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Finding home: the final step of the pigeons' homing process studied with a GPS data logger

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Summary

Experiments have shown that homing pigeons are able to develop navigational abilities even if reared and kept confined in an aviary, provided that they are exposed to natural winds. These and other experiments performed on inexperienced birds have shown that previous homing experiences are not necessary to determine the direction of displacement. While the cues used in the map process for orienting at the release site have been extensively investigated, the final step of the homing process has received little attention by researchers. Although there is general agreement on the relevance of visual cues in navigation within the home area, there is a lack of clear evidence. In order to investigate the final step of the homing process, we released pigeons raised under confined conditions and others that had been allowed to fly freely around the loft and compared their flight paths recorded with a Global-Positioning-System logger. Our data show that a limited view of the home area impairs the pigeons' ability to relocate the loft at their first homing flight, suggesting that the final step of the homing process is mediated *via* recognition of familiar visual landmarks in the home area.

Key words: homing, pigeon, familiar landmark, flight tracks, navigation.

Introduction

Homing pigeons (*Columba livia*) possess the ability to home after displacement even if the release sites are totally unfamiliar to them. This ability also exists in pigeons raised confined in an aviary until the day of the release, provided that they perceive the environmental odours carried by the winds associated with the information of the wind direction (Wallraff, 1966; Wallraff, 1970b; Gagliardo et al., 2001a; Odetti et al., 2003). This evidence, together with the findings that anosmic pigeons are impaired in navigation (Wallraff, 1980; Gagliardo et al., 2006), constitutes the experimental basis of the olfactory navigation hypothesis (Papi et al., 1972; Wallraff, 2005a). This hypothesis predicts that homing pigeons are able to build up a navigational map of the surroundings by associating the olfactory information carried by the winds to the home loft with the directions from which they blow. At the release site pigeons determine the direction of displacement by recognising the prevalent local odours and choose and maintain the goal direction by using a compass mechanism [see also the 'map and compass' concept (Kramer, 1953)]. The olfactory map would therefore allow the pigeons to determine the direction of displacement, without giving them an exact geographical position with respect to the home loft. This view raises the question about how the birds can find home once they have arrived in the vicinity of the loft. It has been suggested that the final step of the homing process, the so-called local navigation, is accomplished by using familiar topographical information in the home area (Schmidt-Koenig and Walcott, 1978; Bingman and Mench, 1990; Guilford et al., 2004; Lipp et al., 2004; Wallraff, 2005a). Nevertheless there is still a lack of convincing evidence regarding the critical role of familiar landmarks in the final step of the homing process.

In the present study we compared the flight tracks of pigeons raised confined in an aviary, thus with a limited experience of the visual landmarks around home, with those of free-flying pigeons, which had an extensive knowledge of the landscape near the loft. The birds were equipped with miniaturised Global-Positioning-System (GPS) data loggers on their back, which allowed a precise reconstruction of their flight path.

Materials and methods

All the pigeons (*Columba livia* L.) used in the experiments hatched in the Arnino field station, Pisa, Italy, and at the time of the releases were about 6–9 months old. The pigeons were bred and kept according to the Italian laws on animal welfare. At the time of fledging (30–35 days after hatching), the pigeons were randomly assigned to two experimental groups as follows.

(1) Prisoner pigeons (P, N=33). The subjects were confined until the day of the experimental release in a large wire aviary (8 m×4 m×3 m) in which they could practice some short flights. From inside the aviary these pigeons could see the other lofts and aviaries placed at different distances (20–95 m away), a red building located 90 m east, a nearby wood east–southeast at about 150 m and open fields in the other directions (see also Fig. 2); a more distant wood (about 800 m away) is visible westward.

Free-flying pigeons (FF, N=20). The birds were housed in a loft from which they could freely exit and perform spontaneous daily flights around the loft. No additional training was given to the birds.

About 1 month before the planned release, the pigeons were equipped with PVC dummies, having the same size and weight as the GPS data loggers, in order to accustom them to carrying the load. The dummy was attached to the pigeon's back by means of a Velcro strip glued on the feathers, which had been previously shortened.

The birds were released once only from Massaciuccoli Lake (home direction 186°; home distance 20 km). The choice of the release site was determined by the habit of the prisoner pigeons, which have the tendency to land soon after being tossed; to prevent them from doing so and to encourage them to fly we performed the experiment from the middle of the lake. The experiment took place in three different years and four release sessions were performed (30/07/2003, P, N=9, FF, N=6; 09/06/2004, P, N=10; FF, N=2; 02/08/2004, P, N=7; FF, N=5; 12/09/2006, P, N= 7, FF, N=7).

The birds were tossed singly. Shortly before the release, the dummy was replaced with a miniature GPS data logger (NewBehavior AG, CH-8057 Zurich http://www.newbehavior.com). All the experimental releases took place in sunny conditions, with no or light wind.

