted that colonial species should have uropygial gland tufts larger than those of solitary species. It must be emphasized that we did not include any representative species of the largest group of birds (i.e., the Oscines) in our analysis because they have not developed uropygial gland tufts (Jacob and Ziswiler 1982).

METHODS

SIZE OF UROPYGIAL GLAND TUFT

We used the quotient of the length of the tuft and the length of the papilla of the uropygial gland provided by Jacob and Ziswiler (1982) as an index of the tuft's relative size, because this ratio may correspond to a specific functional type (Jacob and Ziswiler 1982) and because it represents a measure of the tuft's size that is independent of uropygial gland size. We did not consider the number of feathers of the tuft because this is independent of tuft density (Jacob and Ziswiler 1982) and hence cannot be taken as a proxy for tuft development.

OLFACTORY BULB SIZE, BODY MASS, AND COLONIALITY

We took information on the diameters of the olfactory bulb and cerebral hemisphere, birds' body mass, and their tendency to breed in colonies from Bang (1971) and Bang and Cobb (1968).

From these sources, we obtained information on the sizes of both the uropygial gland tuft and olfactory bulb for a total of 18 species of birds. However, for an additional 10 species with information on tuft size there was also information available on olfactory bulb size for a single congener in the datasets of Bang (1971) and Bang and Cobb (1968). To be able to combine the information on tuft size and bulb size for these taxa, we associated the relative size of these species' bulb with the size of the tuft of congeners included in the dataset of Jacob and Ziswiler (1982), thus assuming that the relative size (i.e., independent of body size) of the olfactory bulb is more similar among species of the same genus than among species of different genera (Steiger et al. 2008). This approach is especially well suited to our data given the high phylogenetic diversity included in our dataset (Table 1). In the case of the rails (genus *Rallus*), Jacob and Ziswiler (1982) provided information on uropygial gland tuft size for a single species (*R. aquaticus*), but information on olfactory bulb size was available for three different congeners, so we used the mean value of bulb size for these species. Thus our dataset comprised a total of 29 species from 20 non-oscine families. Information on the sizes of the uropygial gland tuft and olfactory bulb and on coloniality for these species is shown in Table 1.

DATA ANALYSES

To estimate of relative size of the olfactory bulb, we regressed the diameter of the olfactory bulb ($\log_{10}$-transformed) against that of the cerebral hemisphere ($\log_{10}$-transformed) to remove the allometric effect of the latter variable. Clark et al. (1993) used a similar procedure in an analysis of bulb size in the Oscines. To control for allometric effects of body size, we also entered body mass ($\log_{10}$-transformed) as a covariate in the same multiple regression. Since species are not independent sample units, we used phylogenetic generalized least squares (PGLS) models with an unpublished function by R. Freckleton (pglm3.4.r) in the R statistical environment. First we estimated the phylogenetic signal with the parameter λ, which ranges from 0 (phylogenetic independence) to 1 (species' traits covary in proportion to their shared evolutionary history as predicted by a model of Brownian motion; Freckleton et al. 2002). Then we calculated the maximum-likelihood value of λ, with which we made the phylogenetically corrected regression of olfactory bulb diameter against cerebral hemisphere diameter and body mass. We included the residuals of this model as a covariate in another PGLS model in which the relative size of the uropygial gland tuft ($\log_{10}$-transformed) was the response variable. We added a dummy variable to this model to account for the tendency of species to breed in colonies (code 1) or in isolated pairs (code 0). The phylogenetic hypothesis (see Fig. 1) was taken from the species-level supertree of Davis (2008; available at: http://theses.gla.ac.uk/178/), assuming all branch lengths to equal unity. Davis (2008) created the phylogeny by the supertree method, assembling it from many smaller phylogenies from different sources but having some taxa in common; see Davis (2008) for further details on the supertree method. There was no available phylogeny with known branch lengths for the total number of species included in our study.

RESULTS

The maximum likelihood of λ was 6.61×10^{-5}. At this value, the PGLS model was significant ($F_{2,26} = 18.64$, $P < 0.0001$) and explained 58.9% of the variance among species in the relative size of the uropygial gland tuft. The effect of olfactory bulb size was significant and positive ($b = 1.29$, $t = 2.81$, $P = 0.009$; Fig. 2). The effect of colonial breeding was also significant ($b = 0.58$, $t = 5.12$, $P < 0.0001$), indicating that colonial species have significantly larger uropygial gland tufts than do solitary species (adjusted mean ±SE; colonial: 1.03 ± 0.06, solitary: 0.41 ± 0.03).

