The Condor 97:20–26

HOMING EXPERIMENTS WITH STARLINGS DEPRIVED OF THE SENSE OF SMELL[1]

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Abstract. Three hundred and forty adult European Starlings (*Sturnus vulgaris*) were caught in nest boxes at a colony in southern Germany. Half were made anosmic by bilateral olfactory nerve section; the others were sham-operated and served as controls. The birds were displaced over distances of 30, 60, 120 or 240 km, respectively, either towards east or west. Over 30 and 60 km, both controls and anosmic starlings returned at a rate of 40–50%. Over the longer distances, the return rate of controls remained the same (120 km) or decreased only slightly (240 km), whereas the percentage of anosmic homers was drastically and significantly reduced. The findings are analogous to corresponding results obtained with homing pigeons and strongly suggest that starlings also require perception of olfactory signals for orientation to home over longer distances. Returning to the nest site in the following spring was also significantly lowered by anosmia, suggesting that olfactory navigation is involved in the seasonal migrations.

Key words: Homing; navigation; orientation; olfaction; European starling; Sturnus vulgaris.

INTRODUCTION

There are important reasons why most of the more sophisticated experiments on bird homing have been performed with a domestic strain, the homing pigeon *Columba livia* (see Papi and Wallraff 1992). Investigating wild species only, it would have been impossible to gain the level of insight presently achieved. However, is the homing pigeon a model case for birds in general? It seems advisable to conduct comparative experiments with other species to assess to what degree the conclusions drawn from experiments with pigeons can be generalized.

Most enlightening among these conclusions is the inference that goal-oriented homing of pigeons from unfamiliar areas depends on atmospheric trace substances received by olfaction (see Papi 1986, 1991; Wallraff 1990a, 1990b, 1991; Benvenuti et al. 1992a for review and discussion of divergent views as advanced by, e.g., Waldvogel 1989, Schmidt-Koenig and Ganzhorn 1991, Wiltschko and Wiltschko 1992; see also Benvenuti et al. 1992b, Bingman and Mackie 1992, Schlund 1992, Schmid and Schlund 1993, Kiepenheuer et al. 1993, Wallraff 1993). It is important to know whether this inference holds for other bird species as well.

To date, only two comparative investigations have been published suggesting that swifts *Apus apus* and European Starlings *Sturnus vulgaris* also utilize olfactory input for homing over longer distances (Fiaschi et al. 1974, Wallraff and Hund 1982). Because in the starling, data were insufficient for definitive conclusions, we continued these experiments in another region. Moreover, by displacing the birds over different distances we detected additional analogies between the homing systems of starlings and pigeons.

MATERIALS AND METHODS

Starlings were captured and observed in a colony consisting of 30 nestboxes about 1 km south of the *Ammersee* (about 40 km southwest of Munich) in southern Bavaria, Germany (47°55′N, 11°08′E). The nestboxes were mounted, at several meters distance of each other, in a curved row along a belt of trees at the edge of extended grassland. Each nestbox was permanently equipped with a shutter which could be closed from some distance either by a long cord (in the first five years) or by electric cable connection (in the second five years). From 1984 to 1993 during the incubation period, in most cases between 20 and 30 April, a sample of starlings was caught in these boxes during the morning hours. They were brought to the institute at Seewiesen (road distance 14 km) and transferred there into small cages inside the house where they were fed with mealworms. During the same day they were surgically treated (see below). In the morning of

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[1] Received 1 March 1994. Accepted 8 September 1994.