The miniature GPS data loggers allow the recording of the flight path with an accuracy of about 4 m (Steiner et al., 2000; Lipp et al., 2004). The GPS data logger was adjusted to store one position fix every 10 s. Sometimes some devices were not able to receive the signals from the satellites for a short period, however, resulting in an artefact that corresponds to a straight line in the flight track. The position fixes stored by the GPS data logger included latitude, longitude, speed and time of recording. The device also provided information about altitude, but not precisely enough to allow a reliable analysis. The individual tracks were initially analysed with the MAPINFO software (One Global View, Troy, NY, USA) to extract the following parameters: mean speed (calculated as the ratio between the length of the track and the duration of the active flight), number and duration of stops during the homing flight, and track length. In addition, we calculated an efficiency index relative to two portions of the homing track: EI1, i.e. the ratio between the beeline from the release site to the aviary and the flight path length from the release site to the point at which the track crosses the home latitude; EI2, i.e. the ratio between the beeline from the point at which the track crosses the home latitude to the loft and the track length from this point to the end of the track. When the track was not complete we added the linear distance from the track end to the loft to it. When the birds that arrived directly at the home latitude reached the loft, we assumed the EI2=1.

Uncompleted tracks that stopped before the pigeon reached the home latitude were excluded from the analysis. We analysed the first portion of the track (from the release site to the home latitude) separately from the rest of the track.

The track efficiencies in the two portions of the track (EI1 and EI2, see above) relative to the two experimental groups were compared using the Mann–Whitney U test (Siegel, 1956). The same test was applied for each experimental group to compare the EI2 at two different distance ranges between the point at which the track crossed the home latitude and the loft. The distance ranges considered were 0–800 m and beyond 800 m.

In addition, we analysed the initial orientation of the two experimental groups of birds by considering the direction displayed by the birds when flying at 1500 m from the release site. For each distribution of the initial orientation bearings, a mean vector and homeward component were calculated; the latter ranges from –1.0 to +1.0 and gives an indication of the strength of the group's homeward orientation. The distributions of bearings were tested for uniformity using both the Rayleigh and V-test (Batschelet, 1981). Watson U^2 test (Batschelet, 1981) was used for comparisons among the initial distribution of the two experimental groups. The homing performances of the two groups were compared with the Mann–Whitney U test.

To obtain information about the probable size of the free-flight range of free-flying Arnino pigeons, three inexperienced, 7–9 month old free-flying pigeons, which had not participated in the previous experimental releases (but were carrying GPS dummies), were equipped with the miniaturised GPS data logger for 24 h (10–11 October 2005) and allowed spontaneous flights around the loft in flock with other Arnino pigeons. The day chosen for this observation was sunny and with no wind.

Results

Seventeen out of 20 free-flying (FF) pigeons and 22 out of 33 prisoner (P) pigeons homed after being released from Massaciuccoli. The P-pigeons showed homing performances significantly poorer than the FF-birds (Mann–Whitney U test, P<0.02; see also Fig. 1 for details). All the homed birds that crossed a circle of radius 1500 m from the release point were included in the initial orientation analysis (FF, N=16; P, N=21) and their performances are reported in Fig. 1. Both experimental groups displayed initial orientation distributions significantly different from random according to both the Rayleigh and the V-test (P<0.001 for both groups) and not significantly different from each other (Watson U^2, P>0.2).

As stated in the Materials and methods, we measured the distance at which the spontaneous excursions of three pigeons from the loft usually occurred. From the recorded tracks, it turned out that the spontaneous flights occurred up to a maximum radius of 800 m (see Fig. 2), but most frequently the

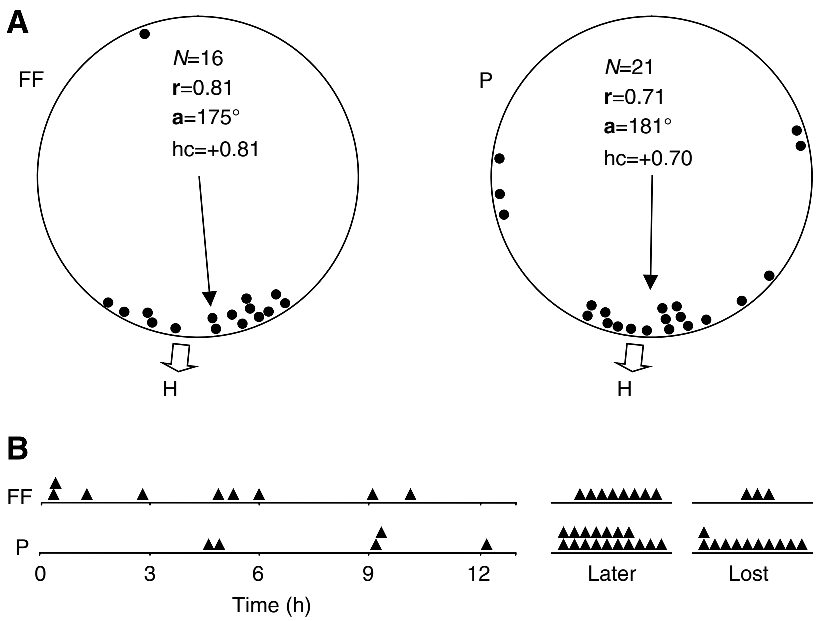

Fig. 1. Initial orientation and homing performance of the free-flying (FF) and prisoner (P) pigeons. Each symbol represents one subject. (A) Initial orientation: the outer arrow represents the home direction; the inner arrow represents the mean vector distribution; *N*, number of birds; **r**, mean vector length; **a**, mean vector direction; hc, homeward component. (B) Homing performance: the homing time (in h); pigeons homed later than the day of the release and birds lost are indicated.

birds remained up to 350–400 m from the loft. Although this recording was performed on only 1 day, it is representative of the habit of our birds (P.I., A.G. and M.S., personal observations).

