

Homing pigeons develop local route stereotypy

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The mechanisms used by homing pigeons (*Columba livia*) to navigate homeward from distant sites have been well studied, yet the mechanisms underlying navigation within, and mapping of, the local familiar area have been largely neglected. In the local area pigeons potentially have access to a powerful navigational aid—a memorized landscape map. Current opinion suggests that landmarks are used only to recognize a familiar start position and that the goalward route is then achieved solely using compass orientation. We used high-resolution global positioning system (GPS) loggers to track homing pigeons as they became progressively familiar with a local homing task. Here, we demonstrate that birds develop highly stereotyped yet individually distinctive routes over the landscape, which remain substantially inefficient. Precise aerial route recapitulation implies close control by localized geocentric cues. Magnetic cues are unlikely to have been used, since recapitulation remains despite magnetic disruption treatment, and olfactory cues would have been positionally unstable under the variable wind conditions, making visual landmarks the most likely cues used.

Keywords: route recapitulation; pilotage; navigation; GPS tracking; homing pigeon

1. INTRODUCTION

Although much is now known about the mechanisms of long-distance navigation in birds (Papi 1992; Wallraff 2001; Wiltschko & Wiltschko 2003) it is far less clear how birds orient within, and build a map of, their local familiar environment. The role of visual landmarks remains a particularly debated issue, despite their obvious candidacy in such highly visual animals. Early work with homing pigeons suggested that visual landmarks were unimportant. Schmidt-Koenig & Schlichte (1972) showed that pigeons wearing frosted contact lenses (allowing them a view of the sun but no other detailed visual features) were still able to reach within a few hundred metres of the home loft. Furthermore, clock-shifted birds appear to remain predictably deviated from the homeward direction upon release from familiar sites unless actually within sight of the loft (Graue 1963; Schmidt-Koenig 1965), even after many releases (Füller *et al.* 1983; Keeton 1969), although the degree of deviation is sometimes smaller than expected (e.g. Wiltschko *et al.* 1994; Wallraff *et al.* 1999; for a review see Chappell (1997)). Nevertheless, familiar visual landmarks have been shown to be important both at the beginning and at the end of the homeward journey. A 5-minute view of a site before release significantly improves homing speeds at familiar sites (Braithwaite & Guilford 1991; Burt *et al.* 1997; Gagliardo *et al.* 2001; Biro *et al.* 2002) but not unfamiliar sites (Braithwaite & Newman 1994). This difference in homing speed is attributed to improved recognition of the release site using familiar visual cues when pigeons are provided with a preview. There has been very little work done on the structure of the birds' map from vanishing point to home, and there are some hints from vanishing data that birds may show persistent deviations from a direct compass bearing to home even from familiar sites (Füller *et al.* 1983; Kowalski & Wiltschko

1987; Wallraff 1994). Nevertheless, current opinion suggests that the role of landmarks is largely restricted to the recognition of position with subsequent goalward orientation specified by an associated compass bearing (as in the mosaic map hypothesis), and that there is no clear evidence that birds' homeward routes may be controlled by direct progression along a sequence of landscape features (a system known as pilotage). At present there is only indirect evidence that any attention at all is paid to ground features during the remainder of the homeward journey (Ulrich *et al.* 1999), although even Schmidt-Koenig & Schlichte's (1972) results indicate that a view of the home loft may be important for the final stage of homing.

A major source of uncertainty about the true nature of the bird's familiar area map must be attributed to limitations in the traditional methods of recording birds' wide-ranging behaviour between release and home. Vanishing point bearings measured by means of binoculars provide only rough orientation data near release; homing speeds only indirectly measure route efficiency; radio-tracking and following by aircraft provide only relatively inaccurate position data. Precision tracking technology for the homing pigeon, which started with compass heading recorders (e.g. Bramanti *et al.* 1988; Bonadonna *et al.* 1997; Holland *et al.* 2000) and has recently been extended to the use of GPS loggers (Steiner *et al.* 2000; von Hünenbein *et al.* 2000), potentially allows far deeper inferences about the relationship between a bird's choice of flight path and the underlying visual landscape (Biro 2002; Guilford *et al.* 2004; Lipp *et al.* 2004; Roberts *et al.* 2004), and offers the prospect of elucidating the map's development without needing to execute drastically disruptive manipulations of the bird's navigational systems (such as clock-shifting). In this study, we used high-resolution GPS loggers to track homing pigeons as they became progressively more familiar with a local homing task.

