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Olfaction in Chicken (*Gallus gallus*): A Neglected Mode of Social Communication?

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Avian olfaction has been neglected for a long time, although pioneering work has been conducted from the 1960th on (Bang, 1960; Bang and Cobb, 1968; Wenzel, 1968, 1971a,b; see also Nevitt and Hagelin, 2009). However, much of this research focused on odor perception in general or on the use of olfactory cues in non-social contexts, e.g., for navigation (Grubb, 1974; Papi et al., 1974; Wallraff, 1979; Gagliardo, 2013) or foraging (e.g., Grubb, 1972; Hutchison and Wenzel, 1980). In addition, this research focused on few avian taxa, in which the olfactory sense was regarded to be important due to large relative olfactory bulbs (Bang and Cobb, 1968). These taxa included, for example, the kiwi (*Apteryx australia*), which has a relative olfactory bulb size of 34% (ratio of the bulb to the hemisphere), the Procellariiformes, i.e., tube-nosed marine birds, with a mean ratio of 29%, and few other species and taxa (Bang and Cobb, 1968).

Within the last decade the use of olfactory cues in the above mentioned topics and avian taxa has been further explored (Nevitt and Bonadonna, 2005; Gagliardo et al., 2011; Amo et al., 2013; Gagliardo, 2013) and, in addition, the social olfactory communication has attracted the interest of research (e.g., Hagelin and Jones, 2007; Caro and Balthazart, 2010; Caspers and Krause, 2013; Caro et al., 2014). Thus, the potential not only of olfactory cues (i.e., information that has not designed for the purpose of communication by natural selection; Danchin et al., 2008) but also of olfactory signals (i.e., information/trait with adaptive function that alter the behavior of receivers; Danchin et al., 2008) became apparent also in avian taxa with smaller relative olfactory bulbs. Olfactory cues have been shown to play roles in inter-specific interactions such as for species recognition (Zhang et al., 2009; Mardon et al., 2010; Krause et al., 2014) or as chemical defenses against predatory species (e.g., Parejo et al., 2013). Olfactory signals are important in intra-specific communication. Offspring related odors (DeLeon et al., 2003; Caspers and Krause, 2011; Amo et al., 2014; Golüke et al., 2016) and the reproductive partners' scent (Bonadonna and Nevitt, 2004) can be recognized. The sex of an individual (Whittaker et al., 2010; Amo et al., 2012a) and kinship (Coffin et al., 2011; Bonadonna and Sanz-Aguilar, 2012; Krause et al., 2012) can be encoded in the scent. Olfactory signals are used for mate choice decisions (Amo et al., 2012b; Whittaker et al., 2013; Caspers et al., 2015) and provide information about the MHC (Strandh et al., 2012; Leclaire et al., 2014).

WHY THE CHICKEN IS INTERESTING

Here, we want to highlight the possible importance of the sense of smell in social communication in another avian species, i.e., the chicken (*Gallus gallus*). The chicken is one of the most commonly used avian species in science (e.g., Rose, 2000; Hillier et al., 2004) and is the most common avian species on the world with ~22-billion specimens kept in captivity for egg and meat production (Nicol, 2015). Thus, a deeper understanding of the use of olfactory communication in chickens would add necessary knowledge to fundamental and applied science which additionally may have consequences for the management and welfare of farmed chicken.

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Chickens show a complex social organization (Zuk et al., 1990a; Collias and Collias, 1996) including defined social relationships (Schjelderup-Ebbe, 1922). They are able to discriminate dozens of individuals from each other (D'Eath and Keeling, 2003) when faced with live conspecifics, whereby the sensory modes underlying this individual discrimination are still unknown. Vocal communication includes about 30 different vocal types (Collias and Joos, 1953; Huber and Fölsch, 1978) that are known to transfer information about e.g., social relationships, status, and level of aggressiveness. Visual components of communication are comb sizes and colourations which correlate with social status (Cloutier and Newberry, 2000) as well as the plumage ornaments of males (Nicol, 2015) that can attract females. Thus, social communication is an essential component in the life of chickens. Whereas, the use of vision (e.g., Zuk et al., 1990b; Cornwallis and Birkhead, 2007) and sound (e.g., Sherry, 1977; Collias, 1987) for social communication are widely recognized the use of olfaction has been largely neglected. This is surprising as the natural forest habitat of chickens is characterized by dimmed light (Wood-Gush, 1971) which limits the use of visual signaling. Furthermore, acoustic signals may increase predation risk and, thus, also their use may be constrained. These communicatory limitations under natural conditions might have been compensated by the use of olfaction in social communication. Understanding whether and how chickens make use of olfactory signals will not only increase our knowledge on the behavior biology of chickens, but additionally could help to improve housing conditions and aspects of animal welfare under commercial conditions.

