RESEARCH ARTICLE

Evidence for discrete landmark use by pigeons during homing

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SUMMARY

Considerable efforts have been made to investigate how homing pigeons (*Columba livia* f. *domestica*) are able to return to their loft from distant, unfamiliar sites while the mechanisms underlying navigation in familiar territory have received less attention. With the recent advent of global positioning system (GPS) data loggers small enough to be carried by pigeons, the role of visual environmental features in guiding navigation over familiar areas is beginning to be understood, yet, surprisingly, we still know very little about whether homing pigeons can rely on discrete, visual landmarks to guide navigation. To assess a possible role of discrete, visual landmarks in navigation, homing pigeons were first trained to home from a site with four wind turbines as salient landmarks as well as from a control site without any distinctive, discrete landmark features. The GPS-recorded flight paths of the pigeons on the last training release were straighter and more similar among birds from the turbine site compared with those from the control site. The pigeons were then released from both sites following a clock-shift manipulation. Vanishing bearings from the turbine site continued to be homeward oriented as 13 of 14 pigeons returned home. By contrast, at the control site the vanishing bearings were deflected in the expected clock-shift direction and only 5 of 13 pigeons returned home. Taken together, our results offer the first strong evidence that discrete, visual landmarks are one source of spatial information homing pigeons can utilize to navigate when flying over a familiar area.

Supplementary material available online at http://jeb.biologists.org/cgi/content/full/215/19/3379/DC1

INTRODUCTION

Research on how pigeons home from distant, unfamiliar sites has been substantially shaped by the justifiably influential map and compass model of Kramer (Kramer, 1959). Less well studied, however, is how homing pigeons navigate when in familiar areas. So-called familiar site navigation first became apparent when homing pigeons, whose navigational map capability was experimentally impaired by inducing anosmia through olfactory nerve sectioning, insertion of nasal tubes or intranasal injection of zinc sulfate, continued to display good homeward orientation and homing performance from release sites they had been to before (Benvenuti et al., 1973; Hartwick et al., 1977; Bingman et al., 1998a), and is thought to be based, at least in part, on visual features in the environment (for reviews, see Holland, 2003; Wallraff, 2005). It was not until the application of global positioning system (GPS) recorders became routine in homing pigeon research that the importance of visual environmental features was experimentally demonstrated (Biro et al., 2002; Biro et al., 2004; Biro et al., 2007; Lipp et al., 2004) (but see Wiltschko, 1991; Wiltschko and Wiltschko, 1998; Wiltschko and Wiltschko, 2001; Holland, 2003).

It has often been assumed that when homing pigeons navigate by familiar, visual features in the environment they do so by relying on what can be referred to as discrete or point-source landmarks (e.g. a large factory tower or a distinctive mountain peak) (Wiltschko and Wiltschko, 1987; Bingman, 1998), which

may be represented as something resembling a cognitive map (O'Keefe and Nadel, 1978). It is therefore surprising that evidence of pigeons using visually recognized, discrete landmarks when homing over a familiar area is lacking. Indeed, the existing evidence from GPS recordings suggests that more linear or continuous visual landscape features, like roads, coastlines and even highway exits, are used for the pigeon's familiar area map rather than discrete landmarks (Lipp et al., 2004; Vyssotski et al., 2009), with a certain amount of 'route loyalty' developing, especially over landscapes with intermediate complexity (i.e. areas with a greater number of visual features, such as buildings, per unit area) (Bonadona et al., 2000; Biro et al., 2002; Biro et al., 2004; Lipp et al., 2004; Meade et al., 2005; Meade et al., 2006; Gagliardo et al., 2009). Thus, pigeon homing over familiar areas may, at least under some circumstances, resemble on a larger scale the panorama navigation of some insect species (e.g. Towne and Moscrip, 2008; Graham and Cheng, 2009).

To examine whether discrete, visual landmarks can be used to guide their homing flights, we trained pigeons from one release site where four large wind turbines (discrete landmarks) were located and a control site that lacked any distinctive landmarks. We predicted that the presence of the turbines would facilitate navigation by enabling the pigeons to fly a more direct path home, allowing them to correct more readily for navigational error following a clock-shift (CS) manipulation compared with homing from the control site without such landmark information.

MATERIALS AND METHODS
Test birds

Fourteen experienced, adult racing pigeons (*Columba livia* f. *domestica* L.) of both sexes, the majority less than 1 year old, were housed at a communal, open-air loft (41°23′43.80″N, 83°37′43.22″E) at Bowling Green State University in Bowling Green, OH, USA. During their first year of life, 10 of the birds were systematically trained to home to their loft from the cardinal compass directions at distances of up to 7.1 km on the north–south axis and 4.7 km on the east–west axis. The remaining four pigeons had obtained experience of up to 43.6 km during previous training and experimental releases. Just prior to the experimental releases reported here, all birds were made familiar with both release sites by being released individually five times from each of the two training sites (see below) in alternating order. All pigeons were hungry at the time of release to ensure motivation to home and no breeding pairs were involved in the releases.

