RESEARCH ARTICLE

Testing cognitive navigation in unknown territories: homing pigeons choose different targets

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SUMMARY

Homing pigeons (*Columba livia*) are believed to adopt a map-and-compass strategy to find their way home. Surprisingly, to date a clear demonstration of the use of a cognitive map in free-flight experiments is missing. In this study, we investigated whether homing pigeons use a mental map in which – at an unknown release site – their own position, the home loft and a food loft are represented simultaneously. In order to test this, homing pigeons were trained to fly to a 25–30 km distant food loft. A total of 131 hungry and satiated pigeons were then released from an unfamiliar site equidistant from the food loft and the home loft. Their vanishing bearings and homing times were assessed conventionally at four sites, and also their flight tracks from one release site by means of GPS loggers. The vanishing bearings of fed and hungry birds differed significantly at all release sites and a highly significant proportion of hungry birds flew to the food loft, while the fed birds headed home. The GPS experiment revealed a number of pigeons flying very precisely to the food loft, others correcting their flight direction after topography-induced detours. This implies that the pigeons knew their geographical position in relation to the targets, and chose a flight direction according to their locally manipulated needs – clearly the essence of a cognitive navigational map.

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Key words: *Columba livia*, pigeon homing, navigation, cognitive map, GPS tracking, orientation, spatial task.

INTRODUCTION

True large-scale navigation, as observed in migratory birds and pigeons, requires goal-oriented behavior in unknown territories. Until now, the map-and-compass strategy, as formulated by Kramer (Kramer, 1953), has been widely accepted. It proposes a position-determination mechanism as the primary step, after which a compass direction to a target is calculated. The compass direction may be updated by position fixes periodically, thus enabling correction of the flight course and detours. Compass mechanisms used for maintaining a target course include celestial cues (azimuth of the sun, stellar constellations), geophysical cues and visual topographic features. So far, most research has been carried out to clarify the nature of the compass mechanisms (Schmidt-Koenig, 1960; Able, 1994; Muheim et al., 2002; Budzynski et al., 2002; Wiltschko and Wiltschko, 2010). However, the investigation of the map step has remained controversial. Models proposed include olfactory-based position finding (Papi et al., 1973; Wallraff, 2005) and theories invoking bi-coordinate magnetic grids or other geophysical cues (Gould, 1998; Walker et al., 2002).

A less obvious but challenging problem that remains is whether position determination during the map step is cognitive (Bennett, 1996; Cruse and Wehner, 2011). Traditionally, a cognitive map refers to a mental representation of spatial relations of objects (Tolman, 1948). In terms of large-scale navigation, do the birds really 'know' where they are and do they have a set of mental spatial coordinates enabling them to choose different courses? Until now, the use of a navigational map has been investigated in either laboratory settings (Cheng, 1994; Kamil and Cheng, 2001; Blaisdell and Cook, 2005; Gibson et al., 2012) or in the natural environment of familiar areas in pigeon homing (Holland, 2003; Bingman et al., 2005; Gagliardo et al., 2009). Vanishing bearings of pigeons released between a former and a new loft provided some evidence for the use of cognitive navigational mapping in homing pigeons (Baldaccini et al., 1976). In addition, most pigeon breeders have experienced the return of pigeons after long periods of absence (either through losses in races or by sales to colleagues), suggesting that pigeons can memorize different loft positions. However, a systematic and experimental study with pigeons released from completely unknown regions is missing.

Displacement experiments with migratory birds have provided evidence of a large-scale navigational map (Åkesson et al., 2005; Thorup et al., 2007; Chernetsov et al., 2008; Holland et al., 2009), as did tracking studies of bartailed godwits crossing the Pacific along different routes (Gill et al., 2009). However, until now, migratory birds were never manipulated locally in terms of setting different compass directions to elucidate whether they are able to choose between memorized targets. Therefore, displacement studies cannot illustrate the use of a cognitive map. A cognitive map requires a minimum of two concurrently memorized sets of target coordinates, and, at an unknown release site, a computation of the bird's own position in relation to the targets to choose a compass direction. Conceptually, it has not been ruled out that pigeons orient according to a navigational principle using only one mental set of coordinates: the home loft. This would allow the birds to navigate home using simpler strategies, e.g. near-automated navigation following various gradient differences (olfactory, magnetic) until they reach home
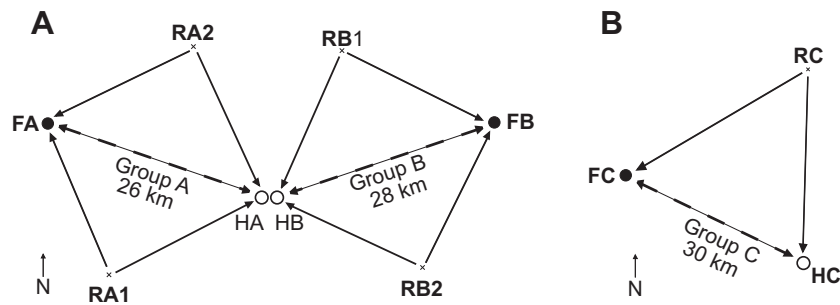
Fig. 1. Scheme of the experimental design of pigeon trainings and releases in the vanishing bearing experiments (A) and in the GPS experiment (B). (A) In Switzerland, group A was trained along the beeline from the food loft FA to the home loft HA whereas group B was trained along the beeline from the food loft FB to the home loft HB, indicated with dashed lines. Release sites for group A are indicated by RA1 (distance to FA 25.5 km, to HA 26 km) and RA2 (distance to FA 21.5 km, to HA 20.5 km) and for group B by RB1 (distance to FB 23 km, to HB 23.5 km) and RB2 (distance to FB 25 km, to HB 28 km). (B) In Italy, group C was trained along the beeline from the food loft FC to the home loft HC. The release site is indicated by RC (distance to FC 31 km, to HC 28 km).

(called 'loftocentric' strategy here). Obviously, such a strategy would not correspond to a cognitive map-and-compass strategy.