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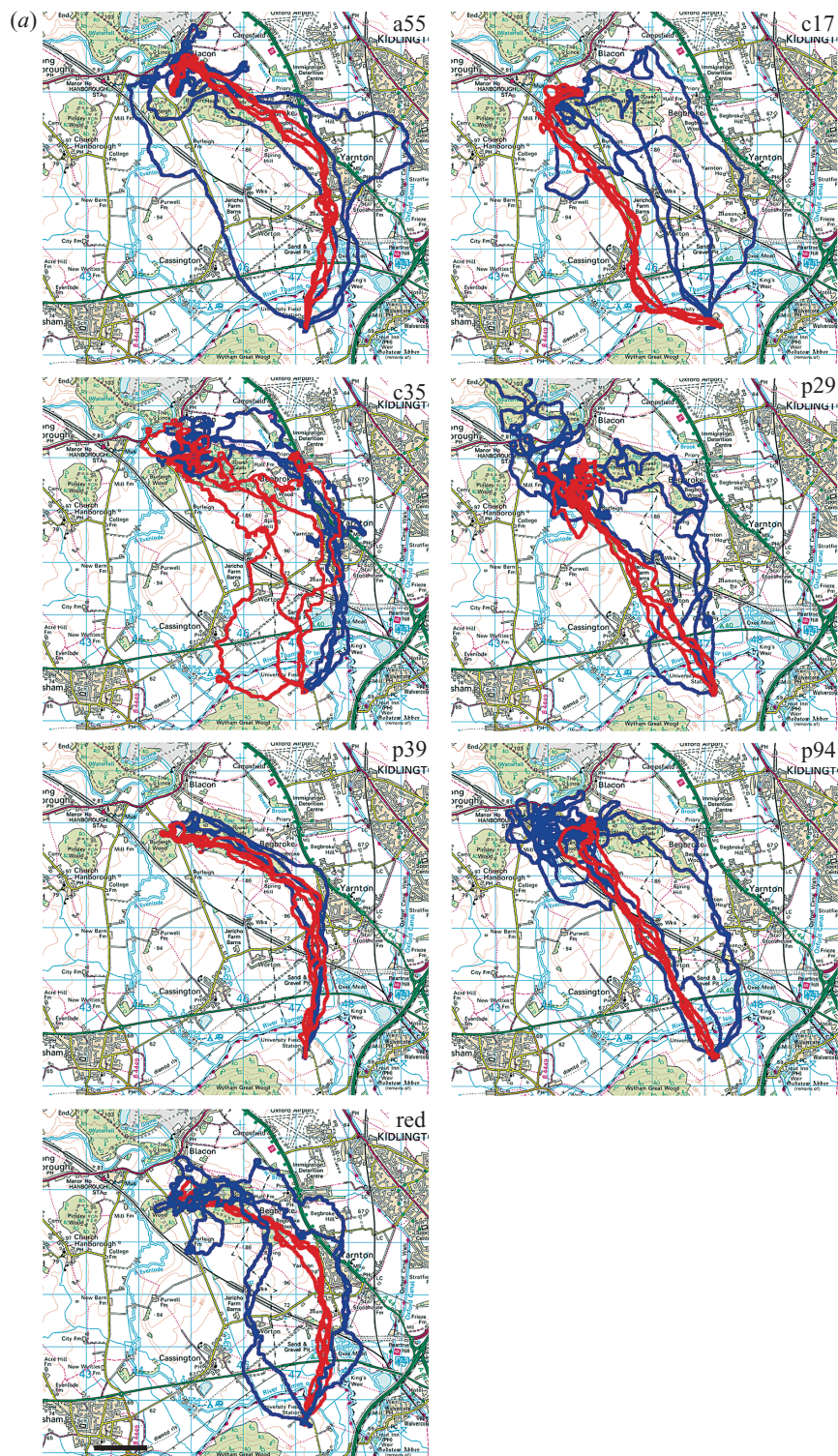


Figure 1. (Continued opposite.)

