

How the viewing of familiar landscapes prior to release allows pigeons to home faster: evidence from GPS tracking

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Summary

Providing homing pigeons with a 5 min preview of the landscape at familiar sites prior to release reliably improves the birds’ subsequent homing speeds. This phenomenon has been taken to suggest that the visual panorama is involved in familiar-site recognition, yet the exact nature of the improvement has never been elucidated. We employed newly developed miniature Global Positioning System (GPS) tracking technology to investigate how access to visual cues prior to release affects pigeons’ flight along the length of the homing route. By applying a variety of novel analytical techniques enabled by the high-resolution GPS data (track efficiency, virtual vanishing bearings, orientation threshold), we localised the preview effect to the first 1000 m of the journey. Birds denied preview of a familiar landscape for 5 min before take-off flew an initially more tortuous path, including a high incidence of circling, possibly as part of

an information-gathering strategy to determine their position. Beyond the first 1000 m, no differences were found in the performance of birds with or without preview. That the effect of the visual treatment was evident only in the early part of the journey suggests that lack of access to visual cues prior to release does not result in a non-specific effect on behaviour that is maintained throughout the flight. Instead, it seems that at least some decisions regarding the direction of home can be made prior to release and that such decisions are delayed if visual access to the landscape is denied. Overall, the variety of approaches applied here clearly highlight the potential for future applications of GPS tracking technology in navigation studies.

Key words: homing pigeon, *Columba livia*, navigation, vision, GPS tracking.

Introduction

Whether homing pigeons rely on the visual landscape to guide their journey home has long been a subject of debate. Although the birds are capable of completing much of the homeward journey even if denied access to detailed visual cues (Schmidt-Koenig and Schlichte, 1972; Schmidt-Koenig and Walcott, 1978), reliance on such cues, when available, has been demonstrated in a series of so-called ‘preview’ experiments over the past decade (Braithwaite and Guilford, 1991; Braithwaite, 1993; Braithwaite and Newman, 1994; Burt et al., 1997; Gagliardo et al., 2001; Biro et al., 2002). In this paradigm, pigeons passively displaced from home are released following a 5 min period during which they are either allowed to view their surroundings or are denied access to visual landscape cues. A robust effect, demonstrated consistently in these studies, is the enhanced homing speed of birds given the preview opportunity. This finding is generally attributed to improved recognition of the release site based on visual cues; however, an alternative explanation is the possibility that a non-specific effect such as increased confidence or motivation to home could account for the

superior homing speeds of birds provided with the preview. Due to the nature of experimental techniques traditionally employed in studies of homing pigeon navigation (Papi, 1992), it has not been possible to pinpoint what aspects of the birds’ behaviour led to the emergence of the difference. Measures of homing performance have included vanishing bearings (compass direction in which a bird is last seen before disappearing from the release site) and homing speeds (calculated from the length of time birds take to arrive at the loft following release), while the exact route taken by the birds to reach home has often remained a mystery.

Previous attempts at reconstructing flight paths have included tracking birds from aeroplanes or helicopters either by eye (Griffin, 1952; Wagner, 1975) or in combination with radiotracking (Michener and Walcott, 1966, 1967), as well as recordings with the aid of an on-board route-recorder of compass headings at regular intervals (Bramanti et al., 1988; Bonadonna et al., 1997). While none of these techniques has established itself as a popular alternative to traditional methods due to high costs and low resolution, the recent development of

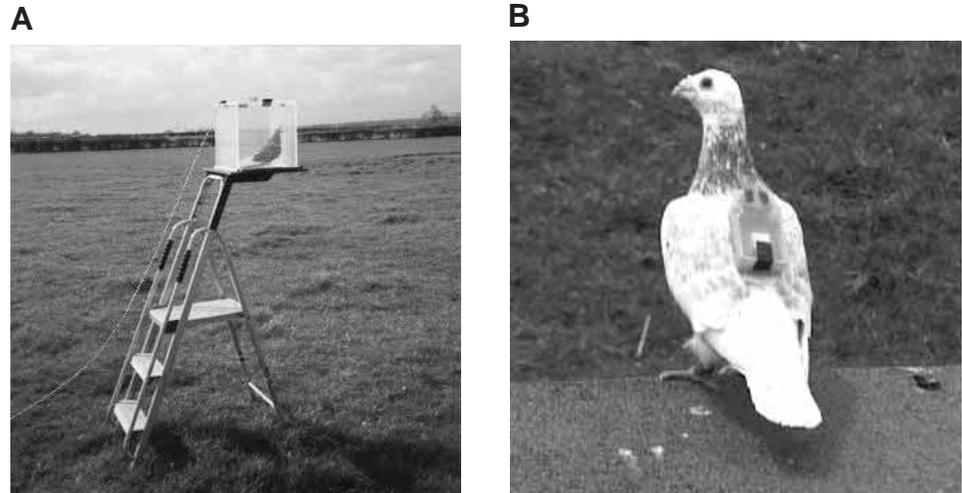


Fig. 1. (A) Homing pigeon inside release apparatus. Depending on the experimental treatment, the vertical sides of the release box either remained transparent (VIS+) or were made opaque (VIS-). (B) Homing pigeon fitted with a GPS tracker. The device is held in a plastic casing and is attached to the back by Velcro.

lightweight Global Positioning System (GPS) tracking (Steiner et al., 2000) represents a step-change in the technology. It is now possible to reconstruct the detail of homing paths highly accurately. We examined tracks recorded from birds with preview (VIS+) and without preview (VIS-) conditions in order to elucidate the effects of this visual treatment at the level of the flight paths themselves. We used short distance releases, shown in the past to reveal the treatment difference most sensitively (Braithwaite, 1993), as well as being valuable in exploring the role of extravisual brain structures implicated in navigational processes (Bingman and Mench, 1990). Whilst GPS technology has been applied in the study of pigeon homing (von Hünenbein et al., 2000; Steiner et al., 2000) and orientation in other birds (Weimerskirch et al., 2002), our work represents the first application of GPS tracking following an experimental manipulation.

Materials and methods

Subjects

12 homing pigeons *Columba livia* L. bred at the University Field Station, Wytham, England were used. Selection of participants was based primarily on two factors: past homing reliability and body mass. All subjects chosen were between the ages of 2 to 6 years, had participated in previous homing experiments, and weighed no less than 480 g. Food, water, minerals and grit were provided *ad libitum*, and the condition of birds (feather condition, body mass) was monitored throughout the study.

