

REVIEW

Route following and the pigeon's familiar area map

Tim Guilford* and Dora Biro

ABSTRACT

Homing pigeons (*Columba livia*) have been the central model of avian navigation research for many decades, but only more recently has research extended into understanding their mechanisms of orientation in the familiar area. The discovery (facilitated by GPS tracking) that pigeons gradually acquire with experience individually idiosyncratic routes home to which they remain faithful on repeated releases, even if displaced off-route, has helped uncover the fundamental role of familiar visual landmarks in the avian familiar area map. We evaluate the robustness and generality of the route-following phenomenon by examining extant studies in depth, including the single published counter-example, providing a detailed comparison of route efficiencies, flight corridor widths and fidelity. We combine this analysis with a review of inferences that can be drawn from other experimental approaches to understanding the nature of familiar area orientation in pigeons, including experiments on landmark recognition, and response to clock-shift, to build the first detailed picture of how bird orientation develops with experience of the familiar area. We articulate alternative hypotheses for how guidance might be controlled during route following, concluding that although much remains unknown, the details of route following strongly support a pilotage interpretation. Predictable patterns of efficiency increase, but limited to the local route, typical corridor widths of 100–200 m, high-fidelity pinch-points on route, attraction to landscape edges, and a robustness to clock-shift procedures, all demonstrate that birds can associatively acquire a map of their familiar area guided (at least partially) by direct visual control from memorised local landscape features.

KEY WORDS: *Columba livia*, Navigation, Route following, Learning, Memory, Vision

Introduction

Birds are nature's masters of long-distance navigation. Especially during the last century, scientific research focused on the homing pigeon (*Columba livia*) as its central model, and most of what we now know about true navigation behaviour in birds [that is, the ability to home efficiently from distant unfamiliar locations and over unfamiliar terrain (Baker, 1978)] comes from work on this paradigmatic species (Wallraff, 2005). Nevertheless, it has long been recognised that once pigeons become familiar with their local environment, their homing behaviour changes, making redundant, or even replacing, the navigational mechanisms that operate from unfamiliar places. This alternative (Bingman and Ioalè, 1989) or second (Papi, 1992) mechanism of homing is thought to involve a familiar area map (Baker, 1982; Holland, 2003), yet despite its potentially wide applicability, the nature of this map has received remarkably little scrutiny. Until relatively recently, debate focused

largely on whether initial orientation at familiar release sites was affected by phase-shift procedures, and hence whether it involved a time-compensated sun-compass (the mosaic map) or whether orientation could be accounted for entirely in terms of guidance by familiar landmarks (pilotage). This debate remains central, but the discovery that pigeons adopt habitual routes home from familiar sites (Meade et al., 2005), and can be precisely tracked doing so, has offered a new avenue by which to investigate how birds control their orientation across familiar terrain. In this paper we summarise what is now known about familiar route following in the pigeon, and discuss how it enlightens our understanding of the familiar area map.

Familiar route following

Whilst earlier experiments with homing pigeons demonstrated that local experience did indeed affect homing performance in various ways and under various conditions (e.g. Bingman and Ioalè, 1989), the precise effects of familiarity on orientation remained opaque. The advent of miniature on-board logging devices [especially GPS (von Hünnerbein et al., 1997; von Hünnerbein et al., 2000; Steiner et al., 2000)] changed this because now the bird's entire route across the landscape could be reconstructed in detail, and the effects of experience or experimental manipulation could be determined precisely.

Route stereotypy

The first experiment to demonstrate systematically the effect of increasing familiarity on orientation throughout the homing flight was published by Meade et al. (Meade et al., 2005). Pigeons were released repeatedly from the same site 5 km from home, and tracked using 1 Hz on-board GPS loggers. Each individual's routes showed considerable variation amongst early flights, but had become largely stereotyped by the end of the experiment (Fig. 1). Meade et al. (Meade et al., 2005) quantified stereotypy by measuring the similarity between routes using the area of the corridor bounded by those routes. Corridor areas reduced significantly between early and late sets of individuals' routes during training, demonstrating a significant increase in stereotypy with repeated flights from the same site. Subsequent studies have refined the measurement of route stereotypy by calculating average nearest neighbour distances between points on the two (or more) routes under comparison (Biro et al., 2006b; Freeman et al., 2011), because corridor areas are affected by route length and not just degree of stereotypy. Typically, stereotypy increases rapidly over the first few (three to five) flights, with a more gradual, perhaps asymptotic, increase as gain in experience continues. Birds typically reach a high level of stereotypy within approximately eight to 10 flights (Fig. 2). Since its original discovery, route following has been demonstrated or visualised in published experiments from at least 13 different sites and at distances of up to 25 km from the home loft (Armstrong 2010; Biro et al., 2004; Biro et al., 2006a; Biro et al., 2006b; Biro et al., 2007; Flack et al., 2012; Pettit et al., 2013). Route following was also suspected, but

Animal Behaviour Research Group, Department of Zoology, South Parks Road, Oxford OX1 3PS, UK

*Author for correspondence (tim.guilford@zoo.ox.ac.uk)

Glossary

Active position fixing

A hypothetical process by which animals actively move towards candidate landmarks in order to determine whether such landmarks match a memorised representation, and hence provide a position fix.

Clock-shift

The procedure by which an animal's internal diurnal clock is re-entrained to an experimentally altered light:dark cycle. Because clock-shifting (or phase-shifting) leads to predictable deviations in the time-compensated sun compass, it can be used to determine what role the compass plays in orientation.

Mosaic map

There is no single accepted definition of the mosaic map. However, perhaps the commonly accepted meaning is of a mosaic of memorised landmark-specified locations with the relationships between locations represented as compass bearings or vectors (Holland, 2003; Wiltschko and Wiltschko, 2009). The principal feature of the mosaic map is that it allows a sparse representation of a wide area because guidance continues beyond each known landmark's view. Because it is not the landmark or pattern of landmarks that directly provide guidance (pilotage), the map rotates if the compass is rotated, e.g. under clock-shift [cf. 'pattern map' and 'point map' (Wallraff et al., 1994)].

Pilotage

Generally defined in the bird navigation literature as navigation that is controlled by direct reference to memorised (usually visual) landmarks without reference to memorised compass instructions (Papi, 1992; Holland, 2003; Biro et al., 2004; Wiltschko and Wiltschko, 2009), although on a smaller scale pilotage is also sometimes used more broadly to include any mechanism (e.g. heading vectors) that might encode the relationship of a goal to known landmarks (Pearce, 2008).

Route stereotypy

The degree to which an animal's route from one place to another resembles its previous routes between these two places. In studies of animal navigation, such as the analysis of detailed pigeon homing trajectories, route stereotypy can be measured, for example, by the average nearest neighbour distance between positions on successive routes, and it can be used to assess the degree of fidelity to a habitual route when individuals are idiosyncratic in their route choice.

Time-compensated sun-compass

Although the sun, as a very distant object, can provide geographic direction regardless of the observer's position (compass information), its apparent motion across the sky during the day means that its direction requires time-compensation to be of general use. Many animals appear able to use the sun in a time-compensated way, as revealed by clock-shifting procedures.

not explicitly demonstrated, in a study in the USA (Mora et al., 2012), and discussed as an important part of individual flight behaviour, but not explicitly measured, in a study in Italy (Dell'Arciccia et al., 2008). At Oxford, route following has so far been found in every experiment in which birds have been tracked over repeated releases from the same site. It has also been shown to be unaffected by magnetic disruption or wind direction (Meade et al., 2005), emphasising that the cues involved are almost certainly visual [an issue that has been well reviewed elsewhere (Holland, 2003)]. The only study of which we are aware that claims to have failed to find route-following behaviour is that of Wiltschko et al. (Wiltschko et al., 2007), which we discuss below.

Route fidelity

A priori the simplest explanation for increasing stereotypy is that birds are, with experience, adopting the most efficient route home – an increasing approximation to the beeline. Route efficiency does indeed increase with successive releases from the same site (e.g.

Meade et al., 2005; Flack et al., 2012; Pettit et al., 2013), but, crucially, this is not the sole reason for increasing stereotypy. Meade et al. (Meade et al., 2005) showed that an individual's final routes were significantly self-similar, and different from the final routes of other similarly trained birds, despite any increased efficiency. This is possible because individuals usually remain substantially inefficient in their approximately stable final routes (the ratio of beeline distance to flown distance remains with a mean typically around 0.83; see Table 1). It indicates that individuals adopt individually idiosyncratic routes home as familiarity increases. This idiosyncrasy implies that routes are likely to depend on individually acquired memories. Idiosyncrasy alone does not tell us definitively the basis of the guidance involved, but important clues are provided by the observation that individual routes tend to be highly constrained within relatively narrow corridors. In Table 1 we present calculated corridor widths for all the studies in which we have gathered data on route development, and this shows a typical mean nearest neighbour distance of approximately 100–200 m in the tracks of locally experienced birds. This implies that memorised guidance control is likely to relate to geocentrically fixed, local features of the landscape.

