RESEARCH ARTICLE

Pairs of pigeons act as behavioural units during route learning and co-navigational leadership conflicts

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SUMMARY

In many species, group members obtain benefits from moving collectively, such as enhanced foraging efficiency or increased predator detection. In situations where the group's decision involves integrating individual preferences, group cohesion can lead to more accurate outcomes than solitary decisions. In homing pigeons, a classic model in avian orientation studies, individuals learn habitual routes home, but whether and how co-navigating birds acquire and share route-based information is unknown. Using miniature GPS loggers, we examined these questions by first training pairs (the smallest possible flocks) of pigeons together, and then releasing them with other pairs that had received separate pair-training. Our results show that, much like solitary individuals, pairs of birds are able to establish idiosyncratic routes that they recapitulate together faithfully. Also, when homing with other pairs they exhibit a transition from a compromise- to a leadership-like mechanism of conflict resolution as a function of the degree of disagreement (distance separating the two preferred routes) between the two pairs, although pairs tolerate a greater range of disagreements prior to the transition than do single birds. We conclude that through shared experiences during past decision-making, pairs of individuals can become units so closely coordinated that their behaviour resembles that of single birds. This has implications for the behaviour of larger groups, within which certain individuals have closer social affiliations or share a history of previous associations.

Key words: pigeon, collective decision-making, route learning, leadership, social relationships.

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INTRODUCTION

Individuals in many bird species obtain a variety of benefits from moving collectively (Krause and Ruxton, 2002). Although in pigeons (*Columba livia*), flying in a flock can be energetically more costly than flying alone (Usherwood et al., 2011), this is offset by a number of advantages. Besides the anti-predatory benefits of group travel, group cohesion can lead to more accurate navigation in situations where the overall orientation of the flock arises from averaging the directional preferences of the single members of the group (Dell'Ariccia et al., 2008; Hamilton, 1967; Simons, 2004). A combination of social habits and prodigious navigational skills (Wallraff, 2005) makes homing pigeons a useful model system for the study of collective navigation (Biro et al., 2006; Flack et al., 2012). Pigeons benefit from route memories that develop over consecutive flights: once enough experience with a route is gathered, these memories will reliably guide birds back to the loft along a remarkably fixed flight path (Biro et al., 2004; Meade et al., 2005). Also, wild rock pigeons, the stock ancestral to homing pigeons, perform daily foraging trips from their colony to feeding grounds and back, seemingly using stable routes (Baldaccini et al., 2000), a process that most likely involves visual memories and reduces the pigeons' level of navigational uncertainty across flights. Nonetheless, because under natural conditions pigeons often travel in small or large flocks rather than individually, one intuitive question that follows is how the presence of a co-navigating partner influences the development of stereotyped routes in homing pigeons. For example, do pairwise trained pigeons develop joint stereotyped homing routes? If so, do joint and individual routes develop in a similar fashion?

Importantly, when homing as a pair, pigeons that possess different preferred homing routes will fly along a path that lies between their two individual routes, provided that these individual routes are within a certain distance from each other (Biro et al., 2006). This suggests that these birds are compromising over their route choice, with the two birds' individual preferences being combined to give a shared route. However, if the distance between the two birds' routes rises above a threshold, one of the pigeons will emerge as the leader and the other as the follower, as seen from the fact that the pair will then follow the leader's path faithfully. In the present paper, we investigate whether and how such leader–follower relationships translate to quadruples composed of pairwise-trained individuals. Although pair-routes may prevail during the homing flights of such quadruples, compromise routes may also be observed, depending on the spatial relationship between the previously established joint routes of the pairs. Furthermore, joint homing can improve navigational efficiency, particularly when decisions are shared (Dell'Ariccia et al., 2008; Simons, 2004) – a phenomenon which could suggest an adaptive explanation for a pigeon's tendency to travel with a co-navigating partner in addition to the more commonly cited anti-predatory accounts. Social bonds and shared experiences developed through joint travel may in turn lead to inter-individual affiliations that enable close coordination of a pair's behaviour even when embedded within a larger flock, much like existing social relationships between familiar conspecifics, sexual partners or

parents and offspring can modify the organisation of social groups in a variety of species (e.g. Griffiths and Magurran, 1999; Sueur et al., 2010).