To test whether pigeons use a loftocentric or a true cognitive map-and-compass strategy, one faces the problem that displaced pigeons usually have only one imprinted and ecologically relevant target, the home loft. To set two ecologically relevant goals for the pigeons, we trained homing pigeons to obtain food at a distant loft, flying to the food loft and back to their home loft repeatedly, thus the birds developed a stereotyped corridor path along familiar landmarks. A group of hungry birds and a group of satiated birds (fed at the release site) were then released at unfamiliar places equidistant to both the food and the home loft. If the loftocentric strategy applies, the hungry birds would need to fly home first and reach the food loft by following familiar landmarks. In this case, there would be no difference in vanishing bearings and significantly longer flight times for the hungry birds to reach the food loft than for the satiated birds to fly to the home loft. In case of a cognitive map-and-compass navigation, we would expect significant differences of initial bearings and equal flight times to the respective targets. In addition, when tracking pigeons by means of GPS loggers, we would expect the direction of the flight paths to approximate the target direction. In the case of a loftocentric strategy, the GPS tracks of hungry birds should not show reorientation toward the target loft before reaching the familiar loft area.

MATERIALS AND METHODS
Vanishing bearing experiments

Young pigeons (*Columba livia* Gmelin 1789) living in mobile lofts of the Swiss army were transferred from the vicinity of Berne across 150 km to Kirchberg (47°25′N, 9°1′E, 695 m a.s.l.), in eastern Switzerland, where none of the pigeons had been before. There, they were placed again in the same mobile lofts. All of the pigeons were 1 or 2 years old and had moderate experience (10 to 15 releases from up to 50 km) at their previous home site. In September 1990, they were accustomed to the new location at Kirchberg during 4 weeks according to standard procedures of the Swiss army and also to a feeding schedule of 48 h interval to increase feeding motivation. Afterwards, the pigeons were trained in two groups: group A from home loft HA learnt to feed at food loft FA 26 km westwards (47°32′N, 8°44′E, 485 m a.s.l.), while group B from home loft HB had to fly 28 km eastwards to food loft FB (47°28′N, 9°22′E, 595 m a.s.l.) (Fig. 1).

First, the pigeons were transported to their food lofts by car every second day and were allowed to feed in the food loft. After feeding, they were transported back. Meanwhile, the pigeons were trained from increasing distances to return home from sites on the beeline to the food loft. Such stepwise training was required because the birds lived at an unfamiliar site. After successful completion of the whole journey back to the home loft, the pigeons were trained to fly into the food loft. They flew first from the vicinity of the food loft; then, with increasing distances, the pigeons managed to fly from the home loft to the food loft, feed there and then return back home. The experimental release sites were chosen to be equidistant from the home and the food loft in an unfamiliar terrain (22 to 26 km to home or food lofts, Fig. 1). Thus, group A (28 pigeons) was released from site RA1 (Mönchaltdorf, 47°19′N, 8°42′E, 440 m a.s.l.) on a sunny day and with no wind. Two days later, the same group (25 pigeons) was released from a new site RA2 (Müllheim, 47°36′N, 9°0′E, 410 m a.s.l.) on a cloudy day, but with visible sun and a northwesterly wind of approximately 30 km h^{-1}. Group B (28 pigeons) was released from site RB1 (Ellighausen, 47°37′N, 9°8′E, 520 m a.s.l.) on a sunny day, partially clouded, with a moderate west wind (5–10 km h^{-1}). Five days later, group B (27 pigeons) was released again but now from site RB2 (Schwägalp, 47°15′N, 9°18′E, 1270 m a.s.l.) on a cloudy day with the sun barely visible and a cool west wind. For all releases, pigeons were transported early in the morning to the release sites and spent 1 h in crates from which they could see and smell the surroundings. Prior to departure, half of the pigeons were randomly selected and were fed at the release site, while the other half remained hungry. The pigeons were released pairwise, alternating pairs of hungry pigeons with pairs of fed pigeons, at intervals of 5 min. Pairwise releasing was carried out to suppress the tendency of the birds to remain in the vicinity of the release site until the release of a companion. For statistics, each pair of pigeons was considered as one data point. Pigeons were not tossed but were allowed to depart from a start box in which they were placed a few minutes before release. This allowed us to assess the departure motivation of the birds.

In order to control for release site effects on the vanishing bearings, and in particular for the possible effect of repeated training from the same direction (Dell'Ariccia et al., 2009a), we released also control pigeons for each experimental group and on the same days. The control pigeons were not trained in the training directions of the experimental pigeons, and thus were not influenced by the same training effect as the experimental groups. However, the control pigeons were released from the experimental sites twice for training. The control pigeons were neither hungry nor fed and flew only to their home lofts located in the vicinity of the targets of the experimental birds.

The vanishing bearings were determined by two independent observers with 8×30 binoculars, and were averaged and rounded to the next 5 deg. The homing times were recorded from an observer at the home loft. Thus, the mean speed (beeline distance between release site and target/flight time) was calculated as an indicator of homing performance. Homing performance was compared between groups with the Mann–Whitney U-test (Siegel and Castellan, 1956). The distributions of vanishing bearings were tested for uniformity using the Rayleigh test (Batschelet, 1981). The Watson U^2-test was used to show any difference between the groups and the Watson–Williams F-test was used to determine any difference in the mean vanishing bearings. The mean vanishing vector (**r**) was computed with the statistical software Oriana (Kovach Computing Services, Pentraeth, Anglesey, UK). The mean vanishing vector shows the mean direction of the pigeons' vanishing bearings and its length (variable between 0 and 1) is a reciprocal measure of angular dispersion (Batschelet, 1981). In addition, the homeward component of the mean vanishing vectors was calculated. The homeward component is the rectangular projection of the mean vanishing vector onto the axis pointing towards home and shows how homeward orientated the group of pigeons was. The number of pigeons choosing either the food or the home loft as their target was analyzed for significance with Fisher's exact probability test.

GPS experiment

Pigeons were kept in a former Swiss army mobile loft in Testa di Lepre (41°55′N, 12°16′E, 35 m a.s.l.), northwest of Rome. These pigeons will be referred to as group C. The food loft FC, also a Swiss army mobile loft and thus familiar to the pigeons, was placed in Santa Severa (42°2′N, 11°58′E, 43 m a.s.l.), 30 m northwest of the home loft HC. The pigeons were mixed in gender, age and experience (1 to 5 years old, average 2 years old). From the beginning of the training, pigeons were fed only every second day and only in the food loft to increase feeding motivation. Over 6 days, the pigeons were brought by car to the food loft, were fed there and then they flew back home in flock. Afterwards, the pigeons were released in the vicinity of the food loft to let them fly into the food loft, feed there and then fly back home. The pigeons were released with increasing distances from the food loft near the beeline from the food loft to the home loft. One month before the experiment, pigeons were equipped with a PVC imitation of a miniature GPS logger to accustom them to the weight and size of the GPS logger (GiPSy2, Technosmart, Rome, Italy). The PVC dummies were fixated with adhesive tissue (Velcro tape), glued on shortened feathers on the back of the birds. The pigeons carried the dummies throughout the training period. At the end of the training phase, the pigeons were equipped with GPS loggers to record their training flights (see supplementary material Fig. S1).