OLFACTION IN THE CHICKEN

The Galliformes have small relative olfactory bulbs ranging from 13.5 to 15% with the chicken (*Gallus gallus*) ranging at the upper edge with 15% (Bang and Cobb, 1968). Wood-Gush (1971) mentioned that the sense of smell is believed to be very poorly developed, although the role of olfaction in the chicken's behavior had barely been investigated. Since that time, however, it has been shown in both, neurobiological (e.g., Tucker, 1965) as well as behavioral studies, that chicken perceive and react to olfactory stimuli (reviewed by Jones and Roper, 1997). Recent studies highlight the enormous number of olfactory receptor genes suggesting an important role of olfaction in many birds including chickens (Steiger et al., 2008; Khan et al., 2015). Also another class of receptors exists for volatile amines, i.e., the trace amine-associated receptors (TAAR), which however seem to be less pronounced in birds (Hashiguchi and Nishida, 2007).

Chickens discriminate and learn about odors and form memories of their home nest odor and their homes' scent (Burne and Rogers, 1995). Familiar odors are preferred throughout life (Jones and Gentle, 1985; Turro et al., 1994) and may reduce fear (Jones and Gentle, 1985). Olfactory cues can also provide information about predators and alarm contexts (Jones and Black, 1979; Fluck et al., 1996). Olfaction also seems to play a certain role during foraging, although it seems to be secondary compared to visual cues (Jones and Roper, 1997; but see Roper and Marples, 1997). Chickens avoid unfamiliar smelling food (Jones, 1987) and adverse reactions gradually appear to graded concentrations of odors (Burne and Rogers, 1996; Marples and Roper, 1997).

Since the seminal review on olfaction in chicken by Jones and Roper (1997) more studies have been published on this topic. However, most of these studies have focused on non-social or mechanistic aspects of odor perception rather than on the potential importance of olfactory social communication. Several studies examined, for example, early experiences or exposure to olfactory cues (Porter and Picard, 1998; Sneddon et al., 1998; Burne and Rogers, 1999; Porter et al., 1999; Bertin et al., 2010, 2012; Hagelin et al., 2013), olfactory memory (Jones et al., 2002; Siddall and Marples, 2008), reactivity to olfactory and gaseous stimulation (Jones et al., 2005; McKeegan et al., 2005, 2006), and to predator cues (Zidar and Løvlie, 2012).

Jones and Roper (1997) already pointed out that research on the use of olfaction in chickens has been mainly conducted using natural or artificial olfactory cues in non-social contexts. Thus, the use of olfaction for social communication remained widely neglected not only in chickens (Jones and Roper, 1997) but in birds in general (Hagelin and Jones, 2007; Caro and Balthazart, 2010; Caro et al., 2014). In chickens only very few studies have addressed aspects of social olfactory communication. Hirao et al. (2009) showed that chicken males prefer females with intact uropygial glands over uropygial glandectomized females for sexual behaviors, suggesting that the uropygial gland and its secretions may act as a source of sexual odorous information. Furthermore, the results of Karlsson et al. (2010) suggest that red jungle fowls have individual body odor profiles.

SOCIAL OLFACTORY COMMUNICATION IN CHICKENS

In the face of the complex social life of chickens (Collias and Collias, 1996; Nicol, 2015), their ability of odor perception (Jones and Roper, 1997), and first hints for the use of olfactory communication (Hirao et al., 2009; Karlsson et al., 2010) we suggest that it will be promising to further elucidate olfaction as a so far almost neglected mode of social communication in chickens. We hypothesize that the role of social olfactory signals is likely to be important in numerous contexts and we suggest to examine social communication in chicken by combining behavioral experiments and analyses of the chemical profiles to understand the underlying processes.

Due to the mating systems of chicken it seems worthwhile, for example, to investigate the role of the males' scent and the link between dominance and body odors. Dominant male chickens sire most offspring (Collias and Collias, 1996; Pizzari and Birkhead, 2000) and it could be tested whether male quality is part of the chemical signal females perceive apart from visual and acoustic signals. It is likely that male courtship displays such as preening, wing-flapping or feather-ruffling behaviors are also used for odor transmission (Wood-Gush, 1971). Such roles of scent in male quality assessment is well known from mammals (e.g., Rich and Hurst, 1998) and there are already hints for this

in some other avian species (Amo et al., 2012b; Whittaker et al., 2013; Caspers et al., 2015).