Release sites

Standard pigeon releases were conducted in September and October 2010 from two release sites located in opposite directions but at similar distances from the home loft. Distinct landmarks were absent at the control release site (41°22′17.80″N, 83°33′8.63″W; home direction 293 deg; distance to loft 6.91 km) (Fig. 1A), while at the turbine release site (41°22′30.25″N, 83°44′49.69″W; home direction 77 deg; distance to loft 10.15 km), four large wind turbines (78 m tall towers with 41 m long blades) were located in the homeward direction at 100 deg (T1, southern-most turbine) to 40 deg (T4, northern-most turbine), ranging in distance between 0.52 km (T1) and 1.41 km (T4) (Fig. 1B; Fig. 3C–F). The turbines were operational during the light wind conditions of the releases (typically at a speed of 0.25 rotations s^{-1}). The area surrounding the loft is highly uniform (predominantly agricultural fields only occasionally punctuated by wood lots) and without any noticeable altitudinal variations because of its position on a former lake bottom. Therefore, the only visual interference on the horizon would be the taller buildings at the center of the city of Bowling Green itself. The control site was therefore chosen not at the same distance from the loft as the turbine site but at a roughly equal distance from the city center to ensure the greatest possible similarity of landscape topography available to the birds from the two sites. Pigeons were test released both pre- and post-CS, first from the turbine site and then from the control site. This order was chosen as higher loss rates were anticipated at the control site following CS, and we wanted to insure that enough pigeons would be released from the turbine site post-CS (see Appendix, point 1). It also addressed the potential criticism that a smaller CS deflection from the turbine site could have resulted from a recalibration of the sun compass after prolonged CS treatment.

Standard pigeon release procedure

All releases were conducted under sunny conditions (usually ≤10% cloud cover and sun disk always visible to ensure the availability of the sun compass during homing) and no more than light winds, and meteorological conditions were closely matched for all critical releases. Non-CS releases occurred in the morning and CS releases 6 h later in the early afternoon. Individually released pigeons were followed by one or two observers using 10×40B (Zeiss) or 10×42 (Nikon Monarch) binoculars until they had vanished from the view of both observers (typically at a distance of about 1.5 km). The vanishing bearing (the direction the pigeon was last observed in before vanishing from view) was recorded to the nearest 1 deg using a suspended-needle magnetic compass (Silva, Model 15T).

We also recorded the vanishing time (interval from the time of release until vanishing) with a stopwatch to the nearest second. The loft was checked for returned pigeons shortly after the completion of a release, at sunset of the release day, and in the morning and at sunset of the following 5 days to retrieve GPS units (see below) and determine return rates for each release.

CS procedure

During the 6 h slow CS, pigeons were housed in a light-tight, sound-isolated room in the Bowling Green State University Animal Facility with an artificial light–dark cycle whose light phase started and ended 6 h after the local sunrise and sunset, respectively. Pigeons were placed in the CS treatment 8 (*N*=10) and 10 days (*N*=4) prior to the post-CS turbine release. Returned pigeons (all pigeons returned on the day of release or within the next 2 days) were immediately transferred from the loft for a further 4–7 days of CS exposure before being released from the control site. A slow shift rather than a fast shift was chosen so that the anticipated post-CS flight direction coincided at both sites with a view of the horizon that was as unobstructed as possible.

Fig. 1. View of the horizon in the home direction for (A) the control site (H, home direction) and (B) the turbine site (T1–4, wind turbines 1–4 with T1 being the southern-most turbine).

GPS data loggers

During flock and individual training flights, pigeons carried dummy weights (20 g) of similar size and shape to the GPS data loggers (45×25 mm and 15 g). During pre- and post-CS test releases some pigeons carried one of two types of GPS receiver. Both types were commercially available differential GPS (DGPS) units that have SBAS (satellite-based augmentation systems) capability with positional accuracy of less than 2 m; namely, TechnoSmArt GiPSy-3 micro-GPS data logger (http://www.technosmart.eu) and PigeonTrack GPS data logger (http://www.pigeontrack.com). The GPS data loggers recorded the tracking signal in a continuous mode at intervals of 1 s. Units were turned on at least 15 min prior to a bird's release to ensure real-time DGPS satellite connectivity. Dummy weights and the two types of GPS data loggers were attached to the pigeon's back between the wings using Velcro strips glued to the pigeon's back (after shortening of the feathers at the attachment site with scissors) and to the underside of the dummy weight or GPS data logger.