All subjects were fitted with a strip of Velcro attached to the back. Feathers between the wings were clipped to approximately 2 mm over a 35 mm (width) \times 90 mm (length) area. Two-component glue (Araldite) was used to attach a strip of 'male' Velcro to this area, making sure that no lateral movement of the strip was permitted. For 2 weeks prior to the experiment, birds lived with Plasticine weights (25 g) attached to the back by Velcro, to accustom them to walking and flying with the load. In the second week, they were taken daily on short-distance (1–2 km) releases with 35 g Plasticine weights

resembling the dimensions of the GPS trackers (see below). Following the end of the experiment, birds were allowed to shed the Velcro through the natural growth of feathers.

Release apparatus

Birds were released from a specially constructed release box mounted on an aluminium stepladder at a height of 1.5 m (Fig. 1A). The box measured 30 \times 30 \times 30 cm and consisted of four vertical Perspex faces, a wire mesh bottom (providing access to local odour cues), and a transparent Perspex lid (permitting view of the sun and the sky). The spring-mounted lid was operated remotely by the experimenter pulling on a 10 m string. The four vertical sides of the box could be made opaque by sliding white Perspex sheets into position along the outer surfaces of the box, whilst access to non-visual environmental cues remained identical under the VIS+ and VIS- conditions.

GPS trackers and data handling

Flight paths were reconstructed using miniature GPS trackers developed for homing pigeons initially at the Swiss Federal Institute of Technology (Bürge and Werffeli, 1999), and now available at NewBehavior (Zürich, Switzerland, <http://www.newbehavior.com>). Including the plastic casing, the trackers measured 71 mm (length) \times 41 mm (width) \times 17 mm (height), weighed 35 g, and consisted of a GPS receiver module with datalogger (μ -blox, Thalwil, Switzerland), antenna, user interface circuits, and a CR2 (3 V) battery (for a full technical description, see Steiner et al., 2000). They were attached to the birds using Velcro strips (Fig. 1B). Time-stamped positional fixes were logged by the trackers every second, and were downloaded after recovery of the trackers using the dedicated software μ -logger. The accuracy of the device in calculating longitude and latitude coordinates has been determined as \pm 4 m (Weimerskirch et al., 2002).

Commercially available Fugawi™ Moving Map software (Northport Systems Inc., Toronto, Canada) was used to superimpose tracks on digitised British Ordnance Survey maps and to calculate track lengths and compass headings.

Table 1. Average performance of birds released following preview of the landscape (VIS+) and those released without preview (VIS-)

Release site*	Treatment	Homing speed (m s ⁻¹)	Track efficiency			Track length within 500 m segments measured from release site (m)		
			Overall	First half	Second half	0–500	500–1000	1000–1500
Binsey	VIS+	13.8 (1.6)	0.79 (0.07)	0.73 (0.10)	0.90 (0.06)	763.3 (154.8)	671.3 (174.5)	674.2 (193.1)
2.9 km, 314°	VIS-	12.3 (3.3)	0.69 (0.18)	0.64 (0.23)	0.87 (0.07)	1036.4 (691.1)	920.3 (702.5)	632.3 (194.6)
Worton	VIS+	10.6 (2.1)	0.64 (0.12)	0.58 (0.15)	0.82 (0.11)	1092.3 (351.1)	855.2 (572.2)	697.8 (251.4)
2.3 km, 153°	VIS-	9.6 (1.8)	0.57 (0.09)	0.49 (0.12)	0.77 (0.09)	1212.5 (354.8)	1089.3 (473.0)	773.7 (243.8)
Wytham Hill	VIS+	15.0 (2.2)	0.71 (0.09)	0.67 (0.10)	0.90 (0.06)	882.5 (169.4)	652.3 (142.5)	644.9 (107.2)
2.0 km, 047°	VIS-	12.3 (3.8)	0.58 (0.16)	0.48 (0.16)	0.92 (0.07)	1366.1 (488.7)	790.1 (441.4)	797.6 (689.8)
St Frid. Farm	VIS+	9.2 (1.4)	0.63 (0.10)	0.56 (0.14)	0.77 (0.06)	1383.6 (637.0)	876.8 (379.8)	832.0 (541.8)
3.9 km, 247°	VIS-	7.3 (2.8)	0.50 (0.15)	0.43 (0.19)	0.72 (0.12)	2663.0 (2832.4)	1445.7 (1053.4)	667.1 (146.4)

*Showing aerial distance and compass direction to home.
Values in parentheses are s.d.

Release sites, training, and testing

Birds were familiarised with four release sites located at distances ranging from 2.0 to 3.9 km from the home loft and distributed in opposite compass directions (Binsey: distance to home, 3.2 km; direction to home, 314°; St Frideswide's Farm: 3.9 km, 247°; Worton: 2.2 km, 158°; Wytham Hill: 2.2 km, 41°). Eight training releases were performed for each bird at all four sites, four as part of a flock, and four as single-tosses. 35 g Plasticine weights were carried throughout training. Subjects were transported to sites by car, inside an aluminium carrying box covered with a white cotton sheet. The eight training releases at each site were interspersed with training at the other sites.

Once training had been completed, birds were tested at the four sites in turn. All subjects received test releases under both the preview (VIS+) and no-preview (VIS-) conditions, with all releases at a given release site being completed within the same day. One at a time, individuals were fitted with a GPS tracker and transferred to the release box with the experimenter's hand cupped over the head to prevent viewing of the landscape. In the VIS+ condition, the opaque vertical sheets were removed to allow access to local visual cues, while in the VIS- condition the opaque sheets were left in place. Birds remained in the box for 5 min, after which the lid was sprung open and they were permitted to exit. After the first release of each day, subjects were collected at the home loft and transported back to the same site for the second release. On average, approximately 50 min passed between the two releases. The order of receiving the VIS+ and VIS- treatments was counterbalanced among the 12 subjects at each site. For each bird, order of receiving the two treatments was counterbalanced across the four sites.

Results

A total of 96 flight tracks were recorded from the 12 subjects (two releases per subject at each of four sites), shown in Fig. 2. The detailed nature of the GPS tracks lends itself to a variety

of ways of analysing the data. We begin by relating the findings of this experiment to those of previous studies using analogous measures, followed by more specialised analyses that are possible only with the aid of the GPS device.