With these ideas in mind, we conducted a series of experiments in which we examined first, whether and how pigeons establish homing routes when trained in pairs, and second, how such joint training influences the pairs' subsequent behaviour in larger flocks. Our work provides insights into both the impact of a partner on the speed and stability of route learning, and collective decision-making in large groups within which different dyads have different levels of prior association.

MATERIALS AND METHODS
Subjects and experimental procedure

We used 16 adult homing pigeons (*Columba livia* Gmelin 1789) bred at the Oxford University Field Station at Wytham (51°46′58.34″N, 1°19′02.40″W). All experimental birds were between 3 and 7 years old, and had homing experience but had never been released from the sites used in the present study. They were trained to carry miniature GPS logging devices (~15 g; i-gotU GT-100 Phototrackers, Mobile Action Technology, Taiwan) attached to their back by a small Velcro strip glued to clipped feathers. For every training and test flight, geographical longitude and latitude were logged by the devices at 1 Hz and with a positional accuracy of approximately ±2.5 m (i.e. when stationary, 50% of fixes remained within a radius of 2.5 m over 24 h). The experiment was performed at two release sites: Church Hanborough (henceforth, R1; distance and direction to home: 6.14 km, 129 deg, respectively) and College Farm (henceforth, R2; distance and direction to home: 7.00 km, 74 deg, respectively). Training at R1 consisted of paired homing flights: each subject was assigned a fixed partner (thus forming eight pairs in total), and the two birds were released 17 consecutive times as a pair, with a maximum of four releases per day. After completing training, we tested pairs in quadruples by releasing two pairs simultaneously from the same release site as that used during training. We repeated such quadruple releases until all possible combinations of our eight pairs had been tested; thus a total of 28 group releases were performed (i.e. seven quadruple releases for each pair).

In addition to these group releases, the same subjects also underwent individual training in order to provide reference data on homing efficiency and track variation changes in birds trained alone. Subjects were required to home singly from R2, 17 times in succession, with a maximum of three releases per bird per day (see Flack et al., 2012).

Data analysis

All analyses were conducted in MATLAB (The MathWorks, Natick, MA, USA). Tracks were initially pre-processed 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 came within 100 m of the loft. When comparing tracks, we analysed only those positional fixes that lay outside a radius of 200 m from the release site to reduce the effect of initial circling behaviour. We explored the acquisition of homing routes when birds were trained in pairs by analysing homing efficiency and route fidelity. 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 of the track. Route fidelity refers to the accuracy with which a bird (or a pair of birds) reproduces the same route repeatedly and is measured as the mean nearest neighbour distance between all constituent points of two tracks.

Additionally, we evaluated a subject's quadruple flight with reference to its immediately preceding paired training flight. To identify subjects as either leaders or followers, we first calculated the expected range of individual track variation between the final set of highly efficient training tracks (i.e. training flights 10–17). We measured the mean nearest neighbour distance between consecutive training tracks and determined their corresponding 99% confidence intervals. Second, we compared the path of each quadruple with the last training flight of both pairs. Leading/following behaviour was then assigned to each pair depending on whether quadruple flights fell within the confidence interval of one or the other pair [for further technical detail on these methods, see also Flack et al. (Flack et al., 2012)].

RESULTS

We began by examining the development of homing routes in pigeons trained in experimenter-assigned pairs. During these paired flights, individual homing efficiency increased as training progressed (nonlinear regression, paired flights: r^2=0.47; Fig. 1A). Furthermore, track variation (nearest neighbour distance to previous training track) decreased with training (Fig. 1B), eventually beginning to asymptote around the sixth to eighth flight and reaching an average inter-route distance of only 241 m by the end of training. Hence, homing pigeons trained exclusively in pairs were able to develop joint stereotyped homing routes, and their route development progressed with an accuracy and on a time scale comparable to those previously reported from individually trained birds (Meade et al., 2005). By also training our subjects in solo releases, we were able to provide a new set of reference tracks for individuals' ability to learn routes when flying alone (Fig. 1A,B). While no formal comparisons can be made because the birds were released from a different site during solo-training (by necessity, as they had already learnt about the first site during paired flights), this data set nonetheless reinforces the similarities in route acquisition between the pair- and solo-training conditions. Note, for example, the similarities in the overall shapes of the two regression curves fitted to the increase in birds' homing efficiency under the two training conditions (Fig. 1A). The decrease in variation between consecutive tracks flown by pair-trained birds is also comparable to that of solo-trained birds (Fig. 1B), although it appears also to hint that at an early stage of route development birds may exhibit less inter-route variation when trained with a partner (this will, however, require further experiments for a formal comparison). Not all pairs stayed together throughout all of their joint training flights. Nonetheless, we found that the probability of pairs splitting decreased markedly as training advanced (Fig. 1C), a phenomenon also revealed by the reduction of the instantaneous distance between training partners during flight (Fig. 1C, inset).

