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SHORT COMMUNICATION

PIGEON HOMING: FAMILIARITY WITH THE RELEASE SITE REDUCES THE RELEASE SITE BIAS

BY UTE KOWALSKI AND ROSWITHA WILTSCHKO
Fachbereich Biologie der Universität, Zoologie, Siesmayerstraße 70, D-6000 Frankfurt am Main, FRG

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When homing pigeons are released, they usually do not depart directly towards home, but deviate from the home direction: the so-called 'release site bias' (Keeton, 1973 as a translation of the German *Ortseffekt* by Wallraff, 1959*a*). These deviations, which were first described by Kramer (1957), vary in size. At most sites, they are not very large, but occasionally may be as much as 180°. Releases at the same site normally produce very similar results, which are independent of weather conditions, age and general experience of the birds (Wallraff, 1959*b*) so that the bias is characteristic for any given location (Keeton, 1973). In view of the modern concepts of a learned navigational 'map' (see Wallraff, 1974; Wiltschko & Wiltschko, 1978, 1982, 1987) it is interesting to know how local experience at the site itself could affect the pigeons' behaviour.

We report here the results of a long-term study in which experienced pigeons were released from the same site more than 60 times. The site, Gau-Bickelheim (49°48′N, 8°01′E) lies on the crest of a hill between vineyards in the Nordpfalz region (56·4 km SW of the loft at Frankfurt am Main; the home direction being 57°).

The test birds were experienced, adult pigeons that had completed numerous homing flights (category V of Wallraff, 1959*b*). They were released singly and watched using 10×40 binoculars until they vanished from sight. The bearings were taken with a compass to the nearest 5°. Between April and September 1981, two groups of pigeons (17 males and 15 females) were released repeatedly from Gau-Bickelheim (the males in the morning and the females at noon according to the breeding schedule), on average three times per week. During this summer, none of these birds was released from any other site. Vanishing intervals were also recorded.

From the vanishing bearings of each release (with $N \geq 8$) the mean vector was calculated and tested for directional preference using the Rayleigh test. The mean value of the vanishing intervals was also determined. The data of the long-term study in 1981 were grouped in six periods according to the number of flights. For each group, we calculated the grand mean of means and determined whether it differed from the home direction 57° according to the confidence interval. The data of two periods were compared statistically using the Watson–Williams test (see Batschelet,

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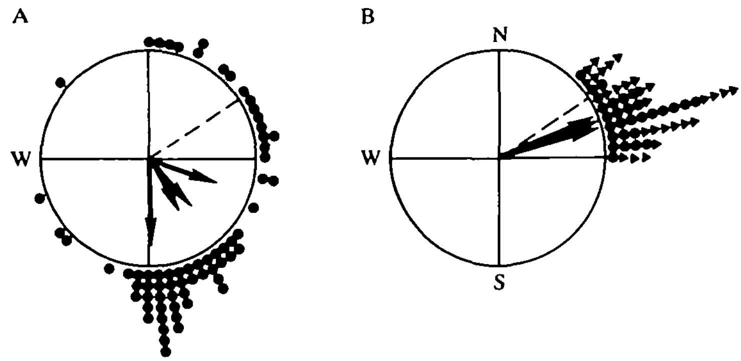

Fig. 1. Orientation at Gau-Bickelheim. (A) Four groups of pigeons released at the site for the first time (for numerical values, see Table 1). (B) Two releases each of two groups of pigeons (triangles, male; circles, female) that had previously homed from the site more than 60 times. The home direction, 57°, is indicated by the dashed line. The symbols at the periphery of the circle mark the vanishing bearings, the arrows represent the mean vectors of the individual releases, with the vector length being proportional to the radius of the circle = 1.

1981). We also calculated the median of the lengths of the mean vectors, and the median of the median vanishing intervals. These types of data for two periods were compared using the Mann–Whitney test.

Fig. 1A shows the individual bearings and the mean vectors (see also Table 1) of four groups of pigeons released at Gau-Bickelheim *for the first time*. Their mean directions showed considerable clockwise deviations from the home direction. Interestingly, the distribution of the bearings was not symmetrical. The majority of birds vanished in the sector between SSE and S, although there was a continuous line of bearings from that peak to the homeward quadrant.

