

# Intraspecific and interspecific chemosignals in birds: a review

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**ABSTRACT:** This review of chemosignals in birds considers intraspecific oriented chemosignals such as pheromones, interspecific chemosignals, and chemical interactions with parasites. Intraspecific chemosignals are known in some seabirds, especially burrow- or crevice-nesting auklets and petrels that breed in large colonies and are often nocturnal on land. Crested Auklets secrete a distinctive scent closely associated with courtship and important in sexual selection. Individually distinctive odours of petrels allow them to identify their own nest and can have a significant role in social relationships. Substances considered as sex pheromones, diesters of 3-hydroxy fatty acids, are produced by female mallards in their uropygial glands during the mating season. In many species of Charadriiformes during nesting monoester waxes are substituted with mixtures of less volatile diester waxes, less easily detected by mammals searching for nests. The tissues, mainly skin and feather of the New Guinean Passerines of the genus *Pitohui* and *Ifrita* contain steroidal alkaloids from the batrachotoxin group probably as a chemical defense. The variation of preen gland secretion in some other Passerines is apparently due to selective pressures caused by ectosymbionts. The auklets' odour, considered as a signal of mate quality, has also a function as ectoparasite repellent: aldehyde constituents of this odour kill and repel ectoparasites. Parasitic nematodes influence grouse digestion and thereby scent emission, making parasitized birds more vulnerable to depredation by mammals. Conversely, scents of some mammalian predators can function as a bird repellent.

**Keywords:** olfactory; pheromone; odor; waxes; parasite

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## 1. Introduction

Birds are the second most species-rich class of vertebrates. In addition to domesticated species, many bird species are bred in zoological gardens, research and other institutes. Many species are endangered and captivity is a chance for their rescue. Thus they become frequent veterinary patients and it is necessary to have specialist knowledge of their biology.

Many types of chemical signals mediate life's processes. Organisms use these signals to orient

and navigate in their environment, and many of them use chemosignals as a signalling factor in inter- and intraspecific relationships. Birds generally have small olfactory bulbs and a poorly developed sense of smell, and are considered to be the animals in which the chemosignals play the minimal role, but they may use similar mechanisms, however the experimental data for these organisms is not so much known (Vickers, 2000). However, a few groups of birds have relatively well developed sense of smell, such as oceanic petrels and some forest vultures that use smell to locate food where

it is not easy to find by sight. Pheromonal signals serve as the primary basis for species-specific mating cues in many vertebrates, but in birds (and in anuran amphibians) it is acoustic signals that play the most important role (Ptacek, 2000).

A comparative analysis of chemosignalling systems responsible for the action of hormones, hormone-like substances, pheromones, etc. in vertebrates, invertebrates and unicellular eukaryotes was provided by Pertseva (1991). Many common features revealed in structural and functional organization of this systems suggest their evolutionary conservatism.

Many types of chemical signals mediate most of life's processes.

Chemically (or visually) mediated interaction within an animal group or society can be an important factor in the organization of their collective activity. In other animal groups, most clearly demonstrable are the principle in social insects, but also in schools of fishes and others, chemical communication is important. In birds, visual (or/and acoustic) signals tend to be most used. Perception of scents is conditioned by the presence of the odorant receptors (ORs) located in the nasal epithelium, at the ciliated surface of olfactory sensory neurons, representing the initial step of a transduction cascade that leads to odor detection. ORs form the largest and most diverse family of G-protein-coupled receptors (GPCRs). They are encoded by a multigene family that has been partially characterized in many animals, mainly vertebrates, including birds (Dryer and Berghard, 1999; Dryer, 2000).

The finding that there exists an ability to perceive scents prior to hatching is very remarkable. The avian's ability to respond to auditory stimuli in prenatal phase of life is known. For comparison, prenatal chemosensory activity has been found in some other classes of vertebrates (fish, amphibians, mammals), and in insects also. In birds the results of experiments demonstrated the positive influence of exposure to a chemosensory stimulus (strawberry aroma) prior to hatching to subsequent chemosensory preferences of newly hatched chicks (while strawberry scent was highly aversive to control chicks, which were not exposed to strawberry scent during embryonal development). Embryos were exposed to strawberry scent from Day 15 to Day 20 of egg incubation by either application of the odour in the surrounding air around the egg, rubbing it onto the shell, or injecting it into the air space in the egg. The

preference of this scent was represented by drinking more strawberry flavoured water and spending more time in a strawberry-scented area than control chicks (Sneddon et al., 1998).