When it turns out that olfactory signals are involved in reproductive processes, a promising next step will be to test whether kinship is recognized based on olfactory signals in chickens. Kin recognition is important to either avoid inbreeding or to benefit from the vicinity of close relatives during chick raising. Olfactory kin recognition is already known from mammals (e.g., Todrank et al., 1998; Mateo, 2003) and some other bird species (Coffin et al., 2011; Bonadonna and Sanz-Aguilar, 2012; Krause et al., 2012).

Furthermore, body odors are mixtures of various substances, including uropygial gland secretion and by-products of every day metabolic processes. Therefore, we expect certain information, such as health status to be more reliable signaled via olfactory cues compared to visual signals, where changes become apparent with a greater delay.

APPLIED PERSPECTIVES OF SOCIAL OLFACTORY COMMUNICATION IN CHICKENS

If olfactory signals play an important role for chickens' social interactions considering the diverse constraints of olfaction in intensive housing conditions may lead to new approaches for understanding and solving welfare problems. Laying hens are kept in sex-homogenous groups and, thus, any communication with males is excluded. Both laying hens and broilers (i.e., chickens for meat production) are artificially hatched and raised without parents and, moreover, are housed in age-homogenous groups. This again restricts aspects of social communication, especially parent-offspring communication. Furthermore, commercial chickens are kept at large group sizes of several thousand individuals which clearly restrict the opportunity of individual recognition (D'Eath and Keeling, 2003). These intensive housings additionally lead to increased ammonia concentrations which negatively affect the olfactory capacities of the birds (Jones et al., 2005). A better understanding of possible consequences of these limitations for social olfactory communication may provide novel insights into some of the most urgent questions in animal welfare research.

For example, olfactory signals might be involved in behavioral disorders often observed in laying hens such as feather pecking (Kjaer and Sørensen, 1997; Jensen et al., 2005). Feather pecking has been found to be related to dust bathing (Vestergaard and Lisborg, 1993), and this behavior is used by chickens to remove feather lipids from the plumage (Scholz et al., 2014). These feather lipids are secreted by the uropygial gland which in turn is involved in the production of the individual's odor. To a certain degree the scent of feathers is linked to the probability that conspecifics peck and eat feathers (McKeegan and Savory, 2001; but see Karlsson et al., 2010). Thus, it seems promising to investigate potential links between dust bath material, individual body odors and the prevalence for feather pecking. Olfaction also might be involved in the problem of cloaca cannibalism as the scent producing uropygial glands are located near the cloaca. Despite possible involvement of olfaction in welfare problems, odors possibly can be used as an olfactory enrichment (Nielsen et al., 2015) and thereby improving the housing of chickens.

Taken together, in our opinion addressing the potential of olfactory social signaling in wild, feral and domesticated chicken is an important new field of research and will lead to important new insights on social communication and on consequences if this mode of communication is constraint.

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REFERENCES

Amo, L., Avilés, J. M., Parejo, D., Peña, A., Rodríguez, J., and Tomás, G. (2012a). Sex recognition by odour and variation in the uropygial gland secretion in starlings. *J. Anim. Ecol.* 81, 605–613. doi: 10.1111/j.1365-2656.2011.01940.x

Amo, L., López-Rull, I., Pagán, I., and Garcia, C. M. (2012b). Male quality and conspecific scent preferences in the house finch, *Carpodacus mexicanus*. *Anim. Behav.* 84, 1483–1489. doi: 10.1016/j.anbehav.2012.09.021

Amo, L., Rodriguez-Girones, M. A., and Barbosa, A. (2013). Olfactory detection of dimethyl sulphide in a krill-eating Antarctic penguin. *Mar. Ecol. Prog. Ser.* 474, 277–285. doi: 10.3354/meps10081

Amo, L., Tomás, G., Parejo, D., and Avilés, J. M. (2014). Are female starlings able to recognize the scent of their offspring? *PLoS ONE* 9:e109505. doi: 10.1371/journal.pone.0109505

Bang, B. G. (1960). Anatomical evidence for olfactory function in some species of birds. *Nature* 188, 547.

