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RESEARCH ARTICLE

Following the sun: a mathematical analysis of the tracks of clock-shifted homing pigeons

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ABSTRACT

We analysed the tracks of clock-shifted pigeons from six releases to determine how they cope with the conflict between their sun compass and other navigational cues. Time-lag embedding was used to calculate the short-term correlation dimension, a parameter that reflects the complexity of the navigational system, and with it, the number of factors involved. Initially, while pigeons were still at the release site, the short-term correlation dimension was low; it increased as the birds left the site, indicating that the birds were now actively navigating. Clock-shifted pigeons showed more scatter than the control birds, and their short-term correlation dimension became significantly smaller than that of the controls, remaining lower until the experimental birds reached their loft. This difference was small, but consistent, and suggests a different rating and ranking of the navigational cues. Clock-shifted pigeons do not seem to simply ignore the information from their manipulated sun compass altogether, but appear to merely downgrade it in favour of other cues, like their magnetic compass. This is supported by the observation that the final part of the tracks still showed a small deviation in the expected direction, indicating an effect of clock-shifting until the end of the homing flight.

KEY WORDS: Navigation, Sun compass, Clock shift, Points of decision, Correlation dimension, *Columba livia*

INTRODUCTION

The use of the sun as a compass in birds was first described in 1950 by Kramer for the starling *Sturnus vulgaris* (Kramer, 1950); at the same time, von Frisch described sun compass use in honeybees, *Apis mellifera* (von Frisch, 1950). These pioneering studies were soon followed by many more, revealing that sun compass orientation is a widespread phenomenon in the animal kingdom. The method of choice for demonstrating sun compass orientation was to alter the animal's perception of time by shifting their internal clock either forward (fast shift) or backward (slow shift), mostly for 6 h – this causes the animals to misjudge the time of the day and, as a consequence, the position of the sun. The resulting deflection from the headings of untreated controls serves as an indicator of sun compass use.

In 1958, Schmidt-Koenig performed the first such 'clock-shift' experiments with homing pigeons, *Columba livia* L. f. *domestica* (Schmidt-Koenig, 1958). The sun compass has since been demonstrated to be a very important component of the avian navigational system. Pigeons have been shown to use the sun compass not only at distant, unfamiliar sites (e.g. Schmidt-Koenig, 1961; Keeton, 1973) but also in the vicinity of their loft to translate the course indicated by their navigational map or their mosaic map of familiar landmarks into a flying direction (e.g. Graue, 1963; Schmidt-Koenig, 1979; Biro et al., 2007). Being established by experience (Wiltschko, 1983), the sun compass is well tuned to the local sun's arc in the pigeons' home region, with the birds adapting their compensation of the sun's movements to the different rates of change in sun azimuth in the course of the day (Wiltschko et al., 2000).

A study on the significance of the sun compass showed that young, inexperienced pigeons rely on this mechanism most strongly, showing the full deflection from untreated controls based on the difference in sun azimuth between the bird's subjective time and the true time of day. When pigeons grow older and get more experienced, however, the deflection decreases, with great scatter, to about 50% in birds aged 2 years and older (Wiltschko et al., 1994). The observation that the deflections were significantly larger in pigeons carrying magnets suggests that old pigeons fly a compromise between the directions indicated by their sun compass and their magnetic compass (Wiltschko and Wiltschko, 2001).

In the present study, we analysed how clock shifting affects the navigational processes itself, using an interdisciplinary approach. With the help of a recently described method derived from dynamic systems theory, we used time lag embedding to determine the short-term correlation dimension. An introduction to dynamic systems theory can be found in textbooks (Kaplan and Glass, 1995; Kantz and Schreiber, 1997). This parameter allowed us to assess the complexity of the system, indicating its degrees of freedom; the method has been rigorously tested in mathematical systems where the exact number of degrees of freedom is known (see Grassberger and Procaccia, 1983). In our specific case, the correlation dimension reflects the number of factors involved in the navigational process (for details, see Appendix). By shifting the pigeons' internal clock, we experimentally caused the two compass systems to give conflicting information – that of the magnetic compass being correct, that of the sun compass being misleading. Also, there may be a conflict between the sun compass and other local navigational factors used, because, as the birds progressed, these factors did not change as expected. How do birds cope with this situation? If they completely ignore the misleading information from their sun compass, this should lead to a marked decrease in the short-term correlation dimension.

RESULTS

The number of tracks is given in Table 1 (data are available from the corresponding author upon request). Fig. 1 gives, as an example, the tracks from the site BD, 17.3 km northeast of the Frankfurt loft; Fig. 2 gives the same tracks, now shaded differently to indicate the short-term correlation dimension. For the tracks of the other releases, see supplementary material Figs S1 and S2.

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Table 1. List of releases, local experience of birds and number of tracks recorded

Site	Home direction (deg)	Home distance (km)	Date of release	Experience	Control			Clock shift		
					n	n_c	Late	n	n_c	Late
BD	230	17.3	12 Jun & 17 Jul 2001	vfs	10	9	–	9	5	1
RB	194	19.2	22 Aug 2001	ufs	4	4	–	6	3	3
BH	167	8.4	18 & 19 Jun 2002	ufs	12	9	1	12	6	1
OT	338	17.9	5 & 8 Jul 2002	ufs	10	8	1	8	5	3
WAL1	67	21.5	7, 9 & 13 Aug 2002	ufs	13	8	2	10	3	7
WAL2	67	21.5	2–5 Sep 2002	fs	10	4	5	9	4	4

vfs, very familiar with the site; ufs, unfamiliar with the site (released there for the first time); fs, familiar with the site.
The Control and Clock shift columns give: n, the number of tracks that could be analysed; n_c, the number of complete tracks; Late, the number of pigeons that returned after the battery expired.

Traditional analysis

For this analysis, we subdivided the tracks into several phases according to the points of decision (see Schiffner and Wiltschko, 2009; Schiffner et al., 2013) into an initial phase, a departure phase and a final homing phase, the last ending when the pigeon reached the loft. The data of the traditional analysis from the six releases are given in supplementary material Table S1. In general, there was a considerable amount of variability and sometimes some seemingly erratic behaviour, so no consistent pattern emerged. Most of the significant differences were found in the tracks from BD, the site most familiar to the pigeons.

Table 2 gives the second-order comparison. The number of points of decision increased significantly in the clock-shifted birds, suggesting a greater necessity to reorient. The difference in the efficiency of the complete tracks did not reach significance; it must be considered, however, that only about two-thirds of the clock-shifted pigeons reached the loft during the time when the battery was still active (see n_h in supplementary material Table S1) – the other tracks ended somewhere in the region, often at a considerable distance from home. In these cases, the true efficiency of the route home was certainly considerably lower, but because the last part of the tracks was not recorded, it cannot be determined. The same applies for the number of points of decision. In this respect, Table 2 does not reflect the behaviour of the clock-shifted pigeons realistically. Altogether, 19 of 54 (35%) experimental birds did not

return in time, compared with 11 of 59 (19%) control birds, but 10 of the experimental pigeons arrived later on the day of release.

During the various phases of the homing flight, we found only few significant differences between clock-shifted pigeons and controls (see Table 2). In the initial phase, while the birds were still at the release site, the behaviour of the two groups was similar. Clock-shifted pigeons had shorter vectors during the departure phase, indicating more scattered, individual headings. The mean headings with respect to home were not significantly different during the initial and the departure phase, although there were considerable deviations between the mean vectors, mostly in the expected counter-clockwise direction (see Table 2; supplementary material Table S1); they differed significantly, however, during the final homing phase.

