

# Hierarchical group dynamics in pigeon flocks

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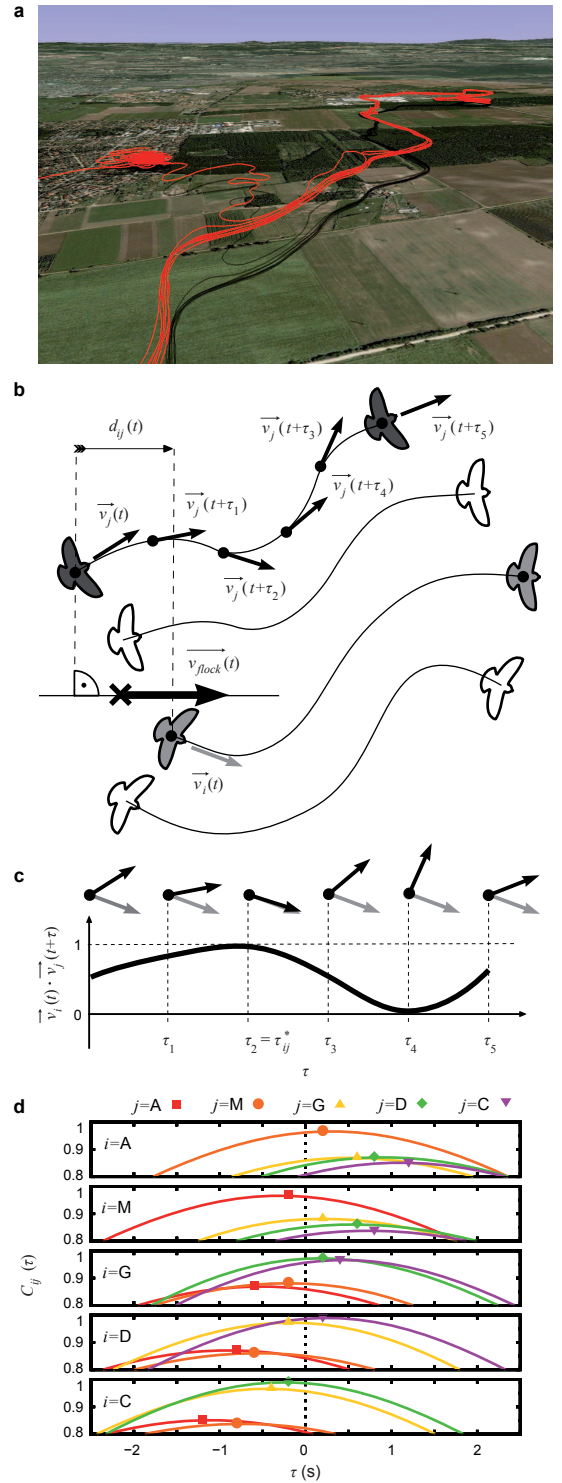
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**Animals that travel together in groups display a variety of fascinating motion patterns thought to be the result of intricate interactive processes among group members<sup>1-3</sup>. Although the most informative way of investigating and interpreting collective movement phenomena would be afforded by the collection of high-resolution spatiotemporal data from moving individuals, such data are scarce<sup>4-7</sup> and are virtually non-existent for three-dimensional group motion within a natural setting because of the associated technological difficulties<sup>8</sup>. Here we present results of experiments in which track logs of homing pigeons flying in flocks of up to 10 individuals have been obtained by high-precision lightweight GPS devices and analyzed using a variety of correlation functions inspired by approaches common in statistical physics. We find a well-defined hierarchy among flock members from data concerning leading roles in pairwise interactions, defined on the basis of characteristic delay times between birds' directional choices. The average spatial position of a pigeon within the flock strongly correlates with its place in the hierarchy, and birds respond more quickly to conspecifics perceived primarily through the left eye – both results revealing differential roles for birds that assume different positions with respect to fellow group members. From an evolutionary perspective, our results suggest that hierarchical organisation of group flight is likely to be more efficient than an egalitarian one, at least for those flock sizes that permit members to perceive and/or individually recognise fellow group members.**