The release site RC for the experiment (Bracciano, 42°10′N, 12°17′E, 325 m a.s.l.) was in northeasterly direction from the home loft, equidistant to the home loft (28 km) and the food loft (31 km) (Fig. 1). None of the pigeons had been in that area before. On the day of the experiment, in July 2009, 23 pigeons were transported by car early in the morning to the release site. The weather was good, with no clouds and no wind, but with a slight haziness, reducing long-distance visibility. There, the pigeons were kept in crates with visual and olfactory access to the environment for 1 h to adapt to the site and to increase motivation to home (Dell'Ariccia et al., 2009b). Then, half of the pigeons were chosen randomly, put into a separate box and fed *ad libitum*. The other half remained hungry. The pigeons were then released in pairs in separate starting crates, alternating two hungry and two fed pigeons, at 5 min intervals between pairs. Beforehand, the PVC dummies were replaced by GPS loggers recording one position fix every 1 s, with an accuracy of approximately 4 m in 95% of the locations. The data were afterwards downloaded from the device to a computer using GiPSy2 software (Technosmart). All files were then imported into the freeware Wintrack (Wolfer et al., 2001) for analysis.

We concentrated on calculating vanishing parameters at 2 km from the release site, a choice in accordance with previous literature (Wallraff, 2005). The vanishing times and the lengths of the vanishing flight tracks were extracted from the data with Wintrack whereas the mean vanishing vectors were computed with Oriana. In addition, the homeward component (the projection of the mean vanishing vector onto the homeward direction) was calculated and is considered as the target-oriented component for both pigeon groups. Other flight parameters were analyzed to show any difference in the homing behavior of both groups: path efficiency (beeline distance between release site and target/track length, in %), homing efficiency (% of path with homeward component >75%), path linearity (beeline/track length in 32 s steps, in %), actual flight speed (GPS ground speed, in km h⁻¹) and homing performance (beeline distance between release site and target/duration of the flight, in km h⁻¹); the latter was calculated to compare with the homing performance of the pigeons in the Swiss experiment. Path linearity is a measure of straightness of the pigeon's track independent of the home direction; the beeline and the track length between two points, 32 s apart, were calculated for the whole track. These parameters were tested for any difference between the two groups with the Mann–Whitney U-test. The vanishing angles were tested for uniformity using the Rayleigh test and the Watson U^2-test was used to show any difference between the groups. A difference in the mean vanishing vector of the two groups was analyzed with the Watson–Williams F-test. The number of pigeons choosing either the food or the home loft as their target was analyzed for significance with the Fisher's exact probability test. On a different day, a control group of pigeons (neither hungry nor fed) was released at the same site to fly home to the same home loft, but no control release was conducted as a comparison to the behavior of the hungry pigeons flying to the food loft because there was no pigeon loft there. Again, each pair was counted as one data point for all statistical analyses.

RESULTS

In all experiments, hungry pigeons chose significantly the feeding site as their flight target whereas fed pigeons chose significantly the home loft as their flight target (Fisher's exact probability test, combining numbers of all releases, $P<0.001$; for each release, $P<0.05$). Overall, 65 out of 69 released hungry pigeons arrived at the food loft and only one at the home loft. And 47 out of 62 released fed pigeons arrived at the home loft and three at the food loft. Only three hungry and 12 fed pigeons were lost.

Vanishing bearing experiments

A summary of all vanishing parameters and homing performances of pigeons that participated in the four releases in Switzerland is shown in Table 1. The vanishing bearings of the hungry and fed pigeons in each release were significantly different (Fig. 2). Six out of eight released groups of experimental pigeons showed also a significant orientation (Rayleigh test, parameter **r**; Table 1). One exception was the release at site RA1 (Mönchaltdorf), where the fed pigeons showed a poor homing success (eight out of 14 were lost) and a scattered initial orientation due to one pair that headed in a direction away from the home loft for unknown reasons and

Table 1. Vanishing bearing parameters and homing performance of all releases in Switzerland

Group	Release site	N	Target loft	n	Lost pigeons	δ (deg)	s	α (deg)	r	Homeward component	t	Homing performance (km h^{-1})
A	RA1	14 f	Home	5 f	8 f	64	7	116	0.60$^{n.s.}$	0.37	4	33
		14 h	Food	13 h	0 h	5	7	347	0.90***	0.81	9	29$^{n.s.}$
	RA2	13 f	Home	12 f	1 f	177	7	128	0.99***	0.65	9	50
		12 h	Food	10 h	2 h	253	6	297	0.56$^{n.s.}$	0.40	7	33$^{n.s.}$
B	RB1	12 f	Home	9 f	3 f	202	6	183	0.69*	0.65	7	30
		16 h	Food	16 h	0 h	132	8	109	0.98**	0.91	10	45*
	RB2	11 f	Home	9 f	0 f	318	7	279	0.96***	0.74	5	49
		16 h	Food	15 h	1 h	12	9	344	0.89***	0.77	9	43$^{n.s.}$

N, numbers of fed (f) and hungry (h) pigeons before release; n, number of either fed or hungry pigeons that arrived at the target loft; δ, direction to the target clockwise from north; s, sample size (pigeons) used for vanishing bearing analysis; α, mean vanishing bearing of the respective fed or hungry sub-group; r, mean vanishing vector; t, sample size (arrived pigeons) used for the homing performance analysis. If t is larger than s, pairs of pigeons separated during the flight. The asterisks refer to the significance levels (*P<0.05, **P<0.01, ***P<0.001, n.s. not significant) of the Rayleigh test (r column) and the Mann–Whitney U-test (homing performance column). These levels are depicted in the homing performance column in the second line to show the difference between the fed and the hungry pigeons at a given release site.

three pairs that headed for the training direction, thus impairing the directionality scores. The control birds supposed to fly to the same target showed largely similar bearings but without outliers (see supplementary material Fig. S2). Northeast of the release site is a mountain chain (1000–1200 m a.s.l.) lying between the release site and the target, the mountain slope starting only a few kilometers away from the release site. Another exception was the release at site RA2 (Müllheim), where the vanishing bearings of the hungry pigeons were not significantly different from random, which was mainly caused by one pair flying in the opposite direction. Also four control pairs of pigeons scattered in the opposite direction. The hungry pigeons were also deviating from the direction to the food loft aligning to the training direction but the control pigeons showed a similar pattern. At the same site, the fed pigeons choose a direction that coincided with the training direction, while the control birds were better oriented homewards.