We next examined the homing flights of quadruples composed of pairwise-trained individuals. First, we determined the instantaneous distance among the four pigeons involved in every quadruple release at all points (i.e. every second) during homing. For each of the four pigeons, we calculated the distance to its known training partner as well as the distance to the remaining two birds. Next, for each of these two sets of data we determined the proportion of the homing flight during which such distance remained below 50 m, a distance that corresponds to the plateau reached during training (see Fig. 1C, inset). We found that individuals spent more time flying closer to their training partners than to the unfamiliar pigeons of the quadruple (related samples Friedman ANOVA, N=28, Q=4.48, P=0.034; Fig. 2A). In these quadruple flights, we also observed that the birds increased their homing efficiency, as compared with the average of the final seven paired training flights
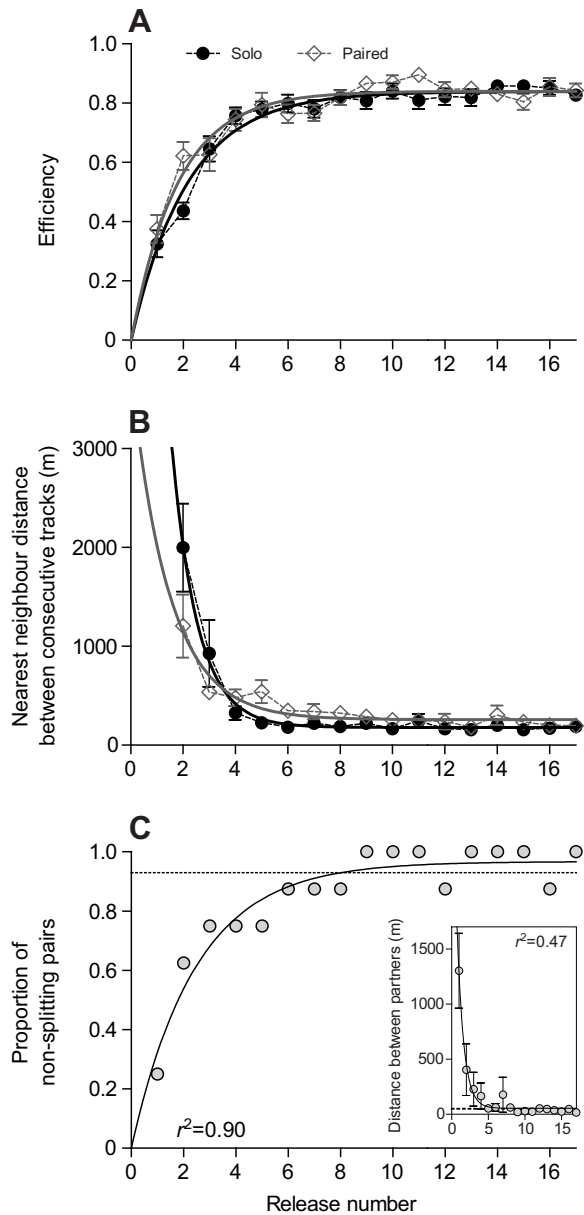
Fig. 1. Training data from homing pigeons released 17 times consecutively from the same release site, either singly or in pairs. (A) Homing efficiency (mean ± s.e.m.) and (B) nearest neighbour distance (mean ± s.e.m.) between consecutive training tracks as a function of training. Data from different birds were averaged according to training protocol. Black circles indicate solo training, white diamonds paired training. Solid lines correspond to fitting of nonlinear regression curves. (C) Proportion of non-splitting pairs as a function of training. Inset is mean (±s.e.m.) instantaneous distance between training partners as a function of training. r^2 shows goodness of fit for nonlinear regression.