Changes in the short-term correlation dimension

The mean short-term correlation dimensions for the six releases and their means are shown in Fig. 3. Numerical data are given in Table 3, separating the first 2000 m (after which the correlation dimension strongly increases) from the central part of the track and from the last 2000 m. A wide range of scatter can be observed, between birds and, to some extent, also between releases and/or sites. However, common trends become visible: the short-term correlation dimension increases significantly with distance, and there is a significantly lower short-term correlation dimension in the clock-
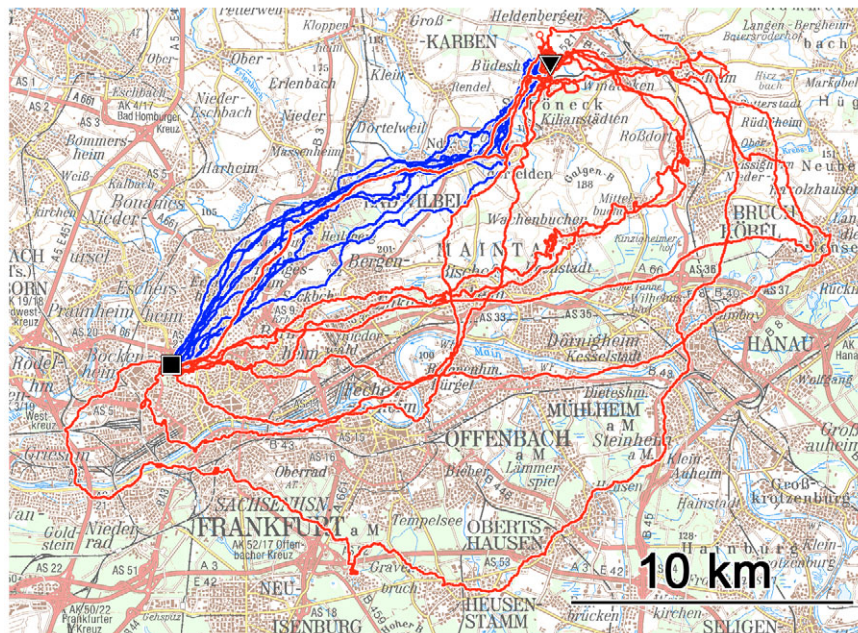

Fig. 1. Tracks of pigeons released at site BD. The release site (17.3 km northeast of the home loft, home direction 230 deg) is marked by a black triangle, the home loft by the black square. Tracks of untreated control birds are given in blue, those of 6 h fast-shifted pigeons in red. Incomplete tracks ending in flight are marked with an open triangle, tracks lost seconds after landing (probably because the contact to the satellites was interrupted) are marked with an open circle, and tracks lost after a longer period of sitting are marked with an open square.
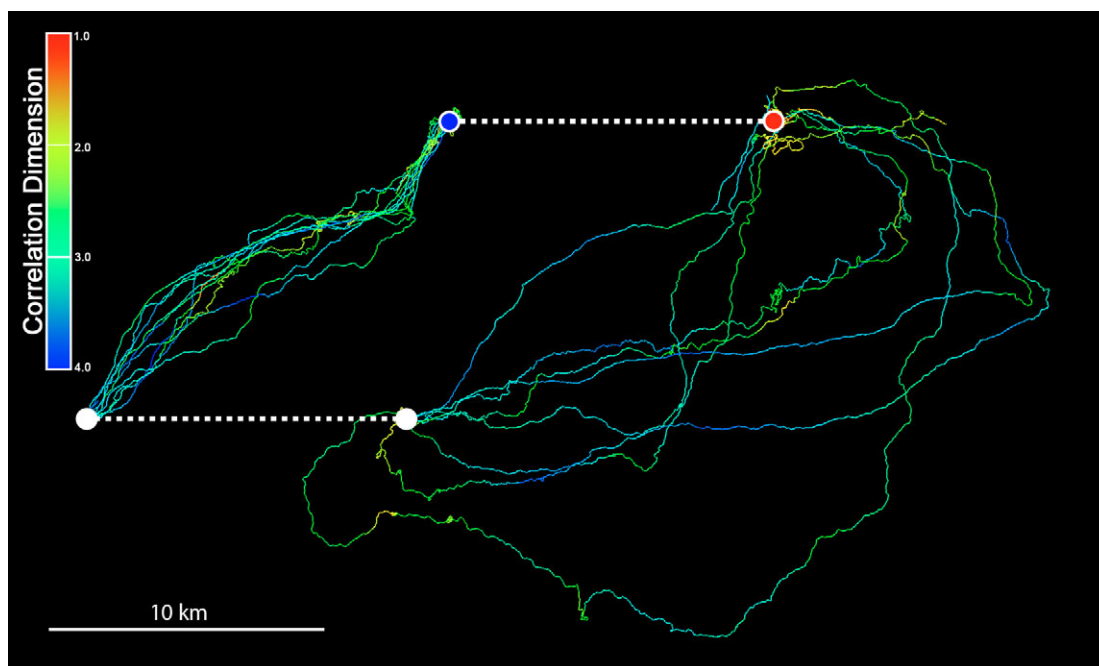
Fig. 2. Short-term correlation dimension of the tracks. The same tracks of pigeons released at BD as in Fig. 1 are shown, with controls and clock-shifted pigeons given separately. The short-term correlation dimension is indicated by the colour of the track (see colour scale). The location of the release site is given in blue for the control birds and in red for the clock-shifted pigeons; the home loft is marked by a white circle.

shifted pigeons for all but the closest site, BH (ANOVA: BD: $P<0.05$; other sites: $P<0.001$; see supplementary material Table S2), indicating an effect of clock shifting.

The reduction is rather small, only of the order of 0.25 degrees of freedom, but it is persistent throughout the entire journey. It becomes more pronounced en route as the pigeons proceed. Looking

at the beginning, the central part and the end of the track separately, a second order analysis reveals no significant difference between clock-shifted pigeons and control birds within the first 2000 m ($T=5$, $P>0.05$, Wilcoxon test), whereas in the later parts of the tracks, when the pigeons are navigating home, the short-term correlation dimensions differ significantly ($T=0$ and $T=1$, $P<0.05$).

DISCUSSION
The observed decrease in the short-term correlation dimension clearly shows that the conflicting information produced by clock shifting leads to subsequent changes in the complexity of the navigational processes. This is the first experimental evidence that the correlation dimension directly reflects changes in the navigational processes and suggests that the method described earlier (Schiffner et al., 2011) can be successfully applied to detect such changes.

The initial phase of the homing flight
The decrease, however, does not seem to manifest itself at the very beginning of the homing flight, but only later, as the birds leave the site. Immediately after release, when pigeons still fly around in the vicinity of the release point, the mean short-term correlation dimensions are rather low, too low to indicate complex navigational processes (Schiffner et al., 2011). This is in agreement with the assumption that the initial phase itself plays little role with regard to making a navigational decision, but rather serves for preparing for the flight, like gaining height and speed, and possibly also for exploring the surroundings, as also suggested in earlier studies (Schiffner and Wiltschko, 2009; Schiffner et al., 2013). However, a first navigational process must already have taken place before the birds begin to fly, because, when released from a cage, pigeons show a tendency to leave in the direction in which they later vanish (Chelazzi and Pardi, 1972; Kowalski, 1994; Mazzotto et al., 1999). This means that the birds have roughly determined their home
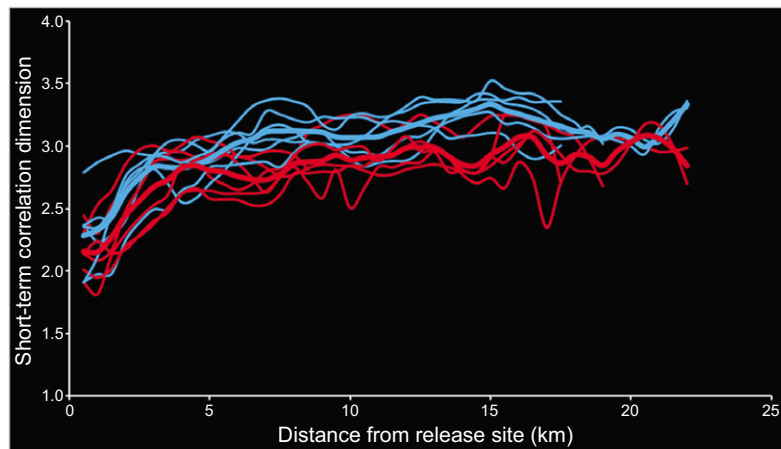
Table 2. Second-order comparison between controls and clock-shifted pigeons (six releases)

Variable	Control	Clock shift	T	P
Complete tracks				
Number of points of decision	1.6	2.0	0	<0.05
Efficiency	0.87	0.85	3	n.s.
Initial phase				
Duration (s)	150	161	5	n.s.
Distance to 1st PoD (m)	1097	779	8	n.s.
Δh (deg)	−10	−51	7.5	n.s.
Vector length r	0.68	0.69	8	n.s.
Steadiness	0.29	0.30	5.5	n.s.
Departure phase				
Δh (deg)	0	−20	5	n.s.
Vector length r	0.82	0.61	1	<0.05
Steadiness	0.84	0.73	9	n.s.
Final homing phase				
Δh (deg)	−7	−20	1	<0.05
Vector length r	0.99	0.98	4	n.s.
Steadiness	0.87	0.85	7	n.s.

