

SEVEN THESES ON PIGEON HOMING DEDUCED FROM EMPIRICAL FINDINGS

HANS G. WALLRAFF

Max-Planck-Institut für Verhaltensphysiologie, D-82319 Seewiesen Post Starnberg, Germany

Summary

Experimental findings obtained in recent years make it possible to recognize and distinguish the most relevant components determining homing flights of displaced pigeons. Conclusions deduced from these experiments, more or less compelling or tentative, are presented in the form of seven theses, supplemented by several subtheses along with reference to empirical data. The principal theses are as follows. (1) Passively displaced pigeons find the way home by using location-dependent signals and not by path integration based on recording of motion. Pigeons are able to home, even from unfamiliar areas, without access to potentially useful information during transport to the release site. (2) Home-related orientation of pigeons in unfamiliar areas requires positional information acquired olfactorily from atmospheric trace gases. Empirically deduced details of olfactory navigation are enumerated (connection with winds and the sun, inaccuracy, spatial range, time course of sampling and memorizing spatial information, etc.). The critical gap in our knowledge, i.e. the nature and spatio-temporal distribution of the substances involved, is provisionally filled by speculation. (3) In familiar areas, known from previous flights, the visual landscape is used additionally to find the way home.

(4) Initial orientation of pigeons does not exclusively reflect home-related navigation but includes components independent of the position with respect to home. Observed bearings are co-determined by a general preference for a certain compass direction and by distracting features of the nearby landscape. (5) Proportions among components controlling initial orientation according to theses 2–4 are highly variable depending on local, temporal and experimental conditions and on the life histories of the pigeons. This complexity greatly restricts recognition of the navigationally relevant components of behaviour at a given release site. (6) Sensory inputs, being neither olfactory nor visual, do not substantially contribute to determining the current position with respect to home. This thesis need not be definitive, but at present no contradicting evidence is available. (7) Pigeon homing is a model case of bird homing in general. Experiments with other species support this thesis. So far, there is no reason to assume that wild birds apply mechanisms fundamentally different from those of pigeons to find the way home.

Key words: bird navigation, olfactory map, atmospheric trace gases, visual landscape, home-independent orientation.

Introduction

In recent years, research on pigeon homing has developed in a peculiarly dichotomous way. On the one hand, our knowledge and understanding have made considerable progress. In my personal view, the overall perspectives are currently much clearer and more promising than ever before. On the other hand, the public image of the field has never before been so adverse and confusing. The reason is another dichotomy. What I call progress, achieved almost exclusively by two research groups, has not been recognized as progress by other researchers in the field. They still preserve a position reached some 20 or 30 years ago, augmented by several more unexplained phenomena and effects accumulated since that time. They argue for a diffuse multifactorial system including a variety of environmental cues, none of which is considered to be crucial or essential. The architecture of the system remains obscure. Noteworthy progress along this line is not in sight, and progress claimed to be made by others is not acknowledged. For observers from

outside the field, it is difficult to cope with the huge quantity of results and controversial discussions they find in the literature. They feel confused and bored and eventually avert their eyes from the whole field.

It is my impression that a great deal of the confusion has been caused by the pigeons themselves, whose behaviour has led the scientists astray. Researchers, focusing their attention on mechanisms of navigation, tend to interpret everything that a displaced pigeon does as an output of a sophisticated machinery endeavouring to find an optimal course home. Yet the pigeons appear less narrow-minded. It seems that home-related navigation is only a fraction, sometimes even a minor fraction, of the orientation behaviour exhibited by the birds after release. The output of the navigation mechanism appears often to be quite weak and uncertain and, moreover, the birds seem not always to be primarily motivated towards flying home as fast as possible. Peculiarities of initial

orientation, as revealed by vanishing bearings observed with binoculars immediately after release, can easily be misinterpreted as indicating peculiarities of the navigational system although they are generated by other oriented activities as well.