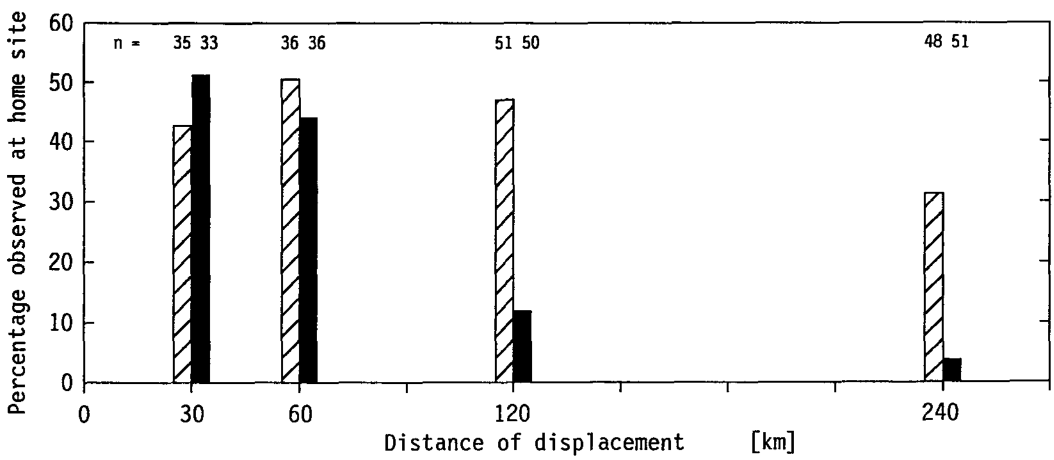

FIGURE 1. Percentages of starlings observed at the home site after displacement over varying distances. Hatched columns, OLF; filled columns, ANO. Percentages are means of percentages per direction as given in Table 1. Sample sizes *n* refer to the number of displaced birds.

the following day, the starlings were transported to the release site by car and set free individually, mostly at intervals of about ten minutes.

To yield long-term anosmia, the olfactory nerves must be cut. In the experimental (anosmic) birds the olfactory nerves were sectioned bilaterally, in an 8–10 min session under anaesthesia with Ketavet, using a method that largely prevents nerve regeneration (Wallraff and Hund 1982, Wallraff 1988). The control (olfactory intact) birds were sham-operated; their olfactory nerves were laid open but not cut. After this treatment, the starlings recovered rapidly and were put back into the cages. They fed on mealworms as before and behaved indistinguishably from untreated birds. Within each sample, sexes were distributed to ANO (anosmic) and OLF (olfaction intact) as equally as possible. Numbers per capture-and-release sample varied between 4 and 19. Each starling was marked individually by a numbered aluminum ring and three colored rings.

Release sites were pairwise east and west of home at approximately 30, 60, 120, and 240 km distance. During the days and weeks following release, the nestbox colony was observed for returners with binoculars and telescopes. The birds were identified by the colored rings and sometimes, when recaptured, additionally by the ring number. Observation occurred at irregular intervals depending on weather and other circumstances. Usually it lasted until feeding of young, i.e., late May or early June. As not each of the observed birds bred again in the colony, and as our observations were not equally intense in each year, we do not believe that we recorded all individuals that actually returned to the colony. However, the probability to be recorded was the same in both OLF and ANO; the observer did not know which bird belonged to which treatment group.

Some 400 m from our colony, there was another colony of 30 nestboxes which was under control of other researchers of our institute. A few of our displaced starlings were observed there, and they were also counted as returning.

We restricted our data to clear categories in that we never displaced the same individual twice. A few starlings that were not recorded after displacement in the same year were found in the colony in the following year. These birds were categorized "not homed."

RESULTS

The principal results are shown in Table 1 and Figure 1. After displacements over 30 and 60 km, about 40–50% of the starlings released were observed back in the colony some time later, independently of whether they could smell or not. A similar percentage of the OLF birds homed from 120 km. Among the ANO birds, however, the return rate was dramatically lower over this distance, reaching only a quarter of the control level. Over 240 km, fewer of the OLF starlings

TABLE 1. Numbers of starlings released, observed in the colony in the same year again ("home"), and not again observed in this year ("lost"); comparisons between control birds (OLF) and anosmic birds (ANO).

						ANO versus OLF			
						Per site		Per 2 sites	
Release site	Type	Released (*n*)	Home (*n*)	Lost (*n*)	Home (%)	Home (%/%)	*P*	Home (%/%)	*P*
30 km W	OLF	17	7	10	41.1	121.7	n.s.	120.4	n.s.
(4 years)	ANO	16	8	8	50.0				
30 km E	OLF	18	8	10	44.4	119.1	n.s.		
(4 years)	ANO	17	9	8	52.9				
60 km W	OLF	15	8	7	53.3	80.5	n.s.	88.0	n.s.
(3 years)	ANO	14	6	8	42.9				
60 km E	OLF	21	10	11	47.6	95.6	n.s.		
(4 years)	ANO	22	10	12	45.5				
120 km W	OLF	26	12	14	46.2	26.0	0.008	25.5	0.0001
(4 years)	ANO	25	3	22	12.0				
120 km E	OLF	25	12	13	48.0	25.0	0.006		
(4 years)	ANO	25	3	22	12.0				
240 km W	OLF	24	9	15	37.5	10.7	0.004	12.9	0.0003
(3 years)	ANO	25	1	24	4.0				
240 km E	OLF	24	6	18	25.0	15.2	0.039		
(3 years)	ANO	26	1	25	3.8				

"Home (%/%)" = percentage of homed ANO in percent of percentage of homed OLF. "*P*" = probability that differences in homing success between OLF and ANO could have arisen by chance (exact Fisher test or χ^2 test based on *n*'s of either one or two release sites, respectively).
Data were collected in 3–4 years per release site as indicated.

homed, but the decrease in ANO was steeper. Only two of the 51 ANO birds were observed back in the colony, against 15 out of 48 OLF's.