PoD, point of decision; Δh, median deviation of the mean headings from the home direction; vector length r, median length of mean vectors based on the headings; T, test statistic of the Wilcoxon signed rank test; n.s., not significant.
Note that the table does not reflect the number of points of decision, the efficiency and the behaviour during the final homing phase realistically, as 19 of 54 experimental birds did not return while the battery was still operating, compared with 11 of 59 control birds.

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Fig. 3. Average short-term correlation dimension for all releases. Control birds are indicated in blue, experimental birds in red. The thin lines indicate the means of the single releases, the thick lines give the average of these means.

course; the extent to which they have already used a compass to transform this course in a flying direction (Kramer, 1957) is not entirely clear. The observation that the deflection in clock-shift experiments increased from the first minute until the pigeons vanished from sight (e.g. Schmidt-Koenig, 1965; Wiltschko et al., 1994) appears to suggest that consulting the sun compass may occur only when the bird is already airborne, possibly only after it has decided to leave the release site.

The traditional variables also appear to speak against navigation immediately after release: the duration of the initial phase until the first point of decision, its distance from the release point and the other variables do not differ between the two groups of birds. There is no indication that pigeons realise that something is unusual and hesitate to leave the site when under the influence of a clock shift. Taken together, this suggests that during the initial phase, pigeons are not yet concerned with navigating (see Schiffner et al., 2011), and therefore clock shifting appears to have little effect on the behaviour during this phase. Only at BD, the site our pigeons knew from several previous homing flights, did we find a significant deflection of the experimental birds from the controls, not only in the initial phase but also throughout the homing flight. Obviously, familiarity with the site and the route home does not diminish the effect of clock shifting here.

Navigating to the loft

After the initial phase, the short-term correlation dimension of the clock-shifted pigeons was consistently lower than that of the control birds, indicating changes in the navigational processes. This allows some careful conclusions on the strategy that pigeons use to overcome the problem of their manipulated internal clock: it seems

that realising that their sun compass is amiss, they do not simply ignore its false information altogether and switch to their magnetic compass. Instead, they appear to continue using sun compass information, yet downgrade it, probably in favour of the magnetic compass. This is suggested by the small decrease in short-term correlation dimension observed in the clock-shifted pigeons – had the sun compass been dropped altogether, we would have expected a somewhat larger decrease (see Schiffner et al., 2011). It seems that clock-shifted pigeons gradually increase the weighting of their magnetic compass, but never fully ignore the information provided by the sun. The higher number of points of decision observed in the clock-shifted birds suggests that they do indeed correct their mistake and adjust their course during the homing flight, but then are again misled by their manipulated sun compass. The deviation from the home course continues to become smaller, but it does not disappear completely. A small, but significant deflection between the two groups remains, and the short-term correlation dimension continues to be a little lower in the experimental birds. This clearly shows that some effect of clock shifting on the navigational processes persists until the pigeons reach their loft. This is in accordance with the observations by Gagliardo and colleagues (Gagliardo et al., 2009; Filannino et al., 2014), who also tracked clock-shifted pigeons with GPS-based recorders and found that the effect of the treatment usually decreased as the birds approached their loft, but was still evident when they reached home.

About two-thirds of our clock-shifted pigeons returned within the ~3 h life-time of the battery. This was well before their subjective day ended, and hence they had not experienced the situation that the sun was still out when they expected it to have already set. It is unclear what the remaining birds did after the beginning of their

Table 3. Short-term correlation dimensions

| Site | Distance (km) | First 2000 m | | | | Central part of track | | | | Last 2000 m | | | |
| | | Control | | Clock shift | | Control | | Clock shift | | Control | | Clock shift | |
		n	Mean	n	Mean	n	Mean	n	Mean	n	Mean	n	Mean
BD	17.3	10	2.89	10	2.48	10	3.02	10	2.98	10	3.36	8	3.10
RB	19.2	4	2.48	4	2.04	4	3.09	4	2.79	4	3.25	3	2.94
BH	8.4	12	2.32	12	2.59	12	2.99	11	2.94	11	3.05	11	2.92
OT	17.9	10	2.47	9	2.21	10	3.12	8	2.86	9	2.95	8	2.97
WAL1	21.5.	10	2.03	12	2.04	9	3.09	11	2.67	8	3.12	5	2.96
WAL2	21.5	9	2.32	10	2.17	8	3.16	8	2.86	5	3.16	6	3.01
Mean			2.42		2.26		3.08		2.85		3.15		2.98

Distance, the distance of the release site from the loft; n, number of tracks involved; Mean, mean short time correlation dimension for the respective part of the track.

subjective night, because their behaviour was no longer recorded. Gagliardo and colleagues (Gagliardo et al., 2009) reported that their clock-shifted pigeons made a stop when their subjective day ended. The great majority of these birds, however, re-started their flight later on the same day. It seems possible that our pigeons behaved in a similar way. About half of the late birds arrived in the afternoon of the day of release; that is, before a sunset and sunrise could have reset the internal clock. They probably relied on their magnetic compass. An important role of the magnetic compass in overcoming clock-shift effects is supported by the observations of Gagliardo and colleagues (Gagliardo et al., 2009): their experimental birds with magnets showed larger deviations and had more problems with reorienting than otherwise un-manipulated clock-shifted pigeons, and more of them got lost. Also, while the pigeons carrying magnets went in random directions when they restarted, the otherwise un-manipulated clock-shifted birds were homeward oriented.

A remarkable observation in our study is the great variability in the behaviour of the experimental birds. Both groups showed a considerable amount of scatter, but the variance among the clock-shifted pigeons was markedly greater, which is in agreement with observations by our Italian colleagues (Bonadona et al., 2000; Gagliardo et al., 2009; Filannino et al., 2014), who also describe a great variability in the responses of clock-shifted pigeons. Evidently, pigeons respond highly individually and have rather different ways of handling the cue-conflict situation caused by their shifted internal clock.

MATERIALS AND METHODS

The study is based on six releases of pigeons whose internal clock was shifted 6 h fast, performed during the summer months of the years 2001 and 2002 (for the exact dates, see Table 1). The releases occurred in the early morning during the overlap between the pigeons' shifted day and the natural day, in sunny weather with no or little wind. The experiments were performed according to the rules and regulations of animal protection in Germany.

Experimental pigeons

The test birds were experienced pigeons from our Frankfurt loft (50°08′N, 8°40′E), all older than 2 years. In their first year of life, they had participated in a standard training programme of flock releases up to 40 km in the cardinal compass directions. Their experience additionally included a number of single homing flights returning from previous homing experiments, the number of which increased with increasing age.

Clock shifting followed standard procedures: the experimental birds were confined in light-tight rooms under a shifted photoperiod that began 6 h before sunrise and ended 6 h before sunset for at least 5 days. This induces a counter-clockwise deflection of their bearings from the untreated controls. The control birds were kept in a photoperiod synchronous with the natural day.

Release sites

The five release sites used in this study – between 8.4 and 21.5 km from the loft – lie in the general region familiar to the birds from training and previous homing flights; their positions are given in Table 1. The site BD was very familiar to the test birds as they had homed 11 times from there in the previous year (see Schiffner et al., 2013). The sites RB, BH, OT and WAL, in contrast, were unfamiliar to the birds in the sense that they had not started a homing flight from there before. In WAL, we performed a second release with the same birds, now familiar with the site, 3 weeks after the first, this time switching the treatments so that the former controls were now 6 h shifted fast and vice versa (see Table 1 for details).

GPS tracking devices and release performance

The GPS tracking devices used were based on the prototype developed by von Hünerbein et al. (von Hünerbein et al., 2000). The recorders were equipped with an embedded patch antenna, a data logger and a 3.3 V CR2 battery with a life time of about 3 h (for details, see Wiltschko et al., 2007). All recorders were set to take a positional fix every second, achieving a precision of ±4 m.