Homing performance is an indicator of how fast a pigeon flew to its target. Hungry pigeons did not significantly differ in their homing performance in comparison with fed pigeons in all releases, with an exception of group B at release site RB1. There, the hungry

pigeons flew significantly faster to the food loft (45 km h^{-1}) than the fed pigeons flew to the home loft (30 km h^{-1}). Overall, the average flight speeds are low and indicate that some pigeons took a rest during the journey.

GPS experiment

The mean vanishing bearings of hungry and fed pigeons were significantly different (Fig. 3). For each group, the distribution of vanishing bearings at 2 km was significantly different from random (Fig. 3A, parameter r). Hungry pigeons' initial orientations can be divided into two groups: one group of hungry pigeons (two pairs and one single bird) chose the direction toward the food loft. The other group of hungry pigeons (three pairs) first flew south. The majority of the fed birds flew in direction of the home loft. Control pigeons (of the fed pigeons), released on a later day, were all heading south (see supplementary material Fig. S2).

Fig. 4 shows all GPS tracks, which confirms that all pigeons flew directly to their assigned target, albeit using different routes. These were inspected in detail on Google Earth maps, providing both flight paths and altitude profiles of the landscape.
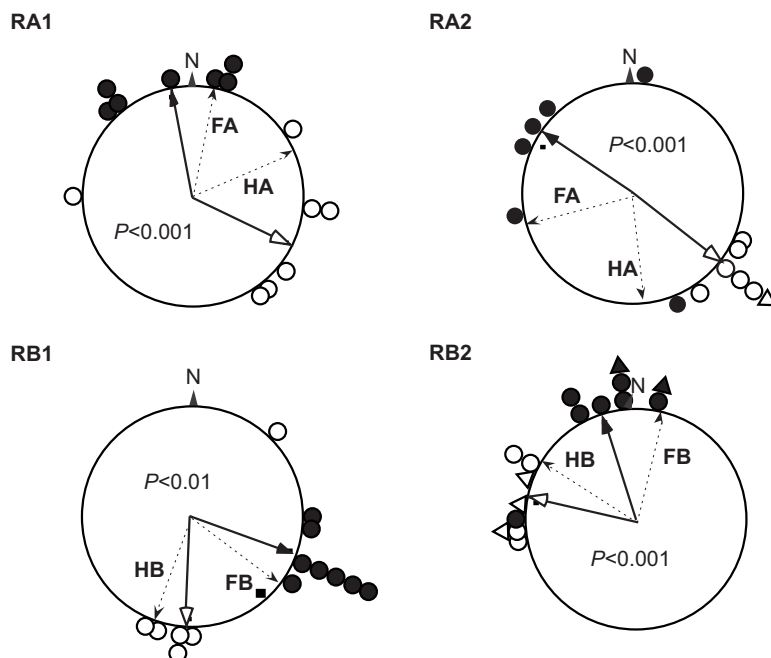

Fig. 2. Vanishing bearing experiments. The black symbols refer to hungry pigeons whereas the white symbols refer to fed pigeons. Circles represent pairs of pigeons, triangles single pigeons. The bold arrows show the mean vanishing bearings of the hungry pigeons with a black arrowhead and of the fed pigeons with a white arrowhead. The dashed arrows show the home loft direction (HA, HB) and the food loft direction (FA, FB). All values are summarized in Table 1. The difference between the hungry and the fed pigeons for each release was calculated with the Watson–Williams F-test for significance (see P-values within the circles). RA1, release site Mönchaltdorf, with 14 pigeons in each group; RA2, release site Müllheim, with 13 fed and 12 hungry pigeons; RB1, release site Ellighausen, with 12 fed and 16 hungry pigeons; RB2, release site Schwägalp, with 11 fed and 16 hungry pigeons.
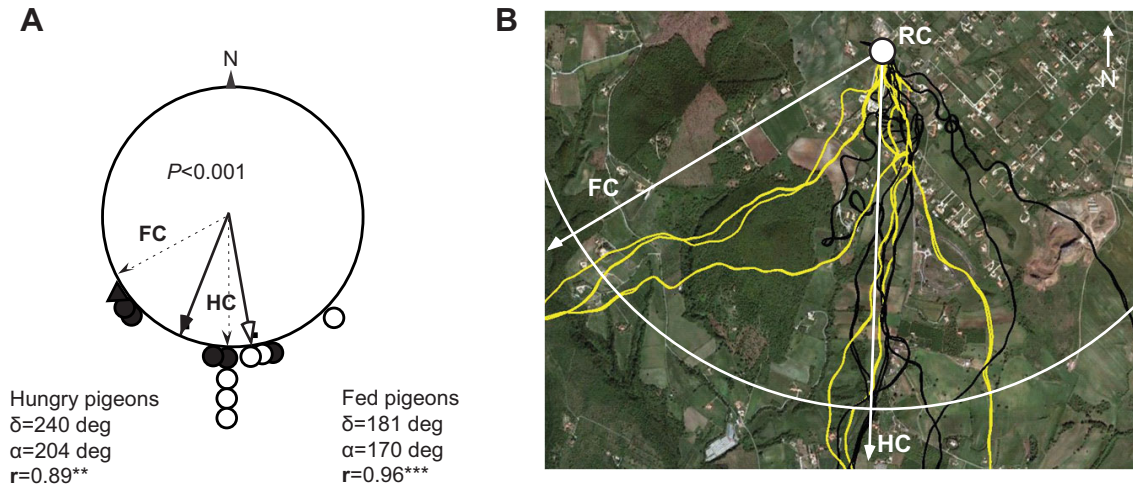
A

B

Fig. 3. (A) Vanishing bearings of the pigeons in the GPS experiment. The black symbols refer to hungry pigeons (*N*=11) whereas the white symbols refer to fed pigeons (*N*=12). Circles represent pairs of pigeons, triangles single pigeons. The bold arrows show the mean vanishing bearings of the hungry pigeons with a black arrowhead and of the fed pigeons with a white arrowhead. The dashed arrows show the home loft direction (HC) and the food loft direction (FC). δ is the loft direction, α is the mean vanishing bearing and **r** is the mean vanishing vector with significance values (***P<0.01, ***P*<0.001) of the Rayleigh test. The difference between hungry and fed pigeons was calculated with the Watson–Williams *F*-test for significance (see *P*-value within the circle). (B) Initial GPS flight tracks from RC. The tracks of the hungry pigeons are in yellow and the tracks of the fed pigeons are in black. The white arrows show the directions from the release site (RC) to the home loft (HC) and to the food loft (FC). The diameter of the circle is 2 km.

