

Exogenous chemical substances in bird perception: a review

J. RAJCHARD

Faculty of Agriculture, University of South Bohemia, Ceske Budejovice, Czech Republic

ABSTRACT: The perception of exogenous chemical substances, olfactory navigation and the use of the olfactory sense by birds to search for food are reviewed. Many results suggest that the olfactory sense is one of the important components of the navigation system in birds. The olfactory mechanisms used by homing pigeons to navigate homeward from distant sites have been well studied. The scent of potential food, carcasses, is a positive attracting percept for Vultures. Procellariiform seabirds (petrels, albatrosses and shearwaters) are able to localize food sources by using their olfactory sense. Procellariiforms are sensitive to scented compounds associated with their primary prey: krill-related odors (pyrazines and trimethylamine), odors associated with phytoplankton (dimethyl sulfide – DMS) and ammonia. Anting is a specific type of behavior of over 200 bird species. Birds probably use anting to control ectoparasites, inhibit the growth of fungi or bacteria, to soothe skin irritated during the molting period, and to remove toxic formic acid from ants prior to their consumption. Insectivorous birds react to insect malodorous substances, produced by insect groups as a chemical defense against predators.

Keywords: anting; food; navigation; olfactory

Contents

1. Introduction
2. Use of the olfactory system for navigation

3. Perception of food odor
4. Anting: a specific bird behavior
5. References

1. Introduction

Although previously it was assumed that the olfactory sense is not powerful in birds, new information suggests that the olfactory sense is also important in these organisms. Detailed knowledge of bird biology and its consecutive application are indispensable for the successful breeding and application of necessary veterinary care in zoological gardens, research institutes, and in the “hobby” breeding of many bird species including worldwide endangered taxa. Among domestic birds, the breeding of and competition between homing pigeons are becoming increasingly popular in many countries. It has now become very important to elucidate the orientation ability of the above mentioned hom-

ing pigeons with respect to precautions against the transmission of bird influenza.

2. Use of the olfactory system for navigation

The mechanisms used by birds to navigate homeward from distant regions have been the focus of much study. Homing pigeons (*Columba livia*) are a popular experimental species. According to some authors magnetic cues are unlikely to be used and olfactory cues can be unstable under the variable wind conditions, making visual landmarks the most likely cues used (Meade et al., 2005).

However, it is necessary to mention that the role of the olfactory system in the homing or orienta-

tion of birds has been investigated in detail only since the beginning of the 1990s. Until then, this method of bird navigation was assigned only little significance within the overall system of navigation. The results of experiments with bird olfactory navigation are somewhat contradictory, but very interesting, and point to the need for further investigations. The results of a series of experiments on homing pigeons, published in 1991 already suggested that more than one factor is involved in their navigation system. The navigation system of pigeons relies on several cues. The absence of one cue can be compensated for by other information. In some experiments the experimental pigeons were exposed to synthetic air. Pigeons probably obtain and process non-olfactory information during the initial part of their transport from the home site to the release site, but the olfactory cues have an important role in their navigation system (Ganzhorn and Burkhardt, 1991). However, Waldvogel and Phillips (1991) conclude that, at least for pigeons raised in New York (and maybe in other geographical locations as well), olfactory cues perceived at the home site do not contribute to the formation of their navigational map.

It has been suggested that homing behavior in pigeons is based on olfactory cues, the Earth's magnetic field or infrasound. It is likely that none of these cues (including olfactory ones) are universally indispensable. The role of olfaction has been investigated using tests of the effects of anosmia on pigeon navigation in different geographical locations. A set of experiments with young inexperienced birds was carried out in southeastern Brazil, a tropical area where olfactory tests had never been run before.

The experimental birds were made temporarily anosmic by washing their olfactory mucosae with a 4% ZnSO₄ solution one day before release, while controls were treated with Ringer solution. Anosmia totally impaired the navigational performance of experimental birds, which were unable to navigate home from sites at relatively short distances away (34–44 km). Pigeon homing in this area evidently depends on olfactory information in the environment (Benvenuti and Ranvaud, 2004).