DISCUSSION

If the uropygial gland produces volatile compounds that birds can perceive and use in intraspecific communication, and if the uropygial gland's tuft plays a role in trapping and

TABLE 1. Relative size of uropygial gland tuft (quotient of length of the tuft and length of the papilla of the uropygial gland), relative size of olfactory bulb (residuals of bulb size diameter regressed against cerebral hemisphere diameter and body mass), body mass, and tendency to breed in colonies for 29 species of birds from 20 families.

Species with information on size of uropygial gland tuft	Species with information on olfactory bulb size[a]	Family	Relative length of uropygial gland tuft	Relative size of olfactory bulb	Body mass (g)	Coloniality[b]
Brahminy Kite (*Haliastur indus*)	Same	Accipitridae	2	–0.113	610	0
Black Kite (*Milvus migrans*)	Same	Accipitridae	4	–0.048	828.5	1
Atlantic Puffin (*Fratercula arctica*)	Same	Alcidae	5	–0.090	383	1
Common Murre (*Uria aalge*)	Thick-billed Murre (*Uria lomvia*)	Alcidae	6	–0.098	919.5	1
Green-winged Teal (*Anas crecca*)	Same	Anatidae	4	0.005	286.5	0
Mallard (*Anas platyrhynchos*)	Same	Anatidae	3.3	0.062	1,119	0
Common Merganser (*Mergus merganser*)	Red-breasted Merganser (*Mergus serrator*)	Anatidae	2.6	–0.061	1090.5	0
Northern Lapwing (*Vanellus vanellus*)	Red-wattled Lapwing (*Vanellus indicus*)	Charadriidae	3.3	0.052	145.5	0
Wandering Albatross (*Diomedea exulans*)	Black-footed Albatross (*Phoebastria nigripes*)	Diomedeidae	15.4	0.310	3195	1
Eurasian Kestrel (*Falco tinnunculus*)	Peregrine Falcon (*Falco peregrinus*)	Falconidae	2	0.004	889.25	0
Common Loon (*Gavia immer*)	Same	Gaviidae	7.3	0.108	3,150	0
Herring Gull (*Larus argentatus*)	Same	Laridae	6.5	–0.052	895	1
Wild Turkey (*Meleagris gallopavo*)	Same	Meleagrididae	0.8	–0.219	5,811	0
Osprey (*Pandion haliaetus*)	Same	Pandionidae	4.3	–0.078	1527.5	1
Great White Pelican (*Pelecanus onocrotalus*)	Brown Pelican (*Pelecanus occidentalis*)	Pelecanidae	24	–0.120	3438	1
Great Cormorant (*Phalacrocorax carbo*)	Same	Phalacrocoracidae	16	–0.111	2254	1
Lesser Flamingo (*Phoeniconaias minor*)	Same	Phoenicopteridae	11	0.144	1500	1
Little Grebe (*Tachybaptus ruficollis*)	Same	Podicipedidae	1	0.039	190	0
Great Crested Grebe (*Podiceps cristatus*)	Horned Grebe (*Podiceps auritus*)	Podicipedidae	10	0.115	394	0
Northern Fulmar (*Fulmarus glacialis*)	Same	Procellariidae	16.6	0.232	795	1
Great Shearwater (*Puffinus gravis*)	Same	Procellariidae	18.3	0.251	849	1
Red-breasted Parakeet (*Psittacula alexandri*)	Rose-ringed Parakeet (*Psittacula krameri*)	Psittacidae	1.9	–0.118	137	0
Common Coot (*Fulica atra*)	Same	Rallidae	5.5	0.115	732.5	0
Common Moorhen (*Gallinula chloropus*)	Same	Rallidae	10	–0.004	348.5	0
Spotted Crake (*Porzana porzana*)	Rudy-breasted Crake (*Porzana fusca*)	Rallidae	2.5	0.003	60	0
Water Rail (*Rallus aquaticus*)	King Rail (*Rallus elegans*), Virginia Rail (*Rallus limicola*) and Clapper Rail (*Rallus longirostris*)	Rallidae	4	0.023	267	0
Eurasian Woodcock (*Scolopax rusticola*)	American Woodcock (*Scolopax minor*)	Scolopacidae	1.1	–0.057	197.5	0
Northern Gannet (*Morus bassanus*)	Same	Sulidae	19	–0.191	2999.5	1
Hoopoe (*Upupa epops*)	Same	Upupidae	1	–0.101	67.05	0

[a]Related species considered when the species with information on the size of the olfactory bulb did not match the species with information on the length of the uropygial gland tuft.
[b]0, solitary; 1, colonial.