Collective movement phenomena in animals include many spectacular and familiar examples: the abrupt splitting of a fish shoal, a seemingly instantaneous change in the same shoal's direction of motion, or, in the case of birds, a synchronised landing are all signs of rapid collective decision-making by group-members, typically on a very short time scale. What behavioural rules govern such phenomena? The most elaborate way to address this question would be to obtain detailed spatiotemporal data on the positions of individuals during group movement. Nevertheless, up to now progress has been hampered by technological difficulties involved in tracking individuals with sufficiently high precision to resolve intra-group spatial relations in fast-moving animal collectives. Indeed, although long ultimate goal, no high-resolution data of spatiotemporal group member positions have thus far been obtained about organisms moving in three dimensions, and over extended distances within their natural environment. As an alternative approach, numerous simulation models have been proposed to obtain insight into the basic laws of collective motion<sup>3,9-11</sup>, yet rarely have detailed comparisons been attempted between these models and experimental data<sup>7</sup>. In addition, whether, for example, all group members are "equal", as most models assume for the sake of simplicity, or whether individual members (one or a small number of leaders) are able to contribute with differential influence to the group's movement decisions<sup>12,13</sup> are questions that become particularly relevant when models of collective motion from statistical physics are applied to the biological world.

Over the last decade, rapid progress in sensor technology has enabled increasingly accurate tracking of free-flying birds, leading to important advances in our understanding of orientation strategies employed by avian navigators<sup>14-17</sup>. Applying advanced technologies to multiple individuals travelling as a group now also provides a novel window onto the rules underlying collective motion in animals<sup>18-22</sup>. In particular, a new generation of GPS devices – capable of capturing movement decisions at the scale of a fraction of a second – allow us to make use of sophisticated evaluation techniques for exploring the influence that individual group members have on a fast-moving collective’s behaviour. We used a combination of state-of-the-art GPS loggers with quantitative methods inspired by statistical physics to produce a detailed mapping of individual directional choice dynamics and potential leading activity within flocks of up to 10 homing pigeons.

We recorded the birds’ movement under two conditions: while the flock was engaged in spontaneous flights near the home loft (“free flights”) and during homing following displacement to distances of approximately 15 km from the loft (“homing flights”; see Fig. 1a and Supplementary Figure 1). To investigate the influence that a given bird’s behaviour had on its fellow flock members as well as on the flock as a whole, we evaluated the temporal relationship between the bird’s flight direction and those of others (Fig. 1b-d). A leading event was said to have occurred when a bird’s direction of motion was “copied” by another bird delayed in time. To quantify such effects we determined the directional correlation delay time  $\tau_{ij}^*$  (measured in seconds) from the maximum value of the directional correlation function  $C_{ij}(\tau) = \langle \vec{v}_i(t) \cdot \vec{v}_j(t+\tau) \rangle$  (where the brackets denote time average) for each pair of birds  $i$  and  $j$  ( $i, j = A..M, i \neq j$ ) in the flock (see Fig. 1d and Supplementary Methods for