Many are of the opinion that displaced homing pigeons and probably also other birds are able to navigate home by deducing positional information from atmospheric trace gases perceived by olfaction. Experiments with pigeons and air analyses suggest a 'preolfactory' concept with a hypotheti-

cal gradient odor map linked with a sun compass (Wallraff, 2004).

Schlund (1992) investigated the behavior of pigeons whose olfactory systems were affected either by the application of a local anaesthetic, ginglyain, to their olfactory epithelium (sham-treated pigeons), or by intra-nasal irrigation with a 18% zinc sulphate solution (anosmic pigeons). In the former case anosmia persisted reliably for only one hour while in the latter case, anosmia persisted for at least five days. Pigeons were released from two different distances (9–24 km, 63–70 km) from home. At shorter distances, sham-treated pigeons and untreated control pigeons were well oriented while individuals treated with zinc sulphate showed no directional preference. At longer distances, pigeons treated with zinc sulphate were oriented but the chosen direction did not correspond with the home direction. The control and the sham-treated pigeons did not show any directional preference. Anosmic pigeons homed but they did so more slowly than the control ones. In further tests at the longer distances, the anosmic pigeons (ZnSO₄ applied to nasal mucosa), but also sham-treated controls, did not show any directional preference whereas the control birds were oriented towards home (Schmid and Schlund, 1993).

Streng and Wallraff (1992) conclude that pigeons may be capable of using olfactory and visual signals simultaneously, although the respective signals are recognized separately by either one of the input channels (vision and olfaction). These authors regard the use of familiar visual landmarks in pigeon homing as still being an open question. However, results of a follow-up study suggest that pigeons in a familiar area, relying on only non-olfactory spatial information, use visual landscape marks to find their way home (Wallraff et al., 1994).

Some results of experiments with anosmic and control pigeons suggest that olfactory and visual cues play a fundamental, but apparently mutually interchangeable role for pigeon orientation. When the experimental pigeons could see their surroundings, both groups of birds, the anosmic and the controls oriented homeward. When visual contact with the landscape was prevented by screens, the anosmic pigeons were disoriented after release (Gagliardo et al., 2001a).

Olfactory access to environmental air features is probably a necessary precondition for homeward navigation from unfamiliar places anywhere on earth. Birds probably use atmospheric conditions

for the development of their “olfactory map”, but the chemical compounds in air, detected by pigeons are still unknown. In a familiar area they can use both olfactory and visual signals (Wallraff, 2001).

Dall’Antonia and Luschi (1993) tested pigeon navigation with respect to the circadian rhythmicity (a group of experimental birds was released from familiar locations after being exposed to a constant bright light). It is important to note that anosmic pigeons were also used in their experiments. None of the birds, including anosmic ones, showed any tendency to orient themselves home. Their homing performances including orientation capability were negatively affected and the distribution was not generally different from random. In the initial orientation of pigeons released from familiar sites it appears that the use of the sun compass plays an important role.

The hypothesis that successful homing pigeon navigation is based on the perception of atmospheric odors is also supported by the results of experiments carried out by Bingman and Benvenuti (1996) in Savannah (southeastern USA). These authors consider the olfactory navigation to be the primary mechanism used by pigeons in different geographical areas.

The impaired homing capabilities in anosmic pigeons (anosmia was again induced by application of zinc sulphate solution to their olfactory mucosa) and also in positive controls (by plugging nostrils) in experiments, in which the pigeons were released at unfamiliar sites (55–79 km from home) was also demonstrated (Benvenuti and Gagliardo, 1996). Walcott (1996) also considers the existence of olfactory pigeon navigation as only one possible way of navigation, along with, e.g., perception of magnetic field. The positional information in homing pigeons and probably other birds is possibly acquired olfactorily from traces of atmospheric gases (Wallraff, 1996).