Fig. 2. Distance between birds and efficiency during quadruple flights. (A) Mean ± s.e.m. proportion of the group flights during which distance between partners and non-partners is less than 50 m. (B) Scatter plots of mean homing efficiency during training (flights 10–17) and quadruple flights. Asterisks represent significant differences ($P<0.05$).

Fig. 3E). In 15 cases, the group followed one of the previously established pair-routes (Fig. 3A; see also example tracks in Fig. 3C,D). Based on these observations, we composed a network of leadership during the quadruple flights. The nodes of this network represent individual pairs, and the edges point from the pair that remained on its own route (i.e. led) to the pair that left its route (i.e. followed the leading pair). The network showed a hierarchical structure with transitive properties (no loops). There was no correlation between a pair's rank in the hierarchy and its route efficiency during previous paired flights (Pearson's $r=-0.44$, $N=8$, $P=0.272$, Fig. 3B). This finding closely mirrors what has been found in individually trained birds (Biro et al., 2006), indicating that the behaviour and interactions of pairs resembled those of individuals.

DISCUSSION

We examined how pigeons learn homing routes when trained in pairs, and how such training influences their subsequent leader–follower relationships when flying in larger flocks. We found that, much like solo-trained birds in our previous experiments (Biro et al., 2004; Flack et al., 2012; Meade et al., 2005), pairs of pigeons trained together also developed idiosyncratic routes over the course of consecutive homing flights. Crucially, the time scale over which the routes developed and the accuracy with which stable routes were recapitulated towards the end of training were clearly comparable between solo- and pair-trained birds, suggesting fundamental similarities in the mechanisms of acquisition and in the navigational processes underlying the recapitulation behaviour. While pair-trained birds tended to split up at some point during the journey in their first few flights, the probability of splitting decreased as training progressed, and birds began reliably to fly close to each other. After this initial phase, pigeons exhibited close coordination of movement with their partners, with potentially both birds' individual navigational experiences contributing to the development of the joint route. This finding is in agreement with previous results showing 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 another's route (Flack et al., 2012).

