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Robustness of flight leadership relations in pigeons

Andrea Flack[a,*,1], Zsuzsa Ákos[b,1], Máté Nagy[a,b,c], Tamás Vicsek[b,c], Dora Biro[a]

[a] Department of Zoology, University of Oxford, Oxford, U.K.
[b] Department of Biological Physics, Eötvös University, Budapest, Hungary
[c] Statistical and Biological Physics Research Group of the Hungarian Academy of Sciences, Budapest, Hungary

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Collective animal movements produce spectacular natural phenomena that arise from simple local interactions among group members. Flocks of homing pigeons, *Columba livia*, provide a useful model for the study of collective motion and decision making. During homing flights, flock members are forced to resolve potentially divergent navigational preferences in order to stay together and benefit from flying in a group. Recent work has demonstrated that some individuals consistently contribute more to the movement decisions of the flock than others do, thereby generating stable hierarchical leader–follower networks. Yet, what attributes of a flying pigeon reliably predict leadership remains an open question. We examined the flexibility of an individual's hierarchical leadership rank (i.e. its ordinal position when flock members are ranked according to the average time differences with which they lead or follow others) as a function of changes in its navigational knowledge. We manipulated already established hierarchical networks in three different flocks, by providing certain individuals with additional homing experience. We found that such training did not consistenly lead to an increase in birds' leadership ranks, and that, in general, the nature of leader–follower interactions between trained and untrained birds remained unaffected. Thus, leadership hierarchies in pigeon flocks appear resistant to changes in the navigational knowledge of a subset of their members, at least when these changes are relatively small. We discuss the implications of our results in light of the potential benefits of structural stability in decision-making networks.

A flock of birds circling over its roosting site is a magnificent aerial display. Theoretical work suggests that these highly synchronized and coordinated movements arise from simple interaction rules, without the need for centralized organization (Vicsek et al. 1995; Couzin et al. 2002; Vicsek & Zafeiris 2012). None the less, we are only just beginning to understand how rules implemented in models relate to those applied by animals. Progress in digital image processing and high temporal resolution tracking has allowed the inference of interaction rules in bird and fish species (e.g. Ballerini et al. 2008; Lukeman et al. 2010; Herbert-Read et al. 2011; Katz et al. 2011). Furthermore, in line with researchers' increasing interest in the role of interindividual differences in shaping interactions (Conradt et al. 2009; Nakayama et al. 2012a), it has been found that flocks of homing pigeons, *Columba livia*, are hierarchically organized, with individuals contributing with different weights to the movement decisions of the flock (Nagy et al. 2010). Such hierarchical networks consist of transitive leader–follower relationships in which birds consistently copy the directional choices of individuals above them in the hierarchy, while being copied by those lower in rank. Little is known about what attributes of a flying pigeon can reliably predict leadership in flocks, although it has been suggested that leadership may be related to individual navigational efficiency (Nagy et al. 2010).

Empirical studies have identified a variety of traits (e.g. age, experience, social rank and motivation; Reebs 2000; King et al. 2008; McComb et al. 2011; Nakayama et al. 2012b) that can modify an individual's propensity to initiate a movement or activity change. Along similar lines, a model by Conradt et al. (2009) suggests that group movements are directed by those specific individuals for whom reaching the goal is most crucial. Several empirical studies support the findings of these models. For example, fish that are deprived of food are more likely to take front positions in shoals than those that are satiated (Krause et al. 1992), and, and lactating female zebra, *Equus burchellii*, initiate movements more frequently than those without dependent foals (Fischhoff et al. 2007). Furthermore, consistent leadership in group movements might be supported by the enhanced knowledge of certain individuals. In several species, including golden shiners, *Notemigonus crysoleucas*, bottlenose

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* Correspondence and present address: A. Flack, Max Planck Institute for Ornithology, Am Obstberg 1, 78315 Radolfzell, Germany.
E-mail address: aflack@orn.mpg.de (A. Flack).
[1] These authors contributed equally.

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dolphins, *Tursiops* sp., and meerkats, *Suricata suricatta*, it has been shown that better informed individuals can change the action of groupmates, using their greater knowledge about their environment (Reebs 2000; Lusseau & Conradt 2009; Bousquet & Manser 2011). With respect to the context of collective motion, recent work has demonstrated that navigationally less experienced birds are likely to follow more experienced conspecifics (Flack et al. 2012). More specifically, the larger the difference in homing experience between two partners, the higher the likelihood that the more experienced bird will emerge as the leader. Additionally, in highly experienced birds the accuracy with which individuals recapitulate previously established idiosyncratic routes when flying solo has been suggested to predict relative influence when flying in pairs (Freeman et al. 2011), suggesting that some aspect of navigational certainty (or perhaps inflexibility) may promote leadership. These findings raise new questions about how variations in navigational knowledge possessed by individual members influence group dynamics in pigeon flocks. If a bird's position in the hierarchy correlates positively with its own navigational experience, we should be able to manipulate the network by providing selected individuals with the opportunity to acquire additional spatial knowledge. In this study, we evaluated whether it is indeed possible to alter individuals' ranks attained during flock homing flights by providing them with additional homing experience before retesting them with their groupmates.