Evidence for the use of olfactory cues in pigeon navigation was also provided by the results of a series of experiments with anosmic pigeons (anosmia was caused by zinc sulphate) carried out in southern England. The disorientational effect of anosmia was smaller at shorter distances (30–39 km), and more significant at longer distance which was tested (66 km). In other experiments with the use of naive (untrained) birds, both control and anosmic pigeons showed poor orientation abilities at short distances (25 km, 36 km, 39 km) from home (Guilford et al., 1998).

Pigeons allowed to smell olfactory cues at a ‘false’ release site (different from the real consequential home site), and subsequently transported to and released from another unfamiliar locality, oriented themselves first toward the false site, i.e., oriented themselves as if the false site were the real home, but eventually homed despite their incorrect initial orientation. The experimental pigeons sometimes flew for a long time in the wrong direction, corresponding with directions toward the false release sites, but later (2 h or more after release) corrected their path to the true homeward direction. The time of correction corresponded with the subsidence of the anaesthesia of their olfactory membranes, applied just prior to release (Dall’Antonia et al., 1999).

In a range of experiments it was assumed that the necessary information about the actual position with respect to home can be obtained from the ratios of three or more chemical compounds, which gradually vary over distances of several hundreds of kilometres, differently in different directions from the home site. The pigeons presumably acquire some knowledge of relevant gradients at their home site. This knowledge is gained by correlating wind directions with specific changes of ratios among a number of chemical compounds in air. However, it is necessary to investigate the above assumptions by additional studies. (Wallraff, 2000).

The results of tests to determine whether pigeons have some sensitive period for learning required olfactory perceptions suggest that the first three months post-fledging is critical for some aspects of navigational map learning (Gagliardo et al., 2001b). The lack of olfactory information (in addition to familiarity with the release site and some unknown site-dependent features) is a factor influencing the extent of deviation due to the clock-shift (Gagliardo et al., 2005a).

Thus, it seems that pigeons need immediate olfactory contact with the local atmospheric conditions. They must have experience with the natural winds at their home site during the most recent several weeks. In a known area around home, pigeons use not only olfactory perceptions but also visual inputs of landscape. From the point of view of neural regulation, the olfaction-based mechanism has been linked to the piriform cortex, while the vision-based mechanism has been associated with the hippocampal formation (Wallraff, 2005).

The piriform cortex is the main projection field of olfactory bulbs of birds. It is evidently necessary

to process olfactory information. Bilateral lesions to this telencephalic region disrupt homing pigeon navigation. The orientation of pigeons with lesions of the right piriform cortex was similar to the intact control birds, whereas the birds with lesions on the left cortex were significantly more disoriented than controls. Both experimental groups were significantly slower than controls. These findings suggest that the integrity of both sides of the piriform cortex is necessary for the successful homing process (Gagliardo et al., 2005b).

In a study focused on the nature of sensory perception it was demonstrated that magnetoreceptors in pigeons are located in the upper beak and that they are innervated by the ophthalmic branch of the trigeminal nerve. An intact ophthalmic branch of the trigeminal nerve but also an intact olfactory nerve are necessary for good homing performance from unfamiliar locations (Gagliardo et al., 2006).

As is obvious from the presented overview, most experiments focused on bird navigation were carried out on homing pigeons. The European Starling (*Sturnus vulgaris*) is another bird species which has been used in corresponding tests. Experimental starlings caught in nest sites in southern Germany were made anosmic by bilateral olfactory nerve section and were then displaced over distances of 30, 60, 120 or 240 km, respectively, either towards the east or west. In this experiment a total of 340 adult birds were used, of which half were made anosmic, and the other half were the control group. From the distances of 30 and 60 km, both controls and anosmic starlings returned at a rate of 40–50%. The return rate of controls was the same from 120 km, and decreased only slightly at 240 km, whereas the percentage of returning anosmic birds was significantly reduced. These results, similar to those obtained with homing pigeons, suggest that European starlings also need olfactory signals for navigation towards home from longer distances (Wallraff et al., 1995).

