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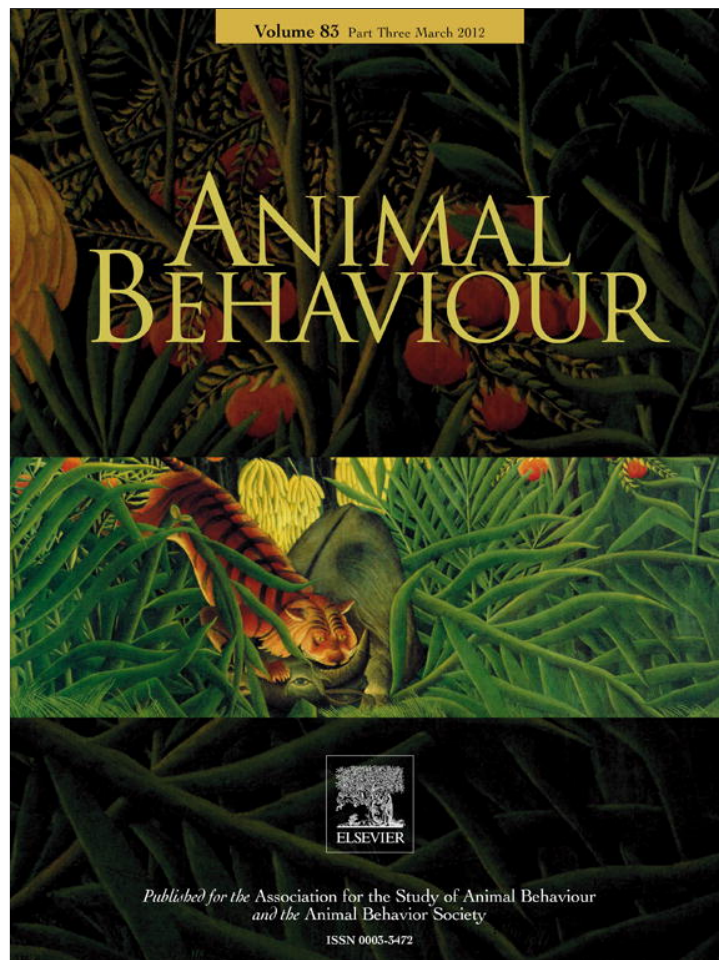
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What are leaders made of? The role of individual experience in determining leader–follower relations in homing pigeons

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Negotiating joint routes during group travel is one of the challenges faced by collectively moving animals, on spatial scales ranging from daily foraging trips to long-distance migrations. Homing pigeons, *Columba livia*, provide a useful model system for studying the mechanisms of group decision making in the context of navigation, owing to the combination of their gregarious nature and the depth of our understanding of their individual orientational strategies. Previous work has shown that during paired flight, if two birds' individually preferred routes are sufficiently different, one bird will emerge as leader whom the other follows. What determines the identity of a leader has important implications for the efficiency of a moving collective, since leaders with higher navigational certainty can increase the accuracy of the group. We examined factors contributing to the establishment of leadership/followership, focusing on the role of previous navigational experience. We tested, on a homing task, pairs of pigeons in which the two partners had relatively greater and lesser prior experience, generated through individual training. Analysis of the GPS-tracked routes taken by such pairs revealed a negative correlation between homing experience and the probability that a pigeon would follow a co-navigating partner. Thus, the larger the difference in experience between two partners, the higher the likelihood the more experienced bird would emerge as leader. Our results contribute to a better understanding of the mechanisms and potential payoffs of collective navigational decision making in species that travel in mixed-experience groups.

One of the most illustrative examples of group decision making in collective animal behaviour concerns the coordinated movement of individuals. Many social animals travel together in groups, over a variety of different spatial scales, from daily foraging or ranging activities to large-scale migrations. Collective travel can yield a multitude of advantages to individual members (including predator avoidance, enhanced foraging efficiency and increased navigational accuracy; Krause & Ruxton 2002). A central problem in the study of group movements concerns the question of how navigational information flows between group members, and of how such flow depends upon the navigational knowledge held by each member of the group (e.g. Couzin et al. 2005; Conradt et al. 2009). Differences in knowledge can stem from various sources, including inherent individual differences in navigational skill or strategy, as well as the amount of experience that group members have gathered through previous encounters with a landscape.

Given such interindividual variation in knowledge, how do groups reach consensus and solve the problem of maintaining a cohesively moving collective?