Route loyalty

Although published before Meade et al. (Meade et al., 2005), Biro et al. (Biro et al., 2004) showed in a subsequent experiment that birds were often attracted directly to their own routes. Route following was replicated from two different sites, now 10 km distant from the loft, but birds were tracked after release from novel locations displaced away from their familiar routes. At distances of up to 1.5 km from the nearest point on the bird's established route corridor, pigeons frequently flew back towards their previous route initially, and then recapitulated the route home after contact. Birds joined their habitual routes significantly sooner than expected by chance, and significantly sooner than would be expected if they had taken a homewards shortcut from the sideways displaced novel release sites. Furthermore, birds rarely crossed their habitual route to continue beyond it once they had made contact, and the contact position induced a homewards shift in orientation. These effects were also seen in a replication at longer distance (Biro et al., 2006a), discussed below. Together, these results indicate that whatever has become attractive about a bird's habitual route is directly perceivable from considerable distance, and is capable of causing geocentrically precise changes in orientation. Because birds were drawn to their habitual routes despite this entailing a detour from the direct route home, the effect was termed 'route loyalty' (Biro et al., 2004).

Whilst the parsimonious explanation for route loyalty is that birds have formed individually memorised routes of landscape features to which they are directly attracted back, it is conceivable that there are small subsets of routes across the landscape that are naturally attractive independent of memory. To test this, Biro et al. (Biro et al., 2006a) conducted experimental off-route releases using yoked controls. Thus, for each bird released from an off-route site chosen for its displacement from that individual's habitual route, a second bird with no history of experience in the same area was also released. Yoked controls were not attracted towards the route, whilst individuals that had previously flown the route were, so attraction back to a bird's own route must be based on memory. Although only conducted at a single site, this experiment (Biro et al., 2006a) also extended the habitual route following phenomenon to 25 km from the loft, and the route loyalty effect to off-route displacements of up to 3 km.

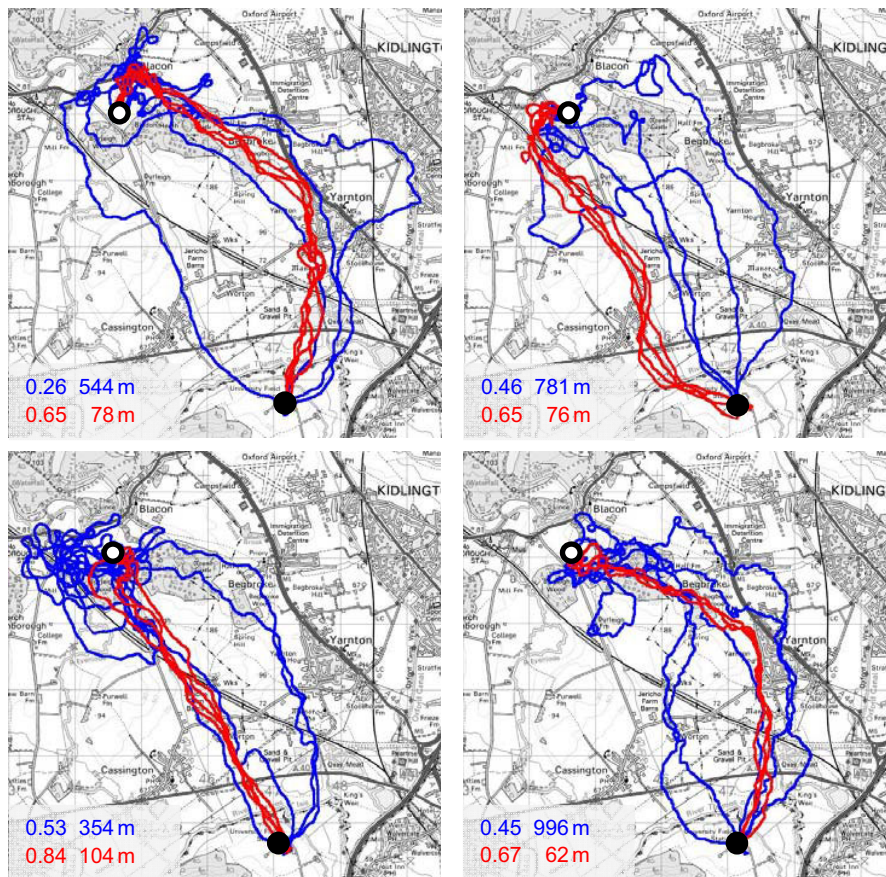


Fig. 1. GPS-tracked flights of four pigeons released 24 times in succession from Bladon Heath (open circle, 5.0 km from home), returning to their loft at the Oxford University Field Station (filled circle). Panels show the first four (blue) and last four (red) flights for each bird. Efficiencies are for the first (blue) and final (red) flight, and corridor widths are calculated on the first (blue) and final (red) flight pairs. Map grid is 1 km². Adapted from Meade et al. (Meade et al., 2005).

Is route following general?

Experiments demonstrating familiar route following have so far been conducted largely by a single research group, and [with the exception of Armstrong (Armstrong, 2010), in Italy; Arnaccio in Table 1] at a single loft (at the Oxford University Field Laboratory). Wiltschko and Wiltschko state that at other lofts, such route stereotypies were not observed [p. 733 (Wiltschko and Wiltschko, 2009)]. In fact, the only independent published attempt to replicate the effect elsewhere to date that we can find comes from a single loft at Frankfurt (Wiltschko et al., 2007; Schiffner et al., 2013). For the one set of releases where formal analysis was undertaken (Wiltschko et al., 2007), pigeons that had been tracked repeatedly from a site 9.1 km from the loft did not apparently show increasing route stereotypy. Data from four additional sites with repeated releases apparently contained too many missing tracks to warrant formal stereotypy analysis (Schiffner et al., 2013), and although lack of route stereotypy is argued by the authors, the track visualisations presented are open to interpretation. What might explain this discrepancy between the Oxford and Frankfurt findings? Pigeons at the 9.1 km site (Wiltschko et al., 2007) were tracked successfully over fewer flights during the experiment itself (nine to 13 releases per bird), over an unspecified time period. However, they had had local training flights around the loft, from sites more distant that were likely to have led to overflight of the experimental site or neighbouring area, and up to six previous releases from the same site itself prior to the start of the study, all of which may have provided familiarity with the route home even before the experiment began. Indeed, the median efficiency of birds' first routes is reported as 0.83 (Wiltschko et al., 2007), already comparable to the efficiencies of route-following birds in other experiments, and

efficiency did not apparently increase during training. The overland section of flights (from 2.5 km after release to 1.0 km before home) was more efficient still (0.92). Wiltschko et al. (Wiltschko et al., 2007) did report that birds showed no increase in route similarity through training, but they did not report testing whether individuals showed routes more similar to their own than to those of other birds (individual idiosyncrasy).