(paired *t*-test, $t_{15}=2.57$, $P=0.022$; Fig. 2B). We therefore determined the extent to which each of the pairs deviated from their pair-routes during quadruple flights. One quadruple split before arrival at the loft (one bird homed individually), and in three cases the inter-route distances were too small to clearly assign leader–follower behaviour. Among the remaining 24 quadruples, in nine cases the birds flew along a compromise route, defined as an intermediate path that deviated from both pair-routes (Fig. 3A; see also example tracks in
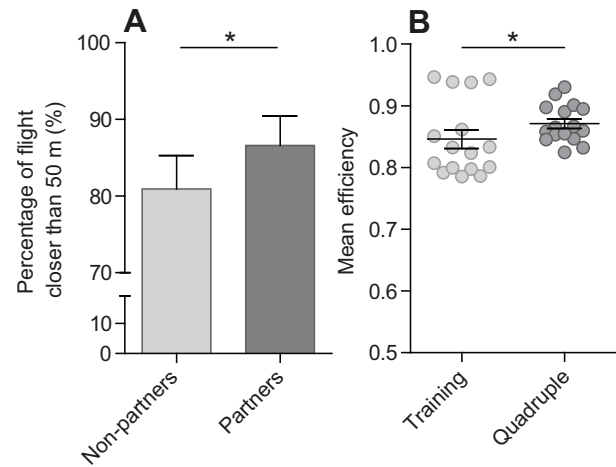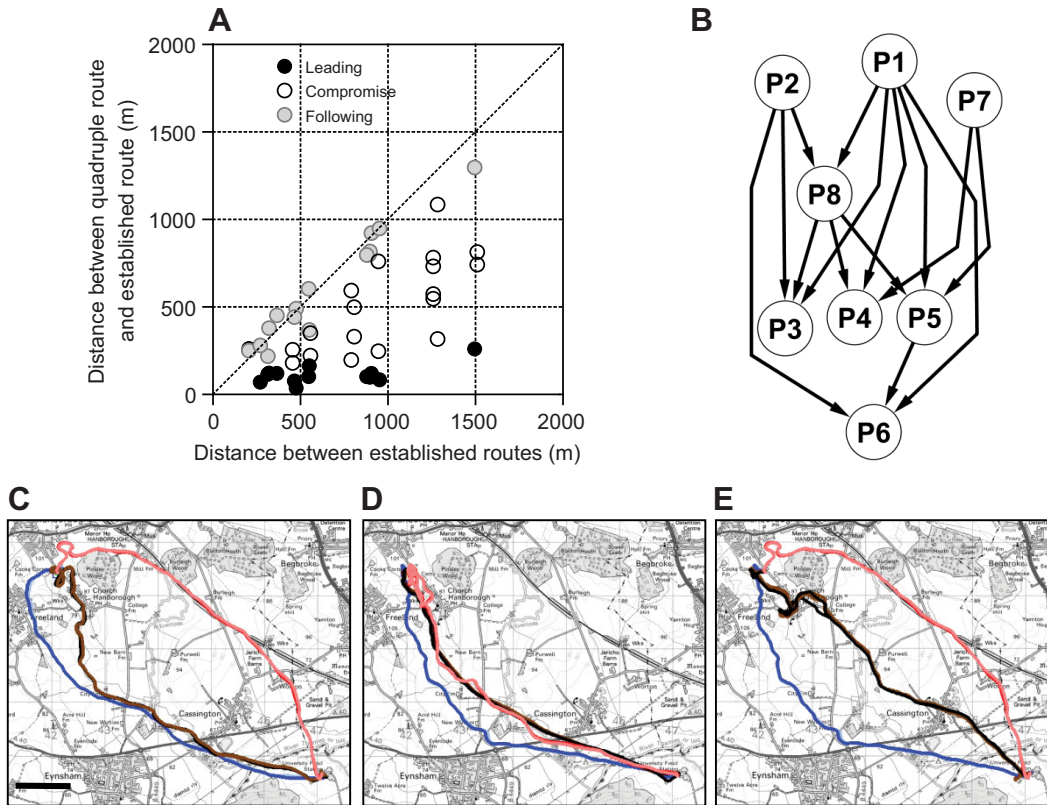
Fig. 3. Leadership and compromise during quadruple flights. (A) Mean distance of birds from their own established routes during quadruple flights as a function of the distance between their own and the other pair's established routes. Birds that followed their own route or the routes of their partners are depicted in black and grey, respectively. Birds that flew along a compromise route are depicted in white. (B) Outcome of specific pairings of pairs. Circles indicate pairs, numbers correspond to the relative rank attained by each pair in terms of homing efficiency during the last training flight (1=most efficient). Solid arrows point from the leading pair of a quadruple to the follower pair. (C–E) Examples of flights performed by training pairs released in quadruples. In each panel, blue and red lines indicate tracks flown during training by pair 1 and pair 2, respectively, and black and brown lines show the flight paths of pair 1 and pair 2 when released together as a group of four. Scale bar, 1 km.

Furthermore, we found that the link between partners established during training continued to be maintained during quadruple flights, as pair members spent more time flying closer to each other than to the two other unfamiliar birds. This link between pair members may have emerged spontaneously, from the pigeons' individual attraction to a common route. While passing over specific features of the landscape, pairwise-trained pigeons might have been attracted towards common familiar homing paths, thereby deviating from other co-navigating birds. Alternatively, repeated interactions during training may have promoted the formation of affiliative bonds based on individual recognition or increased social tolerance between partners, which were then maintained in the form of spatially defined sub-groups during quadruple flights. We argue that pigeons may identify familiar partners among flock members and exhibit a propensity to follow their path, which, as confirmed by joint experience, would lead to a common goal. Past work on different species demonstrated how the establishment of stable relationships based on familiarity can modulate an individual's tendency to follow the movements of a preferred partner (Boissy and Dumont, 2002; Ramseyer et al., 2009). This is in agreement with recent theoretical work on the impact of social networks on collective motion in animals, which suggests that social relationships can affect leader–follower dynamics, the positioning of individuals within the group and the cohesion of the group (Bode et al., 2011).