The pigeons were transported to the release sites in wooden cages in a VW bus and kept without direct view of the sun in the shade of the vehicle while awaiting their release. Immediately before release of a bird, the recorder was equipped with the battery and wrapped in plastic to shield it from water. This package was attached to the pigeon's back by means of a harness made from Teflon tape. The birds were wearing this harness continuously during the summer months; the recorder was placed on the dorsal plate and fixed with Velcro and additional sticky tape. The mass of the recorder including the battery was 35 g; harness and coating added another 7 g to the load. In total, the package was between 5.5% and 9% of the pigeons' mass. Each bird was released singly, alternating between experimental and control birds.

The number of tracks recorded from each site is included in Table 1. Although we always made sure that the GPS receiver had contact with a sufficient number of satellites and was properly working before it was wrapped in the plastic coating, technical problems like temporary satellite loss, battery failure, etc., but also late returns after the battery had run empty led to a number of incomplete tracks (see Table 1).

Data analysis

For the system analysis, we calculated short-term correlation dimensions for the tracks by means of time-lag embedding (a brief summary of the procedure is given in the Appendix) (see Schiffner et al., 2011). In contrast to the true correlation dimension of a track based on all data points, it was calculated as sliding mean over 180 s and averaged for each 500 m step from the release site. This short-term correlation dimension is lower than the true correlation dimension of the entire track, but can be used for comparisons.

To indicate the short-term correlation dimension numerically, we determined separately its mean for the first 2000 m for all pigeons with at least three data points, the mean of the central part of the track for all pigeons with at least five data points, and the mean of the last 2000 m. The mean of these means is given for each release.

We also performed a traditional analysis based on the division of the tracks into distinctive phases by points of decision, which are based on the temporal course of the cumulative velocity and momentary steadiness (a brief summary of the procedure to determine points of decision is given in the Appendix) (see also Schiffner and Wiltschko, 2009; Schiffner et al., 2013). Points of decision divide the tracks into an initial phase, ending with the first points of decision, the subsequent departure phase, which is identical to the final homing phase leading to the loft if there is only one point of decision; otherwise, a separate final homing phase follows, occasionally with intermediate phases before the final homing phase begins.

For the entire track, we determined: (1) the number of points of decision; and (2) the overall efficiency of flight (the length of the track divided by the direct distance). We also determined: (3) the duration of the initial phase till the first point of decision (in seconds); (4) the distance of the first point of decision from the release point (in metres); and, for the various phases, (5) mean headings with respect to the local home direction (i.e. the home direction from the pigeon's momentary position); (6) vector lengths resulting from these headings, reflecting the agreement among pigeons; and (7) steadiness of the flight, calculated as mean vector length from all headings of a pigeon during the respective phase.

In cases with only one point of decision, we took the first 300 s of the final homing phase as a departure phase (see also Schiffner et al., 2013). Rarely occurring intermediate phases were not included in the analysis.

Statistical analysis

The short-term correlation dimensions of the tracks were compared on the first-order level for each site separately by a two-way ANOVA with repeated measurements using a factorial design, with the independent factors being the experimental condition (i.e. control or clock shift) and the distance from the release site at which the short-term correlation dimension estimates were taken. Each individual is treated as repeated measure of the same underlying navigational processes, which is normal in the controls and manipulated in

the clock-shifted birds. When the ANOVA indicated significance, we used the Tukey HSD test to correct for multiple comparisons and look for differences between control and clock-shifted pigeons.

In the traditional analysis, we tested the circular data from control pigeons and those from clock-shifted pigeons for each phase of each release with Rayleigh test and compared them with the Watson–Williams test (if both $r>0.65$) or the Mardia–Watson–Wheeler test (Batschelet, 1981); the other data were compared with the Mann–Whitney U-test. For the second-order analysis, we calculated means for the following variables: 'number of points of decision', 'deviation of the headings from the home direction' and 'vector lengths', and medians for the variables 'duration of the initial phase', 'distance of the first point of decision from the release point', 'overall efficiency' and 'steadiness of the tracks'. Here, data from untreated control birds and clock-shifted pigeons were compared using the Wilcoxon signed rank test. The data of the first 2000 m of the departure phase and the final homing phase were separately compared using this test.

APPENDIX
Calculating the short-term correlation dimension
With respect to time-lag embedding and calculation of the correlation dimension, our study is interdisciplinary, combining navigation research with dynamic systems theory; background information and a general introduction into dynamic system theory can be found in textbooks (e.g. Kaplan and Glass, 1995; Kantz and Schreiber, 1997). The methods are well established and primarily used to describe physical/mechanical systems, but have been applied to biological systems before (for a review, see Skinner, 1994).

According to Takens' embedding theorem (Takens, 1981), an extension of Whitney's theorem (Whitney, 1936), a dynamic system can be fully reconstructed in phase space given a series of observations of the state of the dynamic system, i.e. a time series. In phase space, every degree of freedom or parameter of the system is represented as an axis in a multidimensional space. The number of degrees of freedom is then the minimum number of variables necessary to fully describe the system. For mathematical systems, this is equivalent to the number of terms in the equation; in a physical/mechanical system, it is the number of inputs: e.g. in the case of a robot navigating in a given environment, the number of independent sensors necessary to perform the task. Here, we assumed that for a biological system like pigeon navigation, the correlation dimension, as in the case of the robot, represents the number of independent inputs necessary to navigate.

In our particular case, we were interested in the navigational process of the pigeon, with the time series provided by the tracks recorded during the homing flight. Using time-lag embedding requires no *a priori* knowledge about the number of factors involved and their specific interactions; instead, the methods used here allowed us to create a physical model of the process using only the recorded data. From this model we could then calculate several parameters. In the present study, we focused solely on the so-called correlation dimension, a value reflecting the system's degrees of freedom, i.e. in this particular case, the number of factors involved in the navigational process. The calculation, with some minor enhancements, as described below, was based on the original algorithm proposed by Grassberger and Procaccia (Grassberger and Procaccia, 1983).

First, in order to ensure optimal embedding, we determined the embedding lag for each individual time series. We used the first minimum of the mutual information to determine an appropriate embedding lag (Fraser and Swinney, 1986) and a fixed range of embedding dimensions – from three to five – in order to avoid spurious effects from using different embeddings. For calculation of

the mutual information, we decided to implement a new non-parametric approach in order to circumvent problems with unevenly distributed data. To ascertain that data were always evenly distributed, we divided the data into $\log_2 N$ (with N being the number of data points in the time series) partitions and assigned a fixed number of elements to each partition. This new approach allowed us to get much better convergence and well-defined minima and maxima.

Second, we implemented an algorithm for automatic selection of a proper scaling region, thus ensuring that all values would be selected on objective criteria. This was achieved by embedding the time series three times, with successively increasing embedding dimensions. We then chose the scaling region defined by the minimum in standard deviation over all three embeddings. As the standard deviation tends to decrease as we approach the size of the attractor, the so-called depopulation region, we added some restrictions: (i) the first minimum in standard deviation was used to define an initial estimate; other potential scaling regions with lower standard deviation were ignored, if the resulting correlation dimension fell below this initial estimate (±s.d.); (ii) the size of the scaling region was fixed to 1/4 of the length of the attractor. Although the latter restriction seems to be a rather coarse solution, it ensures that the scaling region will never lie within the depopulation region and allows for better comparison of estimates from different time series.

In order to observe changes in the correlation dimension in the course of the homing flight, we determined short-term correlation dimensions for the tracks. In contrast to the true correlation dimension based on all data points, they were calculated as sliding means over 180 s and averaged for each 500 m step from the release site. This short-term correlation dimension is lower than the true correlation dimension of the entire track, but can be used for comparisons (for details, see Schiffner et al., 2011).

Determining points of decision
Points of decision are determined with the help of two variables, cumulative velocity and momentary steadiness, and their changes with time. Cumulative velocity is defined as the current distance of a pigeon from the release point divided by the time that passed since release – it increases if a pigeon moves away from the release point and decreases if a pigeon slows down, flies perpendicular, heads back, etc. Momentary steadiness is calculated as sliding means of the vector length of 60 consecutive headings determined every 15 s; it approaches 1 if the bird flies straight, has lower values if a bird changes course and would become 0 if a bird flew in circles.