Data analysis

For both pre- and post-CS releases at each release site, we calculated a mean vector (with 95% confidence limits) from the vanishing bearings, which were tested for non-uniformity using the Rayleigh test. The non-parametric Watson U^2-test was applied to test for differences in the distribution of the pre- and post-CS vanishing directions (CS effect) at each release site and an unpaired t-test to determine any significant difference in the size of the CS deflection between the two sites. An unpaired instead of a paired t-test was necessary because, although the releases from the control and turbine sites were carried out with the same group of pigeons, an insufficient number of pigeons provided vanishing bearings for both of any compared releases to carry out a paired t-test (supplementary material Table S1 for vanishing direction of individual pigeons released pre- and post-6 h slow clock-shift treatment at the two release sites). As vanishing intervals are not normally distributed, we calculated medians instead of means and compared the groups using the Mann–Whitney U-test and the Wilcoxon signed-ranks test for unpaired and paired analyses, respectively (birds that had landed were not included in this analysis as information relating to the duration of the landing interval was not available for most birds). Because of logistical constraints, only return rates but not precise homing speeds were recorded. Return rates and the number of pigeons landing after release were compared pre- and post-CS across sites using the Chi-square goodness-of-fit test. A description of the statistical tests can be found elsewhere (see Batschelet, 1981; Zar, 1999).

For each recorded GPS flight track we calculated an overall efficiency index and tortuosity score. The efficiency index reflects how straight the pigeons flew from the release site to the home loft, by dividing the distance of the release site from the loft by the total GPS track length. That is, the longer the GPS track the lower the efficiency index. We also similarly calculated a 2 km efficiency index, which reflects how straight the pigeons flew until reaching a distance of 2 km from the release site for the first time. Statistical comparisons in efficiency indices were carried out with unpaired t-tests (paired t-tests again could not be carried out for the reason noted above). The tortuosity score indicates the frequency and degree of changes in flight direction. For each track, the angular change in flight direction between consecutive 1 s data points (between 119 and 2032 data points per track) was measured and the mean flight vector was calculated. The length of the mean vector was then taken as the tortuosity score.

For the re-projection and plotting of GPS tracks we used the desktop mapping program ArcGIS (Environmental Systems Research Institute Inc., Redlands, CA, USA). Visualized tracks were screened for artifacts and irregularities in the data. In two of the tracks a few data points were missing, probably due to loss of satellite signal, but the tracks are informative nonetheless and thus were used in the analysis. The initial processing of the raw GPS data included re-projection from the geographic coordinate system with WGS84 (World Geodetic System 1984) datum into the Universal Transverse Mercator (UTM) grid system, Zone 17 North, with coordinates expressed in meters. After re-projection the following attributes were extracted or computed: easting and northing, which are the geographic Cartesian coordinates for each GPS point in meters (used to display the tracks in Fig. 3), distance between GPS points (the distance calculated from consecutive GPS points, excluding data points of distance of less than 5 m between recordings based on the assumption that the birds were not flying during such intervals), and total distance flown (in meters) starting from the release site. The non-directional attributes were quantified by univariate and bivariate exploratory data analysis (EDA).

RESULTS AND DISCUSSION
Pre-CS performance
Vanishing directions and homing performance

As seen in Fig. 2A and Table 1, the pigeons released at the control site were well oriented in the homeward direction on their pre-CS test release (Rayleigh test, $P<0.001$). The mean pre-CS vanishing direction fell within the 95% confidence limit of the predicted home direction (deviation from home direction $\Delta H=-17$ deg). Similarly, pigeons at the turbine site (Fig. 2B; Table 1) were also well oriented on their pre-CS test release (Rayleigh test, $P<0.001$) with a vector length comparable to that of the pigeons at the control site and a very narrow 95% confidence interval that did not include the home direction ($\Delta H=+20$ deg). We interpret the failure of the confidence interval around the mean direction to include the homeward direction
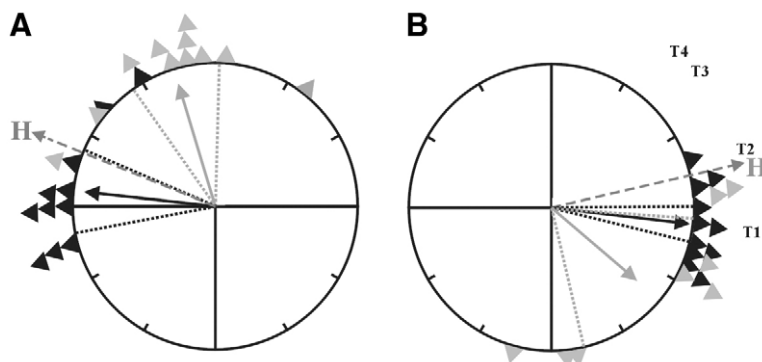

Fig. 2. Vanishing directions of individually released homing pigeons. (A) Control site with pre-clock-shift (CS) (black triangles) and post-CS (6 h slow CS; gray triangles) vanishing directions. Birds were familiar with each release site from five previous training releases. Also shown are mean vanishing vectors (solid arrows) and 95% confidence intervals (dashed lines) for each release as well as the home direction (H). (B) Turbine site; same symbols as control site with wind turbine locations (T1–4).

