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Tree structures are employed by pigeons as leadership structures to flock

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Collective behaviors displaying a variety of fascinating movement patterns are thought to be products of complex interplay among individuals. Previous studies have proposed the hierarchical leadership networks and the coexistence of compromise and leadership in pigeon flocks, but these conclusions have not been confirmed by theoretical or modeling studies. Here, based on the same datasets, using a more reasonable research route, we found a more concise leadership structure in pigeon flocks. i.e., the tree structure, which was verified by our modeling studies. We showed that each individual may follow its only pilot (leader) during collective flights of pigeon flocks, and the only top leader of a certain flock determines the flight direction of the whole flock. Our results confirmed the leadership hypothesis, denying the illusion of compromise between individuals at the same level. The findings shed light on the hierarchical leadership structure in pigeon flocks and have implications for artificial collective systems, e.g., autonomous formation control of multiple unmanned aerial vehicles and unmanned surface vehicles.

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I. INTRODUCTION

The rapid and coherent collective movement of bird flocks containing thousands of individuals is fascinating, exhibiting obvious intelligence and coordination [1]. New monitoring techniques have recently re-engaged interests of a large number of scientists in this collective behavior, allowing for more detailed analysis [2]. For example, small high-precision GPS devices can obtain accurate positional data of individuals in flocks, which can be used for more meaningful and advanced analysis of collective behavior [3–5]. A high-speed 3-dimensional (3D) imaging system has been developed to measure the movements of birds in 3D space [6, 7]. Video recordings have also been used to obtain accurate positional data of individual agents [8–11]. Generally, it is feasible, with accurate positional data, to understand the behavioral and structural properties of collective behaviors through statistical analysis. Researchers have studied the emergence mechanism of collective behaviors experimentally and theoretically for decades, but the mechanism has not been thoroughly revealed. A fundamental question is whether all individuals of a flock have equal status (influence the group decision-making equally and obey the same rules), or the collective behaviors are decided by one or a few individuals, or neither of them, but a more complex mechanism [3, 12–17].

Currently, there are two mainstream propositions. One is that all individuals of a flock follow certain rules equally, and the other is that collective behaviors of a flock are determined by a small number of leaders. The former is sometimes called the “many wrongs” principle, and purports that each individual averages its preferred direction depending on interaction with the neighbors, resulting in a compromise in the choice of direction [18, 19]. The latter claims that one or a few leaders may be able to exert a critical influence on the movement de-

isions of a flock [20]. Ref. [12] shows a theoretical argument that the compromise of all individuals of a flock could make a better decision than the control of one or a few leaders, unless the leader/leaders has/have very superior knowledge. This result also shows, to a certain extent, that it is a better choice to employ the strategy of compromise of all individuals for some low-level organisms which cannot grasp certain information, such as bacteria. Indeed, experimental and theoretical studies have shown that bacterial colonies adopt the strategy of compromise [10, 21]. However, for higher organisms that can master certain information, such as pigeons, the leadership hypothesis should be more appropriate. For instance, Ref. [22] shows that the homing performance of a flock of trained pigeons is better than that of the individuals flying alone. This reflects that there could be a leadership in the pigeon flock, so the individuals mastering the homing information can lead the flock to make a better movement decision. Excitingly, recent studies have shown that a well-defined hierarchy among individuals do exist during flights of pigeon flocks [3, 4], providing strong evidences for the leadership hypothesis. Moreover, hierarchical relationships in pigeon flocks are very stable [23], that is, once hierarchies are formed, they can be quite resistant to change, unless the leaders are misled by external information [24].