Over the past decade, collective motion and group decision making have generated a great deal of theoretical interest (Couzin & Krause 2003; Conradt & Roper 2009; Sumpter 2010). Theoretical work focusing on individual movements and interactions has strengthened our understanding of how individual behaviours scale to coherent collective motion (Couzin & Krause 2003; Vabø & Skaret 2008; Hemelrijk & Hildenbrandt 2011). Additionally, theoretical approaches have generated predictions about the mechanisms through which such group decisions are made, with a broad distinction between processes in which most or all group members contribute to a decision and those in which one or a small number of individuals make decisions for the rest of the group (Conradt & Roper 2009). Simulation models suggest the predictable occurrence of a transition from the latter to the former in groups containing members with divergent directional preferences. The transition is abrupt, and occurs at the point where conflict reaches a critical level (Couzin et al. 2005). Following the transition, leadership is typically assumed by the individual/subgroup with the highest certainty of

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information, or those that place the highest weight on their own information (Conradt et al. 2009). In line with such theoretical work, the role of individual knowledge in determining leadership in real animal groups is of fundamental interest, yet few experiments have attempted to provide the necessary empirical data (e.g. Guilford & Chappell 1996; Reebs 2000; Bousquet & Manser 2011).

Pigeons, *Columba livia*, have long been a model species for the study of animal navigation, where emphasis has traditionally been on the mechanisms that individual birds use to navigate in the field (reviewed in Wallraff 2005). More recently, pigeons have emerged as a system suitable for the study of group decisions, mainly because of the ease with which coordinated movements of flock members can be studied (Biro et al. 2006; Dell'Ariccia et al. 2008; Nagy et al. 2010). Studies have shown that following repeated releases from the same site, homing pigeons come to rely on stereotyped homing routes that show high levels of consistency within individuals but considerable divergence between individuals (Biro et al. 2004; Meade et al. 2005). When two such experienced, 'route-recapitulating' pigeons are released together, they will either fly a compromise route intermediate between their individually preferred routes, or, if the distance between their routes rises above a critical threshold, one of the birds will follow the flight path of the other (Biro et al. 2006; Sumpter et al. 2008).

When experienced pigeons are tested repeatedly, in pairs with different partners, the identities of the leaders and followers condense into a fully transitive hierarchy (i.e. if A follows B and B follows C, then A will follow C; Biro et al. 2006). In fact, even in larger flocks, and in the absence of route recapitulation, a well-defined leadership hierarchy is evident in pairwise comparisons among group members in terms of the initiation and copying of small-scale directional changes (Nagy et al. 2010). These results suggest that in specific pairwise interactions there are one or more attributes of a flying bird that can reliably predict its propensity either to lead or to follow conspecifics. What such attributes are, in other words what determines the probability that one bird will follow the movements of another, is still an open question.

Equally experienced pigeons show differences in route fidelity (i.e. the accuracy with which they follow their routes when flying solo), and route fidelity itself can, at least partially, predict the leading and following behaviour of two co-navigating pigeons. Birds with higher solo route fidelity tend to lead partners with lower solo route fidelity, a result suggesting that leadership may arise from the individual-specific emphasis that birds place on remaining close to their route versus remaining close to their partner (Freeman et al. 2011; see also Conradt et al. 2009 for a theoretical treatment of similar principles). Thus, route fidelity helps to predict leadership when pigeons have the same level of homing experience, but we have yet to explore the effect of different levels of homing experience on the establishment of leader—follower relations. If leading/following behaviour is a function of relative levels of homing experience, we should expect to observe more experienced birds emerge as leaders, supporting the predictions generated by models. Our question here therefore concerns the relationship between the spatial knowledge held by a homing pigeon and the probability that it will follow the movements of a co-navigating partner during a joint trip back to the loft.

To tackle this question, in the present study we used miniature GPS tracking during displacement experiments involving (1) the solo training of homing pigeons up to predefined levels of experience with a route, followed by (2) releases of birds in pairs, constructed such that partners differed in their levels of homing experience. We then examined the outcome of such paired releases, focusing on the degree to which paths flown by the pair resembled the individually preferred routes of the more and less experienced partner.

METHODS

Subjects and GPS Tracking

We used 20 adult homing pigeons bred at the Oxford University Field Station at Wytham (51°46′58.34″N, 1°19′02.40″W). They were kept in a social group of ca. 120 pigeons inside two lofts. Birds normally had free access to the outside, except on the days when the experiments were conducted. Food (a commercially available multigrain mixture), water, minerals and grit were provided ad libitum throughout the study. All experimental birds were between 3 and 7 years old, and had homing experience but had never visited the release sites used in the current study, nor had any experience with paired homing flights. They were trained to carry miniature GPS logging devices (ca. 20 g; i-gotU GT-100 Phototrackers, Mobile Action Technology, Inc., Taiwan) attached to their back by a small Velcro strip glued to clipped feathers. The weight of the devices corresponded to approximately 4% of the average bird's weight (5% for the smallest bird). For every training and test flight, geographical longitude and latitude were logged by the devices at 1 Hz and a positional accuracy of approximately ± 2.5 m (i.e. when stationary, 50% of fixes remain within a radius of 2.5 m over 24 h). The study was approved by the Ethics Committee of Oxford University's Zoology Department.