## 2. Intraspecific oriented chemosignals – do birds use pheromones?

All examined birds have a functional olfactory system and many bird species produce some odours, which makes the presumptive absence of special chemosignals surprising. However examples of birds perceiving social odour have been found. One of them is the crested auklet (*Aethia cristatella*) a small seabird that breeds in very large colonies in crevices on remote oceanic islands. It exhibits a distinctive tangerine-like scent closely associated with courtship. Crested auklets show an attraction to conspecific feather odour and a preference for two chemical components of feather scent (cis-4-decenal and octanal); this secretion increases seasonally. Differential responses to odours, a positive preference for auklet odour, an aversion to mammalian musk and no significant response to tested banana essence (amyl acetate) were found also. This bird species detects plumage odour, particularly in the scented neck region, which is a behavioural basis for odour transmission and the potential for scent assessment during sexual selection (Hagelin et al., 2003).

Another group of birds in which scent recognition has been investigated is the Procellariiformes. Common diving petrel *Pelecanoides urinatrix* and the South-Georgian diving petrel *Pelecanoides georgicus* are able to recognise their nesting burrow by scent alone. For comparison there was also tested a bird species that is known to use olfaction for foraging and nest recognition, the thin-billed prion *Pachyptila belcheri*. In experiments with two-choice T-maze, it was found that individuals of all tested species significantly preferred the odour of their own nest material to that of a conspecific. These results suggest that an individual-specific odour provides an olfactory signature that allows burrowing petrels to recognize their own burrow (Bonadonna et al., 2003a), an ability that may be particularly useful in these birds that only return to land under the cover of darkness to avoid visually hunting predators such as skuas and gulls.

Procellariiform seabirds are prime candidates for these studies, because they have an excellent sense

of smell, many are only active on land at night, they breed in large colonies (in these conditions precise individual recognition is very important), and are monogamous for life. Antarctic prions, *Pachyptila desolata*, which have a musky scent, are able to recognize individual odor cues that probably contribute to the olfactory signature of their own burrows. Prions can recognize their own personal odour also in the presence of a conspecific odour. There is a hypothesis that these birds may also use scents for sex discrimination. The specific role of scent in kin recognition or subsequent mate choice is not yet known. It is supposed that recognition and avoidance to kin scents to prevent inbreeding of these colonial and highly philopatric birds (Bonadonna and Nevitt, 2004).

The chicks of European storm-petrel (*Hydrobates pelagicus*) are able to recognize their own nests by smell, they can apparently differentiate their own body odour, even when tested against the body scent of a conspecific. This species has a well-developed anatomy of olfactory system. Individually distinctive odours allow them to identify their own nest and can have a significant role in social relationships of this bird species (De Leon et al., 2003).

Also the Antarctic prion (*Pachyptila desolata*) can distinguish its own nest from that of conspecifics by olfactory sense alone. The intact and anosmic birds of this species were tested in a maze; only individuals with an intact olfactory sense recognized their own burrow, whereas anosmic birds did not. This ability allows them to locate their own burrow reliably in nesting colony at night, moreover without vocal activity so reducing risk of detection by predators. Well-developed olfactory sense, whose basis is well-developed olfactory anatomical structures comparable to those of mammals thus facilitates an effective protection against predation by skuas (*Catharacta skua lonnbergi*), that hunt this birds by vision and hearing (Bonnadonna et al., 2003b).

Substances with pheromonal activity in the female mallard duck (*Anas platyrhynchos*) have been found. These substances were identified as the diesters of 3-hydroxy  $C_8$ ,  $C_{10}$ , and  $C_{12}$  acids, by mass spectrometry. Cell-free extract from the gland catalyzed conversion of dodecanoic acid to 3-hydroxy-dodecanoic acid which was identified. Described substances with pheromonal activity were found as the major products of the uropygial glands only during the breeding season (Kolattukudy and Rogers, 1987). Among others this information affirms the

functional significance of vertebrate skin glands as producers of pheromones (Quay, 1976).