3. Perception of food odor

Some species of insects produce malodorous substances as a chemical defense against predators including birds. In feeding experiments, six bird species [robin (*Turdus migratorius*), blue jay (*Cyanocitta cristata*), brown thrasher (*Toxostoma rufum*), killdeer (*Charadrius vociferus*), starling

(*Sturnus vulgaris*), and house wren (*Troglodytes aedon*)] demonstrated feeding aversions towards the plant bug, *Lopidea robiniae* (Heteroptera: Miridae). Secretions from the metathoracic glands of this insect contain six major compounds, including (E)-2-hexenal, (E)-2-hexen-1-ol, (E)-2-octenal, (E)-2-octen-1-ol, (E)-2-heptenal, and (Z)-3-octen-1-ol. Bugs discharge a liquid containing these strongly smelling substances when attacked (Staples et al., 2002).

A contrasting situation is presumed for vultures who may be positively attracted by the scent of potential food. Smith et al. (2002) described the exhumation of woodchuck (*Marmota monax*) carcasses by Turkey vultures (*Cathartes aura*) from the soil two days after covering. The authors note that vultures may find food which has been buried and cached by foxes and other predators. However, in the same species (*Cathartes aura*), olfactory thresholds to three by-products of carrion decomposition (butanoic acid, ethanethiol, trimethylamine) were previously examined by Smith and Paselk (1986). The odorant thresholds of these chemicals were relatively high. On the basis of this information the authors raise the question of whether olfaction has general importance in food location by the Turkey vulture.

The Greater Yellow-headed vulture (*Cathartes melambrotus*) uses olfaction to locate food and is capable of locating a carcass in various types of environment including full-grown forest very quickly. Gomez et al. (1994) found that this species of vulture located 63% of provided carcasses, while mammalian scavengers found only 5%. The Greater Yellow-headed vulture is the most abundant vulture in the Amacayacu National Park (Colombia). There is an interspecific competition between Greater Yellow-headed vulture and two related species, the Turkey vulture (*Cathartes aura*) and King vulture (*Sarcorhamphus papa*). It was observed that Greater Yellow-headed vultures were displaced when feeding by both Turkey vultures and King vultures, although they are usually the first animals to locate a carcass.

DeVault et al. (2003) studied scavenging by vertebrates, its importance in the behavior of these animals, and in ecology. These authors note – among others – that vultures are best adapted to use carrion, but nearly all vertebrate predators are also sometimes scavengers. The successful location of carrion by vertebrates is also influenced by their olfactory abilities (in addition to visual abilities,

the speed and efficiency with which they forage it and their thresholds for detoxifying products of decomposition).

Procellariiform seabirds are other birds able to localize food using their sense of smell and have noses with large surface areas filled with olfactory epithelium for detecting odor. This anatomically well developed olfactory system is the basis of an excellent sense of smell. These birds can determine which parts of the featureless ocean are loaded with their prey. Albatrosses and other petrels routinely travel vast distances to forage productive areas where cold water is driven to the surface, providing rich nutrients and zooplankton for foraging. Different species of procellariiforms are sensitive to a variety of scented compounds associated with their primary prey, including krill-related odors (pyrazines and trimethylamine) as well as odors more closely associated with phytoplankton (dimethyl sulfide – DMS). In this manner, the birds are able to identify areas for successful foraging, which may have similarities in smell including high levels of naturally occurring DMS. DMS is an odorous gas associated with areas of high primary productivity, produced by phytoplankton, and the birds eat consequent components of the food chain. DMS and other aromatic compounds could provide information for foraging birds on areas in which food is likely to be found. Birds are able to recognize these signals over thousands of miles of open ocean (Nevitt, 1999a, 2000).