Nagy et al. [3, 4] claimed to have discovered the “leadership network” in free and homing flights of pigeon flocks. In fact, the “leadership network” is just a in-flight hierarchical relationship in pigeon flocks, and it does not reflect the direct leadership relationship between each pair of individuals. We take the leadership relationship between three individuals as an example. When the individuals **C** and **B** are only led by the individuals **B** and **A**, respectively, the corresponding true leadership relationship can be expressed as $\boxed{\mathbf{A} \rightarrow \mathbf{B} \rightarrow \mathbf{C}}$ (the directed edge points from the leader to the follower). However, in the “leadership network” obtained by the method in Refs. [3, 4], there will be a directed edge pointing from the individual **A** to the individual **C** with a larger directional corre-

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lation time delay, i.e., $\boxed{\mathbf{A} \rightarrow \mathbf{B} \rightarrow \mathbf{C}}$. Therefore, the “leadership networks” in Refs. [3, 4] cannot show the true leadership relationship within the flocks. In addition, Xu et al. [25] proposed reciprocal relationships in collective flights of pigeons, and claimed that the compromise and leadership coexist during the flights. They believe that the high synchronization of two pigeons i and j (with the directional correlation time delay $\tau_{i,j} = 0$) is the result of mutual links, i.e., the neighbor compromise mechanism [25]. However, most importantly, the conclusions (leadership networks) in Refs. [3, 4, 25] have a common defect, that is, the leadership networks were only deduced from the data unidirectionally without verification. A more reasonable approach should be “two-way”, that is, a leadership structure is first deduced from the data, and then similar data are reproduced using mathematical models with the structure.

Mathematical models, especially dynamical equations, have been used by mathematicians, physicists and biologists to illustrate interactions or movements of animals [26, 27], even humans [28–30]. The Lotka-Volterra model is an early example of attempts to describe the evolution of systems containing preys and predators. Later efforts used diffusion equations and physical laws to model the movement of social animals, e.g., groups of insects, fish, and herds [31]. Time-discrete models, being used to simulate complex collective behaviors via simple rules, are an initial step to fully understand the nonlinear mechanisms in real complex systems. The Boid model [26], a well-known example, has been used in video games and movies to obtain animated collective behaviors. Another example is the Vicsek model [27], a simpler model of particles, which can describe collective behaviors of huge flocks in the presence of perturbations. Furthermore, recent approaches considered more detailed and realistic dynamical mechanisms, such as the predator-prey model [32], the molecular physics model [33], the zonal interaction model [34], and the metric distance model [20]. However, the previous approaches, modeling collective behaviors with dynamical systems, are generally based on the equal status (compromise) hypothesis, although the hierarchical relationship has been proposed for more than 10 years. Hence, few models consider the hierarchy in bird flocks. As a result, the leadership networks presented in Refs. [3, 4, 25] have not been verified by the corresponding models.

In this article, we proposed a new type of leadership structure, i.e., the tree structure, in pigeon flocks, and developed a model with this leadership structure. The simulated data generated from this type of leadership structure can reproduce the data characteristics of the real flight data of pigeon flocks, which means that our hypothesis is closer to the real leadership structure. We also presented a method to reconstruct specific leaderships via flight data, and the validity of this method is verified by our simulated data. At last, our method was applied to real flight data to obtain leadership relationships in specific flocks. Figure S1 in the Supplementary Information [35] shows the logical organization of this article. The rest of the article is as follows. Section II introduces the method; and then, Section III shows the results, including verification of the model, deduce the leadership structure

from data and application; at last, conclusion and discussion are presented in Section IV.

II. METHODS

Observations suggest that, in nature, an individual often chooses one leader to follow, although the leader may not be the top leader. Here, we assume that the hierarchical leadership structure in pigeon flocks is a tree structure. For convenience, we employ complete binary tree structures in this article. Fig. 1 shows a complete binary tree containing 40 pigeons. Specifically, each follower only follows its only immediate leader, e.g., the individual **C1** only follows the individual **B1**, and the individual **D5** only follows the individual **C3**.

Actual simulations containing N individuals were carried out in a continuous 2D space. At time t , the position vector and velocity vector of the individual i ($i = 1, 2, 3, \dots, N$) can be expressed as $\vec{p}_{i,t}$ and $\vec{v}_{i,t}$, respectively. The time unit Δt is the time interval between two updating of the positions and directions. Consequently, the position vector of the individual i at time $t + \Delta t$ can be obtained, i.e.,

$$\vec{p}_{i,t+\Delta t} = \vec{p}_{i,t} + \vec{v}_{i,t}\Delta t, \quad i = 1, 2, 3, \dots, N. \quad (1)$$

In addition, the velocity $\vec{v}_{i,t}$ is constructed to have a module v (suppose pigeons fly at a constant speed) and a direction given by the unit vector $\vec{a}_{i,t}$, i.e., $\vec{v}_{i,t} \equiv v\vec{a}_{i,t}$.