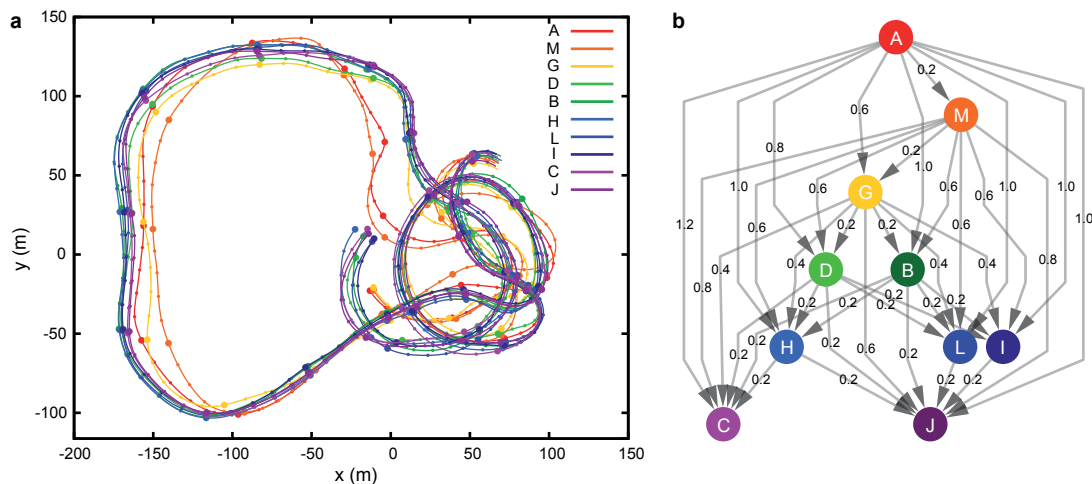
**Figure 1. Summary of directional correlation function analysis for determining leader-follower relationships within a flock.** **a**, Trajectories of a flock of nine pigeons during a homing flight as logged by high-resolution GPS. **b**, Method for determining  $d_{ij}(t)$ , the projected distance of birds  $i$  (light grey) and  $j$  (dark grey) onto the direction of motion of the whole flock at each time step,  $t$ . The cross indicates the center of mass of the flock.  $\vec{x}_i(t) - \vec{x}_j(t)$ , the relative position of the birds, is projected onto  $\vec{v}_{flock}(t)$ , the average velocity of the whole flock. For each pair ( $i \neq j$ ) the directional correlation function is  $C_{ij}(\tau) = \langle \vec{v}_i(t) \cdot \vec{v}_j(t+\tau) \rangle$ . The arrows show the direction of motion,  $\vec{v}_i(t)$ , at each time step. **c**, Visualization of scalar product of the normalized velocity of bird  $i$  at time  $t$  and that of bird  $j$  at time  $t + \tau$  in panel (b). In this example bird  $j$  is following bird  $i$  with correlation time  $\tau_{ij}^*$ . **d**, The directional correlation function  $C_{ij}(\tau)$  during a flock flight (that shown in Fig. 2). For more transparency only the data of birds A, M, G, D and C (in the order of hierarchy for that flight) are shown. The solid symbols indicate the maximum value of the correlation function,  $\tau_{ij}^*$ . These  $\tau_{ij}^*$  values were used to compose the directional leader-follower networks.

further detail). Then, from the pairwise  $\tau_{ij}^*$  values detected within the flock, we composed a directional leader-follower network for each flight. In such a network the nodes represent individual birds, while the edges (links) denote inferred relations between their movements. For every pair, we extracted from  $\tau_{ij}^* = -\tau_{ji}^*$  the positive value as a directed edge pointing from the leader to the follower, and constructed networks by including only those edges whose directional correlation values based on  $\tau_{ij}^*$  were above a given variable minimum,  $C_{\min}$ . The resultant networks were then quantified in terms of the degree of hierarchical organization they exhibited.

We concentrated on analysing velocity correlations because of the well-supported assumption that the information obtainable from spatiotemporal functions has considerably better accuracy than steady global positional data. Since we calculate, e.g., the directional correlation delay data from long series of smoothly changing trajectories averaged over a large number of point pairs, most of the noise is expected to average out. In addition, we found that our GPS devices reproduced *shifts* in the direction of motion much more accurately than global position itself. Thus, quantities based on the interrelations of the derivatives of the trajectories suffer from significantly less uncertainty. We have verified the validity of this assumption quantitatively by generating sample trajectories with given superimposed positional perturbations (see Supplementary Methods).