Table 1. Comparison of vanishing orientation and homing performance pre- and post-6h slow clock-shift treatment at two familiar release sites (with and without distinctive landmarks)

Release site	Treatment	N (n_{van})	α_m (deg)	95% CI (deg)	CS effect (deg)	r	Vanishing time (min:s)	Return rate (%)	Landing rate (%)
Control (293 deg)	Pre-CS	14 (11)	276	±17		0.92***	2:14	100	21
	Post-CS	13 (11)	343	±18	+67 deg**	0.89***	4:05	38	31
Turbine (77 deg)	Pre-CS	14 (11)	97	±7		0.97***	4:43	100	29
	Post-CS	14 (8)	131	±36*	+34 deg$^{n.s.}$	0.78**	4:59	92	57

Release sites are given with the home direction in parentheses. Treatment indicates pre- or post-CS (clock-shift) release. N, number of pigeons released; n_{van}, number of released pigeons with a vanishing bearing (in parentheses). α_m, mean direction at vanishing time. 95% CI, 95% confidence interval for mean vanishing direction. CS effect, clock-shift effect on mean vanishing direction with Watson U^2-test significance level. r, mean vanishing vector length and Rayleigh test significance level. Vanishing time, median vanishing interval. Return rate, percentage of total number of pigeons that returned to the loft. Landing rate, percentage of released pigeons landing at or near the release site (it should be noted that vanishing bearings could sometimes still be obtained from birds that had landed by waiting until the pigeon decided to take flight again and leave the release site).
Significance levels: *$P<0.05$, **$P<0.01$, ***$P<0.001$, n.s., not significant.

to be the result of many of the birds deviating southward to fly around the turbines rather than between them during the initial portion of the flight home (see below).

From both sites, all the pigeons returned to the home loft on the day of their pre-CS release. Looking at the behavior of the pigeons across training, the two release sites were similarly associated with progressively increasing mean vector homeward components. Specifically, whereas during the first two releases the mean homeward component of the pigeon's mean vectors was +0.65 from the control site and +0.59 from the turbine site, mean homeward components of +0.87 from the control site and +0.74 from the turbine site were recorded for the last four training releases prior to CS treatment.

In summary, with respect to vanishing bearings and homing performance, there was very little to distinguish the two release sites prior to the CS; both release sites were associated with increasing homeward components as training progressed and well oriented vanishing bearings close to the home direction on the final release. The only notable difference is that on the pre-CS release the 95% confidence interval around the mean direction did not include the homeward direction from the turbine site.

GPS recordings

In contrast to the traditional homing analyses described above, visual inspection of the recorded GPS tracks revealed interesting differences in the flight behavior of the birds from the two release sites consistent with our prediction of better navigational performance from the turbine site. Notably, compared with the control site (Fig. 3A,B), (1) the pigeons from the turbine site (Fig. 3C,D) generally flew a more direct path to the home loft and (2) there was less inter-individual variation in the flight paths taken.

The visual impression described above was confirmed by statistical analyses on quantitative aspects of the recorded tracks (9 and 11 tracks at the control and turbine sites, respectively). The mean (±s.e.m.) pre-CS efficiency index for the whole track from the control site was 0.64±0.04 (Fig. 4). By contrast, the efficiency index from the turbine site was 0.73±0.02 (Fig. 4), which was significantly greater than that from the control site (one-tailed t-test, $P<0.05$) indicating a more direct path. Even more informative is the mean ratio of the efficiency index of each pigeon's flight up to a distance of 2 km from the release site (i.e. the distance over which the birds' behavior at the turbine site would be most influenced by the obstacle of the turbines, initially leading many of the pigeons to fly a more southerly track with respect to home upon release) when compared with that pigeon's efficiency index over the entire flight (Fig. 4). Here again, there was a significant difference between the two release sites, with the ratio being significantly greater from the control site (1.00±0.05) compared with the turbine site (0.71±0.05) (Fig. 4; one-tailed t-test, $P<0.001$). We interpret this difference to indicate that the pigeons at the turbine site took a straighter path home despite a larger initial displacement from the home direction because of the obstacle of the turbines during the early part of their flight home. The mean pre-CS tortuosity score for the whole track from the control site was 0.52±0.05, whereas at the turbine site it was 0.66±0.03, which reflects a significantly longer mean vector length (one-tailed t-test, $P<0.01$). Up to 2 km from the release site, however, the tortuosity score was significantly greater at the control site (0.62±0.03) than at the turbine site (0.39±0.04; one-tailed t-test, $P<0.001$) indicating a straighter flight path (fewer turns made).

Therefore, although the birds from the turbines overall flew a more direct path home (greater whole-track efficiency index), they flew a more circuitous route up to 2 km from the release site (smaller 2 km tortuosity score). The smaller efficiency index and tortuosity score for the early part of the track are at least in part explained by increased circling behavior before setting on a homeward course as well as many of the pigeons deviating south of the turbines (but a few pigeons did fly near and even between the turbines) away from the homeward direction following release (Fig. 3C,D). Although this finding does not demonstrate that the pigeons were using the turbines to extract positional information for the purposes of navigation, it certainly indicates that they saw and responded to them.