The unit vector at time $t + \Delta t$ of individuals expect the top leader (i.e., the individual **A** in Fig. 1) can be obtained from the expressions

$$\begin{cases} \vec{a}'_{i,t+\Delta t} = F(\vec{a}'_{i,t+\Delta t}, \sigma W_U), \\ \vec{a}'_{i,t+\Delta t} = \frac{\vec{a}_{i,t} + \vec{a}_{j,t}}{\|\vec{a}_{i,t} + \vec{a}_{j,t}\|}, \\ i = 2, 3, 4, \dots, N, \end{cases} \quad (2)$$

where, the manipulate symbol (operator) $F(\vec{a}, \theta)$ means to rotate the vector \vec{a} by an angle θ . W_U is a uniform white noise with a variance of $1/3$ and an average of 0, and $\vec{a}_{j,t}$ represents the direction of the immediate leader of the individual i at time t . $\|\vec{a}\|$ represents the module (magnitude) of the vector \vec{a} .

Because pigeons make a circle-like flight in free flights [17] and their one-dimensional flight trajectory is like a pseudo-periodic time series [36, 37], we use the Lorentz chaotic system to drive the top leader’s flight direction (see the Supplementary Methods in the document named Supplementary Information [35] for further details). $Q_{Lor} = \{\vec{q}_1, \vec{q}_2, \vec{q}_3, \dots\}$ represents the evolutionary time series of displacement vector of the Lorentz chaotic system’s state in the phase plane ($x-z$). In the iterative process, the direction of the top leader $\vec{a}_{1,n}$ can be determined, i.e.,

$$\begin{cases} \vec{a}_{1,n} = F(\vec{a}'_{1,n}, \sigma W_U), \\ \vec{a}'_{1,n} = \frac{\vec{q}_{n+1} - \vec{q}_n}{\|\vec{q}_{n+1} - \vec{q}_n\|}, \end{cases} \quad (3)$$

where, n represents the n th iteration in the system.

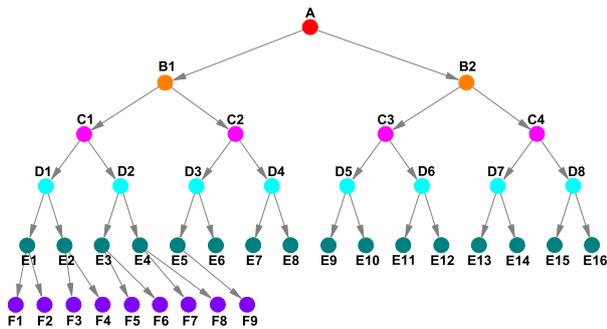


FIG. 1: Hierarchical leadership network of a bird flock containing 40 individuals, which is a complete binary tree (Every level except the last level is completely filled and all the nodes are left justified). Each directed edge points from the leader to the follower. The number of level is 6, and the node in the first level is individual **A**, the nodes in the second level are individuals **B** and **C**.

In all simulations, suppose that the initial positions of all individuals are randomly distributed in a rectangular area ($10m \times 10m$). The initial direction of all individuals points to a common direction (specified as horizontal right in this paper). Parameters were fixed: $v = 10m \cdot s^{-1}$, $\sigma = 0.08\pi$ and $\Delta t = 0.1s$. The dynamic behaviors of pigeon flocks were simulated in a 2D unbounded space through MATLAB code, which is available from the authors on request.