The first group of hungry pigeons that was initially directed toward the food loft first deviated from the beeline by following the shore of Lake Bracciano and then maintained their bearing (azimuth 230–245 deg) until they all reached the mountainous region (450 m a.s.l.), preventing them from seeing the coast (20 m a.s.l.). Once there, they slightly adjusted their course, following valleys down to the coastal area and heading toward the familiar training corridor, following it to the food loft. One hungry pigeon first flew south but then circumvented Lake Bracciano north and northwest to the town Bracciano, where it flew in a circle and then took a new direction (232 deg) for approximately 5 km. At this point it faced forested hills, took a turn south and descended 150 m along a canyon to the village of Cerveteri, from where it gradually turned to the familiar flight corridor.

The second group of hungry pigeons flew initially southward, but all changed their bearing after passing Lake Bracciano (8–10 km from the release site). One pigeon started to change its course early at the mid-eastern border of Lake Bracciano and then headed toward the western hills at 242 deg, almost in parallel to the beeline from the release site to the food loft. One pair flew a longer distance southward but changed their course then more abruptly, heading 214 deg to the hills. One pair of pigeons started to change course gradually when they passed the small lake of Martignano (2 km east of Lake Bracciano), flying a long arc until they adjusted to an azimuth of 243 deg, again almost parallel to the beeline from the release site to the food loft.

All hungry pigeons aligned their flight direction at some stage roughly parallel to the original food loft direction from the release site (240 deg). On average, the deviation from the beeline from the release site to the food loft was 6 deg (±6 deg s.d., mean=236 deg, 95% confidence interval=230–242 deg). An unspecific heading towards the sea would be the bearing of 216 deg (perpendicular to the coastline) and this bearing is outside the confidence interval range of the observed one. Most of the birds maintained the food loft direction until they hit the second topographical obstacle, the mountainous region stretching parallel

to the shoreline. After crossing or flying valleys downhill to the west, most pigeons descended to the coastal plane and followed the familiar highway A12 to the food loft. Highways have been shown to act as guiding cues in pigeon homing (Lipp et al., 2004). After feeding at the food loft, all pigeons flew back to the home loft.

The fed pigeons all flew directly south along the beeline to the home loft. Most of them reached the entrance of a valley 8 km north
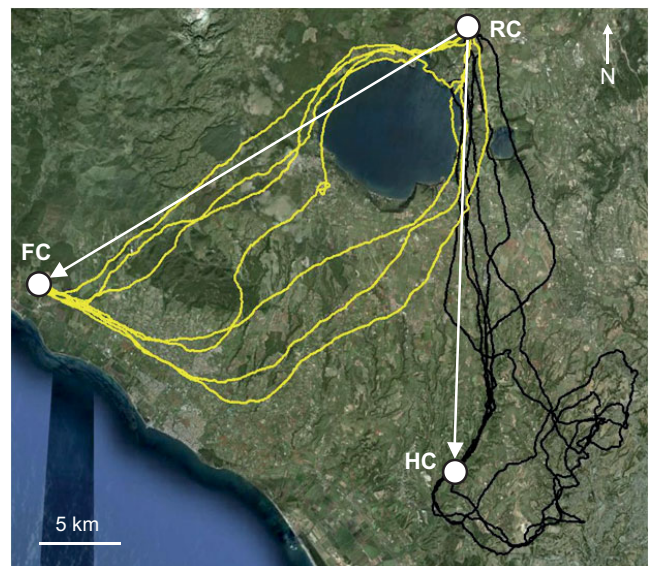

Fig. 4. Flight tracks of all hungry and fed pigeons in the GPS experiment. The yellow tracks show four hungry pairs and three single pigeons. The black tracks show six fed pairs. RC is the release site, FC the food loft and HC the home loft. The large lake is Lake Bracciano, the small easterly lake is Lake Martignano. The distance from the release site to the food loft and home loft is 31 and 28 km, respectively. The direction from RC to FC is 240 deg, from RC to HC 181 deg.

of the loft that led them straight home. One pair of pigeons deviated at the release site in an easterly direction and maintained that course for 20 km until they abruptly corrected their course to the west, where they entered a valley leading them home. Only two pairs of pigeons missed the valley and flew to the east, spending some time exploring the outskirts of Rome. They did return but from the other end of the home valley.

A quantitative analysis of the flight parameters assessed by GPS tracking is provided in Table 2. There was no significant difference between any flight parameter calculated (Mann–Whitney U-test): vanishing time, vanishing track length, homing efficiency, path efficiency, path linearity or mean GPS speed.

DISCUSSION

Our data show that homing pigeons have knowledge of two memorized places in relation to their own position in an unknown area, and that they make a decision where to fly to according to their motivation. In all releases, hungry pigeons departed in significantly different directions from the fed ones, and their flight times were not longer, indicating a direct flight to the target and did not need to fly home first. The GPS experiment showed that approximately half of the hungry birds flew straightforwardly to the food loft, while the other half first flew south and then corrected their bearings in alignment with the initial compass direction to the food loft. The fed pigeons flew directly home. Firstly, these findings strongly support the hypothesis that the pigeons orient according to a map-and-compass strategy, and secondly, they imply that their navigational map is cognitive – they are able to memorize different target locations concurrently.

Vanishing bearings, homing times and GPS flight paths

We predicted that hungry pigeons would choose a different course from fed pigeons if they were able to memorize simultaneously two different target coordinates and choose between them on-site and show similar homing times. Alternatively, in the case of a navigational map consisting of one set of target coordinates only (loftocentric strategy), they should orient homeward first until reaching a familiar terrain and then change the flight path towards the food loft, and thus ought to show prolonged flight times to the target.