Of similar interest is the apparent smaller inter-individual variation in the GPS-recorded flight paths of the pigeons from the turbine site (Fig. 3C,D) compared with the control site (Fig. 3A,B). To quantify and statistically test this impression we calculated the median distance between a pigeon and all other pigeons when the pigeon was at a distance of 5 km from the release sites. A larger mean median distance would indicate a larger spread in the paths flown. A distance of 5 km was chosen because the pigeons were still relatively far from the home loft yet flew far enough from the release sites to produce the spread observed in the flight paths. The mean (±s.e.m.) of the median distance from the turbine site was 972±161 m, while from the control site it was a considerably larger, 1478±180 m. This difference was in line with our visual impression of greater inter-individual variability in the flight tracks from the control site, but just missed statistical significance (two-tailed t-test, $P=0.0506$). One pigeon from the turbine site (pigeon no. 430; in red in Fig. 3C) was, however, a clear outlier, taking a more southerly route compared with all the other pigeons. Excluding that pigeon from the analysis (for both the turbine site and the control site), resulted in a mean of the median distances for the turbine site of
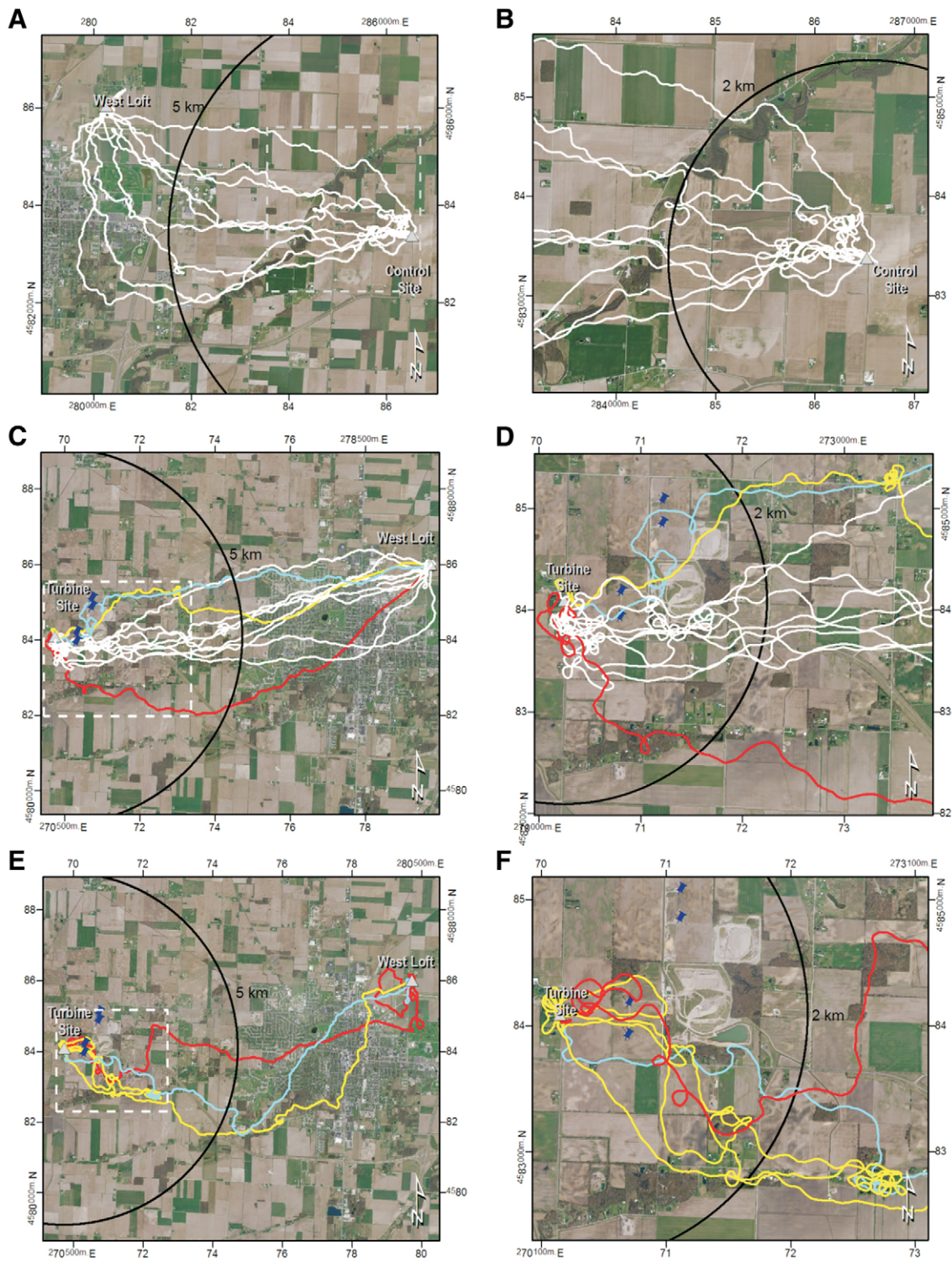
Fig. 3. GPS tracks of homing pigeons released at the control and turbine sites. (A) Full view of the pre-CS tracks at the control site (*N*=9) with the dashed frame encapsulating the enlarged section shown in B. (C) Full view of the pre-CS tracks at the turbine site (*N*=11) with the dashed frame encapsulating the enlarged section shown in D. (E) Full view of the tracks at the turbine site post-CS manipulation (6 h slow CS; *N*=3) with the dashed frame encapsulating the enlarged section shown in F. Tracks for the same pigeon flying in both releases from the turbine site are identified by the color of the track (bird no. 276, 424 and 430 in blue, yellow and red, respectively). The position of the wind turbines is indicated by dark blue push-pins. Units on the axes are easting and northing coordinates (in meters) based on the UTM system (see Materials and methods).