Homing speed

We calculated homing speeds by noting, in the GPS tracks, the time of release and the time of arrival (defined as reaching within approximately 20 m of the home loft) of each bird, and dividing the beeline distance between release site and home by the journey time. In the event of a stopover prior to arrival, the time spent resting was subtracted from the total journey time. Table 1 shows mean homing speeds for birds under the VIS+ and VIS- treatments at all four sites. As with previous studies, the VIS+ condition produces faster homing, with an average 18% improvement in homing speeds over VIS-. When within-individual differences in performance are examined, the effect is similarly seen. At three of the four sites, birds reached home significantly faster under VIS+ (Wilcoxon matched-pairs signed-ranks tests; Worton: $Z=-1.96$, Wytham Hill: $Z=-2.43$, St Frideswide's Farm: $Z=-2.12$; $N=12$ and $P<0.05$ for all three sites; Binsey: $N=12$, $Z=-1.25$, $P>0.05$). Overall, 10 out of the 12 subjects homed on average faster when provided with a view of the landscape at a site prior to release than when denied this preview opportunity: a highly significant result (Wilcoxon matched-pairs signed-ranks test; $Z=-2.67$, $N=12$, $P<0.01$; Fig. 3). Thus, the improvement detected in this experiment is comparable to the 12–18% difference found in birds tested without the GPS load (Braithwaite and Guilford, 1991; Burt et al., 1997).

What do homing speeds calculated on the basis of homing time and homing distance reflect? Birds may take longer to return home for a variety of reasons. Lower absolute flight speeds as well as a tendency to land before reaching home (both of which may suggest a decreased motivation to home) would lead to longer homing times. Alternatively, the latter may also arise when relatively direct paths are replaced by

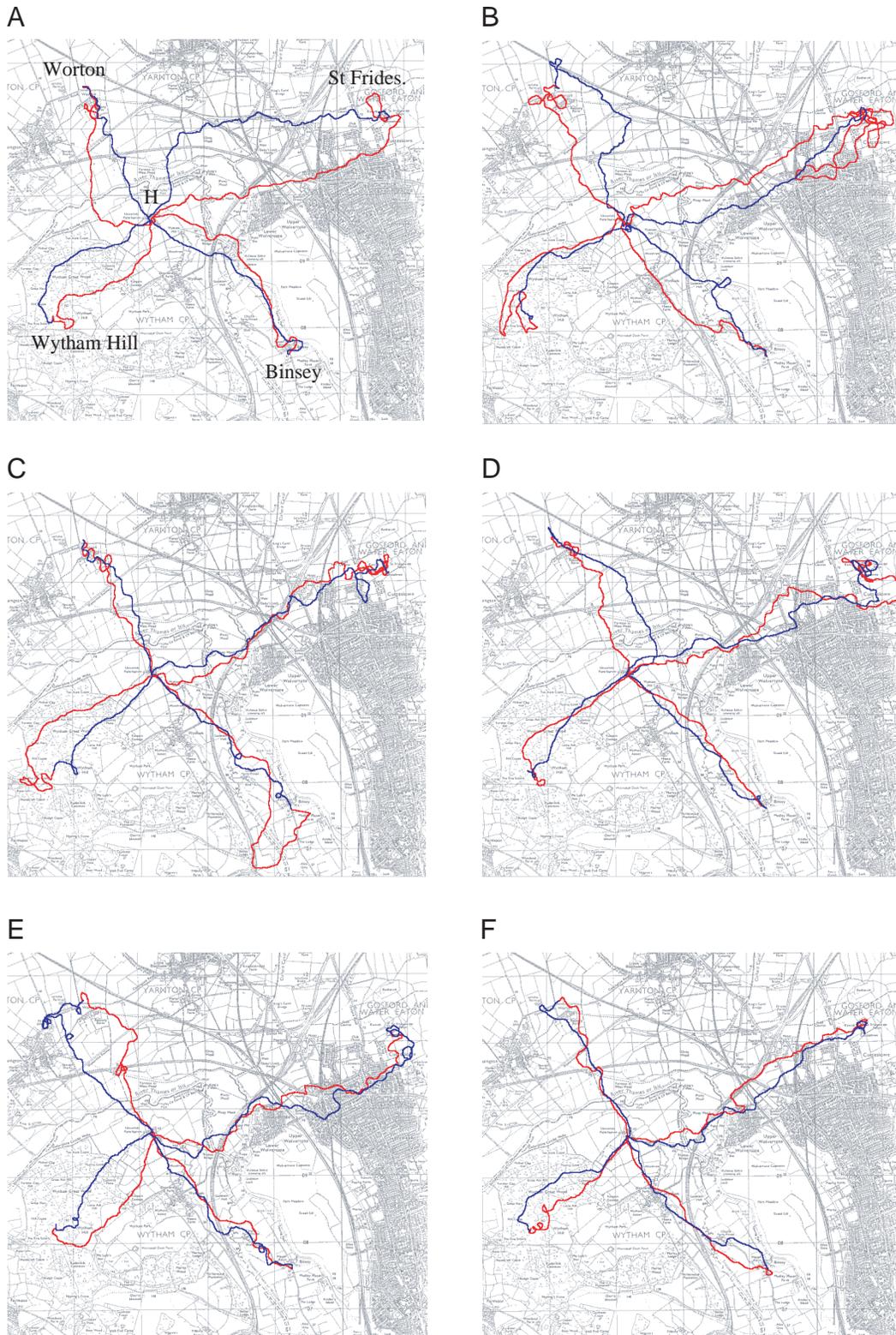
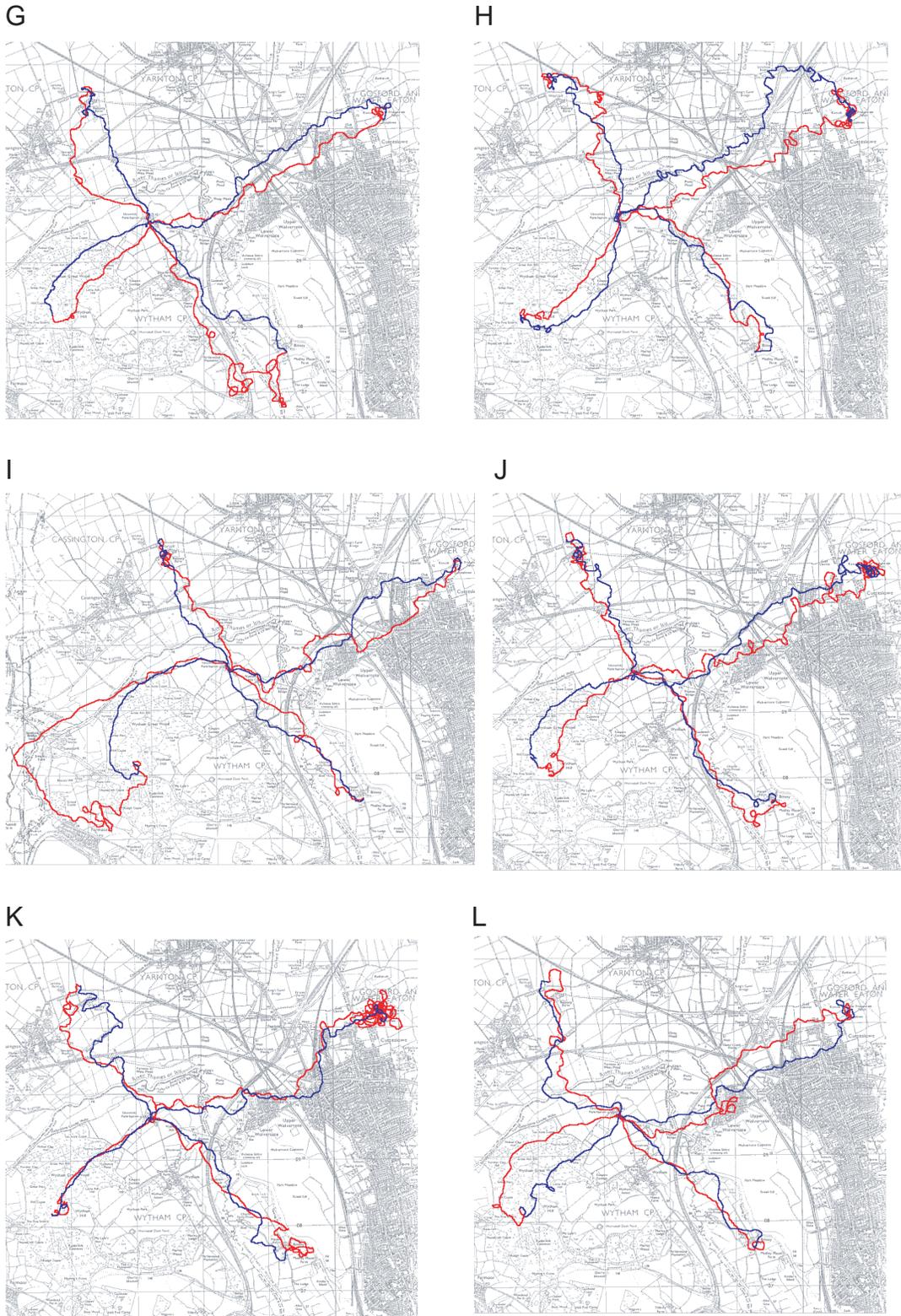