Experimental Procedure

The experiment was performed at two release sites (for locations see Supplementary Figure S1): College Farm (henceforth: R1; distance and direction from home: 7 km, 74°, respectively) and Forest Farm (henceforth: R2; distance and direction from home: 7 km, 260°, respectively). Each of the 20 subjects was assigned randomly to one of two treatment groups, either a high-experience group (henceforth: E+ birds; 10 subjects) or a low-experience group (henceforth: E− birds; 10 subjects). Both groups had a distinct training and testing protocol (Table 1). Training and testing of all subjects were completed at the first site before training at the next site began. Training was conducted on consecutive days, interrupted only by days of unsuitable weather. This was consistent for both treatment groups and release sites.

In the first stage of the experiment, birds from both groups were trained to fly individually from the release site, with the number of flights depending on the treatment group (15 and three flights; see Table 1). By choosing three and 15 flights, we ensured that the ensuing two groups of pigeons were at different stages of route development. Three flights corresponded to the maximum rate of

Table 1
Training and testing protocol for the two treatment groups, E+ and E−

	No. of training flights	Test 1	No. of training flights	Test 2	No. of training flights	Test 3
E+ birds	15	E+/E−	1	E+/E−	1	E+/E−
E− birds	3	E+/E−	5	E+/E−	9	E+/E−

Training flights always involved solo releases; test flights were performed by releasing birds in pairs.

increase in homing efficiency, while by 15 flights improvements in homing efficiency had reached a plateau (see Results). A maximum of three releases were conducted per day. To examine the influence of homing experience on leading/following behaviour, we then randomly assigned each bird a partner from the other group, and released those two birds simultaneously from the same release site as that used during training (E+/E− pairs; Test 1). Subsequently, we decreased the difference in homing experience in E+/E− pairs by giving birds additional solo training flights and repeated the paired test two more times using the same combination of pairs as in Test 1 (Tests 2 and 3; see Table 1). Test releases followed the completion of training with equal delay for both birds of a given pair (and were typically conducted the day after the final training flights of the two birds).

Finally, we repeated the entire protocol at a second release site, and switched the number of training flights assigned to each of the two groups. Thus, tests at the second site consisted of paired releases using the same combinations of birds as at R1, but the E+ became the E− birds and vice versa. Thereby, we asked whether any possible relationship between homing experience and the probability to lead or follow was invariant to the release site or to some individual attribute other than experimenter-controlled homing experience. If experience was the key factor, we expected leader/follower roles to reverse within the same pairs in response to the reversal in levels of experience.

Data Analysis and Comparison Methods

All analyses were conducted in Matlab (The Mathworks Inc., Natick, MA, U.S.A.). Tracks were initially preprocessed by removing any point where the subject moved less than 1 m (which can be interpreted as a stationary bird), or any point after it reached within 100 m of the loft. To compare tracks, we analysed only those positional fixes that lay outside a radius of 1000 m from the release site. This enabled us to examine the similarities between the birds' routes and reduced potential noise created by the birds circling around the release site immediately after release, before assuming a homeward course.

We first examined the development of individuals' routes by focusing on homing efficiency on the one hand and route fidelity on the other. Homing efficiency is defined here as the ratio between the straight-line distance between the release site and the loft, divided by the sum of the direct distances between the neighbouring fixes. Route fidelity refers to the accuracy with which a bird reproduces the same route repeatedly. To estimate track similarity, we used two different methods to compare tracks. The first method, the nearest-neighbour analysis, allowed us to estimate track similarity by computing the spatial proximity between tracks.

For each point along the focal track, we determined the distance to the nearest neighbouring point along the comparison track, and used the average distance across all pairs of points as a measure of track similarity. While this analysis examines the absolute spatial proximity between tracks, homing pigeons may follow landmarks or the movements of co-navigating birds at a variety of distances, making it more difficult to determine leading/following behaviour on the basis of track proximity alone.

Hence, we developed a second method that compares the dynamics of tracks by using the birds' instantaneous flight direction, or heading. For bearing calculations, we determined for every two points along the track the birds' heading relative to the position of the loft. To estimate track similarity during training (within-individual comparisons) or to compare paired flights with previous individual training flights (between-condition comparisons), we defined different track segments according to the distance to the loft: We divided the straight-line distance between the release site and the loft into 18 equal parts (see below) and numbered them consecutively. We then calculated the mean bearings relative to the loft in each segment, and determined the degree of similarity between tracks. To do this, we computed the difference between the mean bearings of the single segments of any given track and the bearings from the corresponding segments of the paired flight. For all analyses involving bearings, we used circular statistical methods (Batschelet 1981). The number of segments (18) was determined using the relationship between efficiency and homing experience as a reference. We fitted nonlinear regression models to the data of homing efficiency as a function of the number of training flights. The equation that gave the best fit ($r^2 = 0.96$) was $Y = Y_0 + a \times \exp(-b \times X)$, where Y is a measure of the efficiency and X is the number of training flights. Next, we used this model to examine how variance of track similarity (Y) during training relates to both the number of training flights (X) and the number of segments. We found maximum r^2 values using 18 segments ($r^2 = 0.97$).