For each pair individuals ($i \neq j$), the directional correlation function is

$$\begin{cases} C_{i,j}(\tau) = \frac{\langle X'_i(t)X'_j(t+\tau) \rangle}{\sigma_i\sigma_j}, \\ X'_i(t) = X_i(t) - \langle X_i(t) \rangle, \\ X'_j(t) = X_j(t) - \langle X_j(t) \rangle, \end{cases} \quad (4)$$

where, $\langle \dots \rangle$ denotes time average. $X_i(t)$ represents the time series of the flight angle $\theta_{i,t}$ (i.e., the polar angle of $\vec{a}_{i,t}$ in the polar coordinate system) of the individual i . σ_i and σ_j represent the standard deviation of the time series $X_i(t)$ and $X_j(t)$, respectively. If $C_{i,j}(\tau)$ reaches its maximum value $C_{i,j}^*$ at τ , τ is called the directional correlation delay time, denoted as $\tau_{i,j}^*$. Positive $\tau_{i,j}^*$ means that the individual i has an effect on the flight direction of the individual j , and negative $\tau_{i,j}^*$ indicates an effect in the opposite direction. Hence, we only consider the positive value of $\tau_{i,j}^*$ ($\tau_{i,j}^* = -\tau_{j,i}^*$) as a directed edge pointing from the influencer to the affected individual.

For convenience, the reconstruction method of leadership structure is detailed in the second part of the RESULTS section.

III. RESULTS

A. Verification of the model

Based on our model, we simulated free flights of pigeon flocks, and reproduced collective behaviors of pigeon flocks

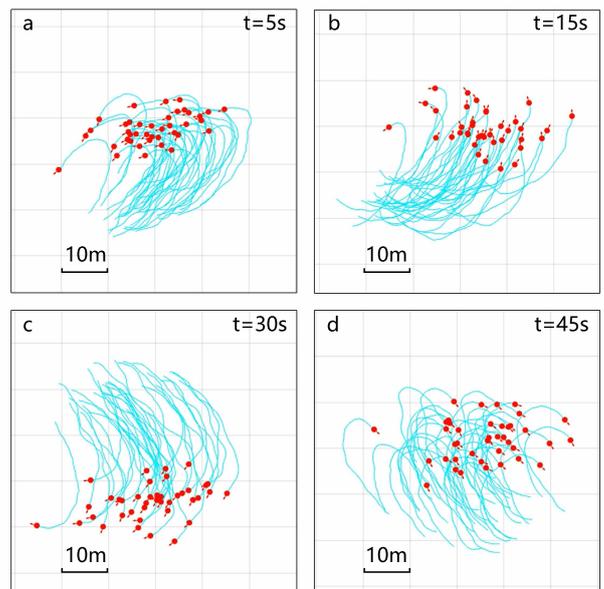


FIG. 2: The flight process of a pigeon flock containing 40 individuals. The red circles with an arrow represent individuals, and the cyan curves represent trajectories that individuals just flew over. Numerical results reproduce the collective flights of pigeon flocks very well. See Movie 1 in the Supplementary Materials for a more vivid flight process.

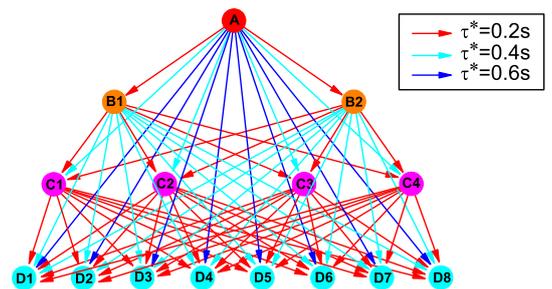


FIG. 3: Directional correlation network of the first four levels. The C^* value between each pair of connected individuals is greater than 0.8 (see the supplementary material named ‘Maximum value of C’ [35]). The time delay τ^* between each pair of individuals in the same level is zero, so the connection between them is not considered, as in Ref. [3].

well. For instance, the top leader completely controls the flight direction of pigeon flock, and when the top leader changes the flight direction, the other sub-leaders change the direction first than the corresponding followers, as shown in Fig. 2 (see also Movie 1 in the Supplementary Materials).