Bang, B. G., and Cobb, S. (1968). Size of olfactory bulb in 108 species of birds. *Auk* 85, 55–61.

Bertin, A., Calandreau, L., Arnould, C., and Lévy, F. (2012). The developmental stage of chicken embryos modulates the impact of *in ovo* olfactory stimulation on food preferences. *Chem. Senses* 37, 253–261. doi: 10.1093/chemse/bjr098

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

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

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

Burne, T. H. J., and Rogers, L. J. (1995). Odors, volatiles and approach-avoidance behavior of the domestic chick (*Gallus gallus domesticus*). *Int. J. Comp. Psychol.* 8, 99–114.

Burne, T. H., and Rogers, L. J. (1996). Responses to odorants by the domestic chick. *Physiol. Behav.* 60, 1441–1447.

Burne, T. H., and Rogers, L. J. (1999). Changes in olfactory responsiveness by the domestic chick after early exposure to odorants. *Anim. Behav.* 58, 329–336.

Caro, S. P., and Balthazart, J. (2010). Pheromones in birds: myth or reality? *J. Comp. Physiol. A* 196, 751–766. doi: 10.1007/s00359-010-0534-4

Caro, S. P., Balthazart, J., and Bonadonna, F. (2014). The perfume of reproduction in birds: chemosignaling in avian social life. *Horm. Behav.* 68, 25–42. doi: 10.1016/j.yhbeh.2014.06.001

Caspers, B. A., Gagliardo, A., and Krause, E. T. (2015). Impact of kin odour on reproduction in zebra finches. *Behav. Ecol. Sociobiol.* 69, 1827–1833. doi: 10.1007/s00265-015-1995-9

Caspers, B. A., and Krause, E. T. (2011). Odour-based natal nest recognition in the zebra finch (*Taeniopygia guttata*), a colony-breeding songbird. *Biol. Lett.* 7, 184–186. doi: 10.1098/rsbl.2010.0775

Caspers, B. A., and Krause, E. T. (2013). "Intraspecific olfactory communication in zebra finches (*Taeniopygia guttata*) – potential information apart from visual and acoustic cues," in *Chemical Signals in Vertebrates 12*, eds M. L. East and M. Dehnhard (Berlin: Springer Verlag), 341–351.

Cloutier, S., and Newberry, R. C. (2000). Recent social experience, body weight and initial patterns of attack predict the social status attained by unfamiliar hens in a new group. *Behaviour* 137, 705–726. doi: 10.1163/156853900502303

Coffin, H. R., Watters, J. V., and Mateo, J. M. (2011). Odor-based recognition of familiar and related conspecifics: a first test conducted on captive Humboldt penguins (*Spheniscus humboldti*). *PLoS ONE* 6:e25002. doi: 10.1371/journal.pone.0025002

Collias, N. E. (1987). The vocal repertoire of the red junglefowl: a spectrographic classification and the code of communication. *Condor* 89, 510–524.

Collias, N. E., and Collias, E. C. (1996). Social organization of a red junglefowl, *Gallus gallus*, population related to evolution theory. *Anim. Behav.* 51, 1337–1354.

Collias, N., and Joos, M. (1953). The spectrographic analysis of sound signals of the domestic fowl. *Behaviour* 5, 175–188.

Cornwallis, C. K., and Birkhead, T. R. (2007). Changes in sperm quality and numbers in response to experimental manipulation of male social status and female attractiveness. *Am. Nat.* 170, 758–770. doi: 10.1086/521955

Danchin, E., Giraldeau, L. A., and Cézilly, F. (2008). *Behavioural Ecology*. Oxford: Oxford University Press.

D'Eath, R. B., and Keeling, L. J. (2003). Social discrimination and aggression by laying hens in large groups: from peck orders to social tolerance. *Appl. Anim. Behav. Sci.* 84, 197–212. doi: 10.1016/j.applanim.2003.08.010

DeLeon, A., Minguez, E., and Belliure, B. (2003). Self-odour recognition in European storm-petrel chicks. *Behaviour* 140, 925–933. doi: 10.1163/156853903770238382

Fluck, E., Hogg, S., Mabbutt, P. S., and File, S. E. (1996). Behavioural and neurochemical responses of male and female chicks to cat odour. *Pharmacol. Biochem. Behav.* 54, 85–91.