2. MATERIAL AND METHODS

(a) Experiment 1

Seven homing pigeons (*Columba livia* L) were selected as subjects. All were successful homers and had been used in previous experiments. All birds were more than 2 years old and at least 450 g in mass. They were fitted with a Velcro strip 30 mm × 70 mm, attached to their back with flexible leather glue applied to trimmed feathers and were trained to carry plasticine dummy weights of 25 g (see Biro *et al.* (2002) for details).

The chosen test release site was Bladon Heath (distance to home 5.0 km, direction to home 153°). The birds were given

numerous training releases, up to 7 km from home in all directions, but were given no training releases from the site and had not been released from the site in previous experiments. Each bird was then released 24 times consecutively from the chosen site, with a maximum of four releases in a day. All 24 tracks for each bird were collected over a period of two months.

During each test release the birds carried GPS logging devices (see Steiner *et al.* (2000) for technical description) attached to the back with Velcro and of mass 28–32 g. Time-stamped positional fixes (accurate to ± 4 m in a horizontal plane; Weimerskirch *et al.* 2002) were logged every second and were downloaded on

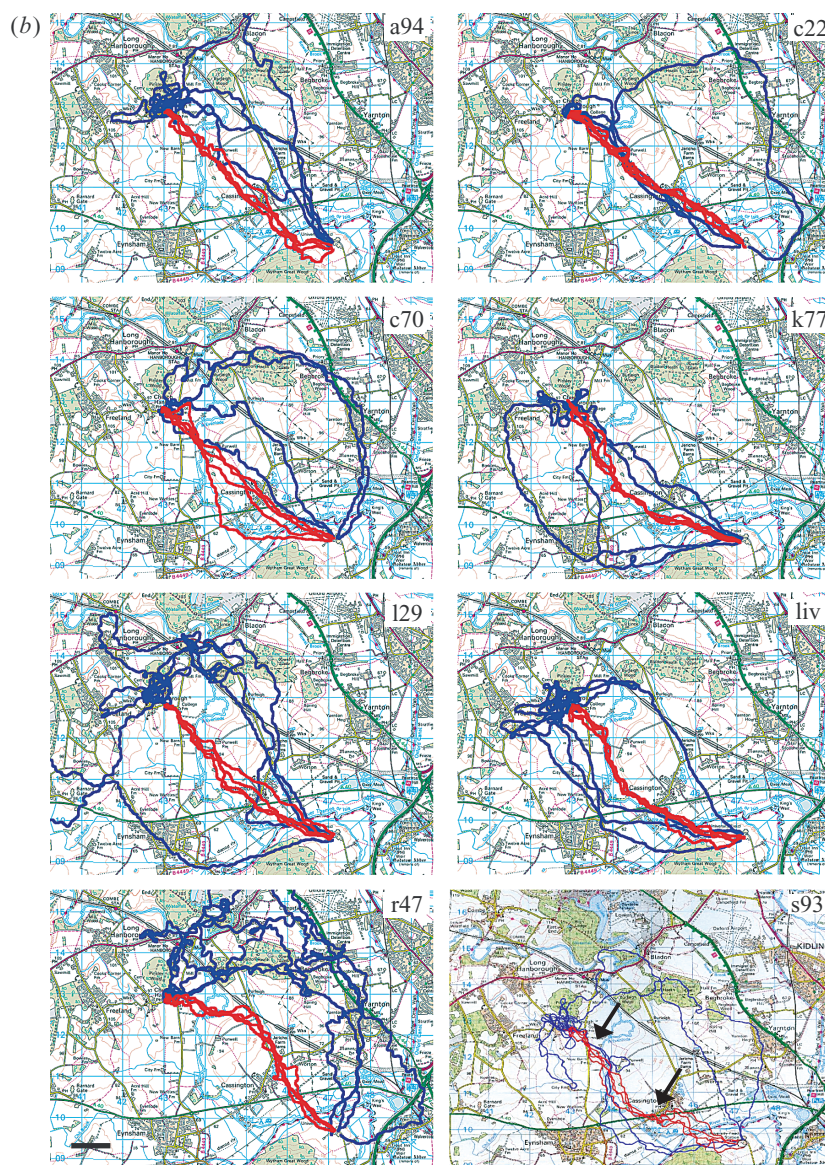


Figure 1. Maps showing the first four and final four flights performed by each bird. The first four flights of each bird are shown in blue. The final four are shown in red. (a) Shows the tracks of the seven birds in experiment 1. (b) Shows the tracks of the eight birds in experiment 2. Bird identities are indicated in the top right corner of each panel. Arrows on map s93 indicate the routes converging in a narrow corridor. In both cases home is to the south-east, with the release sites to the north-west. Scale bar, 1 km.

recovery of the device. The positional data were superimposed onto Ordnance Survey maps using FUGAWI[®] mapping software (copyright 2000–2002, Northport Systems Inc.).

(b) Experiment 2

Eight new homing pigeons (*Columba livia* L), were selected as subjects. A new test release site was chosen (Church Hanborough: distance to home 5.3 km, direction to home 129°). During the training phase, the birds were not released from sites with home direction 40–220° (90° either side of the chosen release site), but they had numerous training releases from all other directions. Each bird also had one training release from the chosen test release site.