In order to further test the validity of our model, we compared the simulated data with the experimental data in Ref. [3]. Specifically, we calculated the $\tau_{i,j}^*$ and $C_{i,j}^*$ between different individuals i and j through the time series of flight angle $\theta_{i,t}$ and $\theta_{j,t}$ (see the supplementary material named ‘Di-

rectional correlation delay time' [35]). And these data are expressed in the form of a network according to the method in Ref. [3]. As shown in Fig. 3, for convenience, we only draw the directional correlation network between individuals in the first four levels. This network is very similar to that in Fig. 2b of Ref. [3]. Specifically, the time delay τ^* between each pair of individuals in adjacent levels is the same. For example, the time delay τ^* between individuals **A** and **B1**, **B3** and **C4**, **C1** and **D3** are all $0.2s$. And the time delay τ^* between each pair of individuals in adjacent levels is smaller, and as the level span becomes larger, the time delay τ^* increases. For example, the time delay τ^* between individuals **A** and **B1** is $0.2s$, between individuals **A** and **C1** is $0.4s$, and between individuals **A** and **D1** is $0.6s$. In addition, the flight directions of all individuals in one flock generally have a large correlation. Therefore, directed edge generally exists between each pair of individuals in different levels.

B. Deduce the leadership structure from data

One can find that the (directional correlation) network in Fig. 3 can not specifically reflect the leadership relationship of the pigeon flock (see Fig. 1). So what we are concerned about is how to deduce the leadership network from the flight data of individuals. Indeed, the higher the level of the leader, the more directed edges it emits (see Fig. 3). From the data in the supplementary material named 'Directional correlation delay time' [35], we can get the number of directed edges emitted by each individual, as shown in Table I. Based on the above characteristic, we can determine the level of all individuals (see Fig. S2 in the Supplementary Information [35]).

In the METHODS section, we pointed out that each individual except the top leader have only one leader, but can have many followers. Next, we will gradually reveal the leadership relationship between individuals in each pair of adjacent levels from top to bottom. Obviously, the leader of the individuals **B1** and **B2** in the second level is the top leader **A**. We use directed edges to represent the leadership relationships between them (see Fig. S3).

Then, we select the leaders of the individuals **C1**, **C2**, **C3** and **C4** from **B1** and **B2**. Since the follower i keeps copying the flight direction of its immediate leader j , the value of $C_{j,i}^*$ between the two individuals should be larger. Table II shows the $C_{i,j}^*$ between the individuals j ($j = \mathbf{C1}, \mathbf{C2}, \mathbf{C3}, \mathbf{C4}$) and i ($i = \mathbf{B1}, \mathbf{B2}$). Therefore, the leadership relationships between the individuals in the two levels can be deduced, that is, **B1** is the leader of **C1** and **C2**, and **B2** is the leader of **C3** and **C4** (see Fig. S4).

In order to expediently identify the leader of each individual in the n th level ($n = 2, 3, 4, \dots$), one can place each individual in this level in the corresponding feature space. For instance, the feature space corresponding to the 3rd level is a 2D space composed of mutually orthogonal $C_{\mathbf{B1},\sim}^*$ and $C_{\mathbf{B2},\sim}^*$ axes, and the coordinates of the individual **C1** in this space are $(C_{\mathbf{B1},\mathbf{C1}}^*, C_{\mathbf{B2},\mathbf{C1}}^*)$. The feature space corresponding to the 4th level is a 4D space composed of mutually orthogonal $C_{\mathbf{C1},\sim}^*$, $C_{\mathbf{C2},\sim}^*$, $C_{\mathbf{C3},\sim}^*$ and $C_{\mathbf{C4},\sim}^*$ axes, and the coordinates of the indi-

TABLE I: The number of directed edges emitted by the individual i , i.e., N'_i , in directional correlation network

Individual i	A	B	C	D	E	F
N'_i	39	37	33	25	9	0

Note: The symbol **B** represents individuals **B1** and **B2**. Similarly, the symbols **C**, **D**, **E** and **F** represent individuals **C1**~**C4**, **D1**~**D8**, **E1**~**E16** and **F1**~**F9**, respectively.