Gagliardo, A. (2013). Forty years of olfactory navigation in birds. *J. Exp. Biol.* 216, 2165–2171. doi: 10.1242/jeb.070250

Gagliardo, A., Ioalè, P., Filannino, C., and Wikelski, M. (2011). Homing pigeons only navigate in air with intact environmental odours: a test of the olfactory activation hypothesis with GPS data loggers. *PLoS ONE* 6:e22385. doi: 10.1371/journal.pone.0022385

Golüke, S., Dörrenberg, S., Krause, E. T., and Caspers, B. A. (2016). Female zebra finches smell their eggs. *PLoS ONE* 11:e0155513. doi: 10.1371/journal.pone.0155513

Grubb, T. C. (1972). Smell and foraging in shearwaters and petrels. *Nature* 237, 404–405.

Grubb, T. C. (1974). Olfactory navigation to the nesting burrow in Leach's petrel (*Oceanodroma leucorrhoa*). *Anim. Behav.* 22, 192–202.

Hagelin, J. C., and Jones, I. L. (2007). Bird odors and other chemical substances: a defense mechanism or overlooked mode of intraspecific communication? *Auk* 124, 741–761. doi: 10.1642/0004-8038(2007)124[741:BOAOCS]2.0.CO;2

Hagelin, J. C., Simonet, J. C., and Lyson, T. R. (2013). "Embryonic domestic chickens can detect compounds in an avian chemosignal before breathing air," in *Chemical Signals in Vertebrates 12*, eds M. L. East and M. Dehnhard (Berlin: Springer Verlag), 363–377.

Hashiguchi, Y., and Nishida, M. (2007). Evolution of trace amine–associated receptor (TAAR) gene family in vertebrates: lineage-specific expansions and degradations of a second class of vertebrate chemosensory receptors expressed in the olfactory epithelium. *Mol. Biol. Evol.* 24, 2099–2107. doi: 10.1093/molbev/msm140

Hillier, L. W., Miller, W., Birney, E., Warren, W., Hardison, R. C., Ponting, C. P., et al. (2004). Sequence and comparative analysis of the chicken genome provide unique perspectives on vertebrate evolution. *Nature* 432, 695–716. doi: 10.1038/nature03154

Hirao, A., Aoyama, M., and Sugita, S. (2009). The role of uropygial gland on sexual behavior in domestic chicken *Gallus gallus domesticus*. *Behav. Process.* 80, 115–120. doi: 10.1016/j.beproc.2008.10.006

Huber, A., and Fölsch, D. W. (1978). *Akustische Ethogramme von Hühnern. Die Auswirkung Verschiedener Haltungssysteme.* Basel: Birkhäuser Verlag.

Hutchison, L. V., and Wenzel, B. M. (1980). Olfactory guidance in foraging by procellariiforms. *Condor* 82, 314–319.

Jensen, P., Keeling, L., Schütz, K., Andersson, L., Mormede, P., Brändström, H., et al. (2005). Feather pecking in chickens is genetically related to behavioural and developmental traits. *Physiol. Behav.* 86, 52–60. doi: 10.1016/j.physbeh.2005.06.029

Jones, E. K., Wathes, C. M., and Webster, A. J. F. (2005). Avoidance of atmospheric ammonia by domestic fowl and the effect of early experience. *Appl. Anim. Behav. Sci.* 90, 293–308. doi: 10.1016/j.applanim.2004.08.009

Jones, R. B. (1987). Food neophobia and olfaction in domestic chicks. *Bird Behav.* 7, 78–81.

Jones, R. B., and Black, A. J. (1979). Behavioral responses of the domestic chick to blood. *Behav. Neural Biol.* 27, 319–329.

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

Jones, R. B., and Gentle, M. J. (1985). Olfaction and behavioral modification in domestic chicks (*Gallus domesticus*). *Physiol. Behav.* 34, 917–924.

Jones, R. B., and Roper, T. J. (1997). Olfaction in the domestic fowl: a critical review. *Physiol. Behav.* 62, 1009–1018.

Karlsson, A. C., Jensen, P., Elgland, M., Laur, K., Fyrner, T., Konradsson, P., et al. (2010). Red junglefowl have individual body odors. *J. Exp. Biol.* 213, 1619–1624. doi: 10.1242/jeb.040279

Khan, I., Yang, Z., Maldonado, E., Li, C., Zhang, G., Gilbert, M. T. P., et al. (2015). Olfactory receptor subgenomes linked with broad ecological adaptations in Sauropsida. *Mol. Biol. Evol.* 32, 2832–2843. doi: 10.1093/molbev/msv155

Kjaer, J. B., and Sørensen, P. (1997). Feather pecking behaviour in White Leghorns, a genetic study. *Br. Poult. Sci.* 38, 333–341.