787±92 m, which was less than half the value from the control site (1678±195 m), resulting in a robust significant difference (two-tailed *t*-test, *P*<0.001).

In summary, the analysis of the GPS tracks revealed a pattern of differences between the turbine site and the control site consistent with the hypothesis of the turbines aiding navigation. The turbine
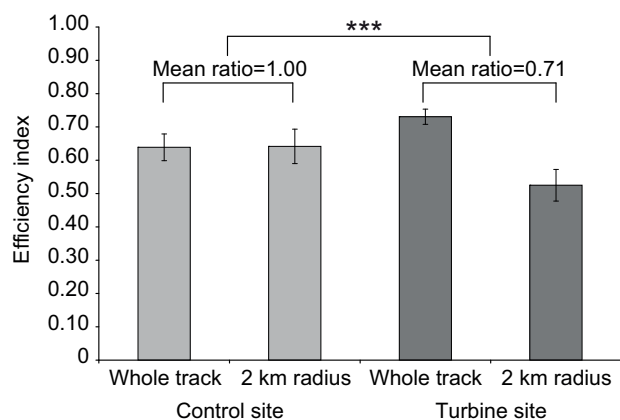
Fig. 4. Mean efficiency index for GPS tracks recorded at the control and turbine sites. Shown is the pre-CS efficiency index for the whole track (the distance of the release site from the loft divided by the length of the whole flight path, and therefore the longer the GPS track the lower the efficiency index) as well as to a distance of 2 km from the release site (2 km divided by the length of flight path to 2 km from the release site). Also indicated is the mean ratio of the 2 km efficiency index for each bird divided by the bird's whole-track efficiency index (***$P<0.001$). Note, the pre-CS whole-track efficiency index from the control site was significantly smaller than that from the turbine site (one tailed t-test, $P<0.05$; not shown).

site was associated with more direct flight paths home and considerably smaller inter-individual variation in those paths. The latter is particularly interesting, because it suggests that the turbines were salient enough to be used in the same way by almost all the pigeons.

Post-CS performance
Vanishing directions and homing performance

As seen in Fig. 2A and Table 1, pigeons released at the control site were also well oriented post-CS (6 h slow CS, Rayleigh test, $P<0.001$). The 95% confidence interval of the post-CS mean vanishing direction was very close to the approximate predicted CS direction (the mean pre-CS vanishing direction +90 deg). As expected, the post-CS vanishing bearings significantly differed from the pre-CS vanishing bearings at the control site. The CS effect (+67 deg relative to the pre-CS release; Watson U^2-test, $P<0.01$) was close to the predicted size and typical of what has previously been found for CS releases from familiar sites (Wiltschko et al., 1994).

By contrast, the majority of the vanishing bearings from the turbine site lay close to the mean pre-CS vanishing direction, with only a few birds vanishing in the expected CS direction. The discontinuous distribution of vanishing bearings reduced the vector length (but still, Rayleigh test, $P<0.01$) and quadrupled the size of the 95% confidence interval compared with the pre-CS turbine release. Importantly, and in notable contrast to the control site, the post-CS vanishing bearings from the turbine site did not differ from the pre-CS vanishing bearings from the same site, with the size of deflection after CS (+34 deg; Watson U^2-test, n.s.) only about half that observed at the control site. Indeed, there was a significant difference in the size of the CS deflection between the two sites (one-tailed t-test, $P<0.05$). Thus, at the control site in the absence of any distinctive landmarks indicating the direction home, the manipulated directional information provided by the sun compass was largely hierarchically dominant over the largely homogeneous visual landmark and landscape features, resulting in the birds leaving

the release site in a direction clearly shifted clockwise from the home direction. The smaller CS deflection at the turbine site indicates that the presence of distinct and discrete visual landmarks can dampen the erroneous sun compass-induced CS effect, enabling the pigeons to steer a course closer to the home direction. As seen in Fig. 2B, more than half the birds appeared to have completely ignored their sun compass, vanishing in a direction indistinguishable from the pre-CS vanishing bearings.