A point of decision was originally defined by the highest increase in the steadiness of flight immediately preceding or during an increase of cumulative velocity when the pigeon departed from the release site. Hence, this definition is independent of the bird's heading when it leaves the release point on a steady course. Frequently, pigeons fly around at the release site and are in the opposite semicircle of the direction in which they are going to leave. In this case, the cumulative velocity first decreases approaching zero, then increases rapidly – here, the highest increase in steadiness preceding the increase in cumulative velocity marks the point of decision (see Schiffner and Wiltschko, 2009).

Over longer distances, most tracks include periods where the pigeons fly steadily towards home and others where they stall and do not increase the distance from the release point continuously. Hence, the temporal course of the cumulative velocity shows periods of increase and periods of decrease of varying length. To

take this into account, sliding means of the cumulative velocity over 60 s are calculated every 15 s, and the value of each of these steps is compared with the preceding one. There are three different types of steps, namely steps with increasing cumulative velocity, steps with decreasing cumulative velocity and steps with no change in cumulative velocity. A period is defined as consisting of at least five steps of the same type, which means that the pigeon was either increasing or decreasing its cumulative velocity over more than 60 s. In order to be able to define periods even when the cumulative velocity is very low, yet shows an overall trend, these five steps can be interrupted by steps with no change in cumulative velocity (Schiffner et al., 2011; Schiffner et al., 2013).

Increasing cumulative velocity is normally associated with an increase in momentary steadiness as defined above (Schiffner and Wiltschko, 2009). A point of decision is indicated by the highest increase in steadiness between two consecutive steadiness values 15 s apart within the period showing the highest mean increase of steadiness over 60 s (five means). This way, we define additional points of decisions by the highest increase of the momentary steadiness following periods where the cumulative velocity remained constant or decreased (see also Schiffner et al., 2011).

Data from the various phases of the individual releases
Supplementary material Table S1 gives the mean respective medians of variables from the initial phase, the departure phase and the final homing phase of the six individual releases.

ANOVA statistics of the short-term correlation dimension
Supplementary material Table S2 gives details on the two-way ANOVA for the short-term correlation dimensions calculated as a sliding mean and averaged for each 500 m segment relative to the home loft for each release.

Figures of the tracks
Supplementary material Fig. S1 gives the tracks from the releases RB, BH, OT, WAL1 and WAL2; supplementary material Fig. S2 gives the same tracks with the short-term correlation dimension indicated.

Supplementary material
Supplementary material available online at
http://jeb.biologists.org/lookup/suppl/doi:10.1242/jeb.104182/-/DC1

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Supplementary Figures of the tracks

1. Figures showing the tracks, with those of clock-shifted pigeons are given in *red*, those of control birds in *blue*. The release site is marked by a black triangle, the home loft by a black square. Incomplete tracks ending in flight are marked with an open triangle, tracks lost seconds after landing (probably because the contact to the satellites was interrupted) with an open circle, and tracks lost after a longer period of sitting with an open square.
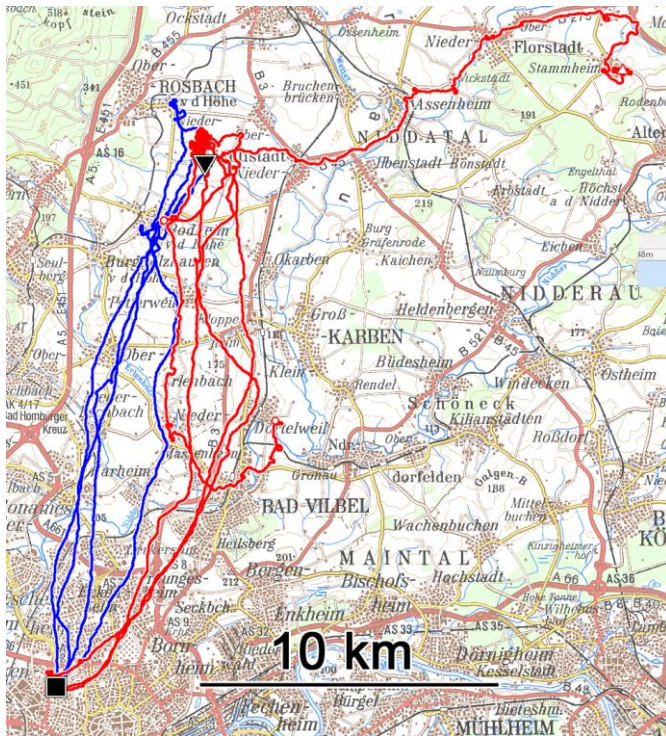

Fig. S1A Tracks of pigeons released at RB, 19.2 km south of the loft, home direction 194°
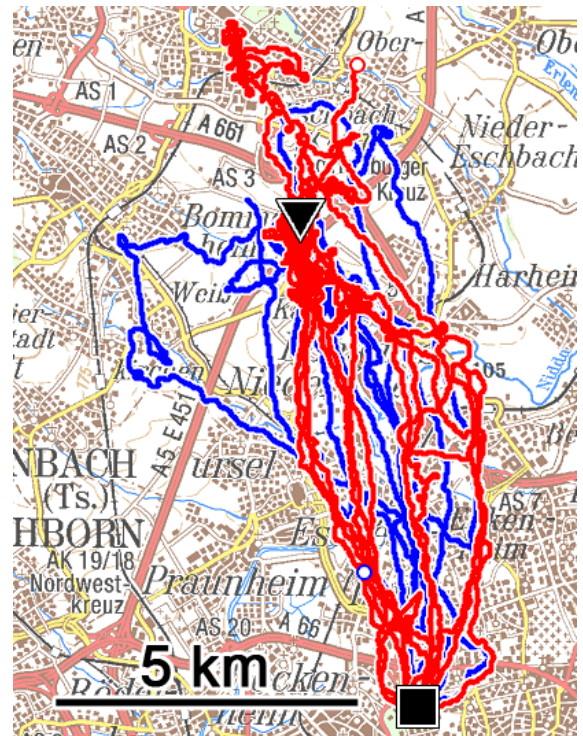

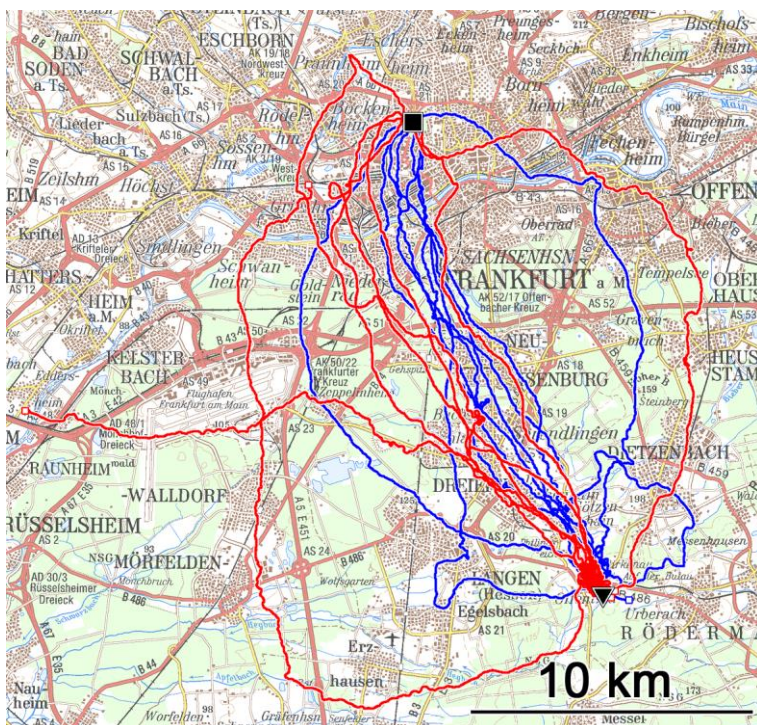**Fig. S1B** Tracks of pigeons released at BH, 8.4 km north-north west of the loft, home direction 167°