In addition to the ANO vs. OLF comparisons made in Table 1, return rates over different distances were compared within ANO and within OLF (using the tests mentioned in Table 1). In ANO, there is no significant difference between 30 and 60 km nor between 120 and 240 km. However, return rates over either 30 or 60 km are significantly different from those achieved over 120 km ($P < 0.001$) as well as over 240 km ($P < 0.00001$). In contrast, no significant differences in return rates between any two of the four distances have been found in OLF (always $P > 0.06$). With all data from displacements over 30, 60 and 120 km pooled, when compared with the 240 km data, $P = 0.047$ is achieved, i.e., still not an impressive statistical significance.

Although the final return rate over the shorter distances was very similar in OLF and ANO, average homing speed appeared to be different. These results are shown in Figure 2A, although the time intervals given there do not represent actual homing times, which in most cases must be considered more or less shorter. Relative comparisons between the two types of treatment are, nonetheless, possible, because numbers per type and release were equal or almost equal, and hence also chances to be detected on a given day. With medians of 9 and 15 days, re-observation intervals of OLF and ANO are different under the Mann-Whitney *U* test with $P = 0.02$.

On the whole, return times were longer over the longer distances (Fig. 2, B vs. A). There is little statistical basis to compare OLF and ANO with respect to homing speeds over more than 100 km because so few ANO starlings homed at all. Their cumulative percentages in Figure 2B are, therefore, more affected by chance events than those of the larger samples. Nevertheless, ANO birds tended to home slower than OLF.

Returned starlings, both OLF and ANO, incubated again and raised young. Observers were unable to distinguish between OLF and ANO returners in any behavioral respect.

No significant differences in any respect were found between males and females. In total, recorded return rates were somewhat larger in the females (OLF: 43.8 vs. 40.0%; ANO: 25.5 vs. 21.9%). It cannot be excluded that these slight differences reflect different chances to be observed rather than different homing performances.

Initial orientation of the starlings was observed. However, most birds landed within the first minute on the ground, on a tree, on a power line or somewhere else. The bearings recorded