One explanation for the failure to show the development of route following is that the birds had already formed a degree of route following before the experiment began. Nevertheless, the degree of route following is not obviously as clear-cut as in the Oxford experiments. The Frankfurt group (Wiltschko et al., 2007; Schiffner et al., 2013) suggest instead that the efficacy of true navigational factors around Frankfurt may make visual route learning naturally subordinate, or even non-existent, at least at this distance. True navigational performance may be relatively poor at the Oxford loft, although experimental data are limited (Guilford et al., 1998). Another possibility is that birds follow single memorised routes more readily, or more faithfully, over some landscape types than others. Armstrong (Armstrong, 2010) used sites where the homeward route encompassed transitions between rural and urban landscape, and found that birds appeared to show less stereotypy over developed areas (Fig. 3). When Mann et al. (Mann et al., 2011) subjected these routes to an analysis that sought to identify important waypoints objectively (see below), there was a noticeable lack of points in urban areas. Thus, even though birds are attracted to edge-containing landscape features (Lau et al., 2006), it is possible that more urban landscapes encourage less coherent route following, perhaps because they provide multiple apparently similar parallel sets of landmark features (such as streets) or, in effect, too

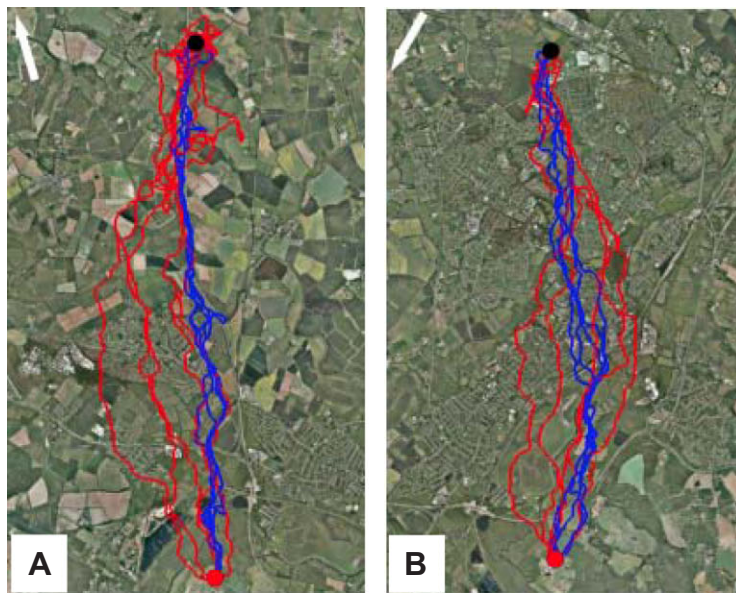
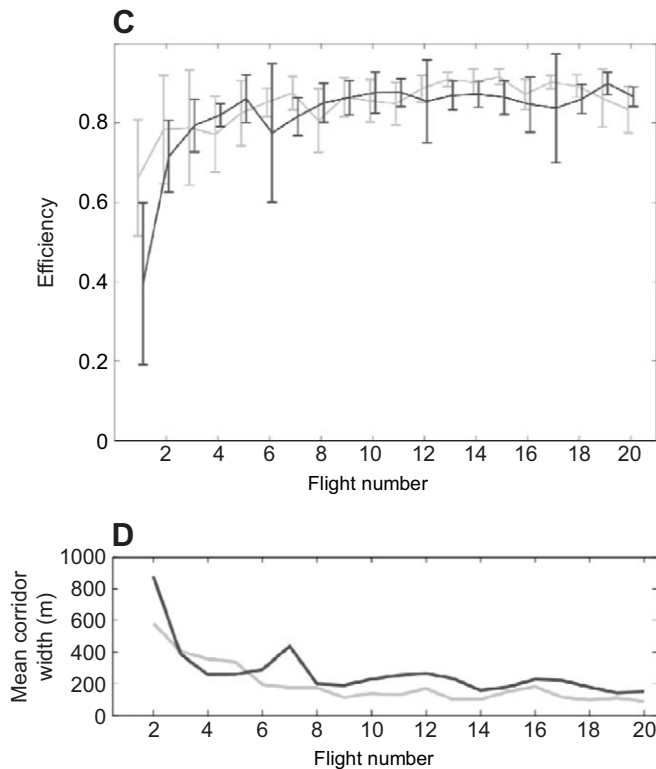


Fig. 2. Sixteen two-year-old pigeons with no previous training were released 20 times in succession in two groups, eight from Weston Wood (10.6 km) and eight from Horspath (10.4 km), and GPS tracked on every flight back to the Oxford loft (data from Armstrong, 2010). (A,B) Single examples of the first four (red) and final four (blue) tracks from the two sites. Arrows indicate north, black circles release sites and red circles the loft. (C) Increase in mean efficiency for the two sites. (D) Mean corridor width (mean distance to previous track) by flight number. In C and D, Horspath is shown by black lines, Weston Wood by grey lines.



much informational complexity. Filannino et al. (Filannino et al., 2013) also showed a probable effect of landscape on the degree to which birds depended on their time-compensated sun compass, rather than direct landmark guidance, when released from multiple familiar sites (in Italy).

Currently, we do not know what restricts the generality of route following, or to what degree. Pigeons can home from places they have been to several times before without obviously following a habitual route, so it is possible that there are three developmental stages to navigation from a single site: true navigation at first, followed by a mosaic-map type representation (see below) as some familiarity is acquired, followed by pilotage along a memorised route as the route becomes thoroughly familiar. It is also possible

that different environments are more or less suitable for the development, or persistence, of each stage. Nonetheless, it seems highly unlikely that route following is a coincidental construct of one particular environment or training regimen (or whatever else might be regarded as peculiar about Oxford). Pigeons may not always develop route following, but the fact that they can robustly do so deserves detailed explanation.

Route development as a localised learning process

Meade et al.'s (Meade et al., 2005) study was the first to show that the effect of familiarity even at sites relatively close to home is quantitative. Even over terrain and at a proximity to home where some familiarity with the landscape might already be expected from

Table 1. Tracking studies with homing pigeons where sufficient releases from the same site have allowed insights into the processes of route development (or its absence)

Study	Distance (km)	Flights	Birds	Efficiency	Corridor (m)	Fidelity	Release site (and remarks)
Meade et al., 2005	5.0	24	7	0.66 {0.69}	112 {80}	Yes*	Bladon Heath {with half-blind bird removed}
	5.3	20	8	0.80	112	Yes*	Church Hanborough (magnetic disruption)
Biro et al., 2004	10.7	20	9	0.85	151	Yes*	Weston Wood
	9.4	20	9	0.80	176	Yes*	High Cogges
Biro et al., 2007	5.1	20	8	0.76	114	Yes	Bladon Heath
	10.6	20	8	0.83	110	Yes	Weston Wood
	9.4	20	8	0.82	171	Yes	High Cogges
	6.1	20	8	0.91	80	Yes	Hinksey Heights
Biro et al., 2006a	25.5	20	9	0.85	207	Yes*	Bury Down
Biro et al., 2006b	5.3	20	4	0.81	105	Yes	Church Hanborough
	10.7	20	6	0.81	107	Yes	Weston Wood
	8.6	20	12	0.84	91	Yes	Greenhill Farm
Armstrong, 2010	10.6	20	8	0.87	88	Yes*	Weston wood
	10.4	20	8	0.85	151	Yes*	Horspath
	13.0	8	19	0.85	534	Yes	Arnaccio
Flack et al., 2012	7.0	17	10	0.85	98	Yes	College Farm (E+ treatment group)
	7.0	17	10	0.85	304	Yes	College Farm (E- treatment group)
	7.0	17	10	0.76	196	Yes	Forest Farm (E+ treatment group)
	7.0	17	10	0.86	156	Yes	Forest Farm (E- treatment group)
Pettit et al., 2013	7.05	18	7	0.86	119	Yes*	South Leigh (demonstrators' pre-training flights)
		15	10	0.91	158	Yes	South Leigh (controls)
	7.73	18	10	0.84	217	Yes*	Elsfield (demonstrators' pre-training flights)
Wiltschko et al., 2007	9.1	15	9	0.82	189	Yes	Elsfield (controls)
		>9–13	9	0.83 {0.92}		No	Main-Taunus-Zentrum (total) {>2.5 km from release}

Efficiency is calculated as the beeline distance divided by the path flown during the final training flight, and corridor widths are calculated as the mean perpendicular distance between the penultimate and final training flights [except in Biro et al. (Biro et al., 2004), where it is amongst the three final flights]. Fidelity refers to claimed demonstration of its presence (yes) or absence (no), either with statistical support (asterisk) or based on visual inspection or other indirect evidence alone (without asterisk).

previous training or spontaneous flights, route following emerges with continued experience. Route development is also gradual, with decreasing effects after an initial rapid improvement. This quantitative improvement is characteristic of learning processes in general (Pearce, 2008), supporting the interpretation that the familiar area map is learnt through direct local experience of the terrain

traversed. Furthermore, where individual birds have been trained at more than one site sequentially, route acquisition appears to proceed independently at each site (e.g. Flack et al., 2012). This independence indicates that even over the limited geographic area spanning the multiple release sites around the loft (perhaps 20 km across), the route-learning process is local to the route itself and