Thirteen birds (8 P and 5 FF) rested for a long period and their tracks stopped before reaching the home area latitude, so their flight paths were not considered in the track analysis. In total we obtained 12 and 14 tracks of FF and P birds, respectively.

In the portion of the flight between the release site and the home latitude, the P birds stopped more often than the FF pigeons (median number of stops was 7/8 for P and 3 for FF pigeons; Mann-Whitney *U* test, $P=0.05$). Once having stopped, the P birds rested significantly longer than the FF pigeons before continuing their homing flights (median of the individual mean stop duration: 2 h 25 min for P and 1 h 26 min for FF; Mann–Whitney *U* test, $P<0.02$). This difference is probably due to P pigeons being in a worse physical condition than FF pigeons. However, during the active homing flight from the release site to the home latitude, the mean speed was not significantly different between the two experimental groups (median mean speed 53.6 $km\,h^{-1}$ for P and 57.8 $km\,h^{-1}$ for FF; Mann–Whitney *U* test, $P>0.2$). Moreover, the efficiency index relative to the first portion of the route (EI1, see Table 1 for details) was not statistically different between the two experimental groups (Mann–Whitney *U* test, $P>0.4$). This suggests that both P and FF birds had a similar motivation to go home and shows that the two experimental groups had similar navigational abilities.

In the second portion of the tracks, the comparison between the P and the FF pigeons revealed that the birds raised in confined conditions displayed a significantly lower efficiency index (EI2, Mann–Whitney *U* test, $P<0.01$; median values: P, 0.04; FF, 1), indicating that once they had reached the home latitude more P birds were unable to approach the loft straightforwardly (see Table 1 for details). In the FF group the EI2 level depended on the distance from the loft when the birds crossed the home latitude (Mann–Whitney *U* test, $P<0.02$). In particular the efficiency index was significantly lower for the distances beyond 800 m. In contrast, the EI2 level of the P pigeons was not significantly

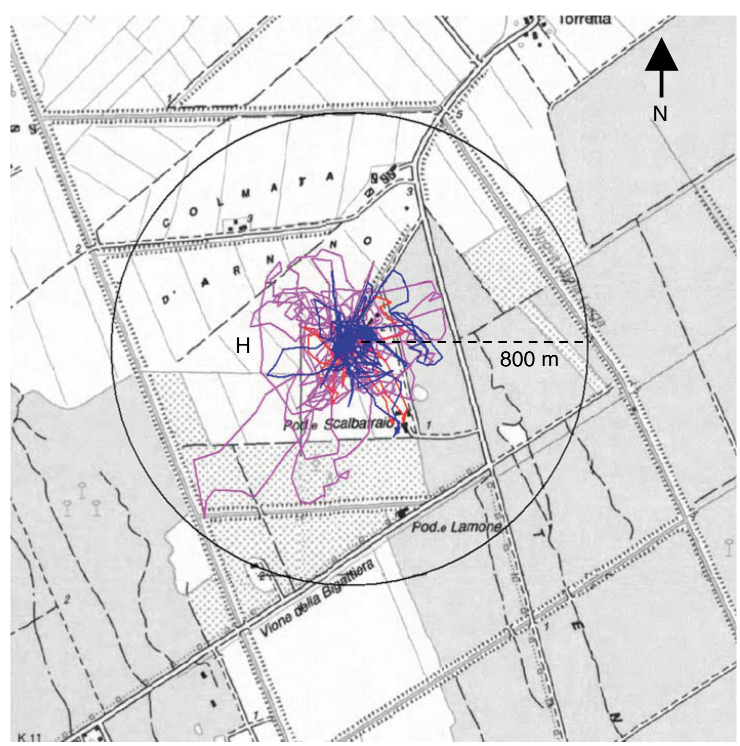

Fig. 2. Tracks of spontaneous flights around the home loft performed by three pigeons. See text for details.

Table 1. *Homing efficiency indices of free-flying and prisoner pigeons*

Prisoner pigeons				Free-flying pigeons			
Subject	EI1	EI2	*d* (m)	Subject	EI1	EI2	*d* (m)
#165	0.68	0.16	3580	#867	0.82	0.78	250
#234	0.71	0.03	930	#860	0.83	0.36	560
#854	0.66	0.05	730	#766	0.79	0.15	3950
#837	0.68	0.0007	26	#742	0.53	1	0
#758	0.76	0.005	9	#701	0.82	1	0
#751	0.47	0.02	400	#745	0.60	1	0
#702	0.54	1	0	#728	0.43	1	0
#733	0.76	1	0	#794	0.51	0.04	1530
#731	0.66	0.13	9	#734	0.38	1	0
#489	0.47	0.07	1680	#235	0.78	0.26	1260
#491	0.69	0.02	830	#195	0.45	1	0
#717	0.44	0.008	200	#755	0.79	1	0
#747	0.77	1	0				
#706	0.44	0.008	760				

EI1, efficiency index relative to the first portion of the track; EI2, efficiency index relative to the second portion of the track; *d*, distance from the loft at which the track crossed the home latitude.

different at the two distance ranges at which the birds crossed the home latitude (Mann–Whitney *U* test, *P*>0.5).