Despite the CS manipulation, 13 of 14 birds returned home from the turbine site post-CS (the one bird that did not return was one that flew off in the expected CS direction). In stark contrast to this, only 5 of 13 birds returned from the control site (Chi-squared goodness-of-fit test, $P<0.01$). The striking difference in homing success post-CS from the two sites is consistent with the vanishing bearing data. Thus, as discussed above, the CS birds from the control site displayed a larger CS deflection relative to the home direction and clearly had difficulty correcting for that initial error. By contrast, the presence of the turbines was associated with smaller deflections and seemingly promoted the successful homing observed from that site. This is consistent with our hypothesis of the turbines acting as visual landmarks that guided the CS pigeons closer to the home direction during initial orientation.

There is of course the possibility that because the critical releases were carried out on two different days, this could have caused the significant differences in navigational strategies and homing performance we observed in the pigeons instead of the presence of the wind turbines at one site. We think this highly unlikely because all 14 pigeons used in the critical releases pre- and post-CS had previously been released 6–7 times from both release sites with good orientation behavior as well as very high return rates and return speeds in each case. Therefore, the birds would have actually experienced more variation in weather, molting condition and motivational factors over the course of several weeks of training flights than during the 2 days of critical releases. Yet, the differences seen in the data were only apparent during the critical releases from the two sites, which occurred within a few days of one another.

GPS recordings

In comparison to the pre-CS GPS tracks, the post-CS tracks are less informative. Because eight of 13 pigeons did not return from the control site after displaying a strong CS deflection in their vanishing bearings, the tracks of the five pigeons that did return are not representative of the group and therefore are not presented (but see supplementary material Fig. S1 for post-CS tracks at the control site). Also, because of technical issues with the GPS data loggers, the flight paths of only three pigeons were recorded post-CS from the turbine site (Fig. 3E,F), but fortunately those three birds had also provided tracks pre-CS from this site. The post-CS flight behavior at the turbine site was characterized by only a weak CS effect seen in the flight paths of the three birds, consistent with the majority of the vanishing bearings for this release. The behavior of all three birds is in line with that of approximately one-third of CS pigeons released at familiar sites, which in the absence of discrete visual landmarks like the turbines, displayed GPS tracks that did not show any or only a reduced CS deflection, but instead followed stereotyped pre-CS routes (Biro et al., 2004). What is notable is that the distance flown, with an inverse effect on efficiency index, for all three birds at the turbine site was greater post-CS compared with their pre-CS values, with the mean whole-track post-CS efficiency index (0.43 ± 0.08, mean ± s.e.m.) being almost half that of the pre-CS value (0.71 ± 0.03) (one-tailed paired t-test, $P<0.05$). Similarly, the

example, at Castor Hill in New York where pigeons inexplicably fly in directions very different from home, and more importantly depart in very different directions compared with other nearby release sites (Keeton, 1974). As such, the data reported here support the hypothesis of a navigational role for discrete visual landmarks in the homing behavior of pigeons.

One notable consideration is the possibility that the infrasound noise produced by the running turbines would have contributed as an auditory landmark in addition to the hypothesized salient visual directional cue provided by the wind turbines. Infrasound cues have previously been proposed to play a role in pigeon navigation (e.g. Hagstrum, 2000). We believe it to be highly unlikely, though, that the pigeons only used auditory spatial information provided by the turbines, just as pigeons are unlikely to follow roads and railway tracks based on sound cues alone. In other words, in contrast to visual cues, sound is a sensory cue that is not easily localized with high precision, and therefore could aid identification of visual landmarks but is highly unlikely to be a persuasive landmark cue in itself. Another alternative interpretation, unlikely but worth noting, is that the presence of the turbines as a familiar landscape feature may have reduced the stress associated with the conflict between the familiarity of the turbine release site and the CS manipulation. This in turn may have caused the pigeons to settle down and switch to the previously learned home direction for the turbine site.

What remains unclear is whether the pigeons used the turbines as landmarks as part of a map for position determination or whether the turbines simply acted as attractor reference points that dampened individual variation in flight paths and prevented the birds, when clock shifted, from flying too far in the CS direction until they were able to orient home by familiar features that may or may not have included the turbines. We look forward to future experiments that explore more thoroughly the conditions that promote the use of discrete visual landmarks and how they may contribute to navigation.

One important factor that led to our conclusion that discrete visual landmarks are likely to play a role in homing pigeon navigation was the dampened effect of the CS manipulation on vanishing bearings from the turbine site. Based on the observation that the effect of CS manipulation on vanishing bearings is almost always somewhat smaller than expected (Wiltschko et al., 1994), two uses of visual environmental features during familiar area navigation by homing pigeons have been suggested. During 'piloting', pigeons use landmarks to reach their goal without the use of any compass information (e.g. Biro et al., 2002; Meade et al., 2005), whereas if landmarks are used in a 'mosaic map', the spatial relationship between individual landmarks is recalled in the form of compass directions (e.g. Bingman et al., 1998b; Wallraff et al., 1999; Kamil and Cheng, 2001). Most recent evidence analyzing GPS tracks of CS pigeons released at familiar sites suggests a dual system that integrates piloting and compass orientation (Biro et al., 2004), and the type of landscape flown over at the time may determine the relative contribution of the two systems (Bonadona et al., 2000; Gagliardo et al., 2005). The results reported here suggest that the final spatial behavioral output of our pigeons from the turbine site, at least following CS, is more akin to piloting.