Fig. 2. Flight tracks of 12 subjects (A–L) reconstructed using GPS data. Position fixes were taken every second. The panels show, for each subject, two releases from each of four sites (locations indicated on first panel were the same for all panels; H, home). Lines in blue, VIS+ tracks; lines in red, VIS– tracks. Map grid, 1 km².

Fig. 2. *Continued*

more tortuous ones. The first two of these possibilities can be discarded: (1) mean instantaneous flight speed (a derived measure calculated by the GPS device at 1 s intervals) did not differ significantly between the two treatments

($20.3 \pm 2.5 \text{ m s}^{-1}$ for VIS- and $20.0 \pm 2.9 \text{ m s}^{-1}$ for VIS+; paired *t*-test, $P > 0.05$), and (2) from the 96 tracks recorded, only in one did a bird land before reaching home. Such homing speeds also indicate that the birds were not substantially

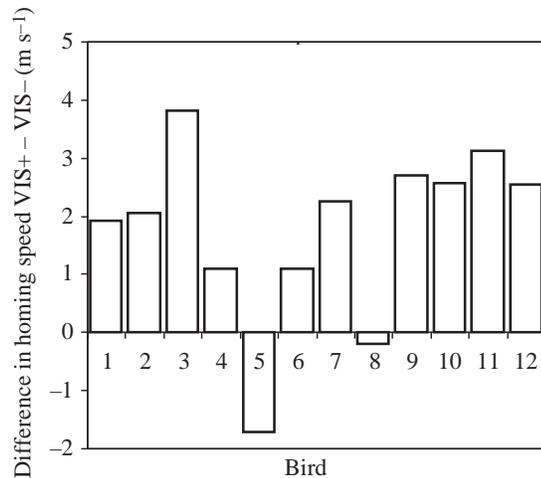


Fig. 3. Mean difference in homing speeds of individual birds following a 5 min pre-release phase, during which they were either allowed to view the landscape (VIS+) or were denied visual access (VIS-). Bars show within-bird differences under the two treatments, calculated as $\text{speed}_{\text{VIS}+} - \text{speed}_{\text{VIS}-}$ and averaged across all four sites.

handicapped in flying by the additional load. The third possibility is examined below.

Track efficiency

Whole journey

Positional fixes logged every second by the GPS device allow a highly detailed reconstruction of the paths taken by birds to be done. We calculated distances moved within each 1 s interval; these, when summed over the whole length of the journey, were used to approximate the total length of track travelled by subjects to reach home. By further dividing track length by the distance to be travelled (i.e. the aerial distance separating a release site from home), the efficiency of the track can be calculated. A completely direct journey home would produce a track efficiency of 1.0, while more tortuous paths would lead to lower values (Batchelet, 1981).

Table 1 lists average track efficiency under the VIS+ and VIS- treatments at the four release sites. As in the case of homing speed, within-bird differences under the two conditions were used for statistical analysis (Fig. 4). The pattern here was highly significant, with all but one bird having on average higher track efficiency under the VIS+ condition (Wilcoxon matched-pairs signed-ranks test, $N=12$, $Z=-2.75$, $P<0.01$). The subject responsible for the single exception (Bird 5; tracks shown in Fig. 2E) consistently flew less efficient paths under the VIS+ condition, a feature that remains evident in the analyses that follow (see Discussion).

Journey segments

Do the differences in track efficiency described above reveal differences between the performance of VIS+ and VIS- birds throughout the length of the route taken or can they be localized to specific segments? To address these possibilities, tracks were broken down into segments in terms of a range of

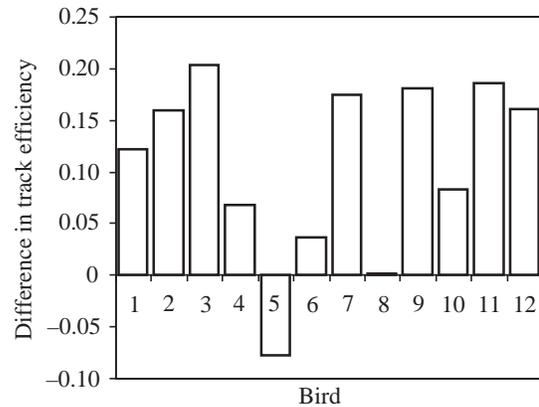


Fig. 4. Average difference in track efficiency (beeline distance/distance travelled) following release under VIS+ and VIS- conditions. Bars show within-bird differences under the two treatments, calculated as $\text{efficiency}_{\text{VIS}+} - \text{efficiency}_{\text{VIS}-}$ and averaged across all four sites.

distances travelled by birds as measured from the release site. First, we divided tracks into two sections, based on the halfway distance between release site and home, and examined track efficiency in the first and second 'halves' of the journey (Table 1).