The FF pigeons' tracks are reported in Fig. 3. These birds were already homeward oriented within 1–2 km from the release site, although some of them did not reach the home area along a straight route, but made a detour along the seashore (Fig. 3A) or more inland (Fig. 3B). However, all of them but two (#794 and #766, see Fig. 3C) stopped at the loft once having reached the home latitude. Pigeon #794 also moved along the coast, but overshot the loft by about 8 km to the south

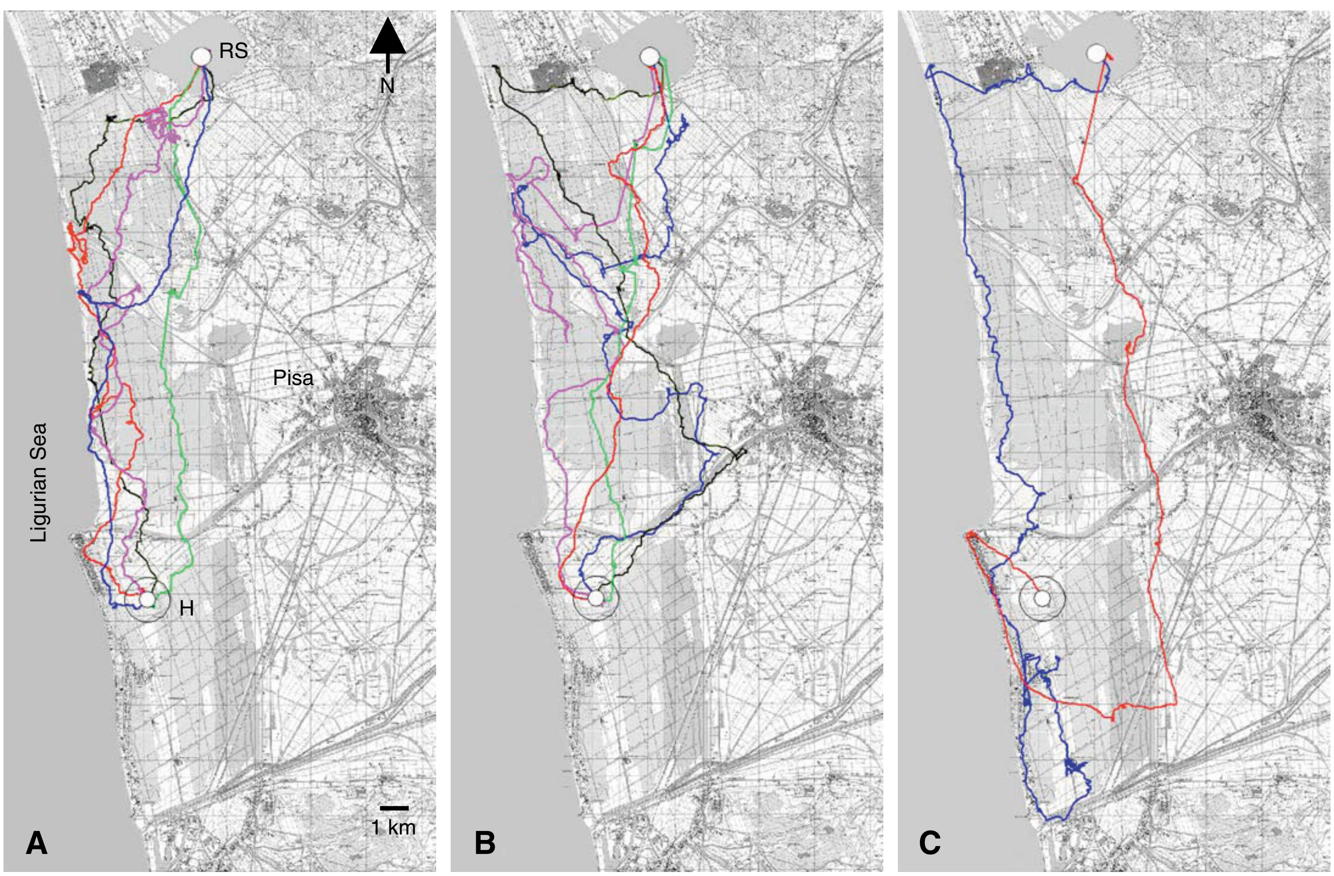

Fig. 3. Tracks of free-flying pigeons. (A) #742 red, #745 black, #195 blue, #235 pink, #867 green; (B) #755 red, #701 black, #734 blue, #728 pink, #860 green; (C) #794 blue, #766 red. H, home; RS, release site.