The birds then had 20 consecutive releases from the test site over the course of four weeks. Each test flight was tracked using the same apparatus as that described in experiment 1. Immediately before test releases each bird was fitted with a neodymium iron boron magnet (Haugh *et al.* 2001). The magnets were 2 mm thick and 3 mm in diameter. They were attached using a 3 mm-wide

strip of adhesive cloth tape approximately 25 mm long, so that the magnet was placed at the base of the cere with the tape stuck to the beak and the feathers above the cere. The magnet was removed on return to the home loft. A maximum of four tracks were recorded in a day.

3. RESULTS

(a) Experiment 1

Figure 1a shows, separately for each bird, the first four and final four tracks recorded in experiment 1. To assess the development of the birds' individual choice of route, we examined track variability over time. As a measure of track similarity, we used a program written in FORTRAN to calculate the area between any given pair of tracks, with small areas indicating a high degree of similarity. The 24 tracks for each bird were divided into groups of four consecutive flights, and the area between every possible pair of tracks within a group was calculated to give a cumulative area for

each group. These values were then plotted against release order (figure 2*a*). Route variability typically decreased progressively, with negative regressions in five out of the seven cases (table 1). Of the two exceptions, one showed high track similarity from the start (p39), and, interestingly, the other (c35), which maintained high track variability, was subsequently discovered to be blind in one eye.

To assess the level of inter-individual variation in route choice, the final flights performed by each bird were compared with the final flights of all other birds in the experiment. To do this, the last three tracks performed by each bird were pooled, creating a set of 21 tracks. These were then randomly reassigned into groups of three, and the areas between all possible pairs of tracks within each new group were calculated and summed to give a cumulative area. This randomization procedure was reiterated 10 000 times to provide a test distribution of track similarity. The cumulative areas between the final three tracks performed by individual birds were then compared with this distribution. Six out of the seven birds had a cumulative area smaller than expected by chance (figure 3*a*). Over a large number of releases, pigeons thus develop tracks that show significantly higher intra- than inter-individual similarity, indicating individual variation in route choice.