Although touched on above, we would like to highlight what we think are interesting comparisons with previous GPS studies from familiar sites. Firstly, Bonadona et al. noted that the degree of deflection following a CS manipulation could vary among different release sites and suggested that the availability of visual landscape information could lead to a reduced CS effect (Bonadona et al., 2000). Our results extend this finding by indicating that discrete

landmarks can have a similar effect and leave us wondering whether in the previous study something resembling discrete landmarks may have been accessible to the pigeons from the release site associated with a small CS deflection (Bonadona et al., 2000). Secondly, Meade et al. noted that homing pigeons trained from familiar sites acquired stereotypical and, more importantly, idiosyncratic flight paths in returning home (Meade et al., 2005; Meade et al., 2006). Similar idiosyncrasy is suggested by the recorded flight paths of our pigeons from the control site. Of more interest, however, is the relative lack of idiosyncrasy from the turbine site, suggesting that the presence of conspicuous, discrete landmarks may be routinely adopted by pigeons in representing a route home and may thus diminish idiosyncrasy/variation across pigeons.

As noted above, the role of discrete visual landmarks and more continuous landscape or panoramic features has attracted the interest of researchers studying hymenopteran navigation (e.g. Towne and Moscrip, 2008; Graham and Cheng, 2009). From a comparative perspective, it is noteworthy that insects navigating on a smaller spatial scale visually exploit both landscape panoramas and discrete landmarks for navigation in a manner that at least resembles the same ability in homing pigeons. For one ant species, the Australian *Melophorus bagoti*, the importance of panoramas even seems to supersede discrete landmarks in guiding navigation from a remote location with respect to the home nest (Wystrach et al., 2011).

One important outcome of the recent findings related to insect navigation is that it has highlighted the question of how discrete landmarks and landscape features/panoramas collectively contribute in guiding navigation. Based on the current study looking at discrete landmarks and more recent landscape-oriented work (e.g. Biro et al., 2002; Lipp et al., 2004), the very same questions about how the different sources of visual information collectively contribute to navigation can be asked of homing pigeons. To answer this question, it will be important to take into consideration differences in scale, point of view and relative speed of movement that might determine how landmarks, continuous landscape features and panoramic characteristics are weighted during navigation by a flying mega-fauna species, such as the homing pigeon, compared with slower moving, small-bodied animals such as insects. Furthermore, it is likely that for homing pigeons there is some flexibility built into the navigational system determining whether landmarks and/or continuous landscape features can supersede sun compass-guided homing depending on the complexity of the landscape the pigeon is flying over as evident from a previous study (Bonadona et al., 2000) and our work. Given that the nearby skyline of Bowling Green would have provided in our study only limited panoramic cues because of the absence of any skyscraper-style buildings and given the fact that we chose the two release sites such that the Bowling Green would have provided similar panoramic cues at both sites, we cannot make any inference as to the relative contribution of panoramic cues in conjunction with a strong landmark cue. We suggest that this interesting issue might be addressed by future studies. A recent study has also indicated that despite route fidelity at familiar sites, a small CS-induced deflection always remains (Biro et al., 2007) suggesting that compass cues are routinely consulted during familiar area navigation. Nevertheless, despite very different evolutionary histories, very different nervous system organizations and navigation over very different spatial scales, the similar challenges in trying to understand landmark and landscape navigation in birds and insects highlights the salience of visual environmental features in shaping the evolution of navigational systems.

CONCLUSIONS

In summary, homing pigeons released from a familiar site characterized by distinct and discrete landmarks displayed a pattern of orientation and flight behavior that resulted in straighter paths home, greater inter-individual similarity in paths flown, and a superior ability to correct for navigational error and return home following CS compared with the same birds released from a site lacking such conspicuous landmarks. Consistent with our predictions as laid out in the Introduction, the data support the hypothesis that discrete visual landmarks can assist navigation in homing pigeons.

APPENDIX

Given that experimental pigeon releases are usually logistically and technically demanding, we would like to make the following suggestions regarding the experimental methods for any future studies.

(1) To ensure a more reliable return rate of pigeons carrying GPS units, we suggest the use of pigeons with at least 2 years of homing experience.

(2) The two types of commercially available GPS units used in this study were only intermittently reliable in their acquisition of data. We are therefore currently looking forward to improvements to the GPS technology available for tracking homing pigeons.

(3) Ideally, enough pigeons should be trained and fitted with GPS units to permit simultaneous post-CS releases at the two sites.

(4) An automated time scoring system installed at the loft and transponder rings attached to the pigeons' feet would have provided additional data in the form of accurate homing times.

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