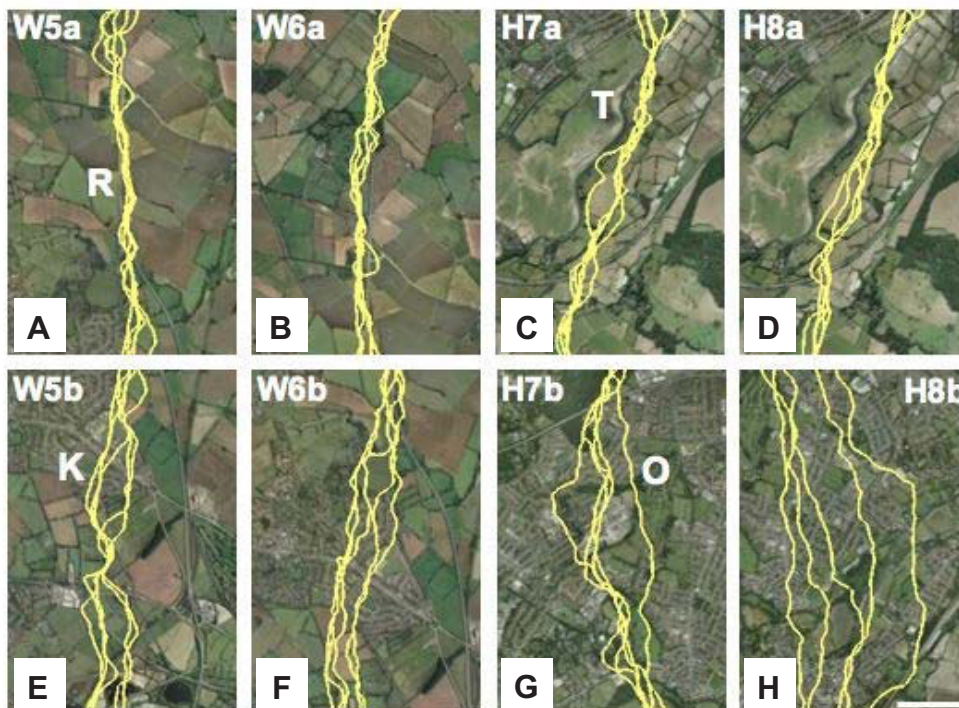


Fig. 3. Selected examples of regions of high (A–D) and low (E–H) trajectory fidelity in the final five (of 20) training flights of four individual pigeons (columns) from two sites, Weston Wood (W) and Horspath (H), overlaid onto satellite images of the underlying topography. Display orientations are approximately normalised for flight direction. Scale bar represents 1 km. Local features are highlighted, including the four-lane road (R), the town of Kidlington (K), Oxford (O) and the River Thames (T). Adapted from Armstrong (Armstrong, 2010).

cannot be accounted for by birds learning geographic relationships, or indeed navigational factors, on a wider scale. If such learning does occur, it is not responsible for route following.

An associative account of route development implies that something about improvement in efficiency, such as getting home quicker, is rewarding to the bird. Parsimoniously, this implies that route inefficiency indicates imperfect knowledge of the best route home, not a lack of motivation to improve directness of the route. This is most obviously the case earlier in the acquisition process, when we can be sure that the bird is working to improve directness because this is what we later find it has achieved. But it is likely to be so throughout the process because even when routes are relatively stable, gradual refinement is often evident.

It is possible that factors other than directness are important to homing birds, for example avoidance of perceived obstacles such as water bodies or forests, or attraction towards favourable stimuli such as places likely to have conspecifics, and that these contribute to route inefficiencies. Wiltschko et al. (Wiltschko et al., 2007) caution against making navigational interpretations of tracking data for this reason. Nevertheless, if such factors were the sole cause of route inefficiency, they should be general to all birds and would not produce individual route idiosyncrasy. Whatever generates idiosyncrasy is individual-dependent, often consistent between flights, and therefore most likely to result from the vagaries of a learning process in which the starting conditions vary greatly amongst individuals as they make their initial flights over the unfamiliar terrain.

Perhaps the strongest evidence that route inefficiency reflects imperfect knowledge even late during the route-acquisition process comes from a study in which relatively stable individual routes were subsequently improved further by paired flights with a second bird (Pettit et al., 2013). Pigeons prefer to fly together, and group navigation often leads to more accurate orientation (Biro et al., 2006b; Dell'Arciccia et al., 2008). In this paired flight study, even naïve partners caused an increase in the efficiency (significantly, when measured as mean distance to the beeline) of birds with already established routes [mean distance to beeline before pairing: 523 m; after: 284 m; Wilcoxon signed ranks test, $P=0.028$, $N=17$; solo efficiency increased from 0.85 to 0.89; Wilcoxon signed ranks test, $P=0.093$, $N=17$ (from Pettit et al., 2013)]. Crucially, these more efficient routes were maintained during subsequent solo flights, so

they were not for some reason inherently unattractive, implying that attraction to the partner exposed birds already following memorised routes to additional shortcuts that then proved rewarding.

The nature of familiar routes

Route tolerance

The details of habitual route structure can offer further insights into the nature of the bird's familiar area map, and we first consider route tolerance. Even when route efficiency has become relatively stable, birds vary in their actual flight paths from one flight to the next. The resulting habitual corridor generally has a scale of 100–200 m across (Table 1), implying that this may be the approximate tolerance distance within which birds attempt to keep memorised landscape features. Wider corridors are seen when birds have had fewer flights (e.g. 534 m after eight flights at Arnaccio). Biro et al. (Biro et al., 2006b) released pairs of birds with different habitual routes from the same site and found that there was an approximate threshold distance of 575 m between their routes, beyond which the pair failed to compromise in a shared trajectory, and either split or one deferred to the other. These birds were conflicted between staying with their memorised route and staying with their flight partner, so a greater tolerance might be expected than when flying alone. Nevertheless, the critical distance from the route is similar (~300 m). Together, these results suggest that guidance from memorised features along the route operates at a perceptual scale of a few hundred metres. Attraction back to routes after off-route displacement can occur over greater distances, up to a few kilometres, but in these cases birds may be forced beyond their normal tolerance, or towards particular landmarks visible from greater distances, and still the scale is relatively local.

Local fidelity variance and waypoints

Although high average fidelity over the entire route tells us that the route has become represented in memory, fidelity also varies considerably along the route. Habitual routes show a beaded structure with sections of higher and lower local fidelity. Informally, we may conjecture that points of local high fidelity, or pinch-points, indicate flight convergence on salient memorised ground features (Fig. 4). Lower-fidelity bowed sections between the high-fidelity sections may indicate error or tolerance of indirectness to the next memorised feature. More formally, peak local fidelity correlates

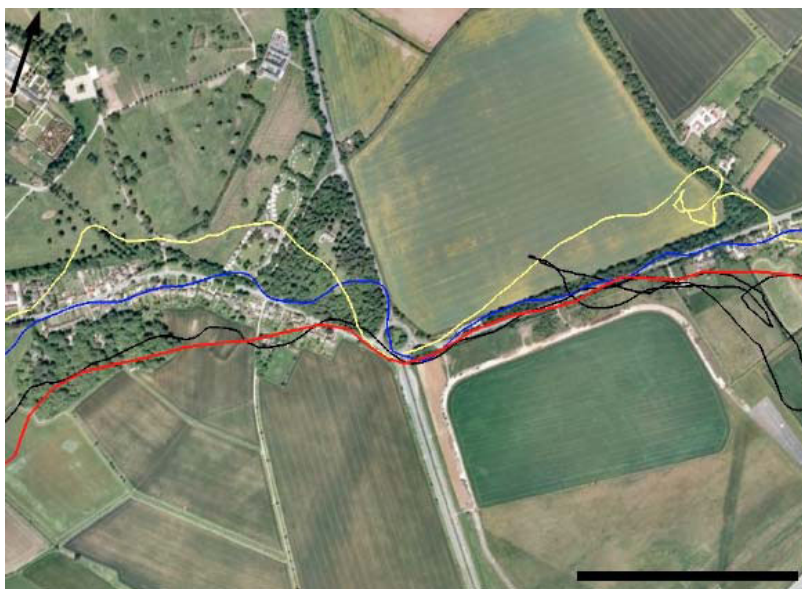


Fig. 4. Four successive tracks of a single route-following pigeon, flying right to left, showing convergence of tracks to a pinch-point coincident with a distinctive underlying ground feature. Scale bar is 1 km; arrow points north. Data from Armstrong (Armstrong, 2010).

with leadership decisions in co-navigating pigeons (Freeman et al., 2011), suggesting that leadership might result from having a greater confidence (or perhaps inflexibility) in the memorised route, which is indicated by very close adherence to the route at particular points. Mann et al. (Mann et al., 2011) dissected the structure of birds' habitual routes using a different approach, by treating repeated flights as a Gaussian process as the output of each bird's attempt to recapitulate its memorised route. This allowed them to identify objectively the positions that best predicted a pigeon's subsequent flights. These positions were often found at distinctive boundaries in the underlying landscape. Local regions of high fidelity, often associated with distinctive ground features, therefore suggest that the structure of a bird's route consists of a series of more strongly attractive memorised local waypoints, as it is hard to see how such intermittent geographical precision could be readily controlled by more distant features. This finding may seem at odds with previous expectations, for example that myopia in the lower visual field would restrict the use of local visual landmarks below and in front of the flying bird (Holland, 2003), but it does not rule out the possibility that more horizontal or panoramic features also contribute in ways that are not inherently obvious in the structure of a bird's route corridor (Filannino et al., 2013). Nevertheless, it does demonstrate that local underlying features are important to guidance in the familiar area, regardless of whether these are in focus.