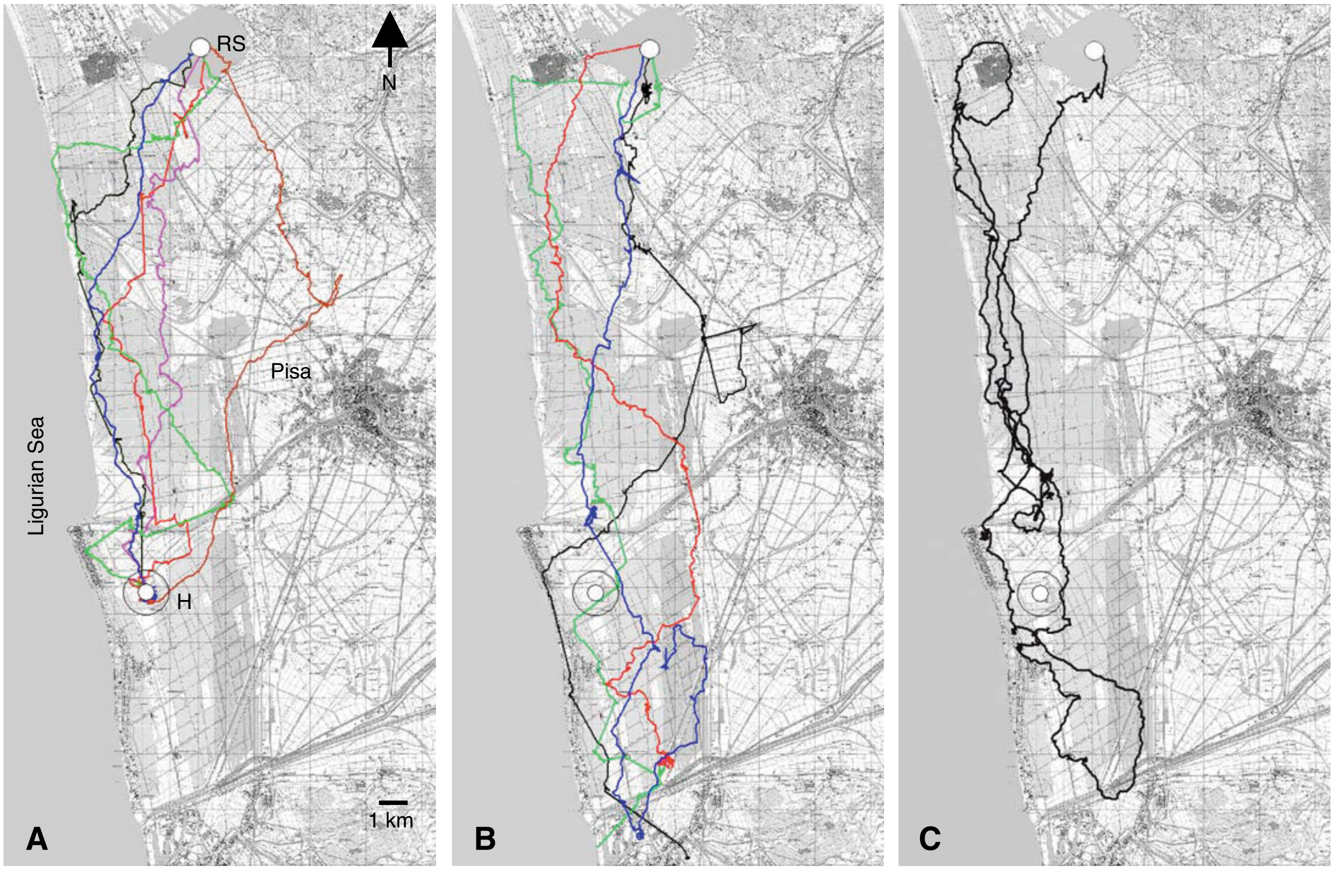

Fig. 4. Tracks of prisoner pigeons. (A) #733 red, #731 black, #758 blue, #747 pink, #702 green, #854 brown; (B) #751 green, #234 blue, #489 black, #165 red; (C) #706. Other explanations as in Fig. 3.

before inverting its route towards home. It is worth noting that this bird, when it approached the home latitude, was flying just over the seashore line at Marina di Pisa and probably could not see its home area behind the thick pine wood, about 25 m high, which extends north–south along the coast. Pigeon #766 was 3.9 km far from home when reaching the home latitude. It is worth noting that this pigeon also flew for a long tract along the edge of a pine wood located east, and this might have impeded sight of the home area. This bird overshot the loft and flew toward south for about 5 km before inverting its route.

Six out of 14 P pigeons stopped in the vicinity of the loft once reaching the home area (Fig. 4A), showing a behaviour similar to the FF. The other eight P pigeons seemed to be unable to recognise the home area and continued their homing flight towards south (Fig. 4B,C and Fig. 5A–C), even passing at a very short distance from the loft.