Next, to identify subjects as either leaders or followers, we used data from the highly efficient tracks of the single birds (i.e. tracks with an average efficiency larger than 0.75; for E+ birds flights 4–17 and 6–17 from release sites 1 and 2, respectively, see also Fig. 1) and calculated the expected range of individual track variation between those tracks. To do so, we determined the corresponding 99% confidence intervals arising from the two measures of track similarity. Using such intervals as a reference, we compared the paired flight of each bird with its own previous training flights and with the previous training flight of its partner. Leading/following behaviour was defined depending on whether or not both paired flights fell within the normal range of variation of the E+ birds. Our rationale for using this criterion was as follows. Since at the time of Tests 1 and 2, E− birds had performed no or only
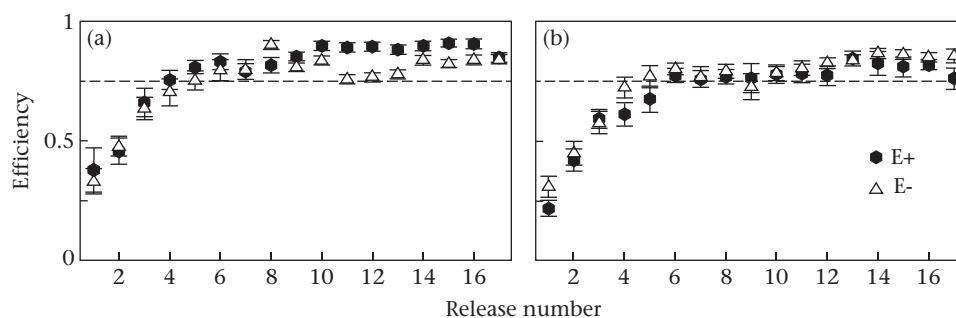
Figure 1. Homing efficiency (mean ± SE) as a function of training. Homing efficiency is the ratio between the straight-line distance between the release site and the loft, divided by the sum of the distances between all neighbouring position fixes along the length of the route flown. Data from different birds were averaged according to group identity and training release. (a) R1, College Farm, (b) R2, Forest Farm. Black circles and white triangles indicate birds with more and less experience, respectively. Dashed lines correspond to an efficiency of 0.75.

a few highly efficient tracks (see Fig. 1), the track variation between consecutive flights was relatively large. We calculated the ratios between the confidence intervals of both groups from the different tests (Table 2). At the time of Test 1, we found that the range of track variation of the E+ birds corresponded to 26% and 1% of the range of variation of the E− birds, according to the relative bearing and the nearest-neighbour analysis, respectively. In Test 2, such a range still corresponded to approximately 59% of the range of variation of the E− birds (see Table 2). Thus, paired flights were likely to fall within the range of the E− birds simply because of the large variation between these birds' tracks, while cases in which pairs flew within the much smaller range of the E+ bird indicated more clearly that they followed the E+ bird's route. Hence, we tested whether or not the paired flights of both birds fell within the normal range of variation of the E+ birds.

RESULTS

We first examined the relationship among training regime, homing efficiency and the development of idiosyncratic routes. We found a positive correlation between path efficiency and the number of solo training flights completed (Fig. 1a, b). Pigeons needed only three flights to increase their homing efficiency drastically. At R1, the fourth flight of the E+ birds already had an average efficiency of 0.75, which then increased gradually until it became asymptotic after six flights (Fig. 1a). At R2, a similar level of efficiency was reached after only five flights (Fig. 1b). This increase in efficiency over consecutive releases did not differ between the two release sites (two-way repeated measures ANOVA: $F_{1,504} = 1.63$, $P = 0.21$). We also found that these experience-dependent changes in homing efficiency were invariant to the training protocol (two-way repeated measures ANOVA: $F_{1,490} = 0.10$, $P = 0.75$). While flying from the first release site, the E+ and E− birds had different efficiency levels only in Test 1, with the E+ birds significantly more efficient than the E− birds (two-sample t test: $t_{18} = 5.5$, $P < 0.001$). Subsequently, in Tests 2 and 3, both groups were equally efficient during homing (two-sample t test: Test 2: $t_{18} = 0.24$, $P = 0.81$; Test 3: $t_{18} = 0.24$, $P = 0.81$). We obtained similar results for the second release site (two-sample t test: Test 1: $t_{16} = 3.8$, $P < 0.01$; Test 2: $t_{16} = 0.73$, $P = 0.48$; Test 3: $t_{16} = 1.77$, $P = 0.09$).