We also examined the distances flown by individual birds over successive releases to investigate whether homeward flights became more efficient over time. Distance travelled was plotted against release number (figure 4*a*). In five out of the seven cases the regressions were significant and negative (table 1), showing that most birds' routes became shorter with an increasing number of releases. However, track length appeared to become asymptotic, as the birds continued to travel substantially longer distances than the beeline path home. Mean track efficiency (calculated as the straight-line distance home divided by the actual distance travelled) in the final flight performed by each bird was 0.66 ± 0.11 (s.d.), with on average an extra 2.6 km travelled in excess of the 5.0 km beeline.

(b) Experiment 2

Figure 1*b* shows the first four and final four tracks of the birds released in experiment 2, after application of magnetic disruption treatment. All the core findings of experiment 1 were replicated. All eight birds performed increasingly stereotyped routes (figure 2*b*, table 1). The cumulative area between the final three tracks of five out of the eight birds was smaller than would be expected by chance, with a further two birds showing results very close to the lower 0.025 confidence boundary (figure 3*b*). In every case the birds became increasingly efficient (figure 4*b*, table 1), while not reaching maximal efficiency (mean track efficiency 0.81 ± 0.04 (s.d.), with an extra 1.3 km travelled in excess of the 5.3 km beeline distance).

4. DISCUSSION

We examined route choice by homing pigeons in 20–24 repeated homing flights from the same release site, as recorded by high-resolution GPS loggers. Three core findings emerged from our analysis. First, tracks of individual pigeons became stereotyped with increasing experience. Second, individuals varied in their choice of tracks. Third, although the birds' tracks became more efficient with

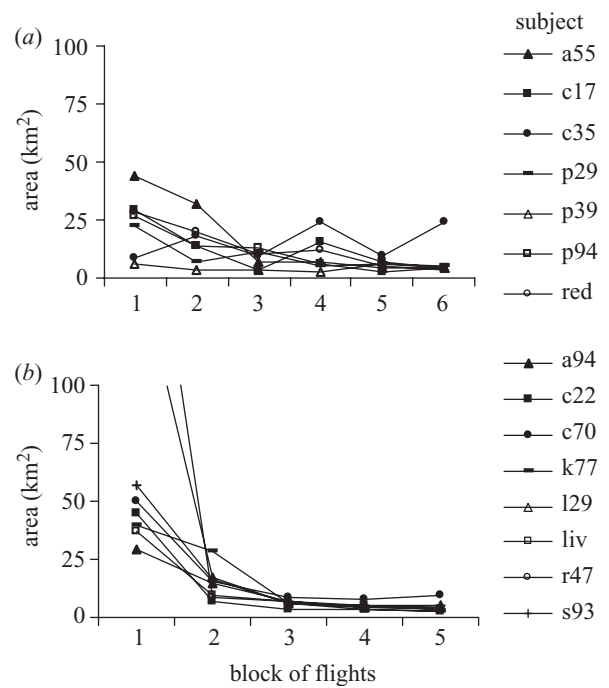


Figure 2. Cumulative area within blocks of four successive flights against release order. Cumulative area was calculated as the sum of areas enclosed by each possible pair of tracks within a group of four. (a) Experiment 1 with six groups of four flights. (b) Experiment 2 with five groups of four flights. Each bird is illustrated by a different symbol.

experience, they remained substantially longer than the beeline distance home.

The finding that pigeons follow highly stereotyped routes even after a large number of releases seems, at first, counterintuitive. During the first few flights from a novel location, birds presumably have only a sparse knowledge of the local area, and it is then that route-recapitulation would most reduce the risk of navigational error. In fact, as birds become more experienced, their routes become more stereotyped. This, coupled with the finding that routes remain inefficient even once fully stereotyped, yet vary between individuals (i.e. there is no single best route that can explain the marginal tortuosity at stability), suggests that the main function of route recapitulation is not to reduce navigational risk. A more probable explanation (though not incompatible with a risk reduction strategy) is that route recapitulation reduces cognitive load in a way analogous to the active vision demonstrated in invertebrates (Collett 1992, 1995; Zeil 1995) and more recently in chickens (Dawkins & Woodington 2000), which is thought to allow minimization of the number of images that must be remembered. The recognition of three-dimensional visual landmarks requires a high memory load because of the range of angles and distances from which landmarks may be viewed. Animals follow stereotyped paths so that landmarks are always encountered from a familiar distance and angle (Ullman 1996). This means that landmarks can be easily recognized only from the set route, but the number of images that must be remembered is greatly reduced.