TABLE II: C^* between different individuals

$C_{i,j}^*$	C1	C2	C3	C4
B1	0.9058	0.9121	0.8819	0.8870
B2	0.8873	0.8859	0.9162	0.9178

vidual **D3** in this space are $(C_{\mathbf{C1},\mathbf{D3}}^*, C_{\mathbf{C2},\mathbf{D3}}^*, C_{\mathbf{C3},\mathbf{D3}}^*, C_{\mathbf{C4},\mathbf{D3}}^*)$. For ease of illustration, Fig. 4 shows the distribution of the individuals **C1**, **C2**, **C3** and **C4** in the feature space $(C_{\mathbf{B1},\sim}^* - C_{\mathbf{B2},\sim}^*)$. Specifically, the coordinates of the individual **C4** are $(0.8870, 0.9178)$, and the larger coordinate is the $C_{\mathbf{B2},\sim}^*$ coordinate. Because the individual corresponding to this coordinate $(C_{\mathbf{B2},\sim}^*)$ is **B2**, one can confirm that the individual **B2** is the leader of the individual **C4**. The method can be generally expressed as

$$\begin{cases} j \leftarrow i, & \text{if } C_{i,j}^* = (C_{\sim,j}^*)_{max}, \\ j \in n\text{th level}, & i \in (n-1)\text{th level}, \\ n = 2, 3, 4, \dots, \end{cases} \quad (5)$$

where, the arrow indicates that the individual j is led by the individual i . $(C_{\sim,j}^*)_{max}$ represents the maximum coordinate of individual j in the feature space. The individual j belongs to the n th level in the hierarchical structure, and the individual i belongs to the $(n-1)$ th level. In addition, it can be seen from Fig. 4 that individuals with the same leader are closer in C^* -space.

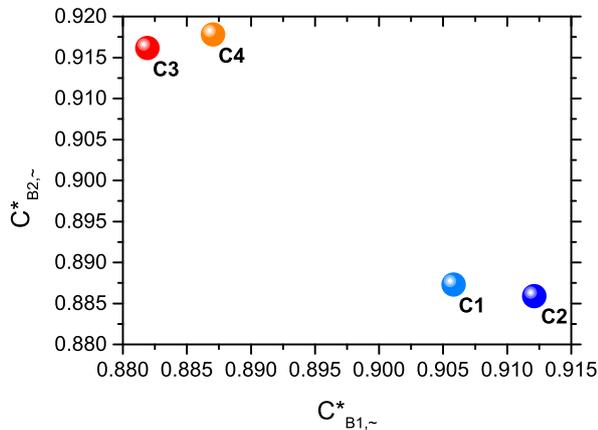
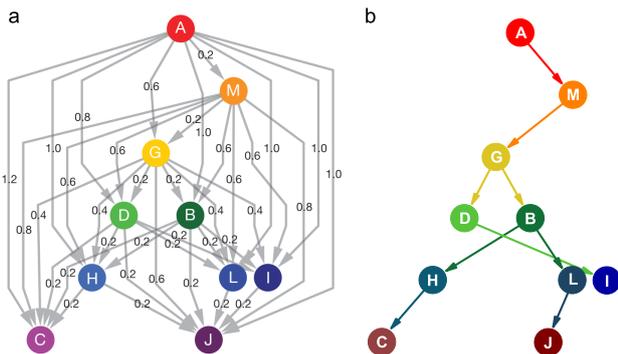
Furthermore, Table III shows the C^* between individuals in the 3rd and 4th levels. One can get the leadership relationship between the two levels (see Fig. S5). Finally, based on this method and combined with the data in the supplementary materials 'Maximum value of C' [35], we deduced the leadership relationships among individuals in the remaining levels. Consequently, we obtained the leadership structure of the pigeon flock (see Fig. S6). One can find that the leadership structure we deduced is exactly the one set in the model. This is a good proof of the validity of our reconstruction method of leadership structure.