The influence of some hormones on production of pheromone substances in mallard duck was also studied (Bohnet et al., 1991; Hiremath et al., 1992). During the mating season female mallards produce sex pheromones, diesters of 3-hydroxy fatty acids, in their uropygial glands. Treatment of estradiol, or a combination of estradiol and thyroxine, caused the proliferation of peroxisomes (in which diesters of 3-hydroxy acids and the enzymes that catalyze the formation and esterification of the 3-hydroxy fatty acids) and that way also production of female pheromones, diesters of 3-hydroxy fatty acids, in the uropygial gland of this bird species are localized. Similar effects including the synthesis of the female pheromones, were induced in the uropygial glands by hormone treatment of males that do not normally produce diesters at any time during their life cycle. The structure and composition of the induced diesters by hormone treatment were identical to natural female pheromones. Monoester synthesizing activities are located in the endoplasmic reticulum.

To a certain extent the molecular core of this hormonal action is known. The peroxisome proliferator-activated receptor (PPAR) gamma 1 cDNA from a duck uropygial gland cDNA library was isolated. PPAR gamma 2 was expressed in both duck and goose uropygial gland (while PPAR gamma 1 was expressed only in the duck gland). Estradiol applique induces peroxisome proliferation and the production of pheromones in the duck uropygial glands, but not in the goose ones, as geese do not produce pheromones. PPAR gamma 2 may be involved in lipid metabolism (Ma et al., 1998).

A further step of knowledge of mallard duck pheromone production was determination of primary structure of a medium-chain fatty acyl-CoA hydrolyase deduced from the cDNA. This enzyme was obtained from the uropygial gland and was designated thioesterase B. The increase of thioesterase B transcript level correlated with peroxisome proliferation and production of described pheromones in the mating season and as a result of estradiol treatment. This enzyme is associated with peroxisomal metabolism or their proliferation (Hwang and Kolattukudy, 1993).

The similarity of substances produced in some animal species with others, which has the function as a chemosignal can be sometimes surprising, but evidently is not functional. For example

the insect pheromonal substances (2R,4R,6R,8R)-4,6,8-trimethyl-2-undecyl formate (lardolurel) and (2R,4R,6R,8R)-4,6,8-trimethyl-2-decyl formate (9-norlardolure with weak pheromone activity) have been synthesized from the corresponding homologous chiral methyl-branched esters which have been obtained from the preengland wax of the domestic goose *Anser anser domesticus* (Morr et al., 1995).

### 3. Interspecific oriented chemosignals

Olfactory cues are an important source of information for many animals, also of the presence of predators. Kats and Dill (1998) mention that the ability of birds to detect predator odours is quite unique.

Other remarkable ability of some bird species are adaptations diminishing smell during their own nesting as a precaution against nest predation. Uropygial gland secretions (preen waxes) showed composition shift in many species of ground-nesting shorebirds and ducks at the start of incubation. The usual mixtures of monoester preen waxes are replaced by mixtures of less volatile diester waxes, that are less readily detected by mammals searching for nests. Diester preen waxes enhance olfactory crypticism at the nest (Reneerkens et al., 2005). Specifically, this phenomenon was originally presented by Reneerkens et al. (2002) in red knot (*Calidris canutus*, Charadriiformes), but it was also found in another 19 sandpiper species. Both sexes of these bird species produced the diester waxes during the incubation period until hatching and to the short period of courtship. The secretion of diester waxes during courtship period indicate their function also as a quality signal for mate choice. Shift in preen waxes composition was not specific for sandpipers breeding in tundra, it also occurred in temperate breeding species, conversely was not found in non-incubating individuals examined: males of curlew sandpipers (*Calidris ferruginea*) and ruffs (*Philomachus pugnax*).

Very interesting is the case of the specific group of Passerines of the genus *Pitohui* and *Ifrita*, living in the New Guinean primavean forest. The tissues, mainly skin and feather of these birds contain steroidal alkaloids from the batrachotoxin group, mainly homobatrachotoxin (arrow poisons known in the central- and South American frog species, belonging mainly to the genera *Dendrobates* and

*Phyllobates*), apparently as a chemical defense. The birds obtain batrachotoxins from dietary sources (probably beetles of genus *Choresine*, family Melyridae). In correlation of batrachotoxins content in bird tissues is warning coloration but also emitting a strong sour odour, which is probably an alarm signal (Diamond, 1992; Dumbacher et al., 1992, 2004).

### 4. The chemical interactions with parasites

It is possible to give the positive reaction in parasites of bird (ticks) to uric acid, excreted by birds (e.g. Yoder et al., 2003) as an example of the chemical relationships between birds and arthropods.