It seems highly likely that our birds' chosen routes were visually mediated. For a terrestrial animal anchored to the

Table 1. Regression coefficients for the change in track similarity and track length over the course of repeated releases in experiments 1 and 2. Similarity was assessed by calculating the sum of areas enclosed by each possible pair of tracks within a group of four consecutive tracks (see figure 2). The distance travelled on each flight was regressed against release number. Asterisks* indicate significance at $p < 0.05$.

bird	cumulative area			distance travelled		
	coefficient	F	p	coefficient	F	p
experiment 1						
a55	-0.000262	13.31	0.022*	-0.273957	16.93	0.000*
c17	-0.000115	2.91	0.163	-0.091520	4.49	0.046*
c35	+0.000055	0.87	0.403	-0.218960	2.21	0.151
p29	-0.000089	4.94	0.090	-0.419170	11.96	0.002*
p39	0.000000	0.00	0.978	+0.020782	4.22	0.052
p94	-0.000149	18.87	0.012*	-0.438960	7.16	0.044*
red	-0.000205	28.52	0.006*	-0.179940	6.88	0.016*
experiment 2						
a94	-0.000169	18.54	0.023*	-0.395639	32.13	0.000*
c22	-0.000286	4.17	0.134	-0.145038	4.11	0.058
c70	-0.000282	4.56	0.122	-0.258346	4.85	0.041*
k77	-0.000312	17.20	0.025*	-0.232105	9.80	0.006*
l29	-0.001330	3.63	0.153	-0.889474	6.65	0.019*
liv	-0.000241	5.70	0.097	-0.402707	16.62	0.001*
r47	-0.001290	3.24	0.170	-0.296770	5.91	0.026*
s93	-0.000404	5.50	0.101	-0.388346	15.00	0.001*

landscape a range of cues might provide the positional control needed to account for detailed route recapitulation, but for an animal flying well above the landscape local visual cues seem to constitute the most likely candidate. It is unlikely that environmental odours could specify such a detailed route, particularly since wind conditions varied considerably between successive flights. (In all but one case the birds experienced wind directions varying across at least three of the four cardinal compass quadrants.) The birds in experiment 2 had their access to potential magnetic cues disrupted in all releases, but their routes were still stereotyped. Previous experiments with identical magnets apparently disrupted magneto-reception successfully, and because our birds only wore the magnets for the brief release periods themselves (Haugh *et al.* 2001), and not constantly in-between, it is most unlikely that they would have been able to adjust to the disruption treatment. Visual cues are also suggested by the fact that one of the only birds that did not develop a highly stereotyped route was found to be blind in one eye.

Our results thus suggest that visual cues are critical to familiar area orientation, not just near release (Braithwaite & Guilford 1991; Biro *et al.* 2002) and on final approach to home (Schmidt-Koenig & Schlichte 1972), but throughout the homeward route, at least over short distances. This is in contrast to established theory, in which it is supposed that birds may encode visual landmark features in a mosaic map, allowing recognition of familiar release points and recall of associated compass bearings, with the compass then being relied on for homeward orientation from those points (Wallraff 1974). There are three possible explanations to account for our results. First, it is possible that the birds used a memorized compass direction from the release site to home and used external landmarks to correct for errors along the route. This seems unlikely, as birds often leave the release site in directions markedly different from that of home. Second, birds may remember a chain of