Identifying features on route

It is inherently difficult to manipulate the landscape experimentally on a meaningful scale for a wide-ranging bird, so the precise nature of the features that make up birds' memorised routes currently remains relatively obscure. Sometimes, however, trajectories so strikingly match features in the underlying landscape that some causal relationship is implied. Most strikingly, pigeons often incorporate into their memorised routes linear or quasi-linear landscape features such as roads, railways, hedgelines, field boundaries and rivers (Meade et al., 2005; Biro et al., 2004; Dell'Arciccia et al., 2008; Mann et al., 2011; Armstrong, 2010; Filannino et al., 2013). Linear feature following is also seen in birds that have not deliberately been trained from a release site (Fiaschi et al., 1981; Ioalè et al., 1994; Biro, 2002; Lipp et al., 2004), suggesting that such features are commonly chosen to structure routes even before familiarity has been gained (see below). Their use as leading lines has also been seen in many long-distance travelling animals (e.g. Baker, 1978), and although some instances may imply physical constraints (such as risks associated with coastlines or forest edges) or advantages (such as dynamic or thermic updraughts associated with ridges or thermal triggers), others seem to offer little physical significance other than as a directional visual cue. More formally, Lau et al. (Lau et al., 2006) demonstrated that pigeon tracks from familiar sites are statistically more likely to pass over edges in the (mixed agricultural/urban) landscape, identified objectively using a Canny edge-detection algorithm applied to satellite photographs, than are the same tracks randomly shifted across the same landscape.

One hypothesis is that linear features are chosen precisely because they provide salience in the route-learning process. This might be because fewer features are required to structure an entire route, because linear features are more robustly identified from different angles of approach, or because they naturally contain directional information similar to that of a compass (T.G. and G. K. Taylor, unpublished). In the last case, we would predict that linear features are more commonly used when they themselves are oriented approximately goalwards (Baker, 1978; Lipp et al., 2004), but whilst

the informal observation that birds often follow linear features appears to support this, birds also cross linear features, but this does not look so obvious to the human eye. Indirect evidence comes from a study showing that pigeon tracks have higher spatiotemporal entropy (unpredictability) over homing approaches that involve crossing linear features rather than flying parallel to them (Guilford et al., 2004; Roberts et al., 2004), but as yet the underlying reasons for choice of linear features remain largely uninvestigated.

In contrast to linear features, the direct influence of individual point-source landmarks is inherently less easy to observe. Memorised waypoints can be inferred from fidelity pinch-points (Freeman et al., 2011) or highly informative locations in a Gaussian process model (Mann et al., 2011), but direct observation is difficult. Some apparently prominent landmarks seem never to exhibit an influence on pigeon homing [such as the tall TV tower at Frankfurt (Wiltshko et al., 2005)]. However, Biro et al. (Biro et al., 2006a) recorded tracks from a release site that did show an apparent influence of distant major landmarks – one a large power station with associated cooling towers, the other a complex of large industrial buildings – during both habitual route following and off-route releases. In an experiment explicitly designed to test for an orientational effect of this same power station landmark in releases from sites around it, Biro (Biro, 2002) saw no attracting influence in birds that had previously flown towards the landmark from one site and were then subsequently released from a second site on the homeward side of the landmark. Instead, birds were homeward orientated, away from the landmark, suggesting either that they ignored the landmark or that they had already acquired sufficient familiarity with the landmark's position in the landscape that they did not simply use it as a waypoint on a single learnt route. More recently, Mora et al. (Mora et al., 2012) argued that birds released from a site close to a wind-turbine array had more consistent tracks home, and were (marginally) less affected by clock-shift, than birds released from a site without such prominent landmarks. Biro (Biro, 2002) used a pseudo-familiarity technique to investigate the influence of a mid-distance village and church steeple, normally on the route home from a familiar site, on the orientation of birds released at a novel site that featured a similar village and steeple but in the direction away from home. A subset of birds was attracted to the village at the second site. Although this is consistent with birds having learnt to pilot home via the village, attraction to human settlements is quite commonly seen in pigeon release experiments (Kiepenheuer, 1993), the so-called village effect (Guilford, 1993), and might have more to do with seeking company than with directional guidance. Clearly, and in contrast to related research on invertebrates (e.g. Wehner, 1998; Graham and Collett, 2002), the difficulty of performing definitive landmark manipulation experiments on a field scale has contributed to our currently weak understanding of the importance of particular, defined landmarks on pigeon orientation, and this is an area where further research is needed.

The nature of place recognition

After being released from a specific site several times, subsequent release from a Perspex box that allowed a 5 min preview of the site resulted in pigeons homing faster than when denied the same preview (Braithwaite and Guilford, 1991; Braithwaite, 1993; Burt et al., 1997), an effect that does not occur at unfamiliar sites (Braithwaite and Newman, 1994) or if birds have not been exposed to the landscape surrounding their loft early in life (Braithwaite and Guilford, 1995). With GPS-tracked birds, Biro et al. (Biro et al., 2002) showed that such recognition led to improved homeward

performance only in the first 1 km out from the release site, not beyond. Results from this previewing paradigm [and similar experiments (Gagliardo et al., 2001)] show that birds' memorisation of places involves vision (reviewed in Holland, 2003). But extensions of the paradigm also indicate that visual landmark recognition can be remarkably localised and view-dependent, prompting Biro et al. (Biro et al., 2003) to liken it to the snapshot mechanism of flying insect orientation (Collett and Land, 1975; Cartwright and Collett, 1982; Cartwright and Collett, 1983). Biro et al. (Biro et al., 2003) allowed pigeons a partial (*ca.* 140 deg) view of a familiar release site (out of just one transparent side of the box) that was either the same during training and testing, or different; the precise direction of the preview (familiar or novel) was crucial to generating the recognition advantage. The effect waned with further releases, suggesting that birds were also acquiring local site familiarity immediately after release from the viewing box. In one experiment, the direction of the view was itself similar in the two treatments, but the release box was moved a few metres sideways to juxtapose two prominent visual features (a gate and a tree) differently in the familiar versus novel release conditions (Biro, 2002). Again, birds experiencing exactly the same view as in training homed faster than those experiencing the reconfigured view.

This view dependence is consistent with other results found in familiar area release experiments. Biro et al. (Biro et al., 2004) showed that pigeons re-joining established routes after displacement to off-route release sites tended to do so in a downstream (homeward) direction once close to the route, suggesting greater attraction to landscape features seen from a more familiar approach direction (although there could be other explanations, such as downstream points being more attractive because they are closer to home). Similarly, the gradual shortcutting of inefficient habitual routes is consistent with small-scale local improvements generated by recognition of landmarks downstream. Meade et al. (Meade et al., 2006) selected release sites that individual (previously tracked) birds were known to have flown over partway home from a more distant site. Although previously overflying a site improved homing speed when a bird was subsequently released from that site (relative to yoked controls), previewing the site from close to the ground did not affect performance. Thus, any recognition advantage produced by prior over-flight of a site did not extend to a ground-based view of the same place, suggesting that familiarity with aerial and ground-based views are substantially independent. More generally, this view-dependent visual memory in birds is thought to result in the use of active vision in which a stereotyped approach route is used to facilitate object recognition on a fine scale (Dawkins and Woodington, 2000).