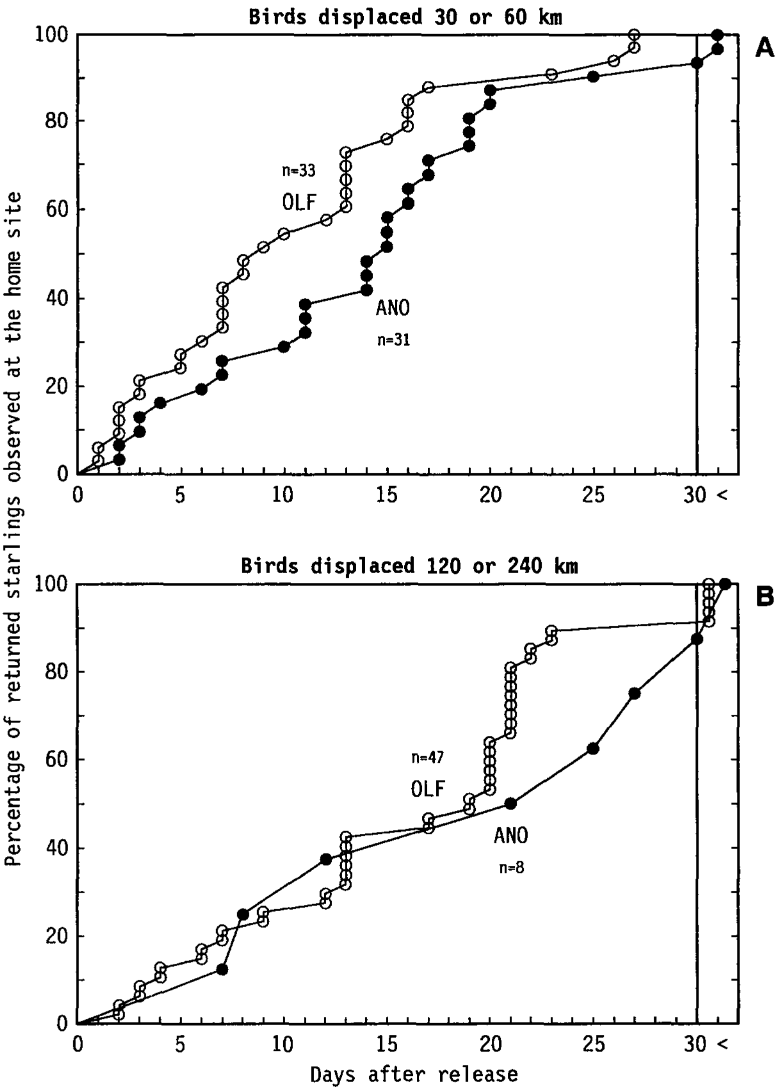

FIGURE 2. Cumulative percentages referring to the time period between release and subsequent observation at home. Only the returned starlings are included (100% = number of birds recorded as homed). In the last column, birds observed more than 30 days after release are pooled.

after several seconds as well as the few vanishing bearings did not show any general preference of the direction towards home.

We counted how many starlings from those re-observed in the year of displacement were again found in the colony during the following spring (Table 2). The percentage was almost four times larger in OLF than in ANO. In five of six cases in which both OLF and ANO birds homed in the first year and at least one bird was again

TABLE 2. Numbers of starlings observed home in the year of displacement and again observed in the subsequent year.

				ANO versus OLF	
Type	1st year (*n*)	2nd year (*n*)	2nd year (%)	2nd year (%/%)	*P*
OLF	63	18	28.6	26.2	0.008
ANO	40	3	7.5		

"%/%" and "*P*" are analogous to Table 1. Notice that 1st-year *n* does not coincide with total *n* in Table 1, because 1993–1994 is not included.

observed in the second year, the percentage of second-year homers was clearly higher in OLF than in ANO; in one case there was almost no difference (1 of 9 OLFs and 1 of 7 ANOs).

DISCUSSION

Anosmia did not notably affect homing success of starlings over distances of 60 km or less, but severely reduced the percentage of homers over distances of 120 km or more. That the return rates were normal after smaller displacements indicates that the anosmic birds were not handicapped in some general way. Obviously the anosmic birds were motivated to home and, in principle, able to use orientational clues in order to find home. One might argue that motivation was sufficient to make a short trip but insufficient to persist in searching for home over a longer period. This cannot be excluded, but seems unlikely for two reasons. (1) If motivation was affected at all, one should expect at least some weak reduction of the homing rate also at short distances and possibly a steady decrease with increasing distance. (2) In corresponding experiments with pigeons, ANO birds were evidently disoriented (see below). Reduced homing speeds (Fig. 2A) might indicate lowered motivation in ANO starlings, but could also indicate difficulties in orientation. In the latter case, eventual achievement of the normal return rate might even express a remarkably strong homing drive in spite of adverse orientation conditions giving rise to delayed success.

In the homing pigeon, it has been shown by several experiments beyond the level of simple nerve sectioning that olfactory deprivation makes orientation conditions adverse, at least in unfamiliar areas. It has been extensively discussed why strong deficits in orientation and homing success of anosmic pigeons are thought to be caused by lack of positional information deduced from airborne odors rather than by non-specific trauma or other disturbances (see Papi 1986, 1991; Wallraff 1990a). It seems quite probable that our results obtained with starlings are analogous to comparable results obtained with pigeons which also show a much steeper decrease of homing success with increasing distance in anosmic as compared with olfaction-intact birds (see Wallraff 1990b: Fig. 1; Papi and Wallraff 1992: Fig. 7.18). In pigeons, it has been shown that from far distant sites anosmic birds did not approach home and merely stopped flying before reaching home (thus indicating lack of motivation), but that the birds were actually disoriented while covering long distances (Wallraff 1989, 1990a).

There are, however, quantitative differences between pigeons and starlings. In the pigeons, deficits in homing success were dramatic over only 30 km distance, even in birds experienced in homing from other sites. From 60 km and more, very few anosmic pigeons ever returned (see also Schlund 1992; for discussion of seemingly divergent results, also quoted by Wallraff and Hund 1982, see Wallraff et al. 1989, p. 60f). Swifts investigated by Fiaschi et al. (1974) were more similar to the pigeons: no bilaterally handicapped swift returned over 47–66 km, in contrast to a 68% return rate of the unilaterally treated controls.