About two-thirds (63%) of pairwise comparisons between birds of a flock produced clearly directed edges ( $C_{\min} = 0.5$ ). That is, birds tended to copy consistently the directional behaviour of particular individuals, while being copied in their orientational choices by others. The average directional correlation delay time was 0.37s ( $\pm 0.27$ s SD) for  $C_{\min} = 0.5$  and 0.32s ( $\pm 0.20$ s SD) for  $C_{\min} = 0.9$ . Such characteristic delay times can thus be taken to represent birds' reaction times in the context of following a persistent change in the direction of motion of neighbouring birds (rather than, for instance, the considerably shorter reflex-like reactions of a startle response<sup>23</sup>).

Crucially, most flights produced a robust hierarchical network (see Fig. 2 for an example), containing only transitive leader-follower relationships (if A follows B, and B follows C, then A follows C). Only 3 of the 15 flights contained directed loops within the network, and across all flights, the proportion of the total number of edges which pointed in the same direction averaged 0.99 ( $\pm 0.03$  SD) (see Supplementary Table 1 for further detail). Furthermore, randomization tests suggest that the

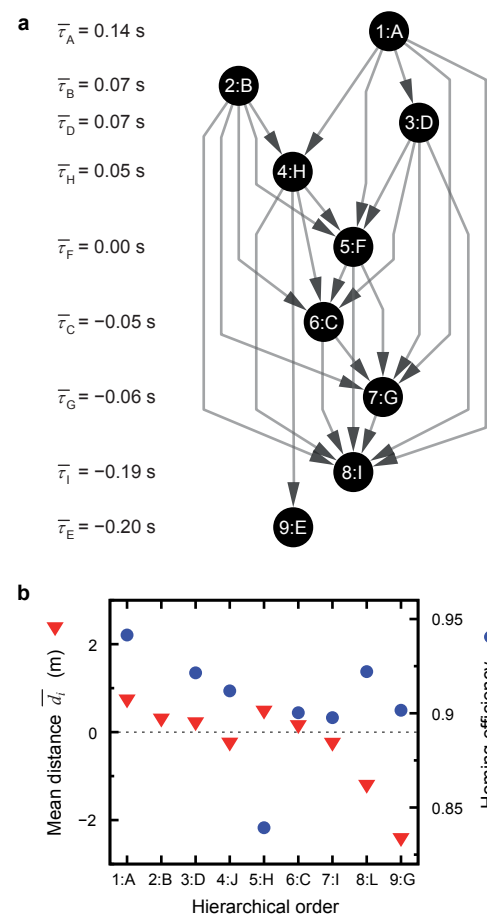


**Figure 2. Hierarchical leadership network generated for a single flock flight.** **a**, 2-minute segment from a free flight performed by a flock of ten pigeons in the vicinity of the loft. The smaller and the larger dots indicate every 1s and 5s, respectively. Each path begins near the centre of the plot. Letters refer to bird identity. **b**, Hierarchical network of the flock for the flight shown in (a). For each pairwise comparison the directed edge points from the leader to the follower (i.e., is oriented such that the average directional correlation delay time for that pair,  $\tau_{ij}^*$ , is positive); values on edges show the time delay (in seconds) in the two birds' motion. For pairs of birds not connected by edges directionality could not be resolved at  $C_{\min} = 0.5$ .

probabilities of obtaining by chance networks with as many or fewer loops as those we observed are extremely low (Erdős-Rényi model for random directed networks,  $p < 0.001$ ; Supplementary Table 1). Hierarchically organised group movement thus appears to be a reliably observable, robust phenomenon in pigeon flocks – opening up a suite of important questions about the roles, identities, and benefits accrued by members that assume the relative ranks of leaders and followers within the group.