Onward guidance in the familiar area

Whilst a crucial role for visual landmarks in the familiar area map is now fairly well established (Holland, 2003), the way in which these contribute to guidance remains uncertain. The prevailing view is that a mosaic of memorised places becomes associated with compass instructions towards home or other goals, and this is sometimes referred to as the mosaic map (Holland, 2003; Wiltschko and Wiltschko, 2009; originally Wallraff, 1974), although, confusingly, the term has also been used more broadly without specifying the need for the compass (e.g. Able, 2001; Bingman and Cheng, 2005). An alternative possibility is that the arrangements of memorised landmarks themselves provide onward guidance, an idea sometimes referred to as pilotage. There is a wide range of cognitive complexity in the potential mechanisms by which pilotage might operate, from simple use of isolated memorised landmarks or scenes

to a flexible appreciation of the spatial relationships amongst them, a research debate that touches on the concept of the cognitive map (e.g. Pearce, 2008), but about which still very little is known empirically at the spatial scale of a wide-ranging bird. Here, the crucial difference is between the use of landmark cues to fix position and their use to provide onward guidance, a difference that was explicitly discussed by Bingman and Ioalè (Bingman and Ioalè, 1989) but not using the same terminology. Under the mosaic map model, familiar landmarks do not provide guidance towards the final goal (onward guidance), this is provided by a memorised compass command. Familiar landmarks are envisaged to provide (or at least aid) a position fix. In the pilotage model, familiar landmarks contribute to both position fixing and direct onward guidance. In reality, the two models are not mutually exclusive of course, but distinguishing them serves to highlight their crucial characteristics and especially the role of memorised compass information.

How might these alternatives work to explain route following in practice? We may visualise route pilotage by imagining that the animal has memorised a chain of landmarks, each of which triggers recognition of a place and recall of a specific onward instruction involving a trajectory inherent in the configuration of the landmark's elements (guidance away from the landmark), or specified attraction towards the next visible landmark in the chain (guidance towards the next landmark). This is a simplification of course, because animals may also use more distant landmarks or panoramas for guidance without needing to be close to them (Filannino et al., 2013), but it serves to help distinguish different elements of the guidance process. Because animals are unlikely always to be precisely in the best position to recognise places, it is likely that attraction towards candidate familiar landmarks is also part of the position-fixing process (a kind of verification seeking), and we term this 'active position fixing' to distinguish it from the execution of a memorised guidance instruction. Active position fixing could also be important in a mosaic map model of route following as part of the initial landmark recognition phase, but it would need then to be followed by onward guidance via a memorised compass instruction once the animal had located its position satisfactorily.

The idiosyncratic structure of habitual routes, the presence of high fidelity pinch-points and other indicators of memorised waypoints, the width and tolerance of flight corridors, and the scale of off-route return to the route (all discussed in earlier sections) are features consistent with what would be expected of pilotage control via a chain of memorised visual landmarks. A traditional mosaic map account would not predict these features because guidance from release to home should be controlled by a compass and remain relatively uninfluenced by the underlying terrain. Indeed, the strength of compass guidance is that it does not require recognition of the terrain over which the animal is traversing. Nevertheless, it is possible that birds could acquire a memorised chain of landmarks, each with a compass instruction coding onward guidance to the next landmark. The attraction to route features seen in off-route release experiments could be accounted for in terms of an active position-fixing process. Whilst it is hard to see what the utility of compass guidance is once memorised locations are within direct visual contact of each other, this is ultimately an empirical question, and a multiple-bearings mosaic-map account of route following remains possible. Certainly, clock-shifting can sometimes affect orientation tasks in birds on a remarkably fine scale in the laboratory (Chappell and Guilford, 1995; Duff et al., 1998; Zimmerman et al., 2009; Wiltschko and Balda, 1989; Wiltschko et al., 1999), and homing pigeons are now known to deviate slightly even when released close to and in direct sight of their loft (Armstrong et al., 2013).

The role of memorised compass guidance during route following

An alternative approach to disentangling the mosaic map and pilotage accounts is to consider the role of the dominant time-compensated sun-compass directly. As an individual habitual route develops, it must involve the acquisition of additional representations involving the landscape to allow the detailed control evident in route stereotypy, but the question of whether it also involves acquisition of additional memorised compass instructions remains open. Biro et al. (Biro et al., 2007) attempted to test this by phase-shifting route-following birds [note that there is a reporting error in Biro et al. (Biro et al., 2007): birds were actually shifted 4 h forwards, rather than backwards, as originally described in Meade (Meade, 2005)]. Deflection after phase-shift was much smaller (usually less than 10 deg) in route-recapitulating birds thoroughly familiar with a release site (20 releases) than in birds not yet sufficiently familiar to show route recapitulation (four releases), in which deflection was similar to that found in birds subjected to more distant familiar site releases (approximately half the full 90 deg deviation). This indicates that control of familiar route following is overwhelmingly via mechanisms that do not require a memorised sun compass for directional guidance. Nevertheless, phase-shifting continues to have a small but persistent effect even on birds that are faithfully following a detailed route home. In many cases birds appear able to recapitulate their memorised route rather precisely, but slightly shifted to the side predicted by time-compensated sun-compass control. This result demonstrates that whilst there is an obvious continued reduction in the effect of clock-shift as birds take up route-following behaviour, it is not completely abolished. It remains to be determined whether this is caused by a residual effect of true navigation, a residual effect of prior memorised compass control from the release site, the acquisition of new compass instructions associated with each place along the memorised route (instructions which have very minor input on guidance), or some other effect of clock-shift yet to be described.

It is just conceivable that time-compensated sun compass guidance is replaced by an alternative (magnetic) compass as birds realise that the former is faulty, but it is not clear why this substitution should be so much stronger during route following than beforehand. Birds might still use compass mechanisms more or less instantaneously for other aspects of flight control, such as compensation for wind drift (measuring angular velocity or steering), but these would not require long-term memory or time-compensation, so would not be affected by phase-shift (T.G. and G. K. Taylor, unpublished). Thus, the likeliest explanation is that at spatial scales at which sufficient landscape familiarity to favour route following can be acquired [which might be easier in some landscapes than others (Filannino et al., 2013)], navigational or mosaic map control is largely, but gradually, replaced by direct landmark guidance, or pilotage. Just as route acquisition is progressive, so too might we expect to be its replacement of the mechanism or mechanisms that guided homing beforehand.

The role of memorised compass guidance on a larger scale

The main evidence that birds acquire a larger-scale mosaic map (perhaps up to a few tens of kilometres) is that clock-shift procedures continue to cause initial deviation at release sites even once they have apparently become familiar, implying continued use of the time-compensated sun compass (reviewed in Holland, 2003). There is disagreement about the strength of this effect, however, with some authors suggesting that the typical clock-shift is seen at familiar sites (Wiltschko and Wiltschko, 2009), and

others suggesting that where special training or conditions (see below) or uncontrolled familiarity can be ruled out, deviation under clock-shift is consistently smaller than at unfamiliar sites, and is accompanied by increased directional scatter (Wallraff et al., 1999), implying less consistent use of the sun compass. The confusing point here is that we need to seek explanation simultaneously both for the continued influence of clock-shifting and for the reduction of this effect. Reduced reliance on the sun compass could, in principle, result from a partial compensation using an alternative (magnetic) compass when birds recognise a conflict between the two, a reduction that should be abolished by applying magnetic disruption (Wiltschko and Wiltschko, 2001). Indeed, there is some evidence that magnetic treatments can restore a small degree of the expected clock-shift deviation at unfamiliar sites (Gagliardo et al., 2009). But, as Gagliardo et al. (Gagliardo et al., 2005) discussed, it is hard to see why this should be encouraged by familiarity with the landscape if no directional information comes from the landscape itself. This would require that birds become inherently more trusting of their magnetic compass, and less so of their sun compass, as they become familiar with the landscape. The alternative account of the reduced clock-shift effect at familiar sites is that rather than indicating a mosaic map representation, it reflects a compromise between conflicting solar compass cues associated with residual true navigational input and direct guidance from the familiar landscape. Experimental evidence shows that olfactory navigational inputs continue to have some influence on orientation, and increase clock-shift effects, at familiar sites (Bingman and Ioalè, 1989; Wallraff et al., 1999), so this residual true navigational interpretation of sun compass involvement seems feasible. Indeed, in Gagliardo et al.'s (Gagliardo et al., 2005) experiment, for example, anosmia explicitly caused birds to decrease their deviation under clock shift at familiar sites, providing clear evidence that some direct guidance information from familiar landmarks had been learnt but was being compromised by conflicting sun compass guidance when birds were able to access their navigational map through smell.