Track efficiency differed significantly in the first half of the journey at two of the four sites (paired t -test, $N=12$; Wytham Hill and St Frideswide's Farm: $P<0.05$, Binsey and Worton: $P>0.05$), but at none of the sites during the second half ($P>0.05$ for all sites). Analysis of within-bird average difference in track efficiency reveals significantly higher track efficiency under the VIS+ condition in the first half of the journey (Wilcoxon matched-pairs signed-ranks test, $Z=-2.67$, $N=12$, $P<0.01$) but not in the second (Wilcoxon matched-pairs signed-ranks test, $Z=-1.65$, $N=12$, $P>0.05$). In addition, the second half of the journey was characterised by significantly higher track efficiency: 0.85 ± 0.09 (second half) versus 0.64 ± 0.14 (first half) under VIS+, and 0.82 ± 0.12 (second half) versus 0.51 ± 0.19 (first half) under the VIS- condition (paired t -tests: $P<0.005$ at all sites and under both conditions). Track efficiency in the second half approached 1, suggesting that by this stage birds tended to deviate little from a beeline track towards home.

To examine the early part of the journey in more detail, we also measured the length of track flown by birds before they passed beyond given distances (in 500 m increments) measured from the release point. Fig. 5 shows that reaching a distance of 500 m from the release site was accompanied by significantly longer tracks in the case of the VIS- treatment (Wilcoxon matched-pairs signed-ranks test, $Z=-2.20$, $N=12$, $P<0.05$), as was passing over a further 500 m (500 m to 1000 m segment: $Z=-2.12$, $N=12$, $P<0.05$). However, no differences between the performance of birds under the two visual treatments were found beyond this point (1000 m to 1500 m segment: $Z=-0.08$, $N=12$, $P>0.05$).

These results therefore confirm that the increase in homing

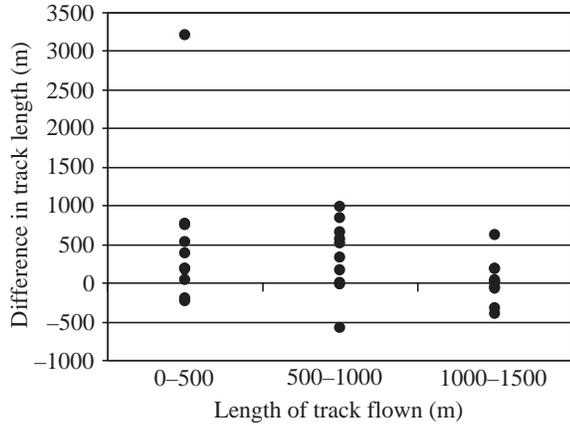


Fig. 5. Effect of visual treatment on the length of track flown by birds ($N=12$) before passing the 500 m, 1000 m and 1500 m boundaries, measured from the release site. Dots show, for each bird, differences in the length of track flown to cross each of the three segments, calculated as $\text{track length}_{\text{VIS-}} - \text{track length}_{\text{VIS+}}$, and averaged across the four release sites.

time and track length associated with the VIS- treatment is not a general effect that is maintained throughout the whole of the homeward journey. Instead, the effect seems localised to the first half, and specifically, to the first 1000 m of the journey, after which the performance of VIS- birds does not differ from that of birds given the VIS+ treatment.

Virtual vanishing bearings

GPS tracks provide data on the orientation of birds relative to home and the release site at any desired point along the journey. We utilised this to collect information on the degree of homeward orientation of VIS+ and VIS- birds at various stages of the flight. In order to relate these findings to the data reported above, bearings were first collected at 500 m

increments: the birds' positions relative to home were measured at the point they first reached the 500 m, 1000 m and 1500 m boundaries measured from the release site. Statistical analyses carried out in this part of the work are standard circular statistical methods (Batchelet, 1981).

Table 2 lists the average angles of heading at the boundaries of each 500 m segment for birds under both treatments and at all four release sites. *V*-tests showed that both treatment groups were significantly homeward-oriented at all sites and at all three distances ($P < 0.05$ for all at 500 m, $P < 0.0001$ for all at 1000 m and 1500 m). Orientation did not differ significantly between treatments at any of the sites and distances (Mardia-Watson-Wheeler test, $P > 0.05$ for all comparisons).

If already well oriented at 500 m, at what earlier point did birds converge on the home direction? We examined orientation at distances less than 500 m from the release point (Table 2). At 125 m only one (VIS+ at Binsey) of the groups was homeward oriented, while by the time birds reached 250 m, all but two of the groups (VIS- at Wytham Hill and VIS- at St Frideswide's Farm) had assumed a mean bearing significantly directed towards home. At none of the sites or distances did the distribution of bearings differ significantly between the VIS+ and VIS- groups (Mardia-Watson-Wheeler test, $P > 0.05$ for all comparisons).

Interestingly, at 125 m, both VIS+ and VIS- birds at Wytham Hill and St Frideswide's Farm were in fact significantly oriented, although not towards home but in equally shifted directions. Possible explanations for this finding will be considered in the Discussion.

Orientation threshold

Whilst work discussed above used distance from the release site as the standard against which to assess the orientation of a group of birds in a given experimental treatment (in this sense being analogous to the traditionally used measure of vanishing bearings, which characterise the degree to which individuals

Table 2. Orientation of birds released following preview of the landscape (VIS+) and those released without preview (VIS-) at various distances from the release site

Site	Treatment	Distance from release site (m)									
		125		250		500		1000		1500	
		θ	r	θ	r	θ	r	θ	r	θ	r
Binsey	VIS+	026°	0.49*	358°	0.68**	002°	0.92***	001°	0.98***	001°	0.99***
	VIS-	041°	0.32	354°	0.40*	346°	0.67**	351°	0.83***	001°	0.98***
Worton	VIS+	017°	0.28	005°	0.44*	351°	0.83***	356°	0.93***	000°	0.98***
	VIS-	327°	0.29	330°	0.60*	002°	0.80***	007°	0.96***	005°	0.98***
Wytham Hill	VIS+	072°	0.82	063°	0.79*	332°	0.79**	354°	0.91***	357°	0.98***
	VIS-	075°	0.83	080°	0.81	347°	0.50*	357°	0.78***	002°	0.83***
St Frid. Farm	VIS+	119°	0.59	046°	0.62*	002°	0.70**	005°	0.90***	357°	0.96***
	VIS-	109°	0.65	041°	0.20	347°	0.61*	354°	0.96***	355°	0.99***

Mean bearing values standardized to home = 0°.

θ , angle of heading; r , circular variance.