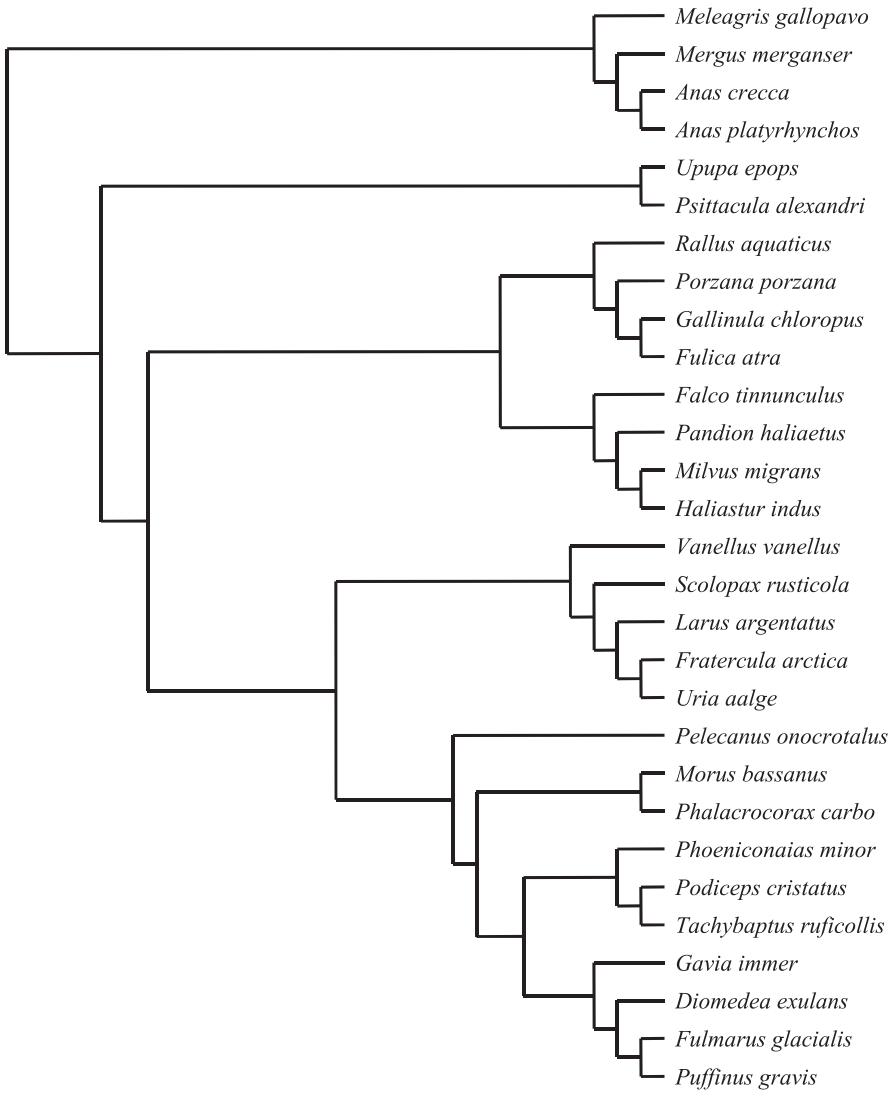

FIGURE 1. Phylogenetic hypothesis used in the study.

spreading such compounds, the adaptive benefits of chemical communication should select for a larger tuft, so that species with better ability to smell should develop larger tufts. Thus we predict a positive association between the relative sizes of the tuft and olfactory bulb, the latter a proxy for the ability to perceive and discriminate odors, across taxa. Our analysis, based on 29 species of birds from 20 families, supported this prediction; species with larger tufts had larger olfactory bulbs. The results also confirmed the prediction that colonial species should have evolved uropygial gland tufts larger than those of solitary species, made on the basis that sociality promotes encounters with conspecifics and increases the prevalence of odor-producing bacteria (Møller et al. 2009). This correlation suggests that the uropygial gland tuft, whose function has remained unknown despite being described long ago (Nitzsch 1840), may play a role in trapping the secretions and odors produced by the uropygial gland. This function is likely for a structure composed of downy feathers that are saturated with gland secretions (Jacob and Ziswiler 1982).