An additional problem with phase-shift evidence for the mosaic map is that with constant directional training birds may become compass entrained, learning to ignore other orientation cues because home is always in a single direction. This over-training effect is probably what contributes to the performance of long-distance racing pigeons always trained from one direction. It is what we might expect from an associative account of orientation if directional experience is highly consistent, and a simple directional response is therefore a good predictor of reward. Nevertheless, it is perhaps rather unlikely to represent the real situation for a bird in its natural familiar area. Dell'Arciccia et al. (Dell'Arciccia et al., 2009) clearly demonstrated this training direction effect without clock-shift in birds released over the sea. But it might also contribute to the strong clock-shift response seen in releases from distant familiar sites. For example, Füller et al. (Füller et al., 1983) is often cited as evidence for the mosaic map (Holland, 2003; Wiltschko and Wiltschko, 2009) because a large deviation was shown under clock-shift following at least 55 releases from the same site >40 km from home. But this effect might have resulted instead from the extensive, long-distance directional training prior to the crucial phase-shifted release (see also Wallraff et al., 1999). Thus, it still remains unclear whether large-scale familiar area orientation is controlled by acquisition of a mosaic map, or is in fact a compromise between decreasing true navigation and increasing direct landmark guidance as landscape familiarity is acquired.

Conclusions

Our analysis indicates just how far short we are of understanding exactly how pigeons, and hence other diurnal birds, utilise either visual landmarks or solar compass cues in familiar area navigation. The bulk of recent evidence suggests that with increasing local experience of sites around the loft, pigeons develop individually idiosyncratic routes or corridors home across the landscape, which are relatively closely controlled by memorised visual landscape features. It is unclear what happens early on in this process, but guidance appears to involve a compromise between direct landmark guidance and compass instructions memorised either as associations with familiar places (the mosaic map) or as part of the navigational map. As familiarity increases, memorised sun-compass instructions appear to have less and less influence on guidance, because clock-shift procedures produce only very small deviations (with the small residual effects of phase-shift having such fine-grained influence that they are currently hard to interpret). For this reason, the attraction to familiar landmarks without resort to stored compass instructions seen from up to a few kilometres in off-route release experiments is most probably indicative of a significant component of landmark guidance during familiar route following. The mosaic map, even a multiple-bearings version, cannot easily account for route following. Thus, a gradual transition to pilotage with increasing local route familiarity is currently the most parsimonious explanation for the bird's detailed familiar area map, although, with evidence largely restricted to experiments from a single laboratory, the case is not yet proven. Furthermore, inferences about the nature of the familiar area map are still derived almost exclusively from the behaviour of birds displaced artificially from their colony, with little understanding yet of how spontaneous exploration contributes to map learning, how information acquired on the outward journey might affect the structure of route following (or birds' dependence on it), or whether habitual route following would continue to dominate orientation if birds were to become familiar with a much more numerous or spatially diffuse array of sites. Spontaneous local flights around the loft (within approximately 1 km) can produce a sufficiently diffuse familiar landscape representation to allow birds approaching from untrained directions (that have been released from unfamiliar sites) to home more directly in the final few kilometres (Gagliardo et al., 2007), but the extent and precise nature of this effect is unknown. Thus, a fundamental question that remains to be investigated is whether a bird's natural familiar area map, once well developed, would continue to consist of a network of independent memorised routes, or whether a richer representation encoding the diffuse relationships amongst many known places might eventually develop, allowing more flexible orientation behaviour (and if so at what spatial scale).

Acknowledgements

We thank Marian Dawkins and Chris Armstrong for valuable comments on an earlier version of this manuscript.

Competing interests

The authors declare no competing financial interests.

Author contributions

Both authors contributed equally.

Funding

T.G. was supported during the writing of this manuscript by Merton College, Oxford, and D.B. by a Royal Society University Research Fellowship.

References

- Able, K. (2001). The concepts and terminology of bird navigation. *J. Avian Biol.* **32**, 174-183.
- Armstrong, C. (2010). *The Familiar Area Orientation Mechanisms of The Homing Pigeon*. DPhil thesis, University of Oxford.

- Armstrong, C., Wilkinson, H., Meade, J., Biro, D., Freeman, R. and Guilford, T. (2013). Homing pigeons respond to time-compensated solar cues even in sight of the loft. *PLoS ONE* **8**, e63130.
- Baker, R. R. (1978). *The Evolutionary Ecology of Animal Migration*. London: Hodder and Stoughton.
- Baker, R. R. (1982). *Migration: Paths through Time and Space*. London: Hodder and Stoughton.
- Bingman, V. P. and Cheng, K. (2005). Mechanisms of animal global navigation: comparative perspectives and enduring challenges. *Ethol. Ecol. Evol.* **17**, 295-318.
- Bingman, V. P. and Ioalè, P. (1989). Initial orientation of anomic homing pigeons based on information gathered at familiar release sites remains homeward directed following clock-shift. *Behaviour* **110**, 205-218.
- Biro, D. (2002). *The Role of Visual Landmarks in The Homing Pigeon's Familiar Area Map*. DPhil thesis, University of Oxford.
- Biro, D., Guilford, T., Dell'Omo, G. and Lipp, H.-P. (2002). How the viewing of familiar landscapes prior to release allows pigeons to home faster: evidence from GPS tracking. *J. Exp. Biol.* **205**, 3833-3844.
- Biro, D., Guilford, T. and Dawkins, M. S. (2003). Mechanisms of visually mediated site-recognition by homing pigeons. *Anim. Behav.* **65**, 115-122.
- Biro, D., Meade, J. and Guilford, T. (2004). Familiar route loyalty implies visual pilotage in the homing pigeon. *Proc. Natl. Acad. Sci. USA* **101**, 17440-17443.
- Biro, D., Meade, J. and Guilford, T. (2006a). Route recapitulation and route loyalty in homing pigeons: pilotage from 25 km? *J. Navig.* **59**, 43-53.
- Biro, D., Sumpter, D. J., Meade, J. and Guilford, T. (2006b). From compromise to leadership in pigeon homing. *Curr. Biol.* **16**, 2123-2128.
- Biro, D., Freeman, R., Meade, J., Roberts, S. J. and Guilford, T. (2007). Pigeons combine compass and landmark guidance in familiar route navigation. *Proc. Natl. Acad. Sci. USA* **104**, 7471-7476.
- Braithwaite, V. A. (1993). When does previewing the landscape affect pigeon homing? *Ethology* **95**, 141-151.
- Braithwaite, V. A. and Guilford, T. (1991). Viewing familiar landscapes affects pigeon homing. *Proc. Biol. Sci.* **245**, 183-186.
- Braithwaite, V. A. and Guilford, T. (1995). A loft with a view: exposure to a natural landscape during development may encourage adult pigeons to use visual landmarks during homing. *Anim. Behav.* **49**, 252-254.
- Braithwaite, V. A. and Newman, J. A. (1994). Exposure to familiar visual landmarks allows pigeons to home faster. *Anim. Behav.* **48**, 1482-1484.
- Burt, T., Holland, R. and Guilford, T. (1997). Further evidence for visual landmark involvement in the pigeon's familiar area map. *Anim. Behav.* **53**, 1203-1209.
- Cartwright, B. A. and Collett, T. S. (1982). How honey bees use landmarks to guide their return to a food source. *Nature* **295**, 560-564.
- Cartwright, B. A. and Collett, T. S. (1983). Landmark learning in bees: experiments and models. *J. Comp. Physiol. A* **151**, 521-543.
- Chappell, J. and Guilford, T. (1995). Homing pigeons primarily use the sun compass rather than fixed directional visual cues in an open-field arena food-searching task. *Proc. Biol. Sci.* **260**, 59-63.
- Collett, T. S. and Land, M. F. (1975). Visual spatial memory in a hoverfly. *J. Comp. Physiol. A* **100**, 59-84.
- Dawkins, M. S. and Woodington, A. (2000). Pattern recognition and active vision in chickens. *Nature* **403**, 652-655.
- Dell'Aricea, G., Dell'Omo, G., Wolfer, D. P. and Lipp, H.-P. (2008). Flock flying improves pigeons' homing: GPS track analysis of individual flyers versus small groups. *Anim. Behav.* **76**, 1165-1172.
- Dell'Aricea, G., Dell'Omo, G. and Lipp, H.-P. (2009). The influence of experience in orientation: GPS tracking of homing pigeons released over the sea after directional training. *J. Exp. Biol.* **212**, 178-183.
- Duff, S. J., Brownlie, L. A., Sherry, D. F. and Sangster, M. (1998). Sun compass and landmark orientation by lack-capped chickadees (*Parus atricapillus*). *J. Exp. Psychol. Anim. Behav. Processes.* **24**, 243-253.
- Fiaschi, V., Baldaccini, N. E., Ioalè, P. and Papi, F. (1981). Helicopter observations of homing pigeons with biased orientation because of deflected winds at the home loft. *Monitore Zoologico Italiano* **15**, 139-153.
- Filannino, C., Armstrong, C., Guilford, T. and Gagliardo, A. (2013). Individual strategies and release site features determine the extent of deviation in clock-shifted pigeons at familiar sites. *Anim. Cogn.* [Epub ahead of print] doi:10.1007/s10071-013-0635-x.
- Flack, A., Pettit, B., Freeman, R., Guilford, T. and Biro, D. (2012). What are leaders made of? The role of individual experience in determining leader-follower relations in homing pigeons. *Anim. Behav.* **83**, 703-709.
- Freeman, R., Mann, R., Guilford, T. and Biro, D. (2011). Group decisions and individual differences: route fidelity predicts flight leadership in homing pigeons (*Columba livia*). *Biol. Lett.* **7**, 63-66.
- Füller, E., Kowalski, U. and Wiltschko, R. (1983). Orientation of homing pigeons: compass direction vs piloting by landmarks. *J. Comp. Physiol. A* **153**, 55-58.
- Gagliardo, A., Odetti, F. and Ioalè, P. (2001). Relevance of visual cues for orientation at familiar sites by homing pigeons: an experiment in a circular arena. *Proc. Biol. Sci.* **268**, 2065-2070.
- Gagliardo, A., Odetti, F. and Ioalè, P. (2005). Factors reducing the expected deflection in initial orientation in clock-shifted homing pigeons. *J. Exp. Biol.* **208**, 469-478.
- Gagliardo, A., Ioalè, P., Savini, M., Lipp, H.-P. and Dell'Omo, G. (2007). Finding home: the final step of the pigeons' homing process studied with a GPS data logger. *J. Exp. Biol.* **210**, 1132-1138.
- Gagliardo, A., Savini, M., De Santis, A., Dell'Omo, G. and Ioalè, P. (2009). Re-orientation in clock-shifted homing pigeons subjected to a magnetic disturbance: a study with GPS data loggers. *Behav. Ecol. Sociobiol.* **64**, 289-296.