This is my impression today, but it was many years before the components contributing to the pigeons' extremely noisy and variable homing behaviour had been sufficiently separated and identified. Eventually, during the last few years, a fairly satisfactory overview may have been achieved. So far, however, my (relative) satisfaction is not shared by everybody else and, therefore, I present my view in the form of seven principal theses and several subtheses, accompanied by brief substantiations and commentaries. The theses are deduced from empirical research, more or less compelling or tentative. For results on which the deductions are based and for comprehensive arguments, I must refer to the literature. For reviews implying my personal view and giving more complete references, see Wallraff (1988, 1990*a,b*, 1991*a,b*); for later published results and arguments, see later titles in the reference list. Reviews largely in agreement with my view are those by Papi (1986, 1991, 1995). Recent results published by Tögel and Wiltschko (1992), Schlund (1992), Schmid and Schlund (1993), Benvenuti *et al.* (1994) and Wiltschko *et al.* (1994) are in accordance with my theses, although the authors discuss them in a more or less different way. Most of the divergent views expressed by others (e.g. Schmidt-Koenig, 1979, 1987; Waldvogel, 1989; Wiltschko and Wiltschko, 1989, 1992; Schmidt-Koenig and Ganzhorn, 1991; Wiltschko, 1991, 1993, 1996; Waldvogel and Phillips, 1991) have been discussed in my/our previous publications.

Thesis 1. Passively displaced pigeons find the way home by using location-dependent signals and not by path integration based on recording of motion

Within certain range limits (in Germany tested up to 300 km from home), orientation and homing performances have not been reduced by exclusion or strong disturbance of potential sources of information during displacement (variable high-speed rotation, irregular variations of the magnetic field, visual and olfactory isolation), even if the site of release was far away from previously visited areas (Wallraff, 1988, 1990*a*). Thus, there is strong evidence against, and no indication favouring, involvement of any kind of path integration based on motion-dependent information.

The above statement does not generally exclude utilization of information picked up during the outward journey. On the contrary, position-dependent information seems to be collected whenever and wherever possible (see subthesis 2.5), i.e. during passive transportation, at the release site and on the way back home (Wallraff and Sinsch, 1988). It is not known whether path integration might be applied by birds returning from an excursion completely performed by active flight.

Thesis 2. Home-related orientation of pigeons in unfamiliar areas requires positional information acquired olfactorily from atmospheric trace gases

If rendered unable to smell environmental odours and released far away from any previously visited places, pigeons do not approach, or even reach, the familiar area around home at a probability level above chance – much in contrast to birds unimpeded in smelling ambient odours (Papi, 1986, 1991, 1995; Wallraff, 1988, 1990*a,b*). Results claimed to be at variance with this statement or, at least, to restrict its validity to certain geographical regions or localities were obtained under conditions of incomplete olfactory deprivation and/or the possible forms of interference covered by theses 3 and 4 were neglected (see Wallraff, 1990*a*, 1991*b*). All the objections so far brought forward against olfactory navigation can be rejected by reasonable arguments (the recent ones by Wiltschko, 1996, included).

It has been proved by a variety of experiments that the dependence of homing on olfactory inputs results from specific navigational deficits and not simply from general disturbances such as may have been caused, for instance, by interference with the birds' central nervous system (for a list of evidence, see Wallraff, 1990*a*, p. 102f).

As shown by filtration of ambient air, positional information is most likely to be gained from gaseous trace substances in the atmosphere. If exposed for some time to natural air at one site, and subsequently released without further contact with ambient odours at another unfamiliar site, pigeons behave as if departing from the site of previous olfactory exposure.

Subthesis 2.1. Knowledge needed to make appropriate use of airborne information at distant sites is acquired at the home site by associating olfactory inputs with wind direction (creation of an 'olfactory map')

Permanent shielding of winds at the home site prevents home orientation from distant sites. Deflection or reversal of winds in the home aviary leads to correspondingly deflected or reversed flight directions upon release. Deflections have been shown to be connected with olfaction. Artificial winds loaded with artificial odours applied at the home site induced initial bearings clustered around a predictable direction when the odours were again applied at the release site (Papi, 1986, 1991; Wallraff, 1990*a,b*, 1991*b*).