Some bird species of Passeriformes order secrete in preen gland various mixtures of homologous monoesters made up of long chain acids and alcohols. Each species has characteristic distribution of esters and is unique to a given species by existence of individual variations. The combination of acids and alcohols to arrive at same molecular compositions varied distinctly between species. There were found distinct differences in number of acids and alcohols that produced the combination of homologous mixtures of esters. The differences both qualitative and quantitative exist also equally as seasonal differences in the secretion components. It is possible that the evolution in variation of preen gland secretion is due to selective pressures caused by ectosymbionts, feather-mites and feather-chewing lice, living on feathers and probably feeding on the secretions and surrounding environments (Haribal et al., 2005).

Douglas et al. (2001) declare that the exogenous application of substances with repellent effect is more frequent in birds, but endogenous production of these is apparently rare. Avian defensive compounds isolated from the feathers and volatile odour of the crested auklet (*Aethia cristatella*) include *n*-hexanal, *n*-octanal, *n*-decanal, *Z*-4-decenal and a 12-carbon unsaturated aldehyde. It is remarkable that two substances of these – octanal and hexanal – are also components of the markedly smelly metasternal gland emissions of heteropteran insects, thus potent invertebrate repellents. The functions of auklet odours are as an ectoparasite repellent and as a signal of mate quality. Authors consider this phenomenon as one of several putative bases for mate selection.

The next investigation clarified the additional facts: the C-12:1 aldehyde is actually two isomers,

(*Z*)-4-dodecenal and (*Z*)-6-dodecenal. Aldehyde constituents kill and repel ectoparasites, antiparasitic efficacy may increase when they are combined in a mixture and with chemical concentration of this mixture. Individuals with higher chemical production probably repel ectoparasites more effectively. The other species of genus *Aethia*, whiskered auklet (*Aethia pygmaea*), produces odorant that is composed predominantly of two odd-numbered aldehydes (heptanal and nonanal) with no detectable unsaturated aldehydes (Douglas et al., 2004).

The empirical evidence that aldehydes emitted by crested auklet function as bird's repellent for a mosquito is in paper of Douglas et al. (2005a). These authors used the synthetic analogues of the auklet odorant, that were strongly repellent to mosquitoes in laboratory trials. This class of aldehydes appears to be potent invertebrate repellents when used by heteropterans against their predators and has broad spectrum in efficacy against ectoparasitic arthropods of birds.

The hypothesis that the specific plumage odours function as chemical defenses against lice in birds was challenged in experiments with pigeon lice exposed to the volatiles emitted by freshly plucked plumage and by whole specimens of the crested auklet. Auklet plumage odorant did not reduce louse life span, and aldehyde odorant in nature did not reduce louse abundance on crested auklets. Indeed, crested auklets (*Aethia cristatella*) had significantly higher louse abundance than other species of this genus, least auklets (*A. pusilla*) – with respect to body size – that nests in close association (Douglas et al., 2005b).

The hypothesis that the antiparasitic function is enhanced by melanin also (example of no smelling antiparasitic substance) was not confirmed in Rock Pigeons (Bush et al., 2006). However a relationship between presence of different pigments and susceptibility to bacterial degradation was found (Grande et al., 2004).

In contrast with that experiment, attraction of avian and other host odours for four species of mosquito: *Culex quinquefasciatus* Say, *Culex tarsalis* Coquillett, *Culex nigripalpus* Theobald, and *Aedes aegypti* (L.) was investigated (Allan et al., 2006). These laboratory experiments were carried out on chicken, human, with only CO<sub>2</sub>, feather and their combinations. Authors describe minutely the differences between attraction of examined objects for these mosquito species. However, it is very important that feathers contribute to the attraction of host-seeking mosquitos *Culex* spp.

Relationships between birds and their parasites and predators are sometimes more complex. One example is relationships between Red Grouse *Lagopus lagopus scoticus* and its parasitic nematode *Trichostrongylus tenuis* and predator – fox *Vulpes vulpes*. Parasitosis itself reduces the survival and breeding production of Red Grouse, similarly affects high predation intensity, however the predators effectively reduce the regulatory role of the parasites, because predators selectively prey on heavily infected birds. Parasitic nematodes cause bird morbidity and thus may influence grouse scent emission and thereby make the parasitized birds more vulnerable to predation of foxes and other mammalian predators. This phenomenon was confirmed in experiments with dogs, that found significantly fewer of the grouse treated with anthelmintic than control (parasitised) birds (Hudson et al., 1992; Dobson and Hudson, 1995).