- Graham, P. and Collett, T. S. (2002). View-based navigation in insects: how wood ants (*Formica rufa* L.) look at and are guided by extended landmarks. *J. Exp. Biol.* **205**, 2499-2509.
- Guilford, T. (1993). Homing mechanisms in sight. *Nature* **363**, 112-113.
- Guilford, T., Gagliardo, A., Chappell, J., Bonadonna, F., Burt de Perera, T. and Holland, R. (1998). Homing pigeons use olfactory cues for navigation in England. *J. Exp. Biol.* **201**, 895-900.
- Guilford, T., Roberts, S., Biro, D. and Rezek, I. (2004). Positional entropy during pigeon homing II: navigational interpretation of Bayesian latent state models. *J. Theor. Biol.* **227**, 25-38.
- Holland, R. A. (2003). The role of visual landmarks in the avian familiar area map. *J. Exp. Biol.* **206**, 1773-1778.
- Ioalé, P., Dall'Antonia, P., Dall'Antonia, L. and Benvenuti, S. (1994). Flight paths of homing pigeons studied by means of a direction recorder. *Ethol. Ecol. Evol.* **6**, 519-527.
- Kiepenheuer, J. (1993). The ambiguity of initial orientation of homing pigeons. In *Proceedings of the Royal Institute of Navigation Conference, 1993, No. 17*. Oxford: Royal Institute of Navigation.
- Lau, K. K., Roberts, S., Biro, D., Freeman, R., Meade, J. and Guilford, T. (2006). An edge-detection approach to investigating pigeon navigation. *J. Theor. Biol.* **239**, 71-78.
- Lipp, H.-P., Vyssotski, A. L., Wolfer, D. P., Renaudineau, S., Savini, M., Tröster, G. and Dell'Omo, G. (2004). Pigeon homing along highways and exits. *Curr. Biol.* **14**, 1239-1249.
- Mann, R., Freeman, R., Osborne, M., Garnett, R., Armstrong, C., Meade, J., Biro, D., Guilford, T. and Roberts, S. (2011). Objectively identifying landmark use and predicting flight trajectories of the homing pigeon using Gaussian processes. *J. R. Soc. Interface* **8**, 210-219.
- Meade, J. (2005). *Tracking Homing Pigeons by GPS*. DPhil thesis, University of Oxford.
- Meade, J., Biro, D. and Guilford, T. (2005). Homing pigeons develop local route stereotypy. *Proc. Biol. Sci.* **272**, 17-23.
- Meade, J., Biro, D. and Guilford, T. (2006). Route recognition in the homing pigeon (*Columba livia*). *Anim. Behav.* **72**, 975-980.
- Mora, C. V., Ross, J. D., Gorsevski, P. V., Chowdhury, B. and Bingman, V. P. (2012). Evidence for discrete landmark use by pigeons during homing. *J. Exp. Biol.* **215**, 3379-3387.
- Papi, F. (1992). *Animal Homing*. London: Chapman & Hall.
- Pearce, J. M. (2008). *Animal Learning and Cognition: an Introduction*. Hove, NY: Psychology Press.
- Pettit, B., Flack, A., Freeman, R., Guilford, T. and Biro, D. (2013). Not just passengers: pigeons, *Columba livia*, can learn homing routes while flying with a more experienced conspecific. *Proc. Biol. Sci.* **280**, 20122160.
- Roberts, S., Guilford, T., Rezek, I. and Biro, D. (2004). Positional entropy during pigeon homing I: application of Bayesian latent state modelling. *J. Theor. Biol.* **227**, 39-50.
- Schiffner, I., Fuhrmann, P. and Wiltschko, R. (2013). Homing flights of pigeons in the Frankfurt region: the effect of distance and local experience. *Anim. Behav.* **86**, 291-307.
- Steiner, I., Bürgi, C., Werffeli, S., Dell'Omo, G., Valenti, P., Tröster, G., Wolfer, D. P. and Lipp, H.-P. (2000). A GPS logger and software for analysis of homing in pigeons and small mammals. *Physiol. Behav.* **71**, 589-596.
- von Hünenbein, K., Klauer, B., Müller, R. and Wiltschko, W. (1997). A GPS based flight recorder for homing pigeons. In *Proceedings of the Conference Global Navigation Satellite Systems, Vol. II* (ed. O. Wiesenau), pp. 561-570. Bonn: Deutsche Gesellschaft für Ortung und Navigation.
- von Hünenbein, K., Hamann, H.-J., Rüter, E. and Wiltschko, W. (2000). A GPS-based system for recording the flight paths of birds. *Naturwissenschaften* **87**, 278-279.
- Wallraff, H. G. (1974). *Das Navigationssystem der Vögel. Ein theoretischer Beitrag zur Analyse Ungeklärter Orientierungsleistungen*. Munich: Oldenbourg.
- Wallraff, H. G. (2005). *Avian Navigation. Pigeon homing as a Paradigm*. Berlin: Springer.
- Wallraff, H. G., Kiepenheuer, J. and Streng, A. (1994). The role of visual familiarity with the landscape in pigeon homing. *Ethology* **97**, 1-25.
- Wallraff, H. G., Chappell, J. and Guilford, T. (1999). The roles of the sun and the landscape in pigeon homing. *J. Exp. Biol.* **202**, 2121-2126.
- Wehner, R. (1998). Navigation in context: grand theories and basic mechanisms. *J. Avian Biol.* **29**, 370-386.
- Wiltschko, W. and Balda, R. P. (1989). Sun compass orientation in seed-caching scrub jays (*Aphelocoma coerulescens*). *J. Comp. Physiol. A* **164**, 717-721.
- Wiltschko, R. and Wiltschko, W. (2001). Clock-shift experiments with homing pigeons: a compromise between solar and magnetic information? *Behav. Ecol. Sociobiol.* **49**, 393-400.
- Wiltschko, R. and Wiltschko, W. (2009). Avian navigation. *Auk* **126**, 717-743.
- Wiltschko, W., Balda, R. P., Jahnel, M. and Wiltschko, R. (1999). Sun compass orientation in seed-caching corvids: its role in spatial memory. *Anim. Cogn.* **2**, 215-221.
- Wiltschko, R., Siegmund, B. and Stapput, K. (2005). Navigational strategies of homing pigeons at familiar sites: do landmarks reduce the deflections induced by clock-shifting? *Behav. Ecol. Sociobiol.* **59**, 303-312.
- Wiltschko, R., Schiffner, I. and Siegmund, B. (2007). Homing flights of pigeons over familiar terrain. *Anim. Behav.* **74**, 1229-1240.
- Zimmerman, P., Nicol, C. J. and Guilford, T. (2009). Involvement of the sun and the magnetic compass of domestic fowl in its spatial orientation. *Appl. Anim. Behav. Sci.* **116**, 204-210.