Krill scent is attractive to some but not all procellariiform species. Birds of some procellariiform species have been exposed to plain or krill (*Euphausia superba*)-scented vegetable oil slicks. The response of Cape petrels (*Daption capense*) is most noteworthy: they were observed most frequently at krill-scented slicks. This species and also southern giant petrels (*Macronectes giganteus*) appeared at krill-scented slicks most quickly (1 min), whereas black-browed albatrosses (*Diomedea melanophris*) were relatively sluggish (3 min). Storm-petrels (*Oceanites oceanicus* and *Fregetta tropica*) and Antarctic Fulmars (*Fulmarus glacialis*) responded in the same manner to krill-scented and unscented slicks (Nevitt, 1999b).

Pyrazines, especially 3-methyl pyrazine, are scented attractants found in macerated Antarctic krill (*Euphausia superba*), a primary prey for many seabird species in this region. Behavioral responses

to 3-methyl pyrazine in comparison with a negative control (unscented vegetable oil) and positive control (herring oil) were also investigated. Responses to pyrazine were highly species specific: cape petrels (*Daption capense*), giant petrels (*Macronectes* sp.) and whitechinned petrels (*Procellaria aequinoctialis*) were observed at least 1.8–4 times more often at pyrazine-scented slicks than at control slicks. Black-browed albatrosses (*Diomedea melanophris*) were only observed at pyrazine-scented slicks and never at control slicks. Wilson's storm-petrels (*Oceanites oceanicus*), black-bellied storm-petrels (*Fregetta tropica*), great shearwaters (*Puffinus gravis*) and prions (*Pachyptila* sp.) were found with equal frequency at control and pyrazine-scented slicks. Behavioral responses to the positive control (herring oil) were less varied. Almost all species (except great shearwaters, *Puffinus gravis*), were observed five times as often at slicks scented with herring oil compared with control slicks. Antarctic procellariiforms probably use species-specific foraging strategies that are more complex than simply the location of prey by scent (Nevitt et al., 2004).

The behavioral response to DMS was also tested in one northern species, Leach's storm-petrel (*Oceanodroma leucorhoa*) in breeding colonies on Kent Island (Canada). Birds were presented with either 5 ml DMS (100 μ mol/l concentration) or a control (water). Birds' reactions to the odor of cod liver oil, a well-established olfactory attractant of procellariiform seabirds foraging at sea were tested too. The results suggest that this bird species can interpret the smell of DMS as information about the localization of food sources. The detection of biogenic sulfur compounds in combination with other cues assists Procellariiform seabirds when searching for food in the sea (Nevitt and Haberman, 2003).

In addition to this, co-operative foraging was proved to be an important component of the foraging strategies of Antarctic seabirds. The influence of both conspecifics and heterospecifics as cues to prey location was investigated in four seabird species: black-browed albatross (*Thalassarche melanophrys*), white-chinned petrel (*Procellaria aequinoctialis*), prion (*Pachyptila* spp.), and diving petrel (*Pelecanoides* spp.). These bird species may forage co-operatively with conspecifics and also heterospecific neighbors within the group of the species investigated. In addition, birds were found to forage together there with groups of penguins and Antarctic seals (*Arctocephalus gazelle*) more frequently than would be expected by chance (Silverman et al., 2004).

In a study of the ontogeny of the olfactory abilities carried out using chicks of some species of seabirds, the blue petrel (*Halobaena caerulea*); the thin-billed prion (*Pachyptila belcheri*); and the common diving petrel (*Pelecanoides urinatrix*), the reactions to DMS, phenyl ethyl alcohol (PEA) and distilled water as a control were tested. The results showed that blue petrel chicks responded to DMS and PEA significantly more than to the control, and that thin-billed prion chicks responded significantly more only to PEA, whereas common diving petrels did not respond significantly to either odourant (Cunningham et al., 2003).