Krause, E. T., Brummel, C., Kohlwey, S., Baier, M. C., Müller, C., Bonadonna, F., et al. (2014). Differences in olfactory species recognition in the females of two Australian songbird species. *Behav. Ecol. Sociobiol.* 68, 1819–1827. doi: 10.1007/s00265-014-1791-y

Krause, E. T., Krüger, O., Kohlmeier, P., and Caspers, B. A. (2012). Olfactory kin recognition in a songbird. *Biol. Lett.* 8, 327–329. doi: 10.1098/rsbl.2011.1093

Leclaire, S., van Dongen, W. F., Voccia, S., Merkling, T., Ducamp, C., Hatch, S. A., et al. (2014). Preen secretions encode information on MHC similarity in certain sex-dyads in a monogamous seabird. *Sci. Rep.* 4:6920. doi: 10.1038/srep06920

Mardon, J., Saunders, S. M., Anderson, M. J., Couchoux, C., and Bonadonna, F. (2010). Species, gender, and identity: cracking petrels' sociochemical code. *Chem. Senses* 35, 309–321. doi: 10.1093/chemse/bjq021

Marples, N. M., and Roper, T. J. (1997). Response of domestic chicks to methyl anthranilate odour. *Anim. Behav.* 53, 1263–1270.

Mateo, J. M. (2003). Kin recognition in ground squirrels and other rodents. *J. Mammal.* 84, 1163–1181. doi: 10.1644/ble-011

McKeegan, D. E., McIntyre, J., Demmers, T. G., Wathes, C. M., and Jones, R. B. (2006). Behavioural responses of broiler chickens during acute exposure to gaseous stimulation. *Appl. Anim. Behav. Sci.* 99, 271–286. doi: 10.1016/j.applanim.2005.11.002

McKeegan, D. E., and Savory, C. J. (2001). Feather eating in individually caged hens which differ in their propensity to feather peck. *Appl. Anim. Behav. Sci.* 73, 131–140. doi: 10.1016/S0168-1591(01)00124-1

McKeegan, D. E., Smith, F. S., Demmers, T. G., Wathes, C. M., and Jones, R. B. (2005). Behavioral correlates of olfactory and trigeminal gaseous stimulation in chickens, Gallus domesticus. *Physiol. Behav.* 84, 761–768. doi: 10.1016/j.physbeh.2005.03.005

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

Nevitt, G. A., and Hagelin, J. C. (2009). Olfaction in birds: a dedication to the pioneering spirit of Bernice Wenzel and Betsy Bang. *Ann. N.Y. Acad. Sci.* 1170, 424–427. doi: 10.1111/j.1749-6632.2009.04016.x

Nicol, C. J. (2015). *The Behavioural Biology of Chickens*. Wallingford, CT: CABI.

Nielsen, B. L., Jezierski, T., Bolhuis, J. E., Amo, L., Rosell, F., Oostindjer, M., et al. (2015). Olfaction: an overlooked sensory modality in applied ethology and animal welfare. *Front. Vet. Sci.* 2:69. doi: 10.3389/fvets.2015.00069

Papi, F., Ioalè, P., Fiaschi, V., Benvenuti, S., and Baldaccini, N. E. (1974). Olfactory navigation of pigeons: the effect of treatment with odorous air currents. *J. Comp. Physiol.* 94, 187–193. doi: 10.1007/BF00611866

Parejo, D., Avilés, J. M., Peña, A., Sánchez, L., Ruano, F., Zamora-Muñoz, C., et al. (2013). Armed rollers: does nestling's vomit function as a defence against predators? *PLoS ONE* 8:e68862. doi: 10.1371/journal.pone.0068862

Pizzari, T., and Birkhead, T. R. (2000). Female feral fowl eject sperm of subdominant males. *Nature* 405, 787–789. doi: 10.1038/35015558

Porter, R. H., Hepper, P. G., Bouchot, C., and Picard, M. (1999). A simple method for testing odor detection and discrimination in chicks. *Physiol. Behav.* 67, 459–462.

Porter, R. H., and Picard, M. (1998). Effects of early odor exposure in domestic chicks. *Reprod. Nutr. Dev.* 38, 441–448.