Eight prisoner pigeons overshot the loft at various distances. In four cases the birds missed the loft by a few hundred metres and in two cases the birds were unable to recognise the loft even when flying over it (see Table 1 and Figs 4 and 5 for details). The other two birds missed the loft flying at a distance greater than 1 km (see Table 1 and Fig. 4B). Three prisoner birds flew in the vicinity of the loft twice without reaching the loft, indicating that they could not recognise the home area (#706, #491, #717, see Fig. 4C and Fig. 5A,C). Pigeon #706 showed the most peculiar route (see Fig. 4C). On its way southwards, it missed the loft by only 660 m, and, after having inverted its flight direction, missed the loft again by 990 m; continuing northwards it reached an area close to the release site (3.7 km from release point). Then it inverted the flight direction again and stopped near the Arno river. The remaining track was not recorded because the GPS battery expired at this point.

The maximum distance recorded southwards was at least 10 km (#489, Fig. 4B); we were not able to determine the distance from the loft at which three birds corrected their orientation because the GPS battery expired (#751, #489, #165 Fig. 4B). Four birds inverted their routes at a distance ranging from 3.3 to 9 km (#706, #491, #837, #717, #234 Fig. 4B,C and Fig. 5A–C).

Discussion

In the present study we tracked for the first time the homing routes of pigeons that had been prevented from previously experiencing an aerial view of the home area, and compared them with those of birds that could perform spontaneous flights around the loft before being released.

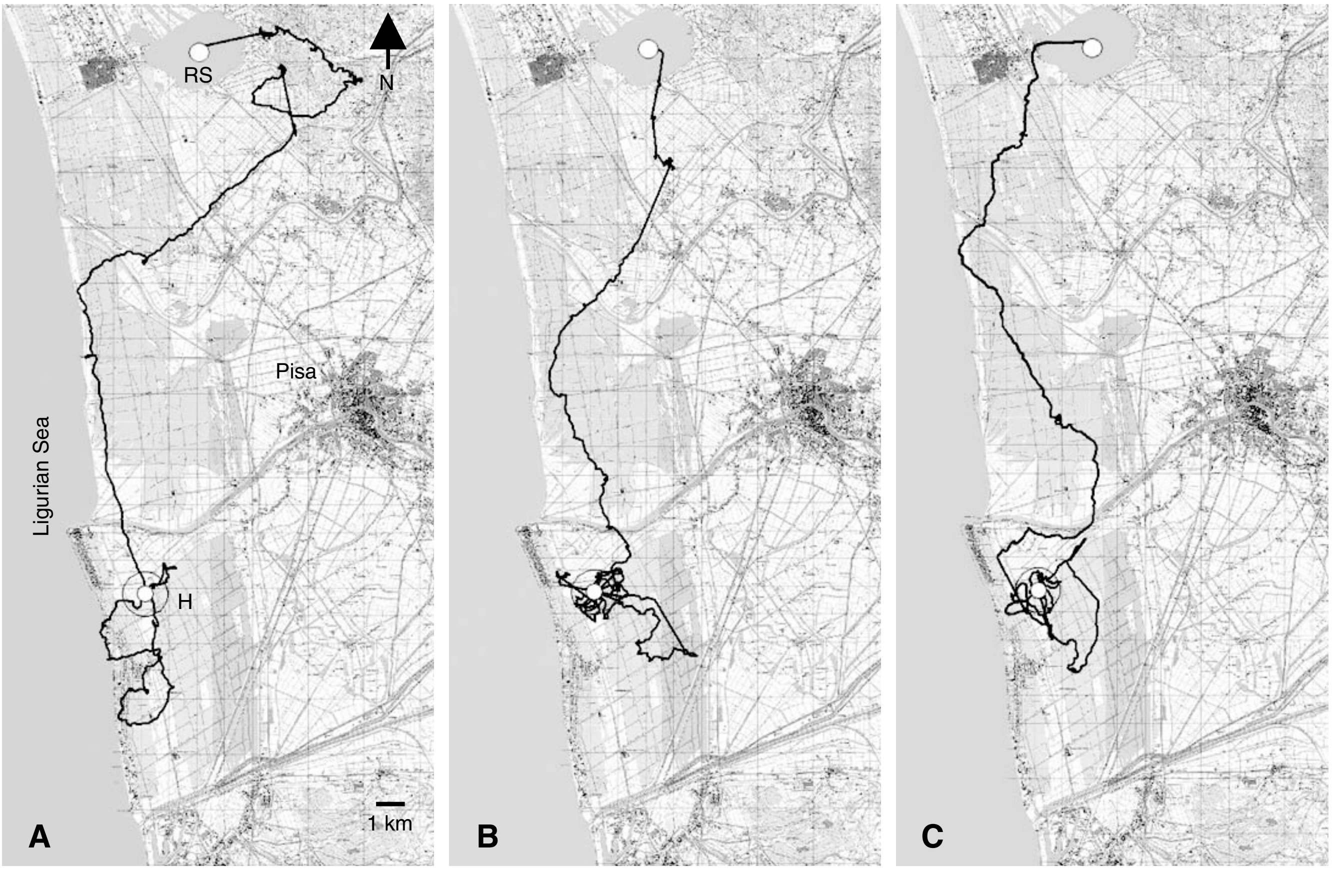

Fig. 5. Tracks of prisoner pigeons. (A) #717; (B) #837; (C) #491. Other explanations as in Fig. 3