The results of another investigation suggest that procellariiform seabirds (petrels, albatrosses and shearwaters) can also detect volatilized ammonia and can use it as a potential signal substance. The tested species, blue petrel (*Halobaena caerulea* Gmelin) is capable of smelling ammonia in natural concentrations of 10^{-11} to 10^{-5} M. Ammonium (NH_4^+) is present in primary waste products. These waste matters are produced by many of the prey species on which procellariiforms forage. The volatilized ammonia (NH_3) and other nitrogen waste products, also scent the terrestrial landscape of sub-Antarctic islands where procellariiform seabirds breed. An ability to smell ammonia may be relevant to both localization of prey and also locating nest colonies: it is used both in foraging and homing behavior. Procellariiform seabirds have large olfactory bulbs, as anatomical and physiological preconditions for this capability (Nevitt et al., 2006).

4. Anting: a specific bird behavior

Many species of passerines (and some bird species of other families) are known to apply ants to their feathers. Anting behavior has been recorded in over 200 birds. Numerous hypotheses exist for why birds ant, including the control of ectoparasites, inhibiting the growth of fungi or bacteria, soothing skin irritated during the molting period, and removing toxic formic acid prior to food consumption. An aquatic passerine, the American dipper (*Cinclus mexicanus*), is one example of anting bird. This bird preens ants onto its remiges. Considering the timing of the dipper's anting episode and the fact that dippers are not known to consume ants, it does not appear that the reason for anting in this species is either molt-irritation or food preparation (Osborn, 1998).

In anting behavior birds hold an ant or another object in the bill and rub it in their plumage. Except ants, many other objects have been used for "anting". The use of a caterpillar for "anting" by a tropical warbler (*Basileuterus tristriatus*) has also been observed (Wenny, 1998).

The food-preparation hypothesis, which argues that birds are anting to remove a distasteful or toxic substance from the ants before eating them was tested in experiments on starlings (*Sturnus vulgaris*). The findings support this hypothesis for this bird species (Judson and Bennett, 1992).

However, Craig (1999) notes that it is very difficult to simply explain behavior of this type. Anting can be passive and/or active; both types of anting has been observed in Africa in 21 passerine species in 10 families in the wild, and in captive birds in a further 27 species of three families, whereas in non-passerine species in Africa only passive anting from four species has been described. The observations of anting were generally rare, which suggests that this behaviour is infrequent. Ants, used by birds for anting, belonged in all determined cases to the sub-family Formicinae.

Revis and Waller (2004) tested polar and non-polar ant secretions from five selected ant species and pure formic acid for bactericidal and fungicidal effects on microbial ectoparasites of feathers. Pure formic acid strongly inhibited the bacteria (two strains of *Bacillus licheniformis*, *B. subtilis*) and fungal hyphae (*Chaetomium globosum*, *Penicillium chrysogenum*, *Trichoderma viride*) tested, whereas the concentrations of formic acid found in the ants, hexane ant-chemical extracts and ant suspensions in deionized water did not. Consequently these authors do not consider that the hypothesis that birds apply ants to control feather parasites has been proved.

Acknowledgement

The author wishes to thank Dr. Hana Cizkova for English revision of the manuscript.

5. REFERENCES

- Benvenuti S., Gagliardo A. (1996): Homing behaviour of pigeons subjected to unilateral zinc sulphate treatment of their olfactory mucosa. *Journal of Experimental Biology*, 199, 2531–2535.