These differences in the effect of anosmia depending on distance suggest species-specific differences not in the basic mechanisms used for homing but in the proportions of their efficiency or in the mode of application. As outlined previously (Wallraff 1991, Wallraff et al. 1994), we assume use of two homing mechanisms. One mechanism is based on visual familiarity with the landscape; its range of operation depends on the range of previous experience with the area surrounding home. The other mechanism is based on atmospheric odors; its range substantially exceeds the range of previous experience. Our results suggest that in starlings the range of visual familiarity was remarkably large. The areas the individual birds had visited before are unknown. These areas need not make up a closed surface with a radius of 60 km. Considerable portions of random search may be involved, and perhaps the tenacity in searching is more developed in the starlings. At first glance, it seems surprising that a highly aerial species such as the swift does not utilize the visible landscape more extensively. However, swifts and pigeons have larger olfactory bulbs than starlings (Bang 1971; see Wallraff and Hund 1982: Fig. 1) and hence their olfactory navigation system may be more effective. Possibly their aerial life makes swifts particularly familiar with the airborne odors of the area; they may devote more attention to olfactory rather than to visual clues. At present, such questions cannot be answered.

The small number of anosmic starlings reaching home over distances of more than 100 km (8 of 101) can be understood on the basis of random search and chance (cf. Griffin 1952, Wallraff 1991). Moreover, it cannot be excluded that occasionally an ANO bird joined an OLF bird and they made the homing flight together. As a third possibility, it is conceivable that in rare cases nerve-cutting was not complete or allowed regeneration. The probability of occasional imperfections in cutting and separating the nerves may have been somewhat higher in the initial experiments reported by Wallraff and Hund 1982. This may, at least partly, explain why return rates of ANO starlings in this previous investigation were greater than in the present series. The difference between the two studies shrinks, however, if only displacements towards west and east are considered.

That a passerine bird with its small olfactory organ (Bang and Cobb 1968, Bang 1971) seems able to evaluate airborne odors for purposes of homing supports the hypothesis that olfactory navigation does not require excessive capabilities of odor discrimination. For quantification of a few key substances, a small sensory apparatus may suffice. The starling's sense of smell is better than originally expected and it is utilized in overt ecological contexts in which the substances involved are at hand (Clark and Mason 1987, Clark and Smeraski 1990).

The return rates of our OLF starlings coincide quite well with those obtained in the classical homing experiments by Rüppell (1935). In his study, 70 out of 186 (=38%) returned from 130 to 250 km. The average rate in our 120 and 240 km displacements is 39% (Table 1). Thus, there is no indication that the sham operations notably impaired the birds.

Although we did not record times of arrival in the colony, it seems clear that most of the starlings did not return in rapid flights over the shortest possible route (cf. Fig. 2). This holds for Rüppell's data as well. The delays may have been caused by difficulties in orientation resulting in more or less extended detours or by a type of slow step-by-step movements involving considerably long periods of feeding and resting, as observed by radio-tracking in Wood Thrushes *Hylocichla mustelina* (Able et al. 1984). Without telemetry, distinguishing between these possibilities is impossible.

The results shown in Table 2 concern the question of whether olfaction is involved in unforced migratory orientation. A much smaller percentage of the originally returning ANO starlings, as compared with OLF birds, returned again during the following spring after having performed the seasonal migrations (which on average may have extended over more than 1,000 km to the western Mediterranean; see Figs. 15f and 16 in Fliege 1984). Following the arguments advanced above, it seems unlikely that this reflects non-specific effects such as increased mortality, decreased motivation, etc. Nevertheless, we should be cautious with these long-term events and should not take them as definite evidence for deficits in home orientation from the winter quarters. However, the finding is a first experimental support of the hypothesis that olfactory navigation is a substantial constituent of the avian migratory system (cf. Wallraff 1991, p. 159).

ACKNOWLEDGMENTS

We thank R. Wahl and M. Neuss for their assistance in conducting the experiments. We thank our colleagues F. Trillmich and H. Biebach for cooperative support, especially for making data available on observations of our starlings in the neighboring colony.

LITERATURE CITED

Able, K. P., W. F. Gergits, J. D. Cherry, and S. B. Terrill. 1984. Homing behavior of Wood Thrushes (*Hylocichla mustelina*): a radio tracking study. Behav. Ecol. Sociobiol. 15:39–43.

Bang, B. C. 1971. Functional anatomy of the olfactory system in 23 orders of birds. Acta Anat. 79 Suppl. 58:1–76.