Next, we examined the development of idiosyncratic routes. Figure 2 illustrates route development of the E+ and E− birds at both R1 and R2 (Fig. 2a, d, respectively). Each column in Fig. 2a, d shows the mean difference in the bird's relative bearing as a function of distance to home (top to bottom) and training (left to right). At the beginning of training (i.e. flights 1–5), individual homing routes were poorly developed and highly variable, but this variability decreased dramatically over the course of the birds' subsequent flights (Fig. 2). There is no evidence of any difference in route development with training protocol (two-way repeated measures ANOVA: R1: $F_{1,270} = 2.59$, $P = 0.12$; R2: $F_{1,240} = 2.98$, $P = 0.054$; Fig. 2b, c, e, f).

Table 3 presents the results of the leadership analysis during Tests 1, 2 and 3 at both release sites. Here, we disregarded flights in which partners split up during homing (pairs were considered to have split

when the partners' instantaneous distance increased above 100 m and never fell below this threshold again). At the time of Test 1, the E− birds had less homing experience (three flights) than the E+ birds (15 flights). While homing from R1, these less experienced pigeons followed the routes of their more experienced partners: the homing routes of all of the six pairs that did not split up during homing fell well within the 99% confidence intervals of the E+ birds. This robust phenomenon was detected by both comparison methods. We obtained similar results for the second release site with the roles of individuals in a given pair reversed, further confirming experience as a key factor in determining leadership beyond other (unmanipulated) individual attributes. In Test 1, all five nonsplitting pairs at R2 followed the routes of the E+ birds according to the relative bearing method (the nearest-neighbour analysis indicated only three of the five pairs). By pooling data from R1 and R2, we found that 11 and nine of the 11 pairs flew within the range of the E+ birds, according to the relative bearing and the nearest-neighbour analysis, respectively.

At the time of Test 2, the E− and E+ birds had made eight and 16 homing flights, respectively. Of the nine nonsplitting pairs released from R1 in Test 2, both methods identified that seven pairs flew within the normal range of individual track variation of the E+ birds. We obtained similar results for the second release site: of the nine nonsplitting pairs at R2 in Test 2, seven pairs flew within the 99% confidence intervals of the E+ birds according to the relative bearing method, although only five according to the nearest-neighbour analysis. By pooling data from R1 and R2, we found that 14 and 12 of the 18 pairs flew within the normal range of the E+ birds, as determined by the relative bearing and the nearest-neighbour analysis, respectively.

At the time of Test 3, both the E+ and the E− birds had performed 17 individual homing flights. Thus, by this stage both groups had gained the same amount of homing experience. By pooling data from R1 and R2, we found that five and nine of the 14 pairs flew within the normal range of the E+ birds, as determined by the relative bearing and the nearest-neighbour analysis, respectively. The different results obtained through the relative bearing and the nearest-neighbour methods demonstrate that the two measures work based on different assumptions, thereby capturing different aspects of track similarity. None the less, they indicate similar general trends, strengthening the idea that our findings are robust.

Next, we examined how the probability of birds following the path of their co-navigating partner changed across the three tests. We measured (1) the extent to which the less experienced birds deviated from their solo routes while flying in pairs (calculated as the difference between the paired flight of each E− bird and its last solo training flight), and (2) how closely the two birds flew together during the test. Figure 3 shows how these two measures related to each other in the three tests. In Test 1 (Fig. 3a), the cluster of data points shown in the upper left area of the plot indicates that the E− birds deviated substantially from their own route while flying close to their partners and all pairs followed the routes of the E+ birds (see example in Fig. 3d). In Test 2, the majority of pairs followed the route of the E+ birds, but the E− birds deviated less from their original route in comparison to Test 1, as seen from the fact that the points in Fig. 3b lie closer to the reference diagonal (see example in Fig. 3e). Moreover, in Test 2 we found pairs following the routes of the E− birds. In the final, third test, the E− birds again showed a smaller deviation with respect to their previous routes, as compared to Test 1. In contrast to the preceding tests, we found that more pairs flew outside the normal range of variation of the E+ birds than those that flew within (Fig. 3c). Figure 3f illustrates an example in which we can no longer reliably evaluate leading/following behaviour owing to the high similarity between the tracks of both, now similarly highly experienced, birds. Such cases became frequent at this stage of route development.