- Benvenuti S., Ranvaud R. (2004): Olfaction and the homing ability of pigeons raised in a tropical area in Brazil. *Journal of Experimental Zoology, Part A – Comparative Experimental Biology*, 301A, 961–967.
- Bingman V.P., Benvenuti S. (1996): Olfaction and the homing ability of pigeons in the southeastern United States. *Journal of Experimental Zoology*, 276, 186–192.
- Craig A.J.F.K. (1999): Anting in Afrotropical birds: a review. *Ostrich*, 70, 203–207.
- Cunningham G.B., Van Buskirk R.W., Bonadonna F., Weimerskirch H., Nevitt G. A. (2003): A comparison of the olfactory abilities of three species of procellariiform chicks. *Journal of Experimental Biology*, 206, 1615–1620.
- Dall'Antonia P., Luschi P. (1993): Orientation of pigeons exposed to constant light and released from familiar sites. *Physiology & Behavior*, 54, 1173–1177.
- Dall'Antonia P., Dall'Antonia L., Ribolini A., Ioale P., Benvenuti S. (1999): Pigeon homing: site simulation experiments with birdborne direction recorders. *Behavioural Processes*, 44, 331–339.
- DeVault T.L., Rhodes O.E., Shivik J.A. (2003): Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos*, 102, 225–234.
- Gagliardo A., Ioale P., Odetti F., Bingman V. P. (2001a): The ontogeny of the homing pigeon navigational map: evidence for a sensitive learning period. *Proceedings of the Royal Society of London, Series B – Biological Sciences*, 268 (1463), 197–202.
- Gagliardo A., Odetti F., Ioale P. (2001b): Relevance of visual cues for orientation at familiar sites by homing pigeons: an experiment in a circular arena. *Proceedings of the Royal Society of London, Series B – Biological Sciences*, 268 (1480), 2065–2070.
- Gagliardo A., Odetti F., Ioale P. (2005a): Factors reducing the expected deflection in initial orientation in clock-shifted homing pigeons. *Journal of Experimental Biology*, 208, 469–478.
- Gagliardo A., Odetti F., Ioale P., Pecchia T., Vallortigara G. (2005b): Functional asymmetry of left and right avian piriform cortex in homing pigeons' navigation. *European Journal of Neuroscience*, 22, 189–194.
- Gagliardo A., Ioale P., Savini M., Wild J.M. (2006): Having the nerve to home: trigeminal magnetoreceptor versus olfactory mediation of homing in pigeons. *Journal of Experimental Biology*, 209, 2888–2892.
- Ganzhorn J.U., Burkhardt J.F. (1991): Pigeon homing – new airbag experiments to assess the role of olfactory information for pigeon navigation. *Behavioral Ecology and Sociobiology*, 29, 69–75.
- Gomez L.G., Houston D.C., Cotton P., Tye A. (1994): The role of Greater Yellow-headed Vultures *Cathartes melambrotus* as scavengers in neotropical forest. *Ibis*, 136, 193–196.
- Guilford T., Gagliardo A., Chappell J., Bonadonna F., de Perera T. B., Holland R. (1998): Homing pigeons use olfactory cues for navigation in England. *Journal of Experimental Biology*, 201, 895–900.
- Judson O.P., Bennett A.T.D. (1992): Anting as food preparation – formic acid is worse on an empty stomach. *Behavioral Ecology and Sociobiology*, 31, 437–439.
- Meade J., Biro D., Guilford T. (2005): Homing pigeons develop local route stereotypy. *Proceeding of the Royal Society of London, Series B – Biological Sciences*, 272, 17–23.
- Nevitt G. (1999a): Foraging by seabirds on an olfactory landscape: the seemingly featureless ocean may present olfactory cues that help the wide-ranging petrels and albatrosses pinpoint food sources. *American Scientist*, 87, 1–6.
- Nevitt G. (1999b): Olfactory foraging in Antarctic seabirds: a species-specific attraction to krill odors. *Marine Ecology-Progress Series*, 177, 235–241.
- Nevitt G.A. (2000): Olfactory foraging by Antarctic procellariiform seabirds: Life at high Reynolds numbers. *The Biological Bulletin*, 198, 245–253.
- Nevitt G.A., Haberman K. (2003): Behavioral attraction of Leach's storm-petrels (*Oceanodroma leucorhoa*) to dimethyl sulfide. *Journal of Experimental Biology*, 206, 1497–1501.
- Nevitt G.A., Reid K., Trathan P. (2004): Testing olfactory foraging strategies in an Antarctic seabird assemblage. *Journal of Experimental Biology*, 207, 3537–3544.
- Nevitt G.A., Bergstrom D.M., Bonadonna F. (2006): The potential role of ammonia as a signal molecule for procellariiform seabirds. *Marine Ecology-Progress Series*, 315, 271–277.
- Osborn S.A.H. (1998): Anting by an American dipper (*Cinclus mexicanus*). *Wilson Bulletin*, 110, 423–425.
- Revis H.C., Waller D.A. (2004): Bactericidal and fungicidal activity of ant chemicals on feather parasites: An evaluation of anting behavior as a method of self-medication in songbirds. *Auk*, 121, 1262–1268.
- Schlund W. (1992): Intranasal zinc-sulfate irrigation in pigeons – effects on olfactory capabilities and homing. *Journal of Experimental Biology*, 164, 171–187.
- Schmid J., Schlund W. (1993): Anosmia in ZNSO₄-treated pigeons – loss of olfactory information during ontogeny and the role of site familiarity in homing experiments. *Journal of Experimental Biology*, 185, 33–49.
- Silverman E.D., Veit R.R., Nevitt G.A. (2004): Nearest neighbors as foraging cues: information transfer in a patchy environment. *Marine Ecology-Progress Series*, 277, 25–36.