V-test for homeward component in mean bearing: * $P < 0.05$, ** $P < 0.001$, *** $P < 0.0001$.

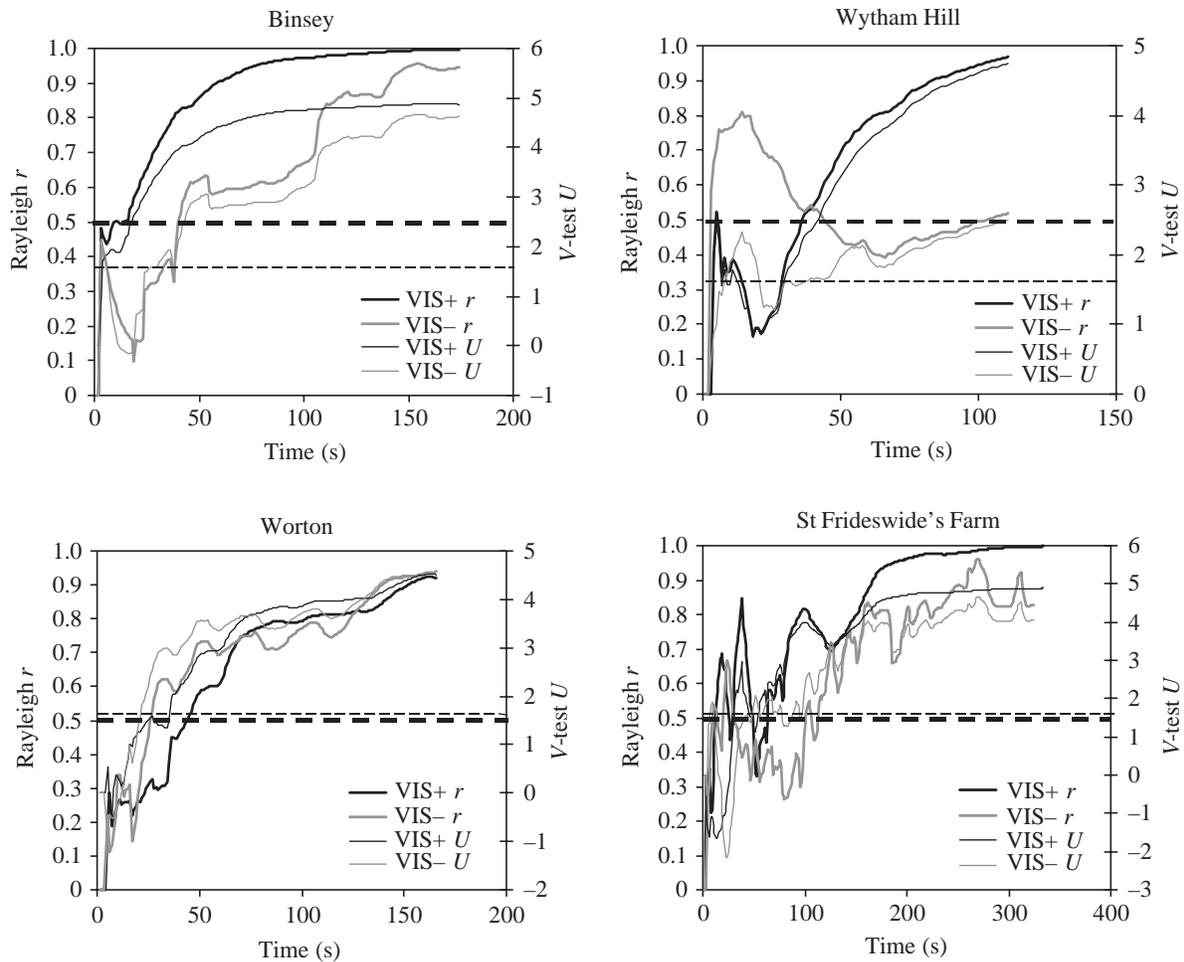


Fig. 6. Orientation of VIS+ (black lines) and VIS- groups (grey lines) at 1 s intervals after release. Thick lines show r -values (thick broken line indicates critical value for Rayleigh test, 0.5 for $N=12$ and $P=0.050$), thin lines show U -test statistic for V -test (thin broken line indicates critical value, 1.64 for $P=0.050$). For any given group, data are shown until the second when the first bird in that group reaches home.

within a group approximate the direction of home or another predicted direction at a particular point in their journey), here we propose an alternative approach. Since we hypothesise that VIS- birds are delayed in their recognition of the release site, it follows that this group as a whole should take longer to select the correct direction of home. We therefore examined how the amount of time needed for groups of birds to reach significant homeward orientation varied with the visual treatment received.

At each site, we calculated the set of bearings that birds in a particular treatment group had assumed relative to the release point at 1 s intervals. That is, data were gathered for 1 s, 2 s, 3 s, etc after release, and for each of these times we determined the mean bearing and circular variance for the distribution of 12 datapoints representing the position of the 12 birds relative to the release site. Performing Rayleigh tests at each interval then allowed us to pinpoint the moment when a group of birds reached significant orientation, and V -tests were used to ascertain whether this orientation was coincident with the direction of home.

Fig. 6 shows, for each of the four sites, circular variance (r) and the V -test statistic U as a function of time after release, along with critical values above which the groups may be said to be significantly oriented. Table 3 shows the number of seconds after which treatment groups at the four release sites no longer displayed random orientation; in other words, the moment when the 12 birds had reached an 'orientation threshold'. At three of the four sites VIS+ birds reached this threshold faster than VIS- birds; at the fourth site (Worton) the difference was the smallest of the four comparisons, but in favour of the VIS- group. By considering the actual positions in space that the birds had assumed at the orientation threshold, it was also possible to calculate the average distance travelled from the release site before the group as a whole reached significant homeward directedness. As expected from the time-based data, these distances are larger for the VIS- group (except at Worton; see Table 3). Overall, birds permitted to view the landscape for 5 min prior to release took, at most, approximately 1 min to reach significant homeward orientation, and were, at such time, on average no further than

Table 3. Time taken for birds in VIS+ and VIS– treatment groups to reach significant orientation following release

Site	Time to orientation threshold (s)		Mean distance from release site at orientation threshold (m) (mean \pm S.E.M.)	
	VIS+	VIS–	VIS+	VIS–
Binsey	7	42	61 \pm 3.5	383 \pm 59.0
Wytham Hill	34	72	305 \pm 21.2	574 \pm 66.0
Worton	36	26	260 \pm 28.9	174 \pm 17.2
St Frid. Farm	64	117	316 \pm 43.3	477 \pm 108.4

Orientation threshold was determined as the first point following release beyond which the Rayleigh test statistic (r) did not drop below significance until birds reached home. In all cases, significant r was accompanied by significant orientation towards home (V -test).