Precise vanishing bearings are difficult to predict because the choice of an actual flight direction is subject to release site, training and home-related peculiarities. Repeated training along a defined compass direction is known to have a significant impact on initial orientation from maritime release sites (Dell'Ariccia et al., 2009a). A good example for a training effect on the initial orientation can be seen at the release site RA2, where the mean vanishing bearing of the hungry birds was 297 deg (training direction 303 deg) and for the fed pigeons 128 deg (training direction 123 deg). However, pigeon groups B and C did not show a training bias in their vanishing bearings. Thus, training effects were not consistent in all groups of pigeons. The topography at a release site might also influence the vanishing bearings, e.g. a mountain chain (1000 m a.s.l.) lying between site RA1 and both lofts might have led to scattered initial orientation of the fed pigeons, causing losses. Release site specificities seem to be consistent when reviewing the mean vanishing bearings of all experimental and control releases: the deviations are all in the same direction despite the differences in training experience and loft origins. These observations can be explained either by a slight navigational error in the position-finding step caused by local factors or by topographical features that deflect the initial flight patterns.

Table 2. GPS vanishing and homing parameters of the release in Italy for group C pigeons

	Fed	Hungry
N	12	11
Expected target loft	Home	Food
n	12	11
s	6	6
Homeward component	0.94	0.72
Vanishing time (min)	2.6	2.1[n.s.]
Vanishing track length (km)	2.6	2.3[n.s.]
t	6	7
Homing performance (km h^{-1})	50	54[n.s.]
Path efficiency (%)	73.8	76.7[n.s.]
Homing efficiency (%)	75.6	67.4[n.s.]
Path linearity (%)	94.9	96.2[n.s.]
Speed (km h^{-1})	68	71[n.s.]

Group C pigeons were released from site RC. N, number of fed and hungry pigeons before release; n, number of fed or hungry pigeons that arrived at the target loft; s, sample size (pigeons) used for vanishing bearing analysis. The vanishing track length is the distance until the bird was 2 km from the release site. t, sample size (pigeons) used for homing analysis. If t is larger than s, pairs of pigeons separated during flight. Speed is the actual speed recorded by the GPS device. There were no significant differences within the group (Mann–Whitney U-test; n.s., not significant).

Homing performance did not differ significantly between hungry and fed pigeons, indicating that the hungry pigeons could not have adopted a homing strategy leading them close to the home loft before reaching the familiar training corridor, as expected if using a loftocentric map. In one release (RB1), the hungry pigeons even homed significantly faster than the fed pigeons and had also the best homeward orientation (0.91) of all releases. Nonetheless, two hungry and two fed groups showed relatively slow average homing performance (29–33 km h^{-1}), which indicates that the homing flight must have been interrupted at times. Taking rests during homing is observed when pigeons are exhausted, insecure or inexperienced.

The results from the GPS experiment not only confirmed the findings of the traditional vanishing bearing observations, but also added valuable information for interpretation of the orientation of pigeons during flight. However, flight tracks are rarely coincident with the beeline to the target, because they reflect a compromise between an initially chosen compass direction and a variety of topographic factors and individual flight strategies. In fact, the initial and maintained compass setting of one group of hungry pigeons, passing Lake Bracciano northerly, represents a rare example of directionality and path straightness, especially after repeated directional training between food and home loft.

An example of an unexpected vanishing behavior is the second group of hungry pigeons (circumventing the lake to the east): they initially followed a route coincident with the beeline to the home loft. There are three possible reasons for the vanishing behavior: (1) choosing a direction towards the home loft, that is, a non-cognitive loftocentric strategy, (2) following fed pigeons flying south towards home, and (3) avoiding Lake Bracciano (note that birds do not need to approach the lake very closely to change direction).

A loftocentric strategy and thus an initial choice of a flight direction towards the home loft is most unlikely because all hungry pigeons had corrected their course already by the time they reached Lake Bracciano or soon afterwards, and then maintained a direction largely coinciding with the initial direction to the food loft. Firstly, and most importantly, the first course corrections occurred 20 km before the home loft, thus far outside of the familiar loft region.

Secondly, after correcting their initial flight bearing, all pigeons aligned their flight direction to the initial food loft direction, which indicates that the pigeons did not head just for the sea (which they could have seen on the horizon). Thirdly, this alignment of the middle part of the flight tracks happened while the pigeons were still in unfamiliar terrain with no distant cues because the pigeons faced a mountain region obstructing the view to the coastal plane (with familiar beacons such as villages and highway A12).

Following fed pigeons flying in the home loft direction is also not very likely because the GPS tracks reveal that the fed pigeons did not pause, indicating a steady and fast flight which hungry pigeons, after 5 min delay, possibly could not track.

Lake Bracciano was obviously a dominant obstacle because all pigeons circumvented it. Avoidance of lakes and other topographic barriers is a well-documented phenomenon (Wagner, 1972; Bonadonna et al., 1997; Dell'Ariccia et al., 2009a). One typical example is a hungry pigeon that was flying south along the border of the lake and changed its course at the shore of the lake, heading towards the food loft until it reached the mountain area.

Despite the different initial orientation of the two groups of hungry pigeons, we do not believe that there are birds that do have a two-target mental map and birds that lack the ability to memorize different goals. Rather, it appears that both hungry groups tried to follow a pre-calculated direction to the food loft. An intriguing question remains: why did the hungry pigeons that avoided obstacles readjust their flight direction not directly towards the food loft but in parallel with the initial beeline from the release site to the food loft? It is possible that flying birds do not update their local position continually but at longer intervals.

The behavior of the fed pigeons was more uniform: all of them departed towards the home loft and corrected their courses 20 km after the release site towards a valley that led them home. The home loft and its surroundings are not perceivable from greater distances because the loft lies within a valley. As observed in an earlier study in this region, pigeons usually fly within a valley and not across (Lipp et al., 2004), which bears a risk of following a 'wrongly' directed valley. The two pairs of pigeons flying easterly might have missed the 'right' valley, and were flying for some time in the outskirts of the city of Rome before returning from a familiar angle into the home valley. Larger cities appear to attract pigeons temporarily in many regions, possibly by the presence of pigeon flocks.

Finally, we would like to emphasize that the results of the vanishing bearing and GPS experiments confirmed the predictions of a cognitive navigational map better than expected.

The GPS-tracked pigeons used a map-and-compass strategy as indicated by direct flight paths with recognizable course corrections. This is of considerable importance for future tracking studies assessing the sensing of geophysical or olfactory cues to establish a homing strategy.