Do, for example, leader-follower relationships within specific pairwise comparisons extend across multiple flights? We calculated the average directional correlation delay times,  $\tau_{ij}^*$ , for all pairs who flew together on at least two occasions and for whom  $C_{\min} = 0.99$ . We found that the overall network thus composed was also hierarchical, containing 9 nodes and 24 edges (Fig. 3a). In addition, we examined the effect of individual birds on the movement of the group as a whole, by assessing the average directional correlation delay time for every bird and the rest of the flock. This measure, denoted  $\bar{\tau}_i$ , allows us in turn to fully resolve hierarchical order among all nine birds, by creating a linear ranking consistent with all available data on edges in the network (see also Supplementary Figures 2 and 3). The perfect correspondence between the order of  $\bar{\tau}_i$  values and hierarchical rank (allowing for relative rankings that cannot be decided on the basis of edges alone; Fig. 3a) confirms that birds higher in the hierarchy were more influential in determining the direction of the entire flock's movement. This finding provides powerful support for our conclusion that certain individuals are able to contribute with relatively more weight to the movement decisions of the flock, through having followers within the group who consistently copy their movement. We note that  $\bar{\tau}_i$  values obtained separately for free and homing flights correlate significantly (Pearson's  $r = 0.797$ ,  $n = 8$ ,  $p = 0.018$ ), suggesting that certain birds have a propensity to act as leaders irrespective of navigational context.

Intuitively, we expect individuals near the front of the group to be responsible for the majority of directional decisions, and there is evidence from a variety of species that this is a reasonable assumption<sup>24,25</sup>. Nevertheless, in flying birds, with a field of vision close to  $340^\circ$  which allows individuals to track the movements of those located behind them, the assumption is less trivial. We therefore determined for each bird its average distance from the centre of the flock projected onto the direction of motion of the flock,  $\bar{d}_i$ . We found a strong correlation between  $\bar{d}_i$  and the overall hierarchical order (red symbols in Fig. 3b; Pearson's correlation for  $\bar{d}_i$  vs.  $\bar{\tau}_i$ ,  $r = 0.863$ ,  $n = 9$ ,  $p = 0.003$ ), which supports the notion that individuals occupying positions near the front of the flock tend also to assume leadership roles (see also Supplementary Movies 1 and 2).



**Figure 3. Hierarchical leadership network generated from multiple flock flights.** **a**, Overall hierarchical network of all birds that flew together on at least two occasions. The directed edge points from the leader to the follower. Only those flight data were used to generate the network where the  $C_{ij}(\tau)$  correlation value was higher than 0.99 for a given pair. The flock-averaged directional correlation delay time for each bird,  $\bar{\tau}_i$ , is indicated on the left; note that it has the same order as the network, as it was used to order those birds between whom relative ranks could not be resolved on the basis of edges alone. **b**, Average projected distance onto the direction of motion of the flock,  $\bar{d}_i$  (red triangles), and solo homing efficiency (beeline distance / distance travelled; blue circles) as a function of the hierarchical order resolved in (a). Solo efficiency data is missing for Bird B, as its GPS logger stopped recording during the flight.

Interestingly, besides the front-back distinction between leaders and followers, we also found evidence of a left-right effect. During homing, the more time a bird spent behind a particular partner, the more likely it was to be flying to that partner's right (and would thus have been perceiving it predominantly through its left eye; Table 1). Birds' visual systems are known to be lateralised<sup>26</sup>, with a superiority of the left brain hemisphere (which receives input contralaterally, from the right eye) in large-scale spatial tasks<sup>27</sup>, and a right hemispheric (left eye) specialisation for social input (such as individual recognition<sup>28</sup>). Accordingly, our data also indicate that when birds perceive a particular partner predominantly through the left eye they respond more quickly and/or strongly to its movements (Table 1) suggesting that, indeed, social information may be preferentially processed through the left-eye/right-hemispheric system.