The average distance that birds had reached at orientation threshold is also shown.

about 300 m from the release point. In contrast, birds denied the preview opportunity took up to 2 min to orient, with an average distance of up to nearly 600 m from the release point.

Search behaviour

Analyses of track length, track efficiency, and initial orientation presented above have shown that VIS– birds spend, on average, more time in the vicinity of the release site than VIS+ birds, as well as taking longer to reach homeward orientation. Do these findings reflect a form of information-gathering in the more ‘uncertain’ VIS– subjects? As previous authors have suggested, must birds given no preview of the landscape accomplish site recognition after release? To examine such behaviour quantitatively, we evaluated the topography of tracks based on the following criterion: minimum progress is made and maximum uncertainty demonstrated when individuals attempting to reach a goal return to a point already visited. Such full circles thus represent a strategy that incorporates search behaviour while ultimately returning the animal to its starting point, thereby ensuring that it does not drift off into yet more unknown territory. Although circling can arise for a number of additional reasons (elevation gain following release, perhaps) a comparison of the circling behaviour in the two treatment groups may reveal whether birds make differential use of the information-gathering potential of circling, depending on pre-release visual experience.

We counted the number of full circles flown by birds under the VIS+ and VIS– treatments. A full circle was defined as any series of points where a bird eventually returned to cross its own track. In comparing the performance of birds under the two conditions, we controlled for different lengths of track flown by taking into account the total duration of the homeward journey.

Table 4 shows the average number of full circles completed per minute of flight time under the two treatments, and Fig. 7

Table 4. Characteristics of search behaviour exhibited by birds subjected to the VIS+ and VIS– conditions

Site	Mean number of full circles completed per minute of flight time		Mean distance from release site at which full circles occur (m)	
	VIS+	VIS–	VIS+	VIS–
Binsey	0.09 \pm 0.04	0.38 \pm 0.13	573 \pm 255	345 \pm 138
Wytham Hill	0.36 \pm 0.09	0.55 \pm 0.14	238 \pm 60	301 \pm 83
Worton	0.35 \pm 0.13	0.74 \pm 0.14	273 \pm 82	548 \pm 133
St Frid. Farm	0.29 \pm 0.09	1.22 \pm 0.42	145 \pm 48	263 \pm 130

Values are means \pm S.E.M.

illustrates individual mean differences in the number of full circles completed by birds under VIS+ and VIS–. The results show that more full circles were flown under VIS– at all four sites (between 0.38 and 1.22 circles min^{-1} under VIS– and between 0.09 and 0.36 circles min^{-1} under VIS+), and that all but two of the subjects completed, on average, more full circles under the VIS– than under the VIS+ condition. This difference was statistically significant (Wilcoxon matched-pairs signed-ranks test, $Z=-2.67$, $N=12$, $P<0.01$). Examining the distribution of full circles with respect to progress made towards home, it appears that the majority occurred in the first half of the journey, with at least 75% within the first 1000 m and at least 95% within the first 1400 m at all sites and under both conditions (see Table 4 for average distance from release site at which full circles occur).

Discussion

The present paper has examined in detail the homing behaviour of pigeons released after a 5 min preview of the

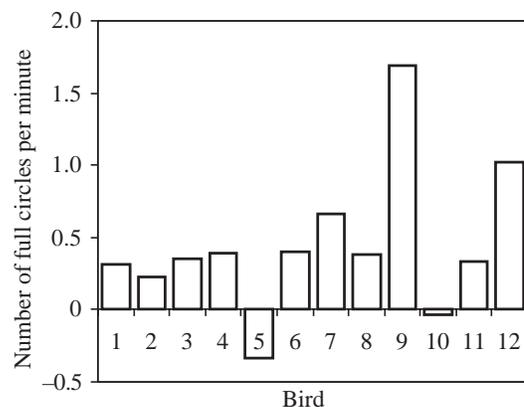


Fig. 7. Average difference in the number of full circles flown per minute following release under the VIS+ and VIS– treatments. Bars show within-bird differences under the two conditions, calculated as number of full circles_{VIS–}–number of full circles_{VIS+} and averaged across all four sites.

landscape with those that were denied the same visual experience. Data was gathered with the aid of a miniature GPS tracking device, allowing the reconstruction of flight paths with extremely high resolution, and enabling a series of analyses novel to pigeon homing studies. Overall, the experiment confirmed the phenomenon demonstrated in previous work (Braithwaite and Guilford, 1991; Braithwaite, 1993; Braithwaite and Newman, 1994; Burt et al., 1997; Biro, et al., 2002) that pigeons home faster when a preview of the surroundings is allowed prior to release. We examined the topography of homing tracks under the two conditions (preview, VIS+ and no preview, VIS-) in an attempt to assess the underlying causes of this difference.

Several explanations of the preview effect have been proposed. Braithwaite and Guilford (1991) were the first to attribute the difference to improved recognition of the release site by VIS+ birds based on visual cues. A potential criticism of this interpretation suggests, however, that the findings may also be explained by a non-specific, general effect, such as lower confidence or motivation to home in VIS- birds. A convincing counterargument is based on the finding that the visual treatment given to birds prior to release has no effect at unfamiliar sites, where visually mediated site recognition would not be expected (Braithwaite and Newman, 1994). Nevertheless, the account proposed by Braithwaite and Guilford (1991) and maintained in follow-up studies relies on a localised effect for the treatment, acting principally in the vicinity of the release site. We attempted to assess whether such a localised effect was indeed responsible for the differences in homing speeds of birds under VIS+ and VIS- conditions, and if so, to characterise the effect in terms of the homing strategy adopted by the two groups.

Overall, homing speeds calculated from the GPS data replicated previous findings: birds homed faster from familiar sites when released following a 5 min preview of the landscape than when denied pre-release visual access to the surroundings. Our study thus validates previously used human observer-based methods such as clocking birds in upon arrival at the loft, showing that these measures do indeed accurately reflect the subjects' homing performance. Furthermore, we found that the difference in homing speeds was due neither to slower flight speeds nor a tendency to delay homing by landing prior to arrival in the VIS- group. Instead, VIS+ birds achieved faster homing by flying a more direct course: they covered less extra track beyond that necessary to reach home. This difference, however, was not evident throughout the whole length of the journey, as additional analyses confirmed a localised effect for the preview treatment. In terms of track efficiency, the performance of birds under the two treatments differed only in the early stages of the flight. Individuals released after a 5 min preview proceeded towards home on a more direct route up to a distance of 1000 m from release, while VIS- birds spent more time straying no further than 1000 m from the site, often returning and crossing their own path (possibly indicating a form of search behaviour). Beyond the 1000 m boundary, no differences in the performance of birds under the two