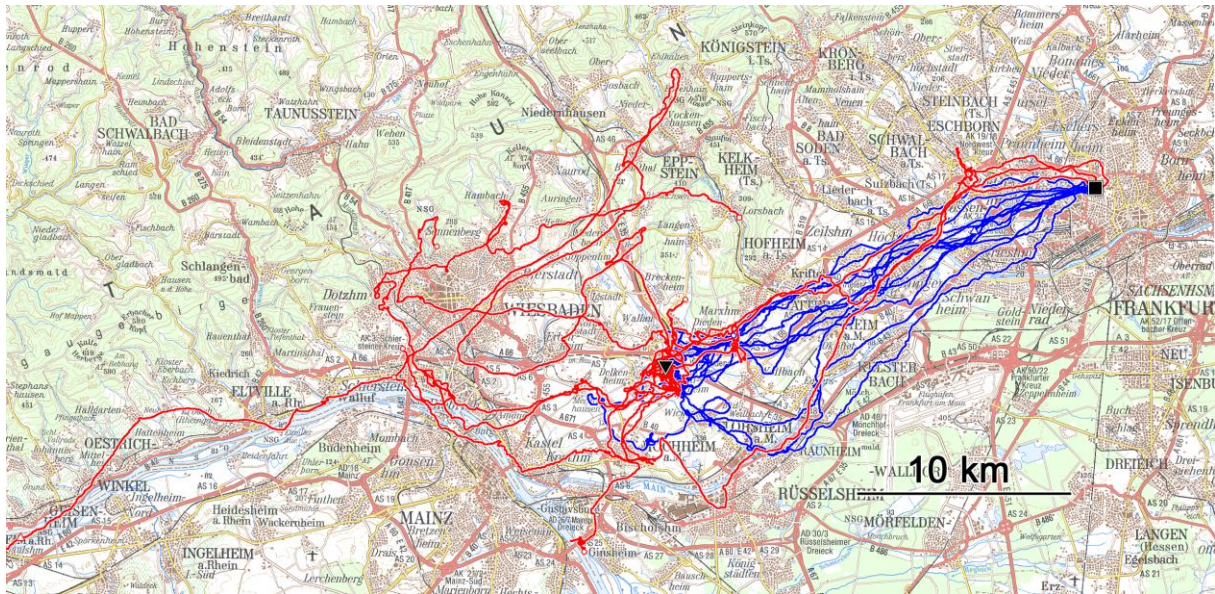**Fig. S1C** Tracks of pigeons released of OT, 17.9 km southeast of the loft, home direction 338°

Fig. S1D Tracks of pigeons unfamiliar with the site, released for the first time at WAL, 21.5 km south-southwest of the loft, home direction 67°
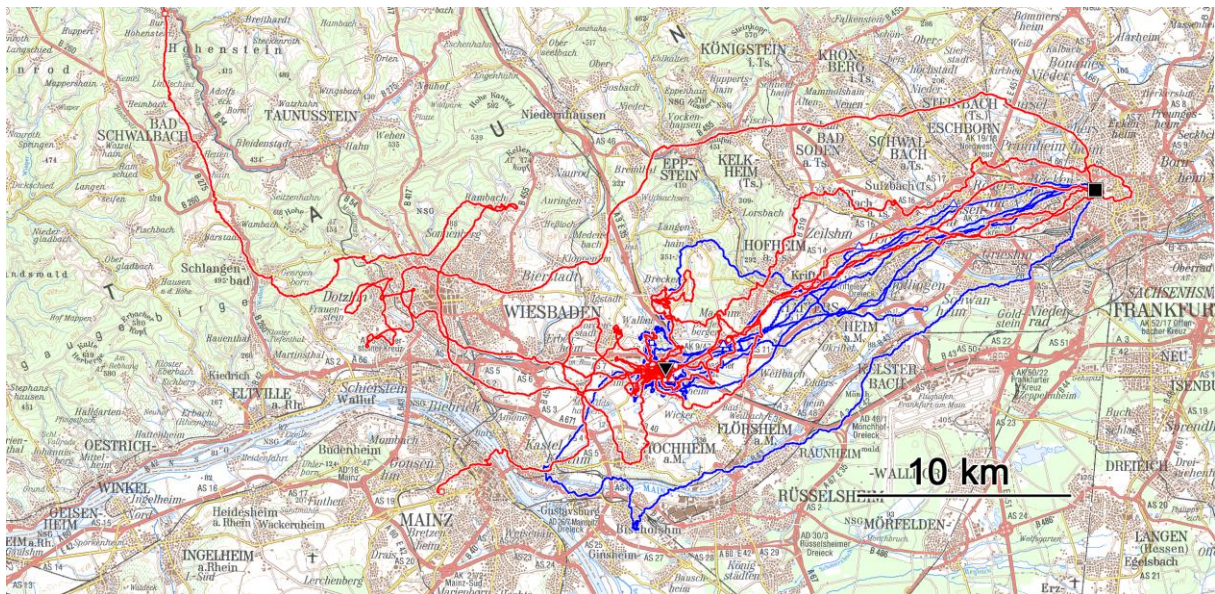

Fig. S1E. Tracks of pigeons familiar with the site, released for the second time at WAL, 21.5 km south-southwest of the loft, home direction 67°

Figures of the tracks with the short-term correlation dimension indicated

The following figures S2A–E give tracks of control and experimental pigeons separately. The release site is marked *blue* for the controls and *red* for the clock-shifted pigeons; the location of the loft is marked in *white*. The value of the short-term correlation dimension is indicated by the color of the tracks, see map legend.
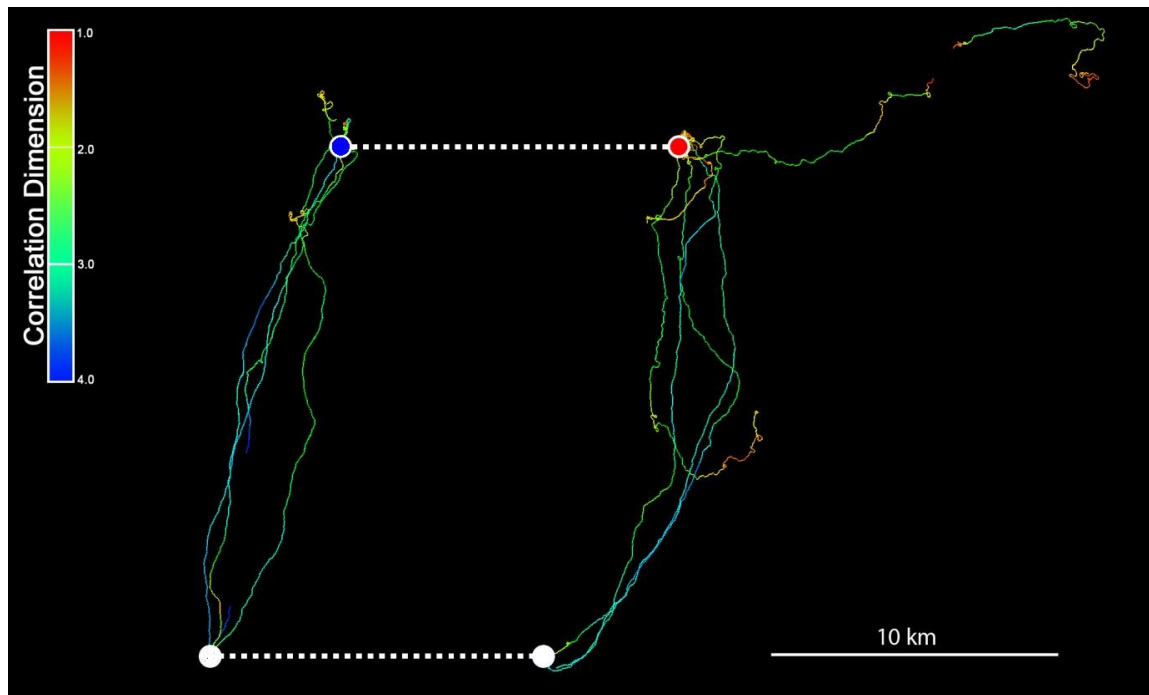