Subthesis 2.2. Directional information, associated with olfactory map information at home and abroad, is derived from the sun's azimuth taking current time into consideration (sun compass)

Shifts of the circadian clock by phase-shifts of the light-dark cycle lead, after release at unfamiliar areas, to deflections of initial bearings corresponding in sign and amount to the angular difference between the actual sun azimuth and the sun azimuth as expected according to the shifted time scale (Wallraff, 1988, 1990*a*). With large clock shifts (e.g. 6h), homing speed and homing success are

drastically reduced. The relationship to olfactory inputs in particular follows indirectly from the fact that in unfamiliar areas no map factors independent of olfaction are known. Moreover, in familiar areas and without natural olfactory input, dependence on the sun compass is weakened (see subthesis 3.1).

Subthesis 2.3. Olfactory map information is noisy and unreliable, thus allowing merely probabilistic orientational decisions

When initial bearings from a number of symmetrically distributed release sites in unfamiliar areas are summarized, they are, on average, homeward-oriented, but directional scatter is considerable. Average homing speeds are usually well below flight speed, at least partly because routes follow smaller or larger detours. The level of performance achievable by the system is represented by the sample as a whole (or its mean and variance) rather than by top individuals, which are at the top largely by chance. This indicates the limited accuracy of the available positional information (Wallraff, 1994a).

Subthesis 2.4. Reliability of olfactory positional information is variable in space and time and limited to a range of, at most, a few hundred kilometres from home

Accuracy of homeward orientation as dependent on olfactory inputs varies among sites around the same loft, among geographic regions, from day to day and with season. Performances are particularly poor under cold winter conditions. Without olfactory *en route* information during the outward journey, pigeons are homeward-oriented only over limited distances which depend on the home site and the direction of displacement and appear to vary from less than 100 to more than 500 km (Wallraff, 1990a,b; Benvenuti *et al.* 1994). Ranges probably depend on orographical and other geographical conditions. Under certain conditions, pigeons deduce seemingly reliable, but positionally incorrect, information from olfactory inputs acquired at a distant site (Wallraff, 1993). Release-site biases of initial orientation due to non-ideal spatial 'coordinates' used by the birds are to be expected. In most cases, however, verification is difficult, because factors not related to the map system co-determine the pigeons' behaviour (see thesis 5).

Subthesis 2.5. Pigeons gather the best possible olfactory map information at any transient position before release and memorize it for potential later usage upon release

To steer approximately homewards, pigeons need not currently be able to smell, provided that they had sufficient opportunity to smell environmental air during the outward journey and/or in the release area before release. Even if pigeons are currently able to smell, previously acquired information is more or less taken into account when directional decisions are made, probably depending on the clarity of previous and current information. Varying deflections caused by outward-journey detours are the result (Papi, 1986, 1991; Wallraff, 1990a).

Subthesis 2.6. Fresh open-field air contains more reliable positional information than stale air between vegetation or in a weakly ventilated container

It makes a difference whether pigeons, deprived of olfaction during release, were able to smell, before release, plenty of ambient air from open country as opposed to air from within a forest or between other types of vegetation (Wallraff *et al.* 1992). Pigeons that were ventilated before release with limited amounts of fresh ambient air were also subsequently impaired in home orientation (Wallraff *et al.* 1984).

Subthesis 2.7. Pigeons cannot immediately draw positional conclusions from ambient air but require some time for sampling of information

Initial homeward orientation is very poor if pigeons are prevented from smelling natural air until immediately before release. Orientation is better in birds ventilated with natural air at the release site over a few hours prior to release, even if they are unable to smell during the take-off itself (Wallraff *et al.* 1984).

Hypothesis. Positional information is deduced from a spectrum of atmospheric trace substances whose proportional composition varies with a fairly regular gradient in any horizontal direction over fairly long distances

This insertion is exceptional, as it is not deduced from empirical findings. It is necessary to fill provisionally the most critical gap in our knowledge. Empirical data on the atmospheric compounds involved and on their spatio-temporal distribution are totally lacking. The empirical findings mentioned above strongly suggest the existence of sufficiently monotonic olfactory gradients over geographically varying ranges. Problems apparently arising from frequent changes of weather, especially winds, must be proposed to be either sufficiently moderate owing to as yet unrecognized physical conditions or to be surmounted by a dynamic olfactory map by which the pigeons take the current type of weather into account (Wallraff, 1989, 1990b, 1991a). I am aware that the state of explanatory hypotheses is still unsatisfactory. However, lack of knowledge about how olfactory navigation operates cannot invalidate empirical evidence that it operates.