That familiarity with the release site might reduce the bias was first indicated in another test series with a group of pigeons that was repeatedly released at Gau-Bickelheim. The data of their first, second and fourth flight are included in Table 1 (the third flight was a flock release).

In the 1981 series, the first flights were flock releases; vanishing bearings were recorded from the seventh flight onwards. The mean directions are given in Fig. 2

Table 1. *Orientation behaviour at Gau-Bickelheim*

Date	Number of bearings	Deviation from home	Vector length	Median vanishing interval (min: s)	
16 May 1977	14	+121°	0·80***	3:53	first flight from site
13 September 1978	19	+92°	0·55**	4:40	first flight from site
30 May 1979	19	+86°	0·58***	3:00	first flight from site
3 April 1981	15	+52°	0·64**	3:25	group A, first flight from site
8 July 1981	11	+40°	0·71**	4:00	group A, second flight from site
29 July 1981	10	+28°	0·75**	3:41	group A, fourth flight from s[illegible]

Significance by the Rayleigh test: $^{**}P < 0{\cdot}01$; $^{***}P < 0{\cdot}001$.

(for the numerical values and ranges of mean directions, vector lengths and vanishing intervals, see Table 2). Both groups of birds reacted very similarly: At first, the bias was approximately 30°; it gradually decreased asymptotically to reach a more or less stable plateau after about 40 flights. The vector lengths increased and the vanishing intervals decreased in the same way. The data for flights 7–15 differed significantly from those recorded for flight 36 onwards.

The data for flight 36 onwards represent a plateau; they do not differ from each other in any aspect. When this stage was reached, the mean directions of the individual samples of both groups varied between 63° and 80°. Their mean at 68–69°, however, still differed significantly from the home direction 57° ($P < 0{\cdot}05$, confidence interval) and thus represents a small, but significant bias.

These results show that the birds were able to modify their orientation as they became increasingly familiar with the test location and vanished closer to the home direction. This dramatic decrease in release site bias appears to contradict earlier observations by Wallraff (1959*a*,*b*) and Keeton (1973) who found no effect of local experience. However, these authors released their test birds fewer times than we did. Our data also show that the effect of the first few flights is not obvious and might easily be overlooked. Keeton (1973) noted that the mean values for pigeons that had

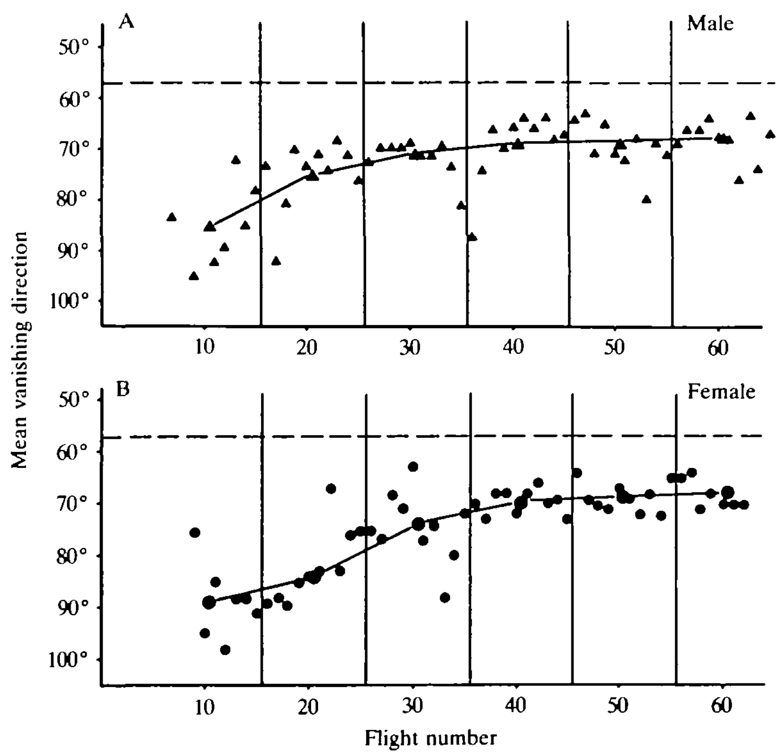

Fig. 2. Position of the mean vanishing direction as a function of the number of releases. The home direction, 57°, is marked as a dashed line. The small symbols give the mean directions of the individual releases; the large, connected symbols indicate the mean of the means of the respective groups of flights (for numerical values, see Table 2). (A) Male birds; (B) female birds.