Our data confirm previously reported observations that pigeons raised confined in an aviary develop unimpaired navigational abilities (Kramer and von Saint Paul, 1954; Kramer, 1959; Wallraff, 1970a; Wallraff, 1970b; Bingman et al., 1990; Ioalè et al., 2000; Gagliardo et al., 2001a; Gagliardo et al., 2001b; Odetti et al., 2003; Gagliardo et al., 2004). In fact, the prisoner pigeons were homeward oriented soon after being released and their initial orientation performance was similar to that of the free-flying pigeons. Moreover, the prisoner birds' tracks in the first portion of the homing route (from the release site to the home latitude) were very similar to those of the birds with a previous free-flight experience around the loft. Although the prisoner pigeons tended to stop more frequently and for longer, they displayed unimpaired navigational abilities and a motivation to home that was similar to the free-flying pigeons. This is shown by similar efficiency indexes, flight speed and orientation for the two experimental groups in the first portion of their track.

By contrast, the pigeons raised under the two different conditions behaved differently in the vicinity of the home area. In fact, more prisoner pigeons seemed to be unable to perform a straight flight path to the loft having once reached the home latitude than free-flying birds, and continued their journey southward, overshooting Arnino. We interpreted this behaviour as a difficulty in recognising the home area, even when passing very close to it. This is probably because the pigeons raised in confined conditions had not had the possibility of experiencing a full view of the landscape around the loft, in contrast to the free-flying pigeons, which could observe the characteristics of the home area in detail and from different perspectives. This is consistent with laboratory and field studies showing that birds find more difficult to recognise objects and landscapes when seen from unusual viewpoints (Dawkins and Woodington, 2000; Biro et al., 2003). Moreover, the pigeons raised confined might have had difficulties in perceiving spatial relationships among the landmarks in the home area, resulting in a less accurate spatial map (Bingman and Mench, 1990). In principle, there could be information other than visual fully available to the free-flying pigeons compared to the prisoner birds, although this is unlikely because acoustic information (for example infrasound coming from the sea) is equally available for both the prisoner and free-flying birds, and there are no magnetic anomalies that could hypothetically be used as a landmark in the area surrounding Arnino.

Interestingly, the only free-flying pigeons to display a behaviour similar to that of the majority of the prisoner birds were two subjects that reached the home latitude at a distance greater than 1 km. Although the home range might be wider for pigeons housed in other aviaries and having different experience, data on the free-flight range of Arnino pigeons show that their spontaneous flights ranged within an 800 m radius. Although the aerial view of the landscape is certainly wider than this range, it is likely that these pigeons, which at the home latitude were flying along the edge of pine tree woods, were prevented from seeing the familiar topographical cues within the free-flight range. Six prisoner pigeons that crossed the home latitude in the immediate vicinity of the loft headed directly towards it. We cannot exclude the possibility that these pigeons could recognise some landmark features even if they had only observed them from inside the aviary and from a limited perspective, but they may also have been attracted by other pigeons on the roof of the aviaries. However, as shown by the statistical analysis, the ability of the free-flying pigeons to head directly to the loft in the final part of their homing journey seems to be conditioned by their distance from it, while the pigeons raised confined can display difficulties in finding the goal even within the free-flight range.

The pigeons that overflew the home area continued their journey in the same direction (south) for some kilometres and eventually they inverted their route, most likely when the map mechanism gave them the information that home was actually in the opposite direction. Our data are consistent with a model proposed by Wallraff (Wallraff, 1991; Wallraff, 2005b), according to which pigeons use two homing mechanisms, one making use of familiar visual landmarks and the other exploiting atmospheric olfactory cues. The efficiency of either mechanism depends on both the distance from home and the level of familiarity with the area. In our case, no bird that overshot Arnino corrected its route before it had flown 3.3 km from the loft, so the olfactory map would seem to be inefficient within this range.

In conclusion, the final step of the homing process seems to be mediated by visual recognition of the landmarks of the home area rather than by the ‘map mechanism’. The critical role of visual features of the home area in the local navigation step is also consistent with previous track studies (Bingman and Mench, 1990; Holland et al., 2000; Guilford et al., 2004; Lipp et al., 2004).

Our data are consistent with a view of a map mechanism that only gives the pigeons information about the direction of displacement, and does not provide any cue about the distance between the release site and home. In fact, if the pigeons had expected to find home after a certain number of kilometres or after a certain flight time, we would probably have observed some of the birds perform a sort of random search near the loft. Actually, after having overshot the loft, our pigeons continued to fly along a straight line before suddenly inverting their route.

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References

Batschelet, E. (1981). *Circular Statistics in Biology*. London: Academic Press.

Bingman, V. P. and Mench, J. A. (1990). Homing behavior of hippocampus and parahippocampus lesioned pigeons following short-distance releases. *Behav. Brain Res.* **40**, 227-238.

Bingman, V. P., Ioalè, P., Casini, G. and Bagnoli, P. (1990). The avian hippocampus: evidence for a role in the development of the homing pigeon navigational map. *Behav. Neurosci.* **104**, 906-911.