Next, we explored how the different directional preferences of sub-groups of pigeons in a small flock are resolved during homing,

by releasing quadruples composed of sub-groups (pairs) of pairwise trained pigeons. Among quadruples in which the two pairs possessed sufficiently dissimilar routes to lead to conflict, we observed two main outcomes, broadly defined as leadership (groups following one of the two pair-routes) and compromise (groups homing along a route intermediate to their established pair-routes). Our results provide empirical evidence to support previously developed theoretical work that investigated the mechanisms by which such group decisions can emerge, with a distinction between processes where a small number decides for the rest of the group and those where the decision is equally shared among members (Conradt and Roper, 2009). Biro et al. (Biro et al., 2006) had previously found that pairs of individually trained pigeons will fly along a compromise route if the distance between the birds' previously established routes lies below a certain threshold (~575 m). By contrast, if this distance exceeds the critical threshold, one bird will follow the path of the other. These findings are in line with theoretical predictions (Biro et al., 2006; Couzin, 2009) indicating that attraction to a route and to a partner will lead to intermediate routes only when the familiar landmarks of each individual are within a critical distance of each other, presumably corresponding to a sensory range. Interestingly, compared with past results describing following behaviour in pairs of individually trained birds, in quadruples we not only observed a greater proportion of intermediate routes overall, but also that these intermediate routes continued to occur at high inter-route distances. Even at average inter-route distances as high as 1500 m we detected

quadruples flying along compromise routes (Fig. 3E), indicating that pairwise-trained individuals tolerate a greater range of disagreements between routes than solo-trained birds. Pigeons appear to be less attracted to their routes when flying in quadruples, a behaviour that seemingly increases their probability of flying along compromise routes. This might be due to birds in larger flocks maximising flock cohesion by reacting more readily to signals from conspecifics, thereby reducing responses to landmarks. Also, pigeons flying in quadruples increased their efficiency relative to paired flight. This result is in agreement with previous data showing that the homing performance of pigeons flying as a flock can be higher than that of birds released individually (Biro et al., 2006; Flack et al., 2012) and supports the predictions of group navigation models (Codling et al., 2007; Hamilton, 1967; Simons, 2004).

The perhaps most surprising aspect of the quadruple tests was the emergence of a fully transitive leadership hierarchy among our pairs. This matched exactly results obtained previously from solo-trained birds tested in pairs, in a design otherwise identical to ours (Biro et al., 2006), and closely resembled the behaviour of single birds in larger flocks, where hierarchies based on initiation and copying of small-scale directional changes (rather than on overall route choice) also showed very high levels of transitivity (Nagy et al., 2010). This suggests that pairs, much like single individuals, may possess stable attributes that they carry over into interactions with new partners, and which thus predict the outcome of any specific pair *versus* pair contest. The lack of a correlation between pair-route efficiency and pair leadership rank suggests that such attributes are independent of the pair's navigational capability in a broad sense [again agreeing with results from solo-trained birds released in pairs (Biro et al., 2006)]. Instead, leadership may emerge out of the relative levels of motivation that different pairs of birds place on following conspecifics *versus* following landmarks along their learnt route, with the pair that attaches more weight to landmarks being the one that emerges as leader. In addition, whatever the attributes that correlate with leadership, whether they arise from some combination of the two birds' individual preferences, or whether they are simply equivalent to the more 'extreme' of the two individuals, are fascinating questions for future experiments.

In summary, we conclude that social bonds and a tendency to travel in groups can influence pigeons' behaviour during route learning and collective decision-making. Pairs develop into a unit through their shared experience of repeated joint flights. Furthermore, such relationships also affect collective decision-making in larger flocks, in that pairs are able to exert their influence as a unit (much like individual birds), form spatial sub-groups when flying with less familiar birds, and are more likely to accept compromise routes than birds in smaller flocks. Therefore, our results not only confirm theoretical predictions that the movement of a flock will depend strongly on its specific composition and on the nature of social relationships within it, but also imply, more broadly, the importance of past histories of joint decision-making among constituent members in shaping the behaviour of groups.

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