Scents secreted by some bird predators can be effective as bird repellents. Mustelid species have scent glands, which produce secretion, containing ortho-aminoacetophenone (OAP). The bird repellency of this substance and its three structural isomers (meta-, para-, alpha-) to European starlings (*Sturnus vulgaris*) was tested. Ortho-aminoacetophenone is the substance chemically and odorously similar of methyl anthranilate. Methyl anthranilate is an effective bird repellent at concentrations greater-than-or-equal-to 1.0% (g/g). OAP was repellent at concentrations less-than-or-equal-to 0.01% in both choice and no-choice feeding tests. The other tested isomers were less effective. Chemically, hydrogen-bonded ring structure formation and basicity predict bird repellent activity (Mason et al., 1991). However, these repellent effects apparently occur through taste rather than through odour.

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### REFERENCES

- Allan S.A., Bernier U.R., Kline D.L. (2006): Laboratory evaluation of avian odors for mosquito (Diptera: Cu-

- licidae) attraction. *Journal of Medical Entomology*, 43, 225–231.
- Bohnet S., Rogers L., Sasaki G., Kolattukudy P.E., (1991): Estradiol induces proliferation of peroxisome-like microbodies and the production of 3-hydroxy fatty acid diesters, the female pheromones, in the uropygial glands of male and female mallards. *Journal of Biological Chemistry*, 266, 9795–9804.
- Bonadonna F., Nevitt G.A. (2004): Partner-specific odor recognition in an Antarctic seabird. *Science*, 306, 835.
- Bonadonna F., Cunningham G.B., Jouventin P., Hesters F., Nevitt G.A. (2003a): Evidence for nest-odour recognition in two species of diving petrel. *Journal of Experimental Biology*, 206, 3719–3722.
- Bonadonna F., Hesters F., Jouventin P. (2003b): Scent of a nest: discrimination of own-nest odours in Antarctic prions, *Pachyptila desolata*. *Behavioral Ecology and Sociobiology*, 54, 174–178.
- Bush S.E., Kim D., Moyer B.R., Lever J., Clayton D.H. (2006): Is melanin a defense against feather-feeding lice? *Auk*, 123, 153–161.
- De Leon A., Minguez E., Belliure B. (2003): Self-odour recognition in European storm-petrel chicks. *Behaviour*, 140, 925–933.
- Deneubourg J.L., Goss S. (1989): Collective patterns and decision-making. *Ethology, Ecology and Evolution*, 1, 295–311.
- Diamond J.M. (1992): Rubbish birds are poisonous. *Nature*, 360, 19–20.
- Dobson A., Hudson P. (1995): The interaction between the parasites and predators of Red Grouse *Lagopus lagopus scoticus*. *Ibis*, 137, S87–S96.
- Douglas H.D., Co J.E., Jones T.H., Conner W.E. (2001): Heteropteran chemical repellents identified in the citrus odor of a seabird (crested auklet: *Aethia cristatella*): evolutionary convergence in chemical ecology. *Naturwissenschaften*, 88, 330–332.
- Douglas H.D., Co J.E., Jones T.H., Conner W.E. (2004): Interspecific differences in *Aethia* spp. auklet odorants and evidence for chemical defense against ectoparasites. *Journal of Chemical Ecology*, 30, 1921–1935.
- Douglas H.D., Co J.E., Jones T.H., Conner W.E., Day J.F. (2005a): Chemical odorant of colonial seabird repels mosquitoes. *Journal of Medical Entomology*, 42, 647–651.
- Douglas H.D., Malenke J.R., Clayton D.H. (2005b): Is the citrus-like plumage odorant of crested auklets (*Aethia cristatella*) a defense against lice? *Journal of Ornithology*, 146, 111–115.
- Dryer L. (2000): Evolution of odorant receptors. *Bioessays*, 22, 803–810.
- Dryer L., Berghard A. (1999): Odorant receptors: a plethora of G-protein-coupled receptors. *Trends in Pharmacological Sciences*, 20, 413–417.
- Dumbacher J.P., Beehler B.M., Spande T.F., Garaffo H.M., Daly J.W. (1992): Homobatrachotoxin in the Genus *Pitohui*: Chemical defense in birds? *Science*, 258, 799–801.
- Dumbacher J.P., Wako A., Derrickson S.R., Samuelson A., Spande T.F., Daly J.W. (2004): Melyrid beetles (Choresine): A putative source for the batrachotoxin alkaloids found in poison-dart frogs and toxic passerine birds. *Proceedings of the National Academy of Sciences of the U.S.A.*, 101, 15857–15860.
- Grande J.M., Negro J.J., Torres M.J. (2004): The evolution of bird plumage colouration: a role for feather-degrading bacteria? *Ardeola*, 51, 375–383.
- Hagelin J.C., Jones I.L., Rasmussen L.E.L. (2003): A tangerine-scented social odour in a monogamous seabird. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 270, 1323–1329.
- Haribal M., Dhondt A.A., Rosane D., Rodriguez E. (2005): Chemistry of preen gland secretions of passerines: different pathways to same goal? why? *Chemoecology*, 15, 251–260.
- Hiremath L.S., Kessler P.M., Sasaki G.C., Kolattukudy P.E. (1992): Estrogen production of alcohol-dehydrogenase in the uropygial gland of Mallard Ducks. *European Journal of Biochemistry*, 203, 449–457.
- Hudson P.J., Dobson A.P., Newborn D. (1992): Do parasites make prey vulnerable to predation – Red Grouse and parasites. *Journal of Animal Ecology*, 61, 681–692.
- Hwang C.S., Kolattukudy P.T. (1993): Molecular-cloning and sequencing of thioesterase-B cDNA and stimulation of expression of the thioesterase-B gene associated with hormonal induction of peroxisome proliferation. *Journal of Biological Chemistry*, 268, 14278–14284.
- Kats L.B., Dill L.M., (1998): The scent of death: Chemosensory assessment of predation risk by prey animals. *Ecoscience*, 5, 361–394.
- Kolattukudy P.E., Rogers L. (1987): Biosynthesis of 3-hydroxy fatty acids, the pheromone components of female mallard ducks, by cell-free preparations from the uropygial gland. *Archives of Biochemistry and Biophysics*, 252, 121–129.
- Ma H.W., Tam Q.T., Kolattukudy P.E. (1998): Peroxisome proliferator-activated receptor gamma 1 (PPAR-gamma 1) as a major PPAR in a tissue in which estrogen induces peroxisome proliferation. *Febs Letters*, 434, 394–400.
- Mason J.R., Clark L., Shah P.S. (1991): Ortho-aminoacetophenone repellency to birds – similarities to methyl