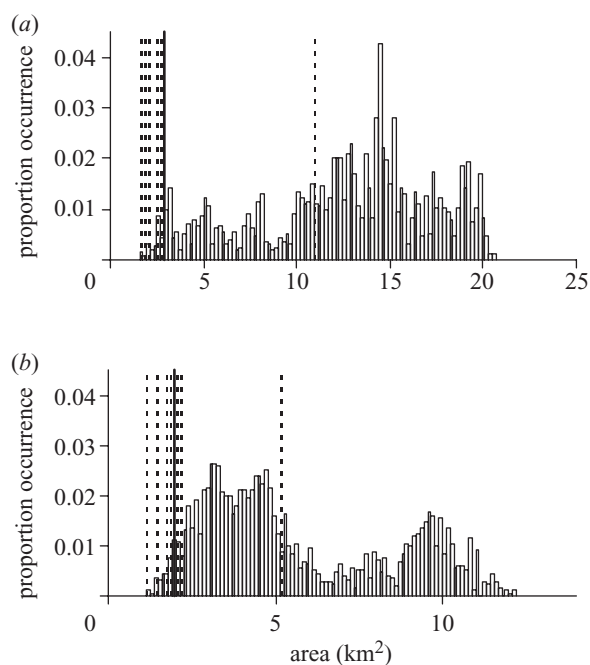


Figure 3. Results of the randomization test for individual variation. The cumulative area for the final three tracks flown by each bird is shown by vertical dotted lines, calculated as the sum of the areas enclosed by each possible pair of tracks within a group of three. The histograms show the distribution of cumulative area when the tracks were assigned randomly into groups of three 10 000 times. The solid line shows the lower 0.025 confidence value. (a) Experiment 1. (b) Experiment 2.

landmarks with an associated compass bearing between each one. An advantage of this model is that it allows for several 'check points' along each route, so that repetition of the characteristic overall shape of the route could be explained. One observation consistent with this second

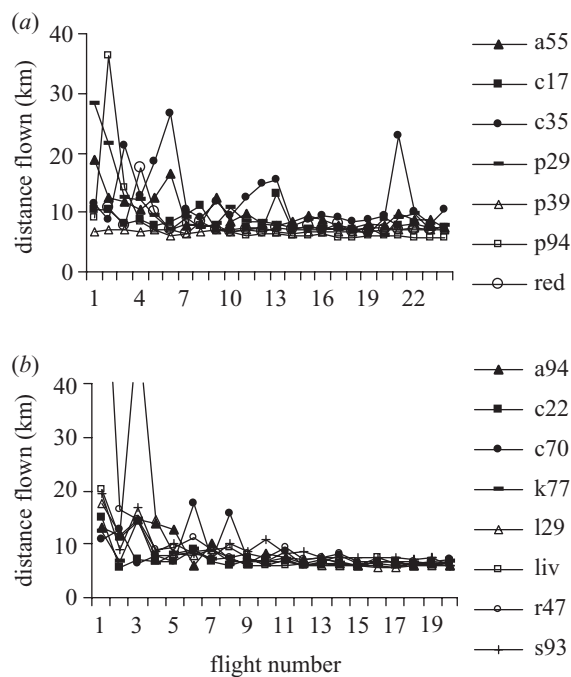


Figure 4. Graph showing the distances flown by individual birds on successive flights. Each bird is illustrated by a different symbol. (a) Experiment 1. (b) Experiment 2.

hypothesis is that although some of the routes were more widely dispersed, most individuals' flights showed convergence onto narrow corridors over various specific locations in the landscape. (The flight paths of s93 provide an example, with arrows illustrating two local constrictions in figure 1b.) The third possibility is that the route is remembered in fine detail with no primary reference to a compass. This model, which is a form of 'pilotage' (Baker 1984; Papi 1992), originally known as 'Type 1 orientation' (Griffin 1952), has the advantage that it accounts for accurate route-recapitulation.

Our more recent work attempts to determine more precisely the nature of cues used and how far the route recapitulation effect extends away from home (Biro *et al.* 2004). In future work we will examine how compass-dependent and compass-independent mechanisms of familiar area orientation may be integrated.

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