Table 2
Ratio in percentage between the 99% confidence intervals of track variation in E+ and E− birds

Relative bearing analysis			Nearest-neighbour analysis		
Test 1	Test 2	Test 3	Test 1	Test 2	Test 3
25.8	58.6	117	0.7	26.2	76

Smaller percentage values indicate smaller confidence intervals for E+ than for E− birds.
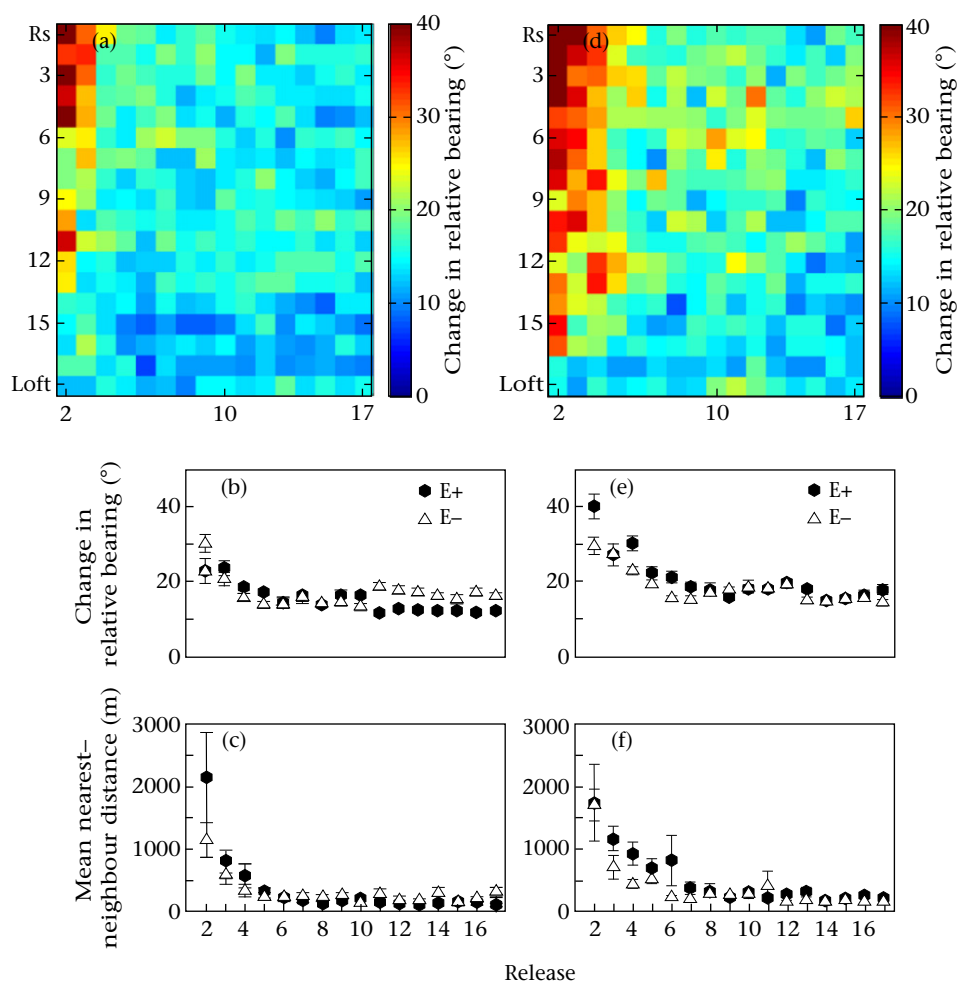
Figure 2. Development of the solo homing routes of birds released at R1 and R2. (a, d) We computed the difference between the mean relative bearing of given segments of any given track and the bearings from the corresponding segments of the preceding flight. Thus, each column depicts the mean difference in the instantaneous flight direction of the birds relative to the loft, or relative bearing, as a function of homing from the release site to the loft (top to bottom) and training flight number (left to right). Data are grouped according to release site: (a) E+ and E− birds at R1, (d) E+ and E− birds at R2. (b, e) Change in relative bearing (mean ± SE) and (c, f) mean nearest-neighbour distance (mean ± SE) as a function of training. Data from different birds were averaged according to group identity.

Table 3
Leading/following behaviour in Tests 1–3

		R1			R2			Both sites
		Within the range of E+	Outside the range of E+		Within the range of E+	Outside the range of E+		
Test 1	RB	6	0	6/6 P<0.05	5	0	5/5 P=0.031	11/11 P<0.001
	NN	6	0	6/6 P<0.05	3	2	3/5 P=0.5	9/11 P<0.05
Test 2	RB	7	2	7/9 P=0.09	7	2	7/9 P=0.09	14/18 P<0.05
	NN	7	2	7/9 P=0.09	5	4	5/9 P=0.5	12/18 P=0.12
Test 3	RB	3	5	3/8 P=0.36	2	4	2/6 P=0.34	5/14 P=0.21
	NN	4	4	4/8 P=0.64	5	1	5/6 P=0.11	9/14 P=0.21