**Table 1. Analysis of laterality effects during group homing flights.**

| Flight number | n  | $Q_{left}$ vs. $Q_{forward}$ |        | $Q_{left}$ vs. $d_{ij}$ |        | $\tau_{left} - \tau_{right}$ |        |                         |        |
|---------------|----|------------------------------|--------|-------------------------|--------|------------------------------|--------|-------------------------|--------|
|               |    | Pearson corr. r              | p      | Pearson corr. r         | p      | mean [s]                     | SD [s] | Student-t test* t-value | p      |
| HF1           | 90 | 0.37                         | <0.001 | 0.32                    | 0.002  | -0.23                        | 0.27   | -8.03                   | <0.001 |
| HF2           | 72 | 0.23                         | 0.048  | 0.25                    | 0.036  | -0.19                        | 0.21   | -7.72                   | <0.001 |
| HF3           | 46 | 0.59                         | <0.001 | 0.62                    | <0.001 | -0.016                       | 0.026  | -4.39                   | <0.001 |
| HF4           | 72 | 0.49                         | <0.001 | 0.54                    | <0.001 | -0.006                       | 0.020  | -2.32                   | 0.023  |

n: Number of data pairs for given flight. The total number represents all possible pairwise comparisons between birds of the flock. For each pair, only those datapoints were analysed where the two individuals were less than 10 m apart (see Supplementary Methods). Note that during HF3, two birds broke away from the group soon after release, and did not have sufficient data at the given distance limit for comparisons with every other flock-mate.

$Q_{left} = t_{left} / t_{total}$ : Left Ratio. For any given pair, time spent with partner positioned on focal bird's left (relative to its direction of motion) divided by the total time spent flying together.

$Q_{forward} = t_{forward} / t_{total}$ : Forward Ratio. For any given pair, time spent by partner ahead of focal bird (relative to the direction of motion of the whole flock) divided by the total time spent flying together.

$d_{ij}$ : Average projected distance onto the direction of motion of the whole flock for each pair.

$\tau_{left} - \tau_{right}$ : Difference of the  $\tau_{left}$  and  $\tau_{right}$  values for any given pairwise comparison, where  $\tau_{left}$  and  $\tau_{right}$  refer to directional correlation delay times calculated separately for datapoints where the partner is positioned to the left and to the right of the focal bird, respectively.

\* The Student t value is calculated on the basis of the distribution of  $\tau_{left} - \tau_{right}$  values obtained when the observed  $\tau_{left}$  and  $\tau_{right}$  pairs are randomly reassigned into novel pairings, and thus tests whether within-bird observed differences in directional correlation delay times are significantly different from the random expectation. In all four flights the mean is significantly lower than 0, suggesting that birds respond faster to their partners when the latter are in view primarily of the left eye.

To explore whether a bird's propensity to lead relates to individual navigational performance, we conducted a single solo homing test, releasing individually those nine subjects who are represented in the overall hierarchy (Fig. 3a). All birds completed the journey individually, although one ("H") flew a considerably longer path than the average for the remaining subjects ( $> \text{mean} + 5 \text{ SD}$ ). When this outlier is excluded, the correlation between order in the leadership hierarchy and homing efficiency approaches significance (Pearson's  $r = -0.71$ ,  $n = 7$ ,  $p = 0.074$ ; blue symbols in Fig. 3b) although not if it is included (Pearson's  $r = -0.29$ ,  $n = 8$ ,  $p > 0.100$ ). Thus, although the current data are equivocal, they are suggestive that leadership may be related to individual navigational efficiency, with birds higher in the hierarchy also demonstrating more accurate solo navigation. Whether such effects would derive from more

motivated or inherently better navigators being better able to assume leadership roles<sup>13</sup>, or from birds that have had more experience leading also having had increased opportunities for navigational learning (the passenger/driver effect<sup>29</sup>) remains an intriguing open question regarding the causes – or indeed consequences – of leadership.