- Smith S.A., Paselk R.A. (1986): Olfactory sensitivity of the Turkey vulture (*Cathartes aura*) to three carrion-associated odorants. *Auk*, 103, 586–592.
- Smith H.R., DeGraaf R.M., Miller R.S. (2002): Exhumation of food by Turkey vulture. *Journal of Raptor Research*, 36, 144–145.
- Staples J.K., Krall B.S., Bartelt R.J., Whitman D.W. (2002): Chemical defense in the plant bug *Lopidea robiniae* (Uhler). *Journal of Chemical Ecology*, 28, 601–615.
- Streng A., Wallraff H.G. (1992): Attempts to determine the roles of visual and olfactory inputs in initial orientation and homing of pigeons over familiar terrain. *Ethology*, 91, 203–219.
- Walcott C. (1996): Pigeon homing: Observations, experiments and confusions. *Journal of Experimental Biology*, 199, 21–27.
- Waldvogel J.A., Phillips J.B. (1991): Olfactory cues perceived at the home loft are not essential for the formation of a navigational map in pigeons. *Journal of Experimental Biology*, 155, 643–660.
- Wallraff H.G. (1996): Seven theses on pigeon homing deduced from empirical findings. *Journal of Experimental Biology*, 199, 105–111.
- Wallraff H.G. (2000): Simulated navigation based on observed gradients of atmospheric trace gases (models on pigeon homing, part 3). *Journal of Theoretical Biology*, 205, 133–145.
- Wallraff H.G. (2001): Navigation by homing pigeons: updated perspective. *Ethology, Ecology & Evolution*, 13, 1–48.
- Wallraff H.G. (2004): Avian olfactory navigation: its empirical foundation and conceptual state. *Animal Behaviour*, 67, 189–204.
- Wallraff H.G. (2005): Beyond familiar landmarks and integrated routes: goal-oriented navigation by birds. *Connection Science*, 17, 91–106.
- Wallraff H.G., Kiepenheuer, J., Streng, A. (1994): The Role of Visual Familiarity with the Landscape in Pigeon Homing. *Ethology*, 97, 1–25.
- Wallraff H.G., Kiepenheuer J., Neumann M. F., Streng A. (1995): Homing experiments with starlings deprived of the sense of smell. *Condor*, 97, 20–26.
- Wenny D. (1998): Three-striped Warbler (*Basileuterus tristriatus*) “anting” with a caterpillar. *Wilson Bulletin*, 110, 128–131.

Received: 2008–03–08

Accepted after corrections: 2008–08–12

Corresponding Author:

Doc. RNDr. Ing. Josef Rajchard, Ph.D., University of South Bohemia, Faculty of Agriculture, Department of Biological Disciplines, Studentska 13, 370 05 Ceske Budejovice, Czech Republic
Tel. +420 387 772 757, e-mail: rajchard@zf.jcu.cz