Thesis 3. In familiar areas, known from previous flights, the visual landscape is used additionally to find the way home

Home orientation is completely prevented by olfactory deprivation only in areas where the pigeons have never been before. In familiar areas, pigeons unable to smell natural air are less clearly deflected by clock-shifts than olfactorily intact birds and show enlarged directional scatter. This observation suggests the use of an extended non-shifted two-dimensional landscape pattern rather than information concerning only the birds' own current standpoint (Wallraff *et al.* 1994).

Subthesis 3.1. The sun compass is also associated with the visual 'topographical map'

The fact that the above-mentioned clock-shifts deflected the olfaction-deprived pigeons at all makes it clear that the birds take notice of the sun's position relative to the landscape. Unexpected discrepancy creates confusion (Luschi and Dall'Antonia, 1993; Wallraff *et al.* 1994).

Subthesis 3.2. Long-distance landscape orientation is based on a wide aerial panorama rather than on a chain of distinct landmarks

Non-olfactory initial homeward orientation occurs not only at the exact sites where the birds had been released before but also at sites at least 10 km away, so that they cannot follow a previously learned sequence of individual landmarks. The pigeons' behaviour as well as the anatomy and physiology of their eyes suggest utilization of large-scale panoramic images rather than human-like foveal scanning (Wallraff *et al.* 1994).

Thesis 4. Initial orientation of pigeons does not exclusively reflect home-related navigation but includes components independent of the position with respect to home

Pigeons deprived of olfactory information in unfamiliar areas and hence showing, in analyses summarizing data from several or many symmetrical release sites, not a trace of home-related orientation, still show considerable similarities with olfactorily intact birds in their initial orientation patterns at the individual sites. This finding indicates the existence of orientation components independent of the spatial relationship to the home site (Wallraff, 1991a; Kiepenheuer *et al.* 1993; Wallraff and Kiepenheuer, 1994). I regard the following three components as being identified.

Subthesis 4.1. Initial courses are more or less modified by nearby features of the surrounding visual landscape

Partly depending on home-site conditions, topographical features such as villages and open or wooded country distract the pigeons immediately after release. This distraction can be shown by statistical analyses including many release sites, but quantification of the effect for a single site is impossible (Kiepenheuer, 1993; Wallraff, 1994b).

Subthesis 4.2. Initial bearings are sometimes modified by the direction that guided the pigeons home in a previous flight

Pigeons, at least those little experienced in homing, tend to depart from the release site in a direction more or less similar to the direction in which they were flown during their last homing trip. The effect is extremely variable in amount (Wallraff, 1991a, 1994a).

Subthesis 4.3. Initial bearings are co-determined by a loft-specific preferred compass direction (PCD)

Many of the very common 'release-site biases' can be explained, to a large extent, by these directional preferences. The origin and the function of the PCD itself, however, are

largely unexplained. The PCD depends on, and can be modified by, prevailing winds at the home loft. The strength of the compass tendency and the specific direction preferred depend on the loft site and on the homing experience of the pigeons; to some degree, they are variable in time (Wallraff, 1990a, 1991a; Papi, 1995; Ioalè, 1995a,b).

Thesis 5. Proportions among components controlling initial orientation according to theses 2–4 are highly variable depending on local, temporal and experimental conditions and on the life histories of the pigeons

This thesis focuses primarily on methodological aspects. Vanishing bearings of individual pigeons observed immediately after release are easily measurable and, for a sample of birds, provide a detailed orientation pattern. However, owing to its composite origin, this pattern needs to be evaluated with appropriate care. Specific effects, experimentally induced or occurring spontaneously, do not necessarily indicate specific functions of the navigation system. Involvement of home-related navigation is not self-evident if only initial orientation is concerned whereas the duration and success of subsequent homing flights are not affected.