We compared the paired flight of each bird with the previous training flight of its partner (E+) and determined whether the pair flew within or outside of the normal range of variation of the E+ bird. The track comparisons were made using two methods: relative bearing (RB) and nearest-neighbour analysis (NN). Each cell shows the number of cases found at R1 and R2. The third column at each site shows the number of pairs that flew within the range of the E+ birds' tracks and the total number of pairs observed at the respective site. P values show the results of binomial tests.
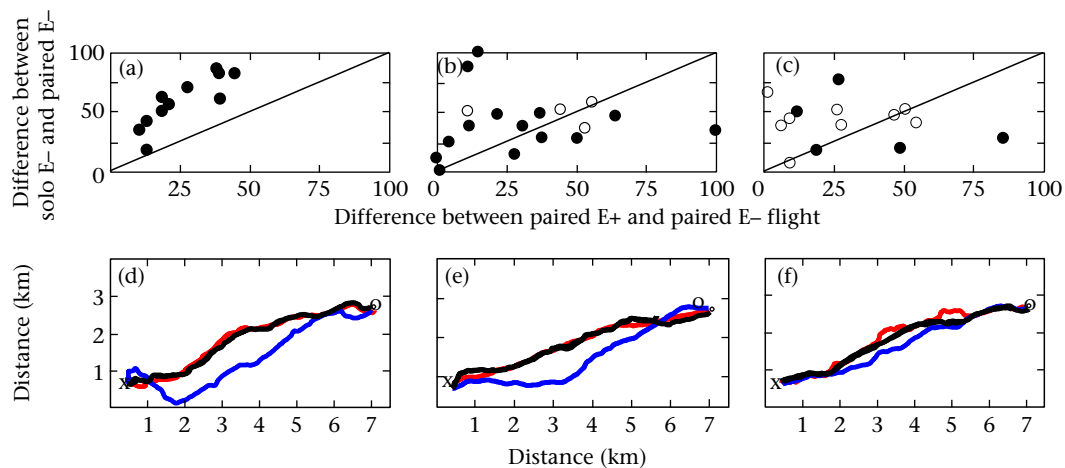
Figure 3. (a–c) The degree of similarity between the paired flight of each E− bird and its last solo training flight as a function of the degree of similarity between the flights of co-navigating pigeons for (a) Test 1, (b) Test 2 and (c) Test 3. Similarity was measured using the relative bearing method. Differences are expressed as percentages of the range between the minimum (0%) and maximum (100%) values recorded for each pair. Pairs that were identified to fly within or outside the 99% confidence interval of the E+ birds are depicted in black and white, respectively. (d–f) Examples of flights for Tests 1–3. In each panel, black lines show flights performed by E+ and E− birds of a pair when released together. Red and blue lines indicate tracks flown individually by E+ and E− birds, respectively, in releases immediately prior to the paired flight. (d) Test 1, (e) Test 2, (f) Test 3. The release point is indicated by an x; the home loft by an o.

Finally, we explored whether birds were more likely to follow a partner with a more efficient route. We measured the difference in homing efficiency between the E+ and the E− birds' last training flight and the extent to which the E− birds deviated from their own route. We did not find a correlation between these two measures in any of the three tests we conducted (Pearson correlation: Test 1: $r_9^2 = 0.04$, $P = 0.58$; Test 2: $r_{16}^2 = 0.1$, $P = 0.19$; Test 3: $r_{12}^2 = 0.1$, $P = 0.24$). In other words, larger differences in route efficiency between the E+ and E− birds of a pair did not result in larger deviations by the E− birds from their own routes.

DISCUSSION

If they are to maintain a cohesive group, animal collectives travelling together must be able to negotiate joint routes even in the presence of conflicting opinions over route choice. This can be achieved when certain individuals have a disproportionately large influence in making navigational decisions (which are then followed by others), or by averaging each group member's preferences for a more 'democratic' decision. Previous work with homing pigeons has confirmed theoretical predictions that the two mechanisms (consensus and averaging) can indeed coexist within the same decision-making scenario, as birds' propensity to rely on one or the other depends on the size of the conflict experienced. Furthermore, we also know that in specific pairwise interactions there are one or more attributes of a flying bird that can reliably predict its likelihood of either leading or following conspecifics (Biro et al. 2006; Nagy et al. 2010). Evidence indicates that leadership may derive from the shifting of the balance between the emphasis that birds place on remaining close to their individually preferred routes and the emphasis they place on remaining close to their partner (Freeman et al. 2011). What roles do individual knowledge and experience play in determining such leader–follower relations? Given that all previous studies have examined leadership phenomena in pigeons with equal levels of homing experience, in the present study we asked whether and to what extent the probability that a bird would follow the path of another depended upon its own level of homing experience relative to that of its partner.