Fig. S2A. Tracks of pigeons released at RB, 19.2 km north of the loft, home direction 194°
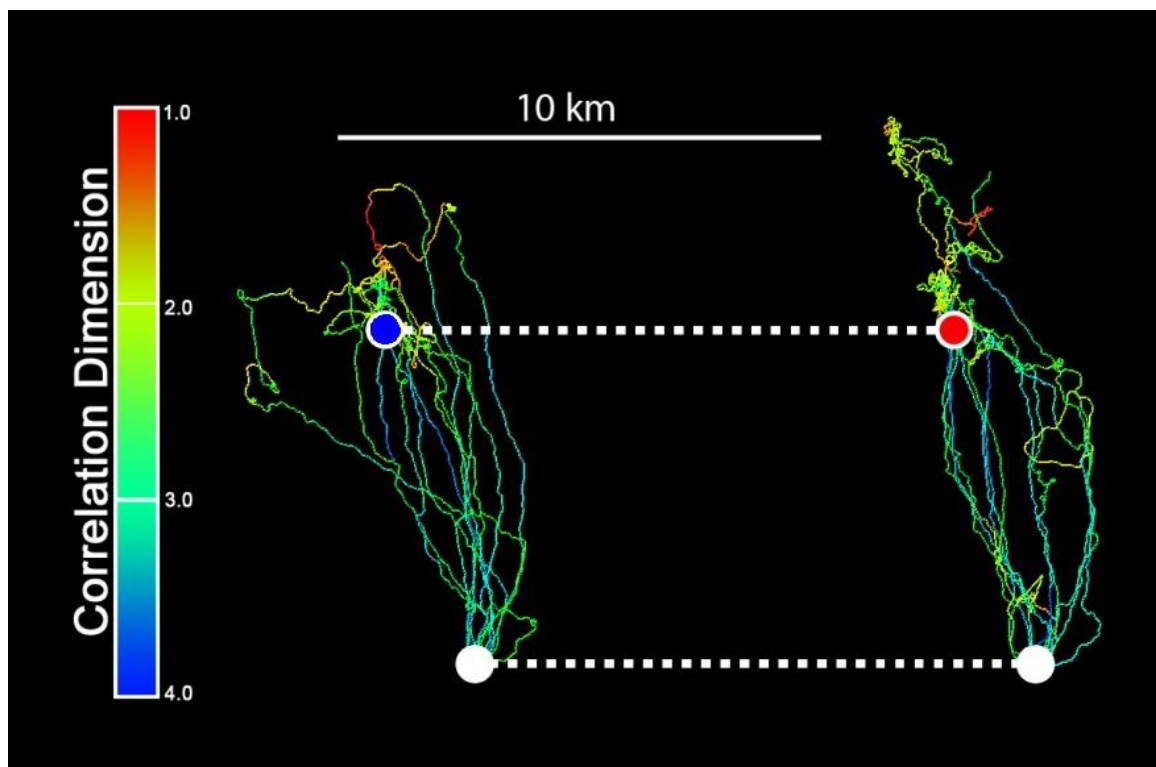

Fig. S2B Tracks of pigeons released in BH, 8.4 km north-northwest of the loft, home direction167°

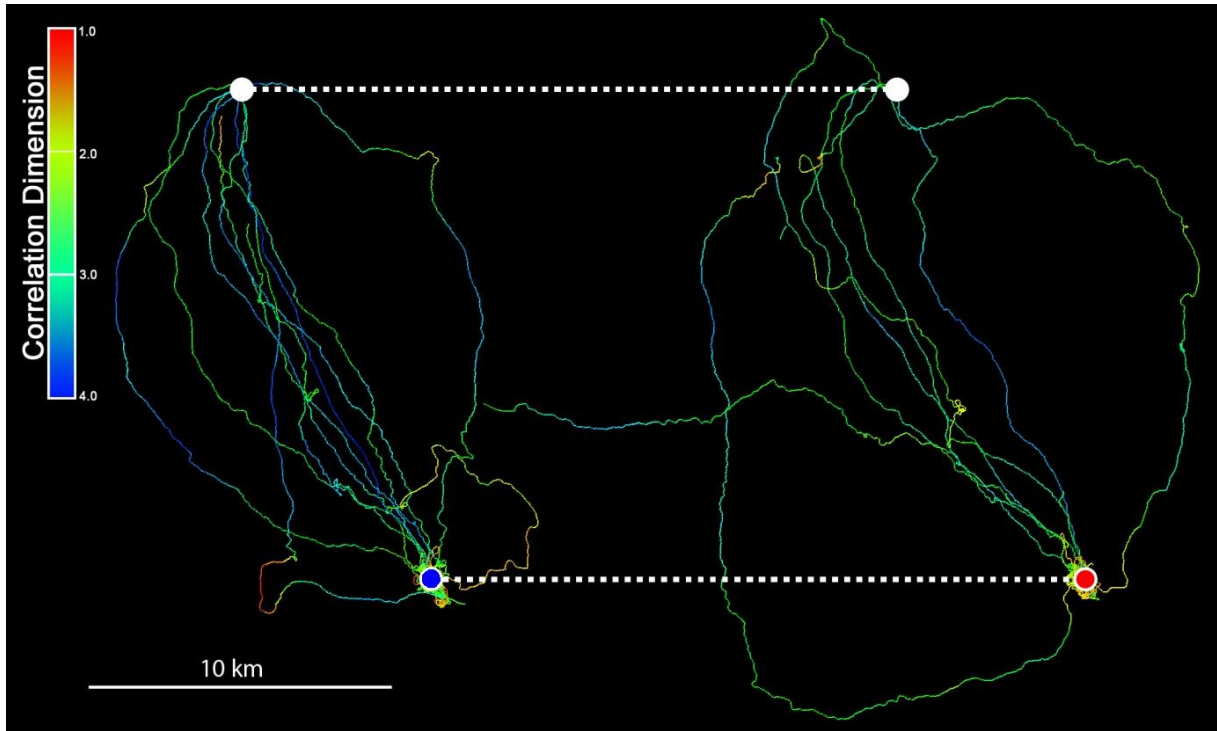**Fig. S2C** Tracks of pigeons released at OT, 17.9 km southeast of the loft, home direction 338°
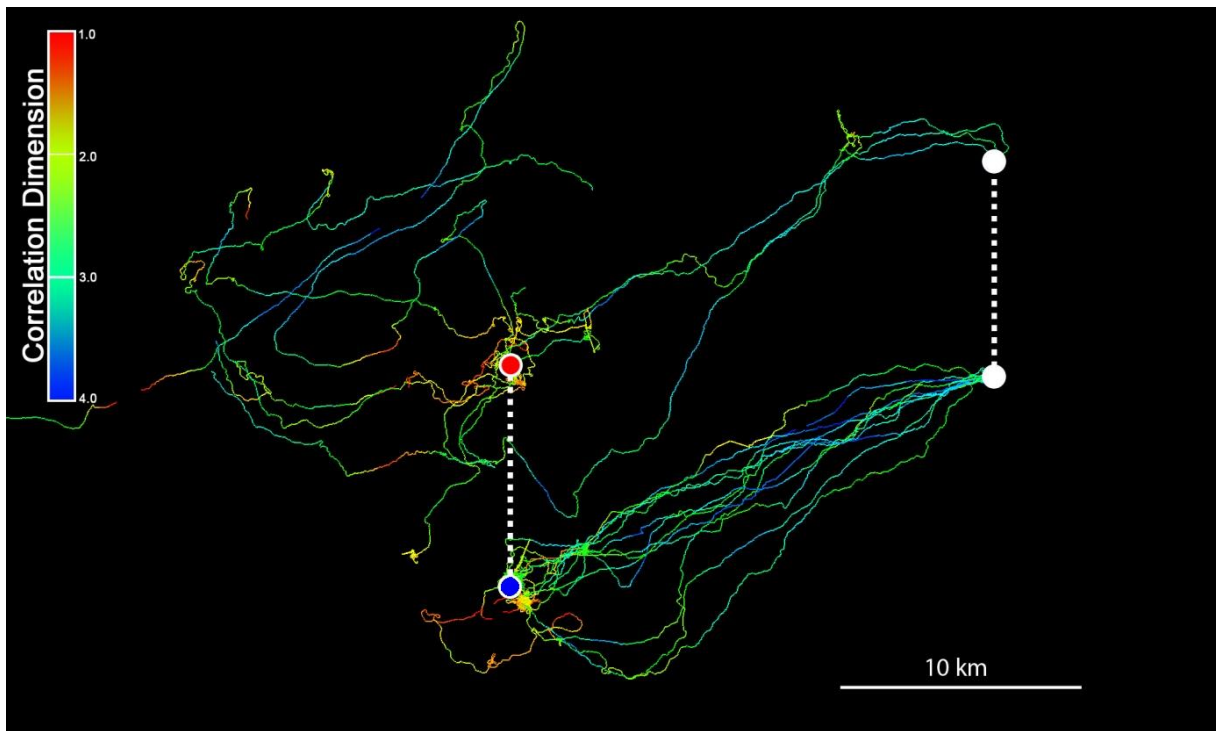