Subthesis 5.1. Without specific experimental interference, it is almost impossible to separate the components for a given release site

Components can be made visible by averaging site-dependent effects in data collected at many symmetrical release sites. At a single site, however, their quantitative contribution to the pattern of initial bearings can, at best, be roughly estimated. Only by experimental exclusion of position-indicating information (according to theses 2 and 3), can the remaining orientation pattern, mostly still non-random, be identified as being independent of such information (Wallraff, 1991a; Kiepenheuer *et al.* 1993).

Subthesis 5.2. 'Release-site biases' are very weak indicators of navigational peculiarities

This subthesis is a consequence of the previous one. Navigation-specific output cannot clearly be separated from other components. Neither the degree of overt homeward-directedness nor the degree of angular deviation from home allows direct conclusions to be drawn on specific properties of local 'map' factors.

Subthesis 5.3. Effects of experimental interference on initial orientation need not indicate interference with the home-finding system, but may result from a proportional change among components affecting behavioural output

Disturbances affecting the animals' motivational state rather than their navigational capabilities, e.g. any kind of stress, appear to retard orientated activities that take spatial relationships to home into account and promote, instead, immediate flights towards the PCD or, perhaps, attractive landscape features (Papi, 1995; Del Seppia *et al.* 1996). Thus, experimentally induced