Rich, T. J., and Hurst, J. L. (1998). Scent marks as reliable signals of the competitive ability of mates. *Anim. Behav.* 56, 727–735.

Roper, T. J., and Marples, N. M. (1997). Odour and colour as cues for taste-avoidance learning in domestic chicks. *Anim. Behav.* 53, 1241–1250.

Rose, S. P. R. (2000). God's organism? The chick as a model system for memory studies. *Learn. Mem.* 7, 1–17. doi: 10.1101/lm.7.1.1

Schjelderup-Ebbe, T. (1922). Beiträge zur Sozialpsychologie des Haushuhns. *Z. Psychol.* 88, 225–252.

Scholz, B., Kjaer, J. B., Petow, S., and Schrader, L. (2014). Dustbathing in food particles does not remove feather lipids. *Poultry Sci.* 93, 1877–1882. doi: 10.3382/ps.2013-03231

Sherry, D. F. (1977). Parental food-calling and the role of the young in the Burmese red junglefowl (*Gallus gallus spadiceus*). *Anim. Behav.* 25, 594–601.

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

Sneddon, H., Hadden, R., and Hepper, P. G. (1998). Chemosensory learning in the chicken embryo. *Physiol. Behav.* 64, 133–139.

Steiger, S. S., Fidler, A. E., Valcu, M., and Kempenaers, B. (2008). Avian olfactory receptor gene repertoires: evidence for a well-developed sense of smell in birds? *Proc. R. Soc. Lond. B* 275, 2309–2317. doi: 10.1098/rspb.2008.0607

Strandh, M., Westerdahl, H., Pontarp, M., Canbäck, B., Dubois, M. P., Miquel, C., et al. (2012). Major histocompatibility complex class II compatibility, but not class I, predicts mate choice in a bird with highly developed olfaction. *Proc. R. Soc. Lond. B* 279, 4457–4463. doi: 10.1098/rspb.2012.1562

Todrank, J., Heth, G., and Johnston, R. E. (1998). Kin recognition in golden hamsters: evidence for kinship odours. *Anim. Behav.* 55, 377–386.

Tucker, D. (1965). Electrophysiological evidence for olfactory function in birds. *Nature* 207, 34–36.

Turro, I., Porter, R. H., and Picard, M. (1994). Olfactory cues mediate food selection by young chicks. *Physiol. Behav.* 55, 761–767.

Vestergaard, K. S., and Lisborg, L. (1993). A model of feather pecking development which relates to dustbathing in the fowl. *Behaviour* 126, 291–308.

Wallraff, H. G. (1979). Olfaction and homing in pigeons. A problem of navigation or of motivation? *Naturwissenschaften* 66, 269–270.

Wenzel, B. M. (1968). Olfactory prowess of kiwi. *Nature* 220, 1133–1134.

Wenzel, B. M. (1971a). "Olfaction in birds," in *Olfaction*, ed L. M. Beidler (Berlin: Springer Verlag), 432–448.

Wenzel, B. M. (1971b). Olfactory sensation in the kiwi and other birds. *Ann. N.Y. Acad. Sci.* 188, 183–192.

Whittaker, D. J., Gerlach, N. M., Soini, H. A., Novotny, M. V., and Ketterson, E. D. (2013). Bird odour predicts reproductive success. *Anim. Behav.* 86, 697–703. doi: 10.1016/j.anbehav.2013.07.025

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

Wood-Gush, D. G. M. (1971). *The Behaviour of the Domestic Fowl*. London: Heinemann Educational Books Ltd.

Zhang, J. X., Sun, L., and Zuo, M. X. (2009). Uropygial gland volatiles may encode for olfactory information about sex, individual, and species in Bengalese finches *Lonchura striata*. *Curr. Zool.* 55, 357–365.

Zidar, J., and Løvlie, H. (2012). Scent of the enemy: behavioural responses to predator faecal odour in the fowl. *Anim. Behav.* 84, 547–554. doi: 10.1016/j.anbehav.2012.06.006

Zuk, M., Johnson, K., Thornhill, R., and Ligon, J. D. (1990a). Mechanisms of female choice in red jungle fowl. *Evolution* 44, 477–485.

Zuk, M., Thornhill, R., Ligon, J. D., Johnson, K., Austad, S., Ligon, S. H., et al. (1990b). The role of male ornaments and courtship behavior in female mate choice of red jungle fowl. *Am. Nat.* 136, 459–473.

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