The mental map problem

The term navigational map is subject to some confusion depending on the field of investigation. In the field of bird migration, the presence of a large-scale navigational map is often inferred by displacement studies of migrants to a point outside their traditional routes from where they correct their course towards the migratory goal (Perdeck, 1958; Thorup et al., 2007; Chernetsov et al., 2008; Holland et al., 2009), or by tracking migratory routes following very different courses (Gill et al., 2009) (for bar-tailed godwits, see http://alaska.usgs.gov/science/biology/shorebirds/barg_photos.php). It appears conceivable that migratory birds memorize both target

and home coordinates, but a displacement experiment cannot prove this because it represents a case of single-target navigation. Migratory birds may have a seasonally dependent set of coordinates, e.g. an internal clock sets the migration program and its target (Berthold, 1996). Unlike migrating birds, albatrosses do not rely on a specific compass bearing home because they forage over thousands of kilometers across the ocean (Bonadonna et al., 2005; Weimerskirch et al., 2002). However, when they home, they still have only one recognizable target for navigation, the breeding site. They may memorize other coordinates, but it cannot be ruled out that their mental map is based on their actual position and distance to the breeding site. Conceptually, single-target maps may include different levels of navigational complexity. The simplest case is that a bird just senses the difference of intersecting gradients (e.g. olfactory, magnetic) and tries to reduce the difference to home, by meandering flight paths, to the levels to which it has been imprinted until it reaches the familiar target region (Wallraff, 2005). In this case, the bird may have no mental map at all, and could return by a largely non-cognitive robot-like procedure. But the directedness of our pigeons' flight paths in the GPS study argues against this homing strategy.

A cognitive navigational map, however, includes a higher level of complexity, particularly so if it involves a position determination at an unknown place. In addition, cognition involves the ability to make choices between targets according to motivation. These conditions, however, cannot be met if the navigational map of the birds contains only one set of goal coordinates. For migratory birds, this means that the displaced birds would need to be manipulated locally to induce a choice between the breeding and the wintering region, entailing bidirectional orientation according to manipulation. Likewise, albatrosses would need to be familiarized with a second target for choosing a course according to motivation. In principle, our approach of establishing a food and a home site emulates, on a smaller scale, the situation of seasonally shuttling migrants, and allowed us to investigate whether the pigeons were holding concurrently different sets of coordinates among which they could select a flight direction.

According to Bennett (Bennett, 1996), at least three requirements must be met in order to show whether animals use a cognitive map: a short-cut must lead across unfamiliar territory, familiar landmarks are not seen, and path integration is not being used. The first requirement of Bennett is clearly fulfilled by our results: from an unfamiliar location, hungry pigeons flew either directly to the food loft across unknown territories or they corrected topographically induced deviations towards the target sites in early segments of the flight. To satisfy the criterion of non-familiarity, the Swiss pigeons had even been moved for 150 km into a test region they had never experienced before. For the Italian birds, a familiar panoramic framework could have been the sea, but the birds had never been anywhere close to the release region before. Also, homing pigeons rarely forage and explore their neighborhood; they usually fly on a direct route home and stay in the vicinity of the loft with a radius of 800 m (Gagliardo et al., 2007), which minimizes the possibility that the pigeons were familiar with areas other than home. At our Italian loft, the familiar home range was larger but did not exceed 4 km, and the pigeons were always trained northwest of the home loft. The training flights were also recorded with GPS (see supplementary material Fig. S1) and they were always confined to a narrow training corridor, far from the release area.

The second requirement, lack of familiar landmarks guiding the pigeons in their initial choice, was clearly met, too. In Switzerland,

new home lofts were established in pre-alpine forested hills without a clear topographic beacon. The food lofts were located in topographically variegated regions with agriculture, human settlements, hills and forests. Likewise, the release sites were situated at the same altitude as the lofts but behind mountainous regions that prevented an outlook. Only release site RB2 was at a higher altitude, but was also within a mountainous region with steep and meandering valleys with a limited vista. In Italy, the GPS tracks showed that the pigeons could indeed recognize a familiar flight corridor, because they changed direction immediately after or shortly before hitting it. However, for topographic reasons explained before, there was no opportunity to see that corridor from the distant sites where the hungry birds corrected their flight paths. Also, the home loft lies within a valley and any possible beacons are not perceivable outside the valley. Thus, visual beacons cannot explain the pigeons' initial choice and course corrections, and can account only for the last part of the flights.

The third criterion of Bennett, lack of path integration, is also confirmed, although it generally plays a lesser role in pigeon homing. Path integration is a common strategy in animal homing that relies solely on the information gathered during the outward journey (Mittelstaedt and Mittelstaedt, 1980), but homing pigeons do not appear to rely on this strategy (Wallraff, 2001). The outward journey can have some influence on the flight track of pigeons (Wiltschko and Wiltschko, 1978; Gagliardo et al., 2009). Possibly, information collected en route might have induced a small bias in initial headings of both the fed and some hungry birds towards the home loft, because the transport route followed largely the beeline from the home loft to the release site. But without any input collected during the drive, pigeons are still able to home (Wallraff, 1980). Also, path integration generally requires active movement during the outward journey (Wehner, 1992), which does not occur when pigeons are passively transported by car.

The results of the GPS experiment are in line with a recent study on fruit bats (Tsoar et al., 2011). Fruit bats were transferred to an unknown region 44 km from their cave. Some bats flew first to a familiar fruit tree and some flew home, thus also heading to different target locations from an unfamiliar terrain. In addition, recent research on spatial tasks with pigeons in a laboratory setting showed that pigeons have a sense of distance (Gibson et al., 2012) requiring cognitive spatial encoding.

Our study provides solid support for the cognitive map hypothesis, showing consistent results under various environmental conditions and with a large number of pigeons. We conducted experiments with pigeons of different age and experience, in different geographical regions, from different release sites, and with pigeons being reared in different home lofts. It is well known that regional factors may influence the employed navigational strategy (Wiltschko et al., 1987a; Ganzhorn, 1992; Walcott, 1996), while another report shows that pigeons from different lofts may differ in vanishing bearings even when the home direction is the same (Wallraff, 1970). Finally, differences in early experiences can also influence the factors used for navigation (Wiltschko et al., 1987b).