treatments were detected. This finding would seem to support Braithwaite and Guilford's (1991) interpretation that the early part of the birds' journey is instrumental in visually mediated recognition of a familiar site, and that individuals not permitted to view the landscape prior to release must accomplish the same task following release. This results in a delay experienced by VIS- birds that, once settled, does not affect the remainder of the homeward journey. Braithwaite's (1993) finding that the treatment effect is no longer detected when birds are released from longer distances (around 10 km) supports this notion – albeit indirectly – as the early information-gathering stage comes to represent a progressively smaller proportion of the journey with increasing distance. Replicating the present study at familiar sites further than 4 km from home would thus constitute a crucial test of this interpretation. Although the difference may disappear in terms of overall homing times, should the treatment effect remain, it will continue to be evident in measures recorded during the initial part of the journey. VIS- birds will be expected to take longer to assume a course towards home than VIS+ birds, fly more tortuous tracks within the first 1000 m, and circle more often near the release site, irrespective of the distance at which the releases are conducted.

Our analysis of headings assumed by birds with respect to the release site revealed that both the VIS+ and VIS- groups already showed significant orientation after 125 m at two of the sites (Wytham Hill and St Frideswide's Farm), but in directions shifted with respect to home. This may have reflected the influence on orientation immediately after release of the landscape and the types of landmarks available at the release site. At Wytham Hill, birds tended to fly initially into a meadow (centred at around 70° from the home direction) rather than over the woods lying in the opposite direction and towards home, while at St Frideswide's Farm, the farm buildings (at 110° from home) could have had a similarly transient attraction. Once the subjects progressed beyond the first 125 m, the effect of these early attractors was no longer evident.

By the time birds reached the 500 m boundary measured from the release site, they were homeward oriented under both VIS+ and VIS-, and remained so for the rest of the journey. However, our second-by-second analysis of birds' positions relative to the release site and the loft revealed that, as a group, VIS- birds generally took longer to reach significant homeward directedness than VIS+ birds. Determining such an 'orientation threshold' based on time after release is a novel way of assessing performance and may provide a convenient way of characterising navigational decision-making in a group of birds subjected to a particular treatment. An important point to note, however, is that the time taken for a population of birds to become significantly oriented says little about the strategies and homing decisions of individuals within it. For example, the relatively large standard errors in the case of the VIS- birds' average distance from the release site at orientation threshold (see Table 3) may reflect a form of bimodality within the group. Some birds were well oriented from the start and had covered a large distance toward home by the time the group as

a whole became oriented, whereas others were initially disoriented and remained in the vicinity of the release site. In addition, a common criticism of the traditional vanishing bearing method also applies to the orientation threshold analysis: recording individual datapoints simply as the position of a bird with respect to the release site does not take into account the direction that the bird is heading in. A bird positioned along the beeline track connecting the release point and home would be considered perfectly oriented even if it was heading directly back towards the former, whilst a bird positioned on the opposite side of the release point would be considered disoriented even if it was already heading directly towards home. Nevertheless, the strict criterion set here (defining orientation threshold as the moment beyond which statistical tests reveal consistent homeward orientation) helps deal with at least the first of these problems. It thus provides the most conservative estimate of the time needed for a group of birds to demonstrate homeward directedness. Overall, the generally longer times needed by VIS- subjects to reach orientation threshold are consistent with the idea that denying birds a view of the landscape prior to release results in delayed site recognition.

There are further indications that birds denied the preview opportunity experience a delay in site recognition. Circling above or near the release site was a characteristic more prominent in VIS- tracks, and we suggest that this feature represents a form of search behaviour in birds that have yet to determine their position relative to home. Although some of these circles are likely to have been the result of birds attempting to gain height following release, such elevation gain itself may have been an important and desired product of the behaviour in terms of information gathering. The higher the bird, the further it may be able to see, and for an individual uncertain of its position, the increased amount of information available to it through this strategy might allow faster recognition. Unfortunately, as we were unable to collect sufficiently accurate altitude data in this experiment, this hypothesis remains, for now, merely speculation. Nevertheless, the treatment difference revealed suggests that the total number of full circles completed, particularly those near the release site, is indeed linked to the nature of the birds' pre-release visual experience.

Some caution is necessary in attributing significance to the localised effect of the preview treatment. Although it has been demonstrated that previewing affects only the early part of the journey home, the influence of factors other than delayed site recognition cannot be entirely discounted. If, as the main alternative to Braithwaite and Guilford's (1991) account suggests, the treatment affects the birds' confidence or motivation to home, instead of their knowledge, a similarly localised pattern may emerge. It may be that such non-specific effects 'wear off' after a certain amount of time in the air, as VIS- birds' motivation/confidence gradually returns. It is difficult to distinguish between the two explanations on the basis of our analyses alone, and the issue of pre-release visual treatment affecting knowledge, motivation or both, remains

problematic. The case of one bird (Fig. 2E) is of particular interest. This subject performed consistently better under VIS- than VIS+ (indicated by faster homing, less tortuous paths, and less circling under VIS-), suggesting that its orientational decisions were affected differently by the additional sensory information available through the preview opportunity. Gagliardo et al. (1999) have suggested that individual preference may play a role in the types of cues that pigeons primarily attend to at familiar sites. It may be that landmarks visible prior to release (nearby farm buildings, villages, open fields, etc) exerted a particularly strong influence in the case of this bird, attracting visits prior to the subject's assuming a course towards home. Such effects of the landscape on initial orientation have been documented in the past (Dornfeldt, 1982; Kiepenheuer, 1993), although whether they are mere distractions or, instead, whether visits to particular types of landmarks have a navigational function (Guilford, 1993) is still unclear. Another intriguing possibility is an interaction between both motivational and knowledge factors: for a bird already confident of its position relative to the loft prior to take-off, attempting to fly directly home may be less of an immediate priority. However, since the opposite pattern was observed in all of the remaining subjects, such speculation cannot at present be further tested.

In conclusion, it is clear from the present experiment that visual treatment prior to release affects subsequent homing performance. 5 min previews of the landscape at familiar sites enhance homing speeds by reducing the amount of time birds spend near the release point before taking up a course towards home. GPS tracking provides data in sufficient detail to examine differences in the paths flown by birds with or without preview; however, precisely how behaviour near the release site reflects search attempts at site recognition remains to be clarified until we understand more about the interaction between the birds' vision, knowledge and movement in flight. Nevertheless, the variety of analyses facilitated by the GPS data clearly illustrate the immense power of the technique. Combined with further manipulations of the availability to homing pigeons of different types of sensory information, GPS tracking will undoubtedly continue to provide valuable data for evaluating orientational decisions in a bird with known start and goal positions.

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