Table 2. *Orientation behaviour of pigeons that were repeatedly released at Gau-Bickelheim*

	Number of tests ($N \geq 8$)	Deviations from home mean (range)	Vector lengths of the releases median (range)	Median vanishing intervals (min:s) median (range)
Male				
Flights 7–15	7	+28° (15°–38°)	0·77 (0·65–0·94)	3:29 (2:06–5:02)
Flights 16–25	10	+18° (11°–35°)	0·90 (0·67–0·96)	2:58 (1:51–4:04)
Flights 26–35	10	+14° (11°–24°)	0·94 (0·87–0·98)	2:30 (1:59–3:01)
Flights 36–45	10	+12° (7°–30°)	0·97 (0·91–0·98)	2:18 (1:36–2:54)
Flights 46–55	10	+12° (6°–23°)	0·97 (0·95–0·98)	2:19 (2:07–3:15)
Flights 56–65	10	+11° (6°–19°)	0·97 (0·76–0·97)	2:22 (1:34–3:10)
Female				
Flights 7–15	7	+32° (19°–41°)	0·84 (0·76–0·94)	3:10 (2:12–3:34)
Flights 16–25	9	+27° (18°–32°)	0·97 (0·87–0·99)	2:46 (1:55–3:19)
Flights 26–35	10	+17° (6°–31°)	0·97 (0·92–0·99)	2:41 (1:53–3:26)
Flights 36–45	10	+13° (9°–16°)	0·98 (0·97–0·99)	2:32 (2:09–3:25)
Flights 46–55	10	+12° (7°–15°)	0·98 (0·97–0·99)	2:16 (1:43–2:29)
Flights 56–62	7	+11° (7°–14°)	0·98 (0·96–0·99)	2:20 (2:00–3:10)

previously homed from Castor Hill were significantly closer to the home direction than those for birds that were unfamiliar with the site; this he interpreted as a fortuitous effect. The reduction in bias which he observed (23°) is, in fact, very similar to the one that we found after only two or three homing flights.

It is generally the case that with increasing flying experience the pigeons are better able to orient towards home (e.g. Wallraff, 1959*b*, 1978; Keeton, 1974). However, even very experienced birds still showed deviations from the home direction (examples have been published by Wallraff, 1959*a*; Windsor, 1975; Grüter, Wiltschko & Wiltschko, 1982). In our study, all the birds were very experienced from the outset. So it appears that *local* rather than general flying experience reduced the bias to a mere 12°.

A large bias means a long detour, at least at the beginning of the return flight, and shortening the distance to be covered would be an obvious advantage. It is an interesting question how extensive familiarity with the release site enables pigeons to change their initial orientation and to depart closer to home. A fortuitous effect caused by K-variation (cf. Keeton, Larkin & Windsor, 1974) cannot explain the decrease of the initially large bias (U. Kowalski, E. Füller & R. Wiltschko, in preparation).

An obvious possibility is that the pigeons changed their navigational strategy as they became familiar with the location and followed a sequence of known landmarks (Griffin, 1955). Such piloting was, however, excluded in the 1981 series by a clock-shift experiment: when their internal clock was shifted backwards by 6 h at the end of the series, the pigeons showed a typical clockwise deviation from the mean of controls (Füller, Kowalski & Wiltschko, 1983, fig. 1b). This clearly demonstrates that even after more than 60 homing flights the birds still determine their home direction as a *compass direction*, as described by the map and compass model (Kramer, 1953).

This implies that the pigeons, after becoming familiar with the release site, must have begun to interpret the local factors differently. Originally, the local map factors indicated a southeasterly direction. But the birds might have realized that they always had to correct their initial course to a more northerly bearing when checking their flight direction *en route* during the homing flight. Because of this experience they started the later flights on a more northerly course.

Our findings show that the navigational system is not rigid, but remains flexible even in experienced old pigeons. These birds can modify their map to include new experiences and to associate a specific local combination of factors with a new course. Local landmarks may have helped them to recognize the locality.

Nevertheless, a small bias remained. However, detours caused by this 12° deviation from the true home direction are probably negligible and might well lie within the normal fluctuations of the homeward course.

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