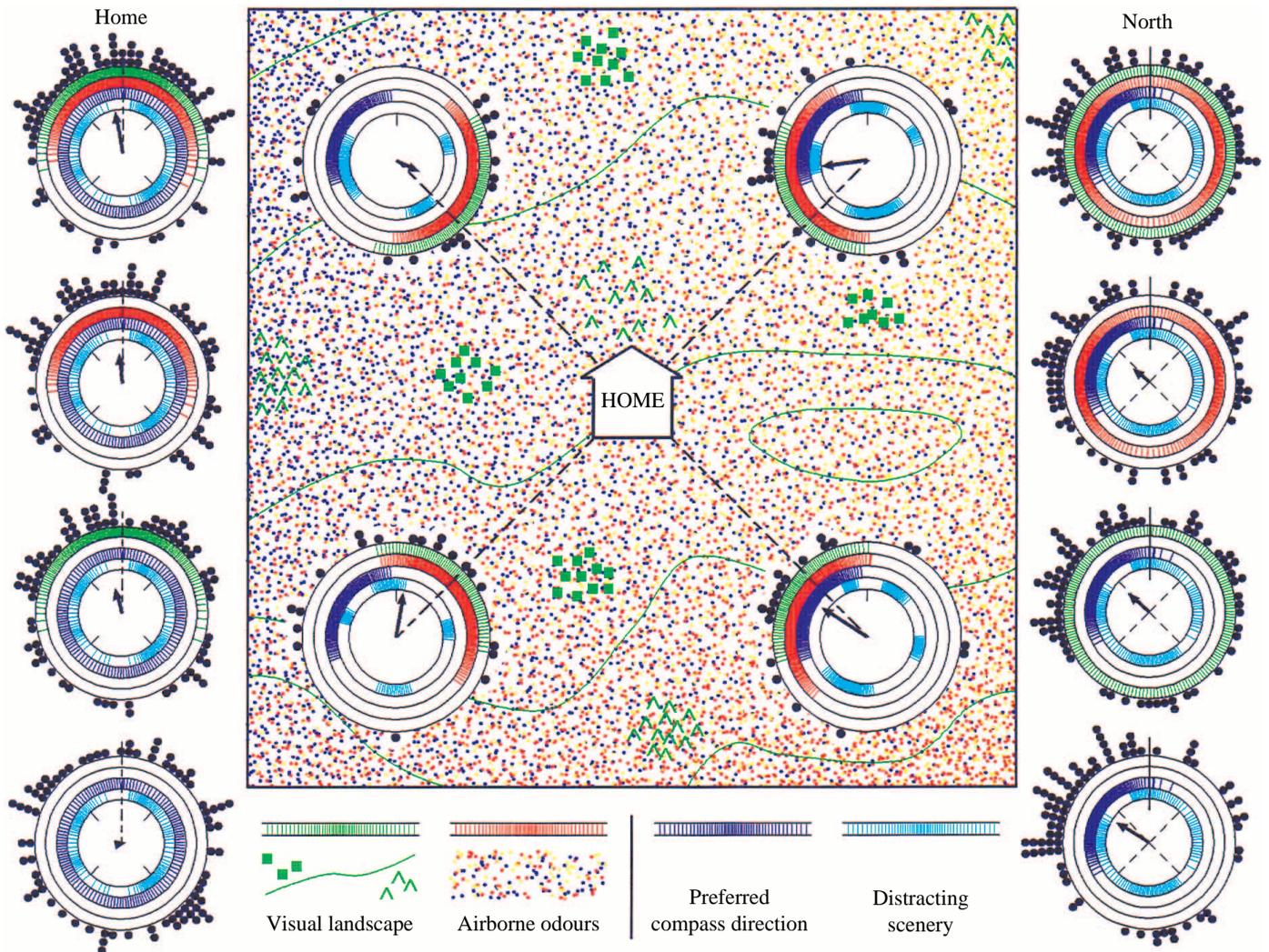


Fig. 1. Scheme showing the principal components determining initial orientation of pigeons. Coloured areas on concentric rings indicate degrees and ranges of probability to tend towards the respective directions under the influence of four components. In areas familiar from earlier flights, birds can estimate the approximate direction of home by means of the visual landscape as well as by evaluation of atmospheric odours. Yet their initial orientation is also influenced by directional tendencies that are independent of the position with respect to home: a generally preferred compass direction (PCD) and some propensity to approach or avoid distracting topographical features of the immediate surroundings. Schematically and hypothetically, any position in the field shown is characterized by a unique proportional density composition of three odorous compounds symbolized by blue, red and yellow dots. Initial bearings of samples of 20 pigeons, departing under the influence of probabilities induced by the four components and of stochastic noise, are shown as filled circles on the periphery of each diagram. Central arrows indicate mean vectors derived from these bearings (maximum vector length 1 = radius of outer circle). The uppermost diagrams to the left and right of the central field show orientation-inducing component probabilities together with pigeon bearings for the four sites pooled, on the left with the direction towards home pointing upwards and on the right with north pointing upwards. The other diagrams at the sides result after removal of position-indicating information: visual information is lacking if the area is unfamiliar, i.e. if the birds have never been there before; olfactory information can be removed experimentally. With neither of these two sources of positional information available, the pigeons do not show any orientation towards home, but the preference for a particular compass direction, northwest in the example, is now most pronounced (lowermost diagrams).

directional shifts may result from non-specific influences which have nothing to do with home orientation.

Thesis 6. Sensory inputs, being neither olfactory nor visual, do not substantially contribute to determining the current position with respect to home

This thesis will be disproved as soon as evidence contradicting it is presented. Up to now, such evidence is

lacking. Manipulations of magnetic conditions, for instance, never prevented homing from distant sites. Experimental effects restricted solely to initial orientation do not prove the involvement of the home-finding mechanism (see thesis 5).

Thesis 7. Pigeon homing is a model case of bird homing in general

There is no reason to assume that birds belonging to other

species apply mechanisms fundamentally different from those used by pigeons to find the way home from familiar or unfamiliar distant sites, although behavioural details may differ. There is experimental evidence that thesis 1, thesis 2, thesis 4 (PCD), and probably thesis 3, are also valid for at least some wild species (Rüppell, 1936; Matthews, 1984; Wallraff *et al.* 1995).

Conclusion

Fig. 1 gives a schematic overview of the composite origin of pigeon orientation as proposed by theses 2–4. By maintaining the basic structure of the system, but changing proportional relationships among its components, a wide variety of orientation patterns can be produced. Quantitative relationships shown in the figure are arbitrary, as the rules according to which different environmental signals and internal tendencies mutually influence each other, are weighted and are processed are unknown.

The most crucial gap in our knowledge does not concern the birds but rather their environment. As long as we have no empirical data on potentially exploitable sources of information in the atmosphere, olfactory navigation of pigeons and other birds remains not only enigmatic but seemingly impossible or, at least, inconceivable. Nevertheless, experimental data clearly show that olfactory navigation operates. The resulting dilemma cannot be solved by denying or ignoring empirically established facts. Instead, we should accept the challenge and try to solve the dilemma by directing future research into the empirically untouched gap.