METHODS

Subjects and Experimental Procedure

We used 30 adult homing pigeons bred at the Oxford University Field Station at Wytham, Oxford, U.K. (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 4 and 8 years old, and had homing experience but had never visited the release site used in the current study. They carried miniature GPS logging devices (see below) attached to their back by a small Velcro strip glued to clipped feathers. All releases were performed from Radford (distance and direction to home: 15.7 km, 151°, respectively). The experiment had three phases. First, we trained three flocks of 10 birds (designated groups A, B and C), by releasing all 10 birds of a flock simultaneously at the release site (Phase I: group training). Each flock performed eight group training flights, with a maximum of two releases per day. We then calculated for each group a leadership hierarchy among flock members using the methods described in Nagy et al. (2010). In Phase II (solo training), we allowed three randomly chosen individuals from each flock to gain additional homing experience by performing 10 individual flights from the same site (one of these nine birds was lost during its eighth individual training flight, and therefore did not participate in the third phase for group C). Finally, in Phase III (group tests), we released each original flock six more times to evaluate any changes in the hierarchy's structure, in particular whether the additional homing experience resulted in any changes in the ranks attained by the three individuals that had received additional solo training. Phase I was completed in 10 days, Phase II in 6 days and Phase III in 3 days, with releases conducted on all consecutive days when weather conditions were favourable (dry and with winds <7 m/s).

GPS Device and Data Handling

The GPS device was based on a commercially available product (Gmsu1LP, from Global Top), weighed 13 g, and was capable of logging time-stamped longitude, latitude and altitude data at 10 Hz. The geodetic coordinates provided by the GPS were converted into x, y and z coordinates using the Flat Earth model. These coordinates were smoothed by a Gaussian filter ($\sigma = 0.2$ s), and we used a cubic B-spline method to fit curves onto the points obtained with the 0.1 s sampling rate. Only the x and y coordinates were used for analysis (average number of data points recorded per bird ± SD was 176 107 ± 15 423). In independent tests, using the devices in fixed relative positions to each other, the deviation between real and measured distance was 0.00 ± 0.34 m (mean ± SD). This degree of accuracy is sufficient for calculating directional correlation delay functions that characterize relations among the birds' movements (see Fig. A1 and the Appendix for further details).

Data Analysis

To evaluate the effect of training on homing performance, we calculated homing efficiency and homing time for each flight. Efficiency was measured by dividing the straight-line distance between the release site and the loft by the actual distance travelled by the bird to reach home. Homing time was the length of time that elapsed between release and the bird reaching a radius of 250 m from the loft. These two measures are, of course, not independent of each other, although the relationship between them can vary to some extent as a function of the bird's speed. In addition, to measure the trained birds' change in homing performance, we calculated the difference in efficiency and homing time between the average of the first two and the average of the last two solo training flights in Phase II.

To determine leader–follower relations inside the flock, we calculated the directional correlation delay for each pair of birds i and j ($i \neq j$). The directional correlation delay of a pair is $C_{ij}(\tau) = \langle \vec{v}_i(t) \cdot \vec{v}_j(t+\tau) \rangle_t$, where $\vec{v}_i(t)$ is the normalized velocity of bird i at time t and $\vec{v}_j(t+\tau)$ is the normalized velocity of bird j at time $t+\tau$. Note that $C_{ij}(\tau) = C_{ji}(-\tau)$. We then determined the maximum value of the $C_{ij}(\tau)$ correlation function at τ^*_{ij}, $C_{ij}(\tau^*_{ij})$. We identified the corresponding τ^*_{ij} as the directional correlation delay time. τ^*_{ij} values focus on the relationship between specific pairings of individuals while ignoring hierarchy changes caused by other flock members. Note also that $\tau^*_{ij} = -\tau^*_{ji}$. Negative τ^*_{ij} values mean that the flight directional changes of bird i fall behind that of bird j, and can thus be interpreted as a case of j leading. To compare relationships among flock members before and after the solo training we focused on pairwise τ^*_{ij} values, averaged across pre- and post-training separately. For every specific pair ij, we averaged those τ^*_{ij} values that exhibited a $C_{ij}(\tau^*_{ij})$ larger than 0.95. Because the relationships between specific pairings are nonindependent data points, we used the number of individuals as our sample size for correlations between pre- and post-training τ^*_{ij} values. Only edges with values higher than 0.02 were retained. We chose this conservative value as our threshold to reduce the amount of erroneously introduced edges while ensuring that there is no loss of information.

For the calculation of the $C_{ij}(\tau)$ correlation function, we included only those pairs of data points from birds i and j where the two birds were a maximum of 100 m apart (i.e. $d_{ij} < 100$ m). We chose this threshold based on the distributions of interindividual distances (see Fig. A2). A bird's closest neighbour was less than 10 m away in 71% of all recorded data points (see inset of Fig. A2). However, to be able to detect potential interactions between more distant flock members we used a threshold of 100 m, although only a few data points fall into this bin category.

By averaging the τ^*_{ij} values of bird i and the rest of the flock, we obtained a second measure, denoted τ_i. Because of full transitivity of each hierarchy, this measure allowed us to resolve fully the