Our results clearly demonstrated that less experienced pigeons are likely to follow more experienced conspecifics. The difference in homing experience between our two experimental groups of co-navigating pigeons was the largest in the first of our three tests. Under these conditions, all pairs flew within the range of the more experienced birds' preferred path. Similarly, we found that the majority of less experienced birds followed their more experienced partners in the second test, in which differences in levels of experience were reduced but still existent. However, by the time the final test was conducted, and both groups had had the same number of training flights, we observed roughly equal probabilities to lead or follow for the previously more or less experienced birds. This means that some of the birds that had previously followed a (more experienced) partner were able to become leaders once their experience rose to equal that of their partner. These results held at both release sites where we conducted replicates of the experiment, suggesting that the outcome is invariant to release site location. Furthermore, since the training regimes of the birds were reversed between the two sites (with more experienced birds at the first site becoming the less experienced ones at the second), the results also confirm the robustness of the effect over other individual differences that may determine the emergence of leaders. Taken together, the results clearly indicate that different levels of homing experience accounted for the observed group differences in leading/following behaviour.

In the present study we used homing efficiency and route fidelity as measures of a pigeon's level of experience and navigational knowledge, manipulated by controlled exposure to a specific navigational task during training. Our results document how, over the course of repeated releases from a given site, both homing efficiency and route fidelity increase first dramatically and later gradually until they become asymptotic. Such findings match previous results by Meade et al. (2005), who reported that as birds become more experienced, their routes become more efficient and increasingly stereotyped. Experiments by Wallraff (1959) also suggested that homing success increases with experience, but that specific knowledge of a release point is of much less importance than general homing practice. If this were the case, the efficiency observed at our second site would have been higher than that observed at the first site, which would have prevented us from evaluating the behaviour at both release sites in a combined analysis. Our results did not match these previous findings: the rate of

increase in efficiency over consecutive releases did not differ between the two release sites.

Our results additionally suggest that there is a short sensitive period in the development of a route, during which pigeons are more likely to respond to conspecifics by following the latter's route. Studies have described that a pigeon's propensity to fly together with other birds is relatively low during its very first flight from an unknown site irrespective of its partners' knowledge (Heinroth & Heinroth 1941; Guilford & Chappell 1996). This suggests that on encountering a new location, birds may prioritize the processing of available navigational information in order to compute their own directional decision, and that at this stage, stimuli arising from other birds (even those more experienced) may not be salient enough to initiate a following reaction. The present study shows that just a few additional flights are sufficient to induce different behaviour. After those initial flights, birds may have gained enough experience to allow them to attend to and to follow the movements of partners. Whether such following behaviour also represents a learning opportunity (i.e. whether birds following conspecifics during this potential sensitive period acquire navigational knowledge about routes) is an open, and highly interesting, question that will be the basis of future work.

Our findings are in line both with theoretical predictions and with empirical studies on different model systems suggesting that naïve or inexperienced individuals follow those more experienced. For example, several studies have reported, across a broad range of taxa, a relationship between information and leadership. Cliff swallows, *Petrochelidon pyrrhonota*, follow their colony neighbours (Brown 1986), while trained shoaling fish can manipulate the direction of the group (Reebs 2000). A recent study on meerkats, *Suricata suricatta*, has shown that trained individuals are more likely to initiate group departure than untrained individuals (Bousquet & Manser 2011). In agreement with these empirical reports, theoretical work by Couzin et al. (2005) and Conradt et al. (2009) has shown that individuals with the highest certainty of information or greater assertiveness can spontaneously emerge as leaders during group movement.

While our experiments necessarily involve a level of artificiality to provide experimental control, it seems likely that the same advantages found here in following more experienced birds when an individual is itself inexperienced should also exist in feral pigeon or ancestral rock dove populations. Group members are always likely to vary in local experience and age, providing information-gathering advantages, and reducing navigational risks, to inexperienced individuals in following others. Indeed, we may expect these advantages to be fairly general to socially foraging species that range widely.

In sum, our results have implications for a better understanding of how problems of collective decision making are solved in species that travel in mixed-experience groups. We can assume that each member of a group possesses particular features (e.g. age, experience, social rank or sex) that might modify its own behaviour towards others as well as the behaviour of its conspecifics towards it. Evidence indicates that numerous types of individual differences and state- or status-dependent characteristics, such as level of dominance (King et al. 2008), hunger (Krause et al. 2000), boldness (Harcourt et al. 2009) or lactation state (Fischhoff et al. 2007), can influence leadership and followership across a range of species (reviewed in King et al. 2009). Further studies on the role of individual variation among group members in determining the organization of group decision making are certain to prove fruitful for improving our understanding of both the mechanisms and the adaptive significance of information transfer, coordination and learning in animal collectives.

Supplementary Material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.anbehav.2011.12.018.

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