References

- BENVENUTI, S., IOALÈ, P. AND NACCI, L. (1994). A new experiment to verify the spatial range of pigeons' olfactory map. *Behaviour* **131**, 277–292.
- DEL SEPPIA, C., LUSCHI, P. AND PAPI, F. (1996). Influence of emotional factors on pigeon initial orientation. *Anim. Behav.* (in press).
- IOALÈ, P. (1995a). Preferred compass directions of homing pigeons in Italy. *Boll. Zool.* **62**, 13–21.
- IOALÈ, P. (1995b). The preferred compass direction of homing pigeons can be affected by suitable screening of the home loft. *Ethol. Ecol. Evol.* (in press).
- KIEPENHEUER, J. (1993). The ambiguity of initial orientation of homing pigeons. In *Orientation and Navigation – Birds, Humans and Other Animals*, paper no. 17. London: The Royal Institute of Navigation.
- KIEPENHEUER, J., NEUMANN, M. F. AND WALLRAFF, H. G. (1993). Home-related and home-independent orientation of displaced pigeons with and without olfactory access to environmental air. *Anim. Behav.* **45**, 169–182.
- LUSCHI, P. AND DALL'ANTONIA, P. (1993). Anosmic pigeons orient from familiar sites by relying on the map-and-compass mechanism. *Anim. Behav.* **46**, 1195–1203.
- MATTHEWS, G. V. T. (1984). 'Nonsense' orientation in mallard; a resumé and an investigation of the mechanism of a sun-compass. *Wildfowl* **35**, 81–92.
- PAPI, F. (1986). Pigeon navigation: solved problems and open questions. *Monit. zool. ital. (N.S.)* **20**, 471–517.
- PAPI, F. (1991). Olfactory navigation. In *Orientation in Birds* (ed. P. Berthold), pp. 52–85. Basel: Birkhäuser Verlag.
- PAPI, F. (1995). Recent experiments on pigeon navigation. In *Behavioural Brain Research in Naturalistic and Semi-naturalistic Settings* (ed. E. Alleva, A. Fasolo, H. P. Lipp, L. Nadel and L. Ricceri), pp. 225–238. Dordrecht: Kluwer.
- RÜPPELL, W. (1936). Heimfinderversuche mit Staren und Schwalben 1935. *J. Orn.* **84**, 180–198.
- SCHLUND, W. (1992). Intra-nasal zinc sulphate irrigation in pigeons: effects on olfactory capabilities and homing. *J. exp. Biol.* **164**, 171–187.
- SCHMID, J. AND SCHLUND, W. (1993). Anosmia in ZnSO₄-treated pigeons: loss of olfactory information during ontogeny and the role of site familiarity in homing experiments. *J. exp. Biol.* **185**, 33–49.
- SCHMIDT-KOENIG, K. (1979). *Avian Orientation and Navigation*. London: Academic Press.
- SCHMIDT-KOENIG, K. (1987). Bird navigation: has olfactory navigation solved the problem? *Q. Rev. Biol.* **62**, 31–47.
- SCHMIDT-KOENIG, K. AND GANZHORN, J. U. (1991). On the problem of bird navigation. *Persp. Ethol.* **9**, 261–283.
- TÖGEL, A. AND WILTSCHKO, R. (1992). Detour experiments with homing pigeons: information obtained during the outward journey is included in the navigational process. *Behav. Ecol. Sociobiol.* **31**, 73–79.
- WALDVOGEL, J. A. (1989). Olfactory orientation by birds. *Curr. Orn.* **6**, 269–321.
- WALDVOGEL, J. A. AND PHILLIPS, J. B. (1991). Olfactory cues perceived at the home loft are not essential for the formation of a navigational map in pigeons. *J. exp. Biol.* **155**, 643–660.
- WALLRAFF, H. G. (1988). Navigation mit Duftkarte und Sonnenkompaß: das Heimfindervermögen der Brieftauben. *Naturwissenschaften* **75**, 380–392.
- WALLRAFF, H. G. (1989). Simulated navigation based on assumed gradients of atmospheric trace gases (models on pigeon homing, part 2). *J. theor. Biol.* **138**, 511–528.
- WALLRAFF, H. G. (1990a). Navigation by homing pigeons. *Ethol. Ecol. Evol.* **2**, 81–115.
- WALLRAFF, H. G. (1990b). Long-distance navigation of homing pigeons based on airborne olfactory signals. In *ISOT X: Proceedings of the 10th International Symposium on Olfaction and Taste* (ed. K. B. Døving), pp. 26–35. Oslo: GCS A/S.
- WALLRAFF, H. G. (1991a). Conceptual approaches to avian navigation systems. In *Orientation in Birds* (ed. P. Berthold), pp. 128–165. Basel: Birkhäuser Verlag.
- WALLRAFF, H. G. (1991b). Critical comments on the discussion about olfactory navigation in homing pigeons. *Verh. dt. zool. Ges.* **84**, 368.
- WALLRAFF, H. G. (1993). Correct and false olfactory orientation of homing pigeons as depending on geographical relationships between release site and home site. *Behav. Ecol. Sociobiol.* **32**, 147–155.
- WALLRAFF, H. G. (1994a). To be the first in pigeon homing: championship or luck? *Anim. Behav.* **47**, 833–846.
- WALLRAFF, H. G. (1994b). Initial orientation of homing pigeons as affected by the surrounding landscape. *Ethol. Ecol. Evol.* **6**, 23–36.
- WALLRAFF, H. G., BENVENUTI, S. AND FOÀ, A. (1984). Pigeon navigation: time course of olfactory signal processing and dependence on fresh environmental air. *J. comp. Physiol. A* **155**, 139–150.
- WALLRAFF, H. G. AND KIEPENHEUER, J. (1994). Relationships between initial orientation and subsequent homing of individual pigeons. *Anim. Behav.* **47**, 821–832.