Fig. S2D Tracks of pigeons *unfamiliar* with the site, released for the first time at WAL, 21.5. km south-southwest of the loft, home direction 67°.
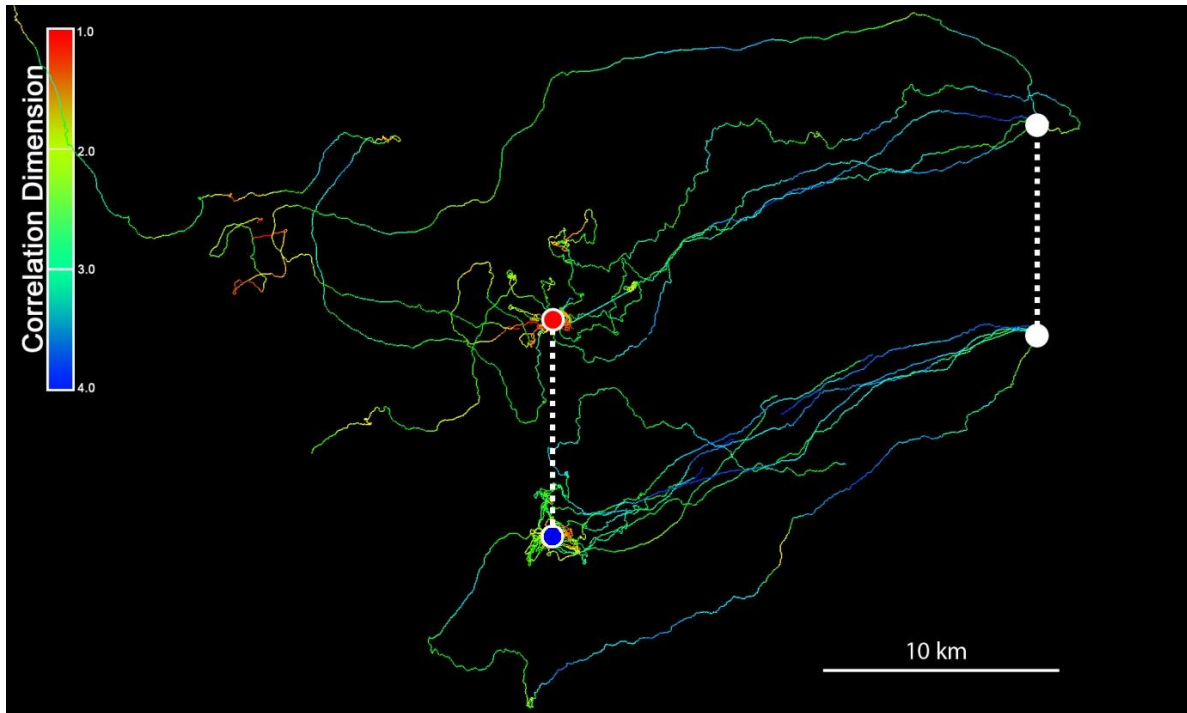
Fig. S2E Tracks of pigeons *familiar* with the site, released for the second time at WAL, 21.5. km south-southwest of the loft, home direction 67°.

Supplementary Table S1

Data from the various phases of the individual releases

site	tr.	n_c	PoDs	eff.	n_b	dur.(s)	dist.(m)	Δh	r	stead.	Δh	r	stead.	n_h	Δh	r	stead.
			Entire Track					**Initial Phase**				**Departure Phase**				**Final Homing Phase**	
BD	C	9	1.8	0.88	9	150	1342	**- 12°**	0.98	0.55	**- 14°**	0.93	0.91	10	**+8°**	**0.99**	0.88
BD	CS	5	2.4	0.81	6	128	597	**- 132°***	0.45	0.36	**-117°***	0.79	0.83	8	**- 25°***	**0.82***	0.78
RB	C	4	1.3	0.93	4	150	659	- 10°	0.74	0.31	+9°	1.00	0.87	4	+2	0.99	0.93
RB	CS	3	1.7	0.95	6	135	565	- 36°	0.84	0.31	- 30°	0.83	0.71	3	- 19	0.99	0.95
BH	C	9	1.2	0.86	10	135	1070	- 8°	0.33	0.40	- 9°	0.73	0.85	11	- 14°	0.99	0.84
BH	CS	6	1.3	0.87	7	195	1727	- 66°	0.54	0.23	- 35°	0.43	0.76	11	- 7°	0.98	0.87
OT	C	8	1.6	0.91	9	150	1292	- 39°	0.77	0.24	- 22°	0.91	0.82	9	-18	0.95	0.9
OT	CS	5	2.2	0.89	8	158	661	- 23°	0.91	0.30	- 30°	0.89	0.74	5	-29	0.98	0.89
WAL1	C	8	2.3	0.86	10	**120**	534	+23°	0.35	0.21	+22°	0.30	0.60	11	-10	0.99	0.85
WAL1	CS	3	3.7	0.84	10	**165***	986	+143°	0.24	0.38	+172°	0.21	0.73	3	- 20	0.97	0.83
WAL2	C	4	1.5	0.77	9	165	1123	- 120°	0.62	0.27	**+102°**	0.32	0.58	5	-3	0.99	0.8
WAL2	CS	4	1.8	0.71	8	188	897	- 130°	0.85	0.24	**- 58°**	0.33	0.68	5	-13	0.98	0.78

Abbreviations: tr, treatment: C, untreated control pigeons; CS, pigeons clock-shifted 6 h fast. n_c, number of complete tracks; PoDs, mean number of Points of Decision; eff., median overall efficiency of complete tracks. n_b, number of tracks for which the initial phase and the departure phase could be analysed, n_h, number of tracks of which the final homing phase could be analysed. dur.(s), duration of the initial phase to the first Points of Decision in seconds; dist. (m), distance of the first Point of Decision from the release point in meters. Δh, headings with respect to the local home direction; r, vector length of the headings; stead,. median steadiness of flight. Significant differences (P < 0,05) between clock-shifted and control pigeons are marked by an asterisk and indicated in bold.

Supplementary Table S2

ANOVA statistics of the short-term correlation dimension

The short-term correlation dimensions were compared for each site separately by a two way ANOVA with repeated measurements using a factorial design, with the independent factors being (a) experimental treatment, that is, control of clock-shift, and (b) distance from the release sites at which the short-term correlation dimension estimates were taken. When the ANOVA indicated significant differences, we used the Tuckey HSD test to look for differences between controls and clock-shifted pigeons. The test statistics are given in table S1 below

Results of Two way ANOVA for the short-term correlation dimension

Site	Df_w	Control v.s. Clock-shift			Distance From Release Site			Interactions		
		Df_b	F	Sig.?	Df_b	F	Sign?	Df_b	F	Sig.?
BD	355	1	5.94	*	45	2.945	***	34	1.397	n.s.
RB	582	1	22.26	***	38	2.751	***	38	0.447	n.s.
BH	583	1	0.05	n.s.	16	5.562	***	16	1.153	n.s.
OT	255	1	39.32	***	42	3.597	***	36	0.592	n.s.
WAL1	731	1	52.72	***	75	5.407	***	43	0.549	n.s.
WAL2	532	1	74.27	***	95	3.138	***	43	0.743	n.s.

Df_b, degrees of freedom between groups and Df_w, degrees of freedom within groups; F, F-Value of the Anova, with $F(Df_b, Df_w)$, which in the case of $F(1,x)$ is the same for the ANOVA and the Tuckey HSD test; significance levels: n.s, not significant; *, $p<0.05$; ***, $p<0.001$.