Biro, D., Guilford, T. and Dawkins, M. S. (2003). Mechanisms of visually mediated site recognition by the homing pigeon. *Anim. Behav.* **65**, 115-122.

Dawkins, M. S. and Woodington, A. (2000). Pattern recognition and active vision in chickens. *Nature* **403**, 652-655.

Gagliardo, A., Ioalè, P., Odetti, F. and Bingman, V. P. (2001a). The ontogeny of the homing navigational map: evidence for a sensitive learning period. *Proc. R. Soc. Lond. B Biol. Sci.* **268**, 197-202.

Gagliardo, A., Ioalè, P., Odetti, F., Bingman, V. P., Siegel, J. J. and Vallortigara, G. (2001b). Hippocampus and homing in pigeons: left and right hemispheric differences in navigational map learning. *Eur. J. Neurosci.* **13**, 1617-1624.

Gagliardo, A., Ioalè, P., Odetti, F., Kahn, M. C. and Bingman, V. P. (2004). Hippocampal lesions do not disrupt navigational map retention in homing pigeons under conditions when map acquisition is hippocampal dependent. *Behav. Brain Res.* **153**, 35-42.

Gagliardo, A., Ioalè, P., Savini, M. and Wild, J. M. (2006). Having the nerve to home: trigeminal magnetoreceptor *versus* olfactory mediation of homing in pigeons. *J. Exp. Biol.* **209**, 2888-2892.

Guilford, T., Roberts, S., Biro, D. and Rezek, I. (2004). Positional entropy during pigeon homing II: navigational interpretation of Bayesan latent state models. *J. Theor. Biol.* **227**, 25-38.

Holland, R., Bonadonna, F., Dall'Antonia, L., Benvenuti, S., Burt de Perera, T. and Guilford, T. (2000). Short distance phase shifts revisited: tracking clock-shifted homing pigeons (Rock dove *Columba livia*) close to the loft. *Ibis* **142**, 111-118.

Ioalè, P., Gagliardo, A. and Bingman, V. P. (2000). Hippocampal participation in navigational map learning in young homing pigeons is dependent on training experience. *Eur. J. Neurosci.* **12**, 1-9.

Kramer, G. (1953). Wird die Sonnenhöhe bei der Heimfindeorientierung verwertet? *J. Ornithol.* **94**, 201-219.

Kramer, G. (1959). Recent experiments on bird orientation. *Ibis* **101**, 399-416.

Kramer, G. and von Saint Paul, U. (1954). Das Heimkehrvermögen gekäfigter Brieftauben. *Ornithol. Beobach* **51**, 4-12.

Lipp, H.-P., Vyssotski, A. L., Wolfer, D. P., Renaudineau, S., Savini, M., Tröster, G. and Dell'Omo, G. (2004). Pigeon homing along highways and exits. *Curr. Biol.* **14**, 1239-1249.

Odetti, F., Ioalè, P. and Gagliardo, A. (2003). Development of the navigational map in homing pigeons: effects of flight experience on orientation performance. *Anim. Behav.* **66**, 1093-1099.

Papi, F., Fiore, L., Fiaschi, V. and Benvenuti, S. (1972). Olfaction and homing in pigeons. *Monit. Zool. Ital. N. S.* **6**, 85-95.

Schmidt-Koenig, K. and Walcott, C. (1978). Tracks of pigeons homing with frosted contact lenses. *Anim. Behav.* **26**, 480-486.

Siegel, S. (1956). *Nonparametric Statistics for the Behavioural Sciences.* New York: McGraw-Hill.

Steiner, I., Bürgi, C., Werffeli, S., Dell'Omo, G., Valenti, P., Tröster, G., Wolfer, D. P. and Lipp, H.-P. (2000). A GPS logger and software for analysis of homing in pigeons and small mammals. *Physiol. Behav.* **71**, 589-596.

Wallraff, H. G. (1966). Über die Heimfindeleistungen von Brieftauben nach Haltung in verschiedenartig abgeschirmten Volieren. *Z. Vergl. Physiol.* **52**, 215-259.

Wallraff, H. G. (1970a). Über die Flugrichtungen verfrachteter Brieftauben in Abhängigkeit vom Heimatort und vom Ort der Freilassung. *Z. Tierpsychol.* **27**, 303-351.

Wallraff, H. G. (1970b). Weitere Volierenversuche mit Brieftauben: wahrscheinlicher Einfluss dynamischer Faktoren Atmosphäre auf die Orientierung. *Z. Vergl. Physiol.* **68**, 182-201.

Wallraff, H. G. (1980). Olfaction and homing in pigeons: nerve-section experiments, critique hypotheses. *J. Comp. Physiol.* **139**, 209-224.

Wallraff, H. G. (1991). Conceptual approaches to avian navigation systems. In *Orientation in Birds* (ed. P. Berthold), pp. 128-165. Basel: Birkhaüser.

Wallraff, H. G. (2005a). *Avian Navigation: Pigeon Homing as a Paradigm.* Berlin: Springer Verlag.

Wallraff, H. G. (2005b). Beyond familiar landmarks and integrated routes: goal-oriented navigation by birds. *Connect. Sci.* **17**, 91-106.