In conclusion, our data indicate that pigeons have the ability to memorize different target locations, and to establish a spatial relationship between themselves and their position in an unknown territory, the essence of a cognitive navigational map. Possibly, with age and homing experience, the birds build up a mental map containing an increasing number of memorized positions facilitating efficient homing. Clearly, further studies are needed to test this hypothesis and to explore the sensory basis of this large-scale navigational map.

LIST OF ABBREVIATIONS

FA	food loft of group A
FB	food loft of group B
FC	food loft of group C
HA	home loft of group A
HB	home loft of group B
HC	home loft of group C
n	number of pigeons arrived at target
N	number of pigeons released
$\mathbf{r}$	mean vanishing vector
RA	release site of group A
RB	release site of group B
RC	release site of group C
α	mean vanishing bearing
δ	direction to the target

AUTHOR CONTRIBUTIONS

H.-P.L. conceived and designed the experiments; N.B., G.D.A. and G.D.O. performed the experiments; N.B. and D.P.W. analyzed the data; N.B. and H.-P.L. wrote the manuscript; and G.D.A. and G.D.O. revised the manuscript (agreed and approved by all authors).

COMPETING INTERESTS

No competing interests declared.

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Fig. S1. Flight tracks of 11 pigeons flying in the training corridor. FC refers to the food loft and HC to the home loft. The red symbol is the training release site. The pigeons were released from the training site, then they flew first to the food loft and after resting there for one to two hours they were released to fly back home.
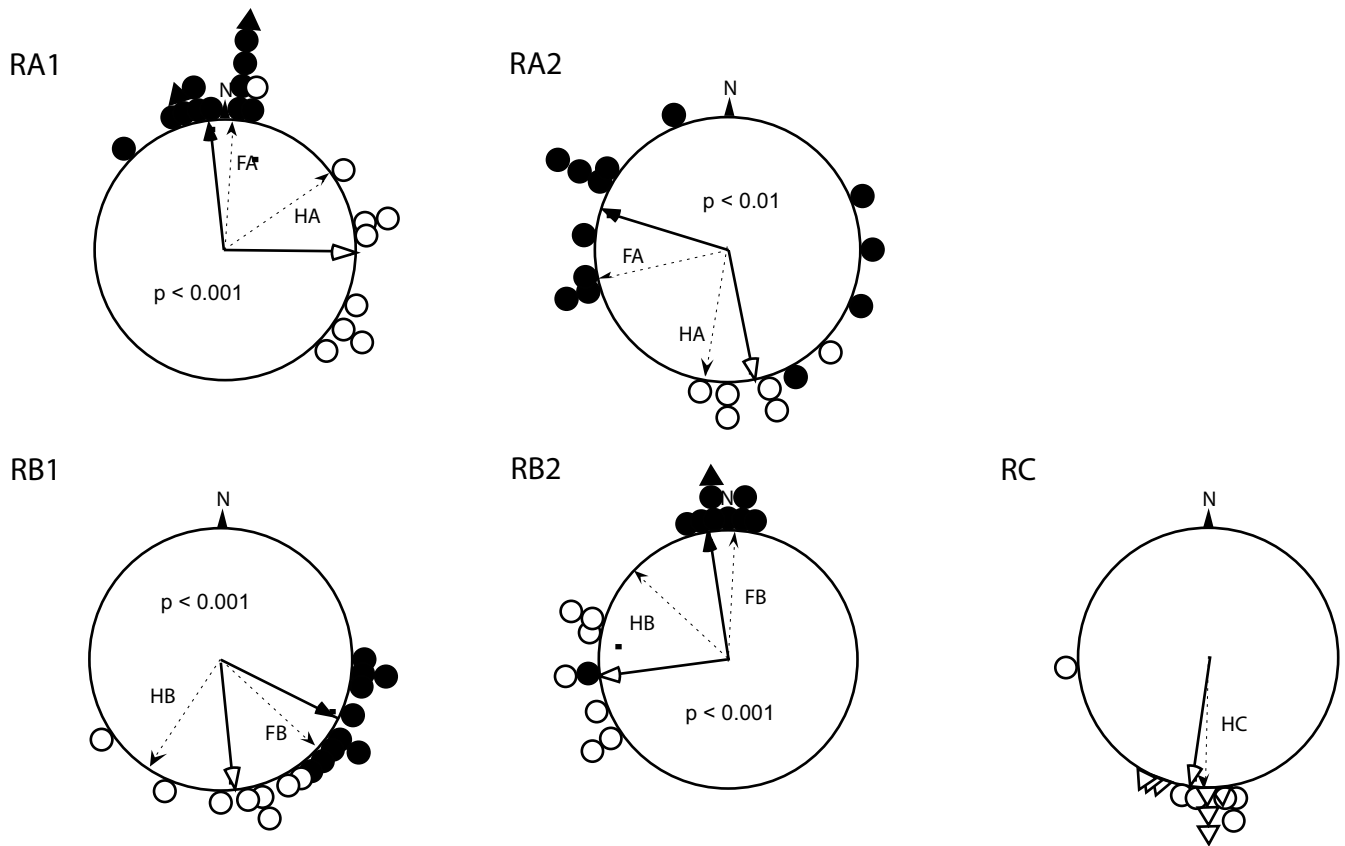
Fig. S2. The vanishing bearings of control pigeons in all releases. The control pigeons flew always to their home loft. For simplification, the direction to the lofts are depicted as HA, HB or HC when comparing with the direction of the fed pigeons (home direction) in the experimental releases and with FA, FB or FC when comparing with the direction of the hungry pigeons (food loft direction) in the experimental releases. The black symbols depict pigeons that flew to their home loft which corresponds to the direction of the food loft in the experimental releases, the white symbols depict the pigeons that flew to their home loft which corresponds to the direction of the home loft in the experimental releases. Circles represent pairs of pigeons, triangles single pigeons. The bold arrows show the mean vanishing bearings of the 'hungry' pigeons with a black arrowhead and of the 'fed' pigeons with a white arrow head, the dashed arrows show the home loft directions. RA1, release site Mönchaltdorf with 18 'fed' and 24 'hungry' pigeons. RA2, release site Müllheim, with 12 'fed' and 26 'hungry' pigeons. RB1, release site Ellighausen, with 16 'fed' and 20 'hungry' pigeons. RB2, release site Schwägalp, with 14 'fed' and 19 'hungry' pigeons. RC, release site Bracciano, with 19 pigeons flying to the home loft but no data of pigeons flying to the food loft direction. The difference between the pigeons following either direction for each release was calculated with the Watson–Williams F-test for significance (see P-values within the circles).