- anthranilate. *Journal of Wildlife Management*, 55, 334–340.
- Morr M., Proppe C., Wray V. (1995): Synthesis of asymmetrical methy-branched chiral ketones from the corresponding homologous wax esters – a new synthesis of the insect pheromone lardolure and of 9-norlardolure. *Liebigs Annalen*, 11, 2001–2004.
- Pertseva M. (1991): The evolution of hormonal signalling systems. *Comparative Biochemistry and Physiology A*, 100A, 775–787.
- Ptacek M.B. (2000): The role of mating preferences in shaping interspecific divergence in mating signals in vertebrates. *Behavioural Processes*, 51, 111–134.
- Quay W.B. (1976): Structure and function of skin glands. In: Muller-Schwarze D., Mozell M. M. (eds.): *Chemical Signals in Vertebrates*. Plenum Press, New York.
- Reneerkens J., Piersma T., Damste J.S.S. (2002): Sandpipers (Scolopacidae) switch from monoester to diester preen waxes during courtship and incubation, but why? *Proceedings of the Royal Society of London Series B, Biological Sciences*, 269, 2135–2139.
- Reneerkens J., Piersma T., Damste J.S.S. (2005): Switch to diester preen waxes may reduce avian nest predation by mammalian predators using olfactory cues. *Journal of Experimental Biology*, 208, 4199–4202.
- Sneddon H., Hadden R., Hepper P.G. (1998): Chemosensory learning in the chicken embryo. *Physiology and Behavior*, 64, 133–139.
- Vickers N.J. (2000): Mechanisms of animal navigation in odor plumes. *The Biological Bulletin*, 198, 203–212.
- Yoder J.A., Domingus J.L., Luerman G.C. (2003): Uric acid-induced arrestment as a possible bird host cue (kairomone) in nymphs and adults of the lone star tick, *Amblyomma americanum* (L.). *International Journal of Acarology*, 29, 399–402.

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