- WALLRAFF, H. G., KIEPENHEUER, J., NEUMANN, M. F. AND SINSCH, U. (1992). Microclimatic origin of inhaled air affects olfactory navigation of homing pigeons. *Experientia* **48**, 1153–1158.
- WALLRAFF, H. G., KIEPENHEUER, J., NEUMANN, M. F. AND STRENG, A. (1995). Homing experiments with starlings deprived of the sense of smell. *Condor* **97**, 20–26.
- WALLRAFF, H. G., KIEPENHEUER, J. AND STRENG, A. (1994). The role of visual familiarity with the landscape in pigeon homing. *Ethology* **97**, 1–25.
- WALLRAFF, H. G. AND SINSCH, U. (1988). The role of 'outward-journey information' in homing experiments with pigeons: new data on ontogeny of navigation and general survey. *Ethology* **77**, 10–27.
- WILTSCHKO, R. (1991). The role of experience in avian navigation and homing. In *Orientation in Birds* (ed. P. Berthold), pp. 250–269. Basel: Birkhäuser Verlag.
- WILTSCHKO, R. (1993). Pigeon homing: release site biases and their interpretation. In *Orientation and Navigation – Birds, Humans and Other Animals*, paper no. 15. London: The Royal Institute of Navigation.
- WILTSCHKO, R. (1996). The function of olfactory input in pigeon orientation: does it provide navigational information or play another role? *J. exp. Biol.* **199**, 113–119.
- WILTSCHKO, R., KUMPFMÜLLER, R., MUTH, R. AND WILTSCHKO, W. (1994). Pigeon homing: the effect of a clock-shift is often smaller than predicted. *Behav. Ecol. Sociobiol.* **35**, 63–73.
- WILTSCHKO, R. AND WILTSCHKO, W. (1989). Pigeon homing: olfactory orientation – a paradox. *Behav. Ecol. Sociobiol.* **24**, 163–173.
- WILTSCHKO, W. AND WILTSCHKO, R. (1992). Pigeon homing: the effect of temporary anosmia on orientation behavior. In *Chemical Signals in Vertebrates VI* (ed. R. L. Doty and D. Müller-Schwarze), pp. 435–442. New York: Plenum Press.