Nonetheless, the differential benefits of leading and following highlight the notion that hierarchically organised group motion may bring individual-specific benefits to group members. In human collectives, hierarchical organisation is widespread – companies, armies, research groups all incorporate hierarchical structures – suggesting that such organisation may be an effective solution that endows the collective's members with additional benefits. Indeed, diversity in social roles has been argued to scaffold the emergence of cooperation in humans<sup>30</sup> – in part applicable to other social-living species faced with the problem of group coordination. As for the original question whether the direction of birds in a flock is determined primarily by following a leader or by more egalitarian, yet unknown self-organizing mechanisms, our quantitative results suggest that nature offers a third and beautiful solution: the roles according to which birds tend to follow each other are arranged into a hierarchy, with a continuous spectrum in levels of leadership. Moreover, these roles are manifested in a dynamically changing fashion, i.e., only in average, since the leading role of a given bird fluctuates in time over a wide range of time intervals. Such dynamic segregation of roles into leaders and followers may, from an evolutionary perspective, favour the emergence of hierarchically organised groups over ancestrally (presumably) egalitarian collectives. Thus, our results are potentially far-reaching since the kind of collective decision making situation flocks face when selecting a common direction has appealing analogies in many other systems, ranging from other animal congregations through swarms of robots to groups of people.

## Methods

**Subjects and experimental protocols.** 13 homing pigeons, all aged between 1 and 5 years, participated in the experiments. All had had previous homing experience and most had previously competed in races (>100 km) for young pigeons. Birds were habitually allowed to fly freely outside the loft twice a day. All subjects (labelled A to M) were initially equipped with plasticine dummy weights (16 g, same size and weight as the GPS logger), affixed to the back with an elastic harness, to habituate them to flying and living with a load. We collected GPS data from three types of releases: free flights of flocks around the home loft (11 flights in total; with flocks spending on average 12 min in the air), homing flights in flocks (4 flights; all participating subjects released simultaneously), and individual homing flights (one per subject). Group homing flights were conducted from release sites located 13.7-14.8 km from the loft; the single solo flight from 15.2 km (600 m from one of the sites used during group releases). The different types of flights were interspersed in the following order: 1 free, 1 flock homing, 1 free, 3 flock homing, 1 individual homing, and 9 free. In most cases, flocks consisted of 10 (8 flights) or 9 (5 flights) pigeons, while on two occasions the flock numbered 8 individuals, and once only 7 participated. A maximum of two flights were conducted per day, between 22nd of August and 26th of September 2008. In total, GPS devices logged 32 h of flight time, representing 580,000 datapoints gathered for analysis.

**GPS device and data handling.** The GPS device we developed was based on a commercially available U-blox (Thalwil, Switzerland) product. It was capable of logging 30,000 datapoints (latitude, longitude, and altitude coordinates and time), measured 2.5 x 4.5 cm, and weighed 16 g (3-4% of the subjects' body weight). The temporal resolution of the device was 0.2 s. Immediately before recorded flights the dummy was replaced by the GPS device, and upon recapture of the birds at the loft the device was removed and the log files downloaded to a computer. 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 ( $\sigma = 0.4$  s), and the cubic B-Spline method was used to fit curves onto the points obtained with the 0.2 s sampling rate. Occasionally, the device failed to log every second or third point; in such cases we interpolated the position of the missing datapoints by averaging those recorded



immediately before and after. As with the GPS measurement the error of the z coordinate is much larger than that in the horizontal directions, we used only x and y in our analysis. In independent tests we confirmed that the accuracy of the x and y global coordinates was in the range of 1-2 m. While this degree of accuracy does not permit accurate determination of spatiotemporal configurations of individuals within the flock, it is nevertheless sufficient for calculating various relevant correlation functions that characterise relations among the birds' motion (see Supplementary Methods).

**Supplementary Information** accompanies the paper.

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**Author Contributions.** Zs. A. and T.V. designed the experiments. Zs. A. and M.N. performed the experiments, M.N and D.B. designed the evaluation of data. M.N. performed the analysis and the visualization of data. D.B. and T.V wrote the paper.

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