Birds have traditionally been considered to differ from mammals in the ability to smell, frequently assumed to be insignificant in birds, although an increasing number of studies shows that birds can perceive and use volatile compounds in intraspecific communication (e.g., Caro and Balthazart 2010). Secretions from the uropygial gland appear as the most likely source of bird odors (Leclaire et al. 2011, Whittaker et al. 2010, 2011, Zhang et al. 2010, Amo et al. 2012). Thus it is likely that a structure such as the uropygial gland tuft, which concentrates gland secretions (Jacob and Ziswiler 1982) and thus probably traps and spreads their odor, provides

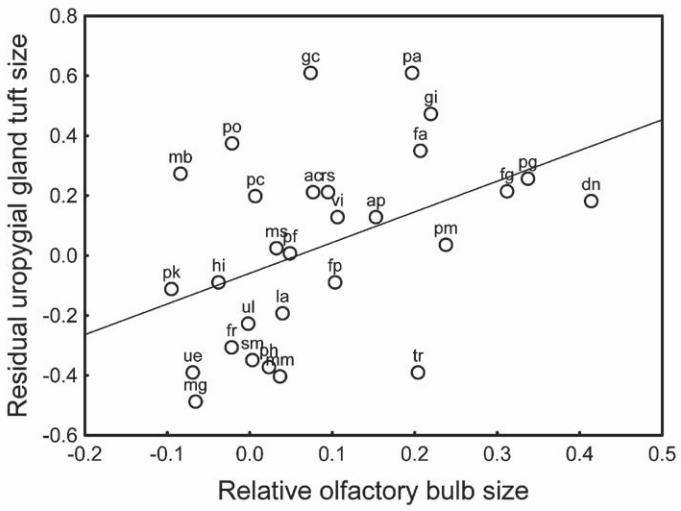

FIGURE 2. Relationship between the relative size of the uropygial gland tuft and the relative size of the olfactory bulb in 29 species of birds. The residual figures of the response variable (i.e., independent of the effect of colonial breeding) are shown. The line is the regression line. Species coded as follows: ac, *Anas crecca*; ap, *Anas platyrhynchos*; dn, *Phoebastria nigripes*; fa, *Fulica atra*; fg, *Fulmarus glacialis*; fp, *Falco peregrinus*; fr, *Fratercula arctica*; gc, *Gallinula chloropus*; gi, *Gavia immer*; hi, *Haliastur indus*; la, *Larus argentatus*; mb, *Morus bassanus*; mg, *Meleagris gallopavo*; mm, *Milvus migrans*; ms, *Mergus serrator*; pa, *Podiceps auritus*; pc, *Phalacrocorax carbo*; pf, *Porzana fusca*; pg, *Puffinus gravis*; ph, *Pandion haliaetus*; pk, *Psittacula krameri*; pm, *Phoeniconaias minor*; po, *Pelecanus occidentalis*; rs, *Rallus* spp.; sm, *Scolopax minor*; tr, *Tachybaptus ruficollis*; ue, *Upupa epops*; ul, *Uria lomvia*; vi, *Vanellus indicus*.

an adaptive benefit to birds in which olfaction plays a greater role in intraspecific communication. It is interesting to note that the human species, which has lost most of its body hair during the course of evolution because reduced hair reduces overheating (Ruxton and Wilkinson 2011), has conserved some body parts covered by hair that seems to be involved in trapping body odors that transmit information on genetic diversity regarding the major histocompatibility complex (Vollrath and Milinski 1995, Kohl and Francoeur 2002). Certain hairs specialized in soaking up and emitting pheromones play a similar role in other mammals (Wyatt 2003). Our study thus suggests that the tuft of the uropygial gland of birds and certain hair types present in humans and other mammals that trap and emit volatile substances (as well as structures with similar functions in other animals as distant phylogenetically as insects; see Wyatt 2003) may represent cases of adaptive convergence caused by the benefits of increasing the perception by others of body odors.

Some groups of birds that are known to use the odor of uropygial gland secretions in intraspecific communication, such as the Oscines (Whittaker et al. 2011), have not developed uropygial gland tufts (Jacob and Ziswiler 1982). The remaining groups that are known to not have developed tufts are the Cuculiformes, Columbiformes, Caprimulgiformes, Apodiformes, and Meropidae (Jacob and Ziswiler 1982), all, except the Columbiformes, closely related phylogenetically (Davis 2008). Thus it is possible that phylogenetic constraint is responsible for the absence of the uropygial gland tuft and that some alternative mechanisms to enhance the transmission of body odors may have evolved in these groups of birds, although future studies should investigate this possibility. Future studies should also investigate intraspecific variability in the size of the uropygial gland tuft. We hypothesize that intraspecific variability in the size of this structure may depend on an individual's phenotypic quality if uropygial gland secretions convey information on aspects of individual quality and the tuft thus acts as an amplifier of such information (Hasson 1997, Galván and Sanz 2008).

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