Bang, B. C., and S. Cobb. 1968. The size of the olfactory bulb in 108 species of birds. Auk 85:55–61.

Benvenuti, S., P. Ioalè, and F. Papi. 1992a. The olfactory map of homing pigeons, p. 429–434. *In* R. L. Doty and D. Müller-Schwarze [eds.], Chemical signals in vertebrates VI. Plenum Press, New York.

Benvenuti, S., P. Ioalè, A. Gagliardo, and F. Bonadonna. 1992b. Effects of zinc sulphate-induced anosmia on homing behaviour of pigeons. Comp. Biochem. Physiol. 103A:519–526.

Bingman, V. P., and A. Mackie. 1992. Importance of olfaction for homing pigeon navigation in Ohio, USA. Ethol. Ecol. Evol. 4:395–399.

Clark, L., and J. R. Mason. 1987. Olfactory discrimination of plant volatiles in the European Starling. Anim. Behav. 35:227–235.

Clark, L., and C. A. Smeraski. 1990. Seasonal shifts in odor acuity by starlings. J. Exp. Zool. 255:22–29.

Fiaschi, V., A. Farina, and P. Ioalè. 1974. Homing experiments on swifts *Apus apus* (L.) deprived of olfactory perception. Monit. Zool. Ital. (N.S.) 8:235–244.

Fliege, G. 1984. Das Zugverhalten des Stars (*Sturnus vulgaris*) in Europa: Eine Analyse der Ringfunde. J. Ornithol. 125:393–446.

Griffin, D. R. 1952. Bird navigation. Biol. Rev. 27: 359–390.

Kiepenheuer, J., M. F. Neumann, and H. G. Wallraff. 1993. Home-related and home-independent orientation of displaced pigeons with and without olfactory access to environmental air. Anim. Behav. 45:169–182.

Papi, F. 1986. Pigeon navigation: solved problems and open questions. Monit. Zool. Ital. (N.S.) 20: 471–517.

Papi, F. 1991. Olfactory navigation, p. 52–85. *In* P. Berthold [ed.], Orientation in birds. Birkhäuser Verlag, Basel.

Papi, F., and H. G. Wallraff. 1992. Birds, p. 263–319. *In* F. Papi [ed.], Animal homing. Chapman & Hall, London.

Rüppell, W. 1935. Heimfindeversuche mit Staren 1934. J. Ornith. 83:462–524.

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 W. Schlund. 1993. Anosmia in $ZnSO_4$-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., and J. U. Ganzhorn. 1991. On the problem of bird navigation, p. 261–283. *In* P.P.G. Bateson and P. H. Klopfer [eds.], Perspectives in ethology, Vol. 9. Plenum Press, New York.

Waldvogel, J. A. 1989. Olfactory orientation in birds, p. 269–321. *In* D. M. Power [ed.], Current ornithology, Vol. 6. Plenum Press, New York.

Wallraff, H. G. 1988. Olfactory deprivation in pigeons: examination of methods applied in homing experiments. Comp. Biochem. Physiol. 89A:621–629.

Wallraff, H. G. 1989. The whereabouts of non-homing homing pigeons: recoveries of normal and anosmic birds, paper no. 10. *In* RIN 89—Orientation and navigation: Birds, humans and other Animals. Royal Institute of Navigation, London.

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, p. 26–35. *In* K. B. Døving [ed.], ISOT X: Proc. 10th Int. Symp. Olfaction and Taste. GCS A/S, Oslo.

Wallraff, H. G. 1991. Conceptual approaches to avian navigation systems, p. 128–165. *In* P. Berthold [ed.], Orientation in birds. Birkhäuser Verlag, Basel.

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., and K. Hund. 1982. Homing experiments with starlings (*Sturnus vulgaris*) subjected to olfactory nerve section, p. 313–318. *In* F. Papi and H. G. Wallraff [eds.], Avian navigation. Springer-Verlag, Berlin.

Wallraff, H. G., M. F. Neumann, and U. Sinsch. 1989. Orientation and homing success of experienced and inexperienced anosmic pigeons. Ethol. Ecol. Evol. 1:47–64.

Wallraff, H. G., J. Kiepenheuer, and A. Streng. 1994. The role of visual familiarity with the landscape in pigeon homing. Ethology 97:1–25.

Wiltschko, W., and R. Wiltschko. 1992. Pigeon homing: the effect of temporary anosmia on orientation behavior, p. 435–442. *In* R. L. Doty and D. Müller-Schwarze [eds.], Chemical signals in vertebrates VI. Plenum Press, New York.