C. Application

As mentioned above in the METHODS section, Fig. 2b in Ref. [3] is not the leadership structure of the pigeon flock. Here, based on the method in this article, we deduced the leadership structure of the flock via the experimental data in Ref. [3]. Figure 5 shows the directional correlation network

TABLE III: C^* between different individuals

$C^*_{i,j}$	D1	D2	D3	D4	D5	D6	D7	D8
C1	0.9264	0.9262	0.8818	0.8956	0.8681	0.8505	0.8353	0.8471
C2	0.9034	0.9018	0.9182	0.9143	0.8487	0.8384	0.8381	0.8483
C3	0.8652	0.8645	0.8555	0.8546	0.9195	0.9165	0.8832	0.8935
C4	0.8585	0.8660	0.8637	0.8652	0.8930	0.8919	0.9153	0.9199

FIG. 4: Distribution of individuals in space ($C^*_{B1,~} - C^*_{B2,~}$).FIG. 5: Comparison of the directional correlation network, **a**, and the corresponding leadership network, **b**. Subplot **a** quotes from Ref. [3], and subplot **b** is the leadership network, constructed using the method in this article. For the convenience of comparison, we kept the original position of each node in subplot **b**.

and the corresponding leader network of the flock. It can be seen that the leadership network is relatively simple compared to the directional correlation network. It also shows that the leadership relationships in a flock are not complicated, and collective flights are just dynamic processes in which a large number of individuals follow their only leaders to fly.

IV. CONCLUSION AND DISCUSSION

We have found that the leadership structures in collective movements of pigeon flocks are tree structures, which are

more concise than those in Refs. [3, 4, 25]. We also developed a model to verify the validity of the tree structure. Our results have shown that each individual may follow its only pilot (leader) in collective flights, and the only top leader determines the flight direction of a certain flock. Our findings have confirmed the leadership hypothesis, denying the compromise [25] between individuals at the same level.

Our results show that all directed edges between non-adjacent levels and some ones between adjacent levels in the hierarchical networks in Refs. [3, 4] do not represent a direct leadership relationship, but only the existence of correlation. Accordingly, the “leadership networks” in Refs. [3, 4] are actually “correlation networks” including hierarchical structures. Excitingly, this article proposed a method to extract the leadership network from a “correlation network”.

Xu et al. [25] think that the correlation time delay $\tau_{i,j} = 0$ means a coordinated interaction exists between the pair of pigeons i and j , as a result, a mutual (reciprocal) link exists between them. However, our results including the simulation results confirmed that the mutual (reciprocal) links may not exist. Our findings show that when the leadership structure in a pigeon flock is a tree structure, the movements of individuals in the same level (i.e., $\tau_{i,j} = 0$) will show a very strong synchronization, and the movements of individuals led by the same leader have a larger correlation coefficient. Consequently, the phenomenon of strong synchronization is not caused by the mutual (reciprocal) link, and the larger correlation coefficient with $\tau_{i,j} = 0$ is the result of being led by the same leader.

By comparing our simulated data with the experimental data, it can be seen that the tree structure dominates the flight formation of pigeon flocks, while the compromise mechanism (interactions) among individuals (e.g., the repulsion to prevent collision between individuals, the attraction to prevent individuals from moving away from each other, and the polarization force to make the direction consistent) is not shown, at least in general.

Ref. [17] shows that, during flights of pigeon flocks, the intermittent interaction (alignment, polarization force) between each pair of individuals is not required at every moment, but intermittent. This mechanism can help substantially reduce the requirements of information processing or/and communication, reducing costs of the intra-group communication and energy of information processing or/and communication [17]. Here, we find that the leadership structure is more concise than previously reported, so it is more energy-saving in information processing or/and communication. Consequently, applying the leadership structure to autonomous formation control of unmanned vehicles can save energy for the whole sys-

tem.

Ref. [38] shows that birds (budgerigars) have strong anti-collision ability and can effectively avoid collision even if they don't fly in a narrow space. Therefore, during flights of flocks, pigeons may not consider the interaction forces (attraction and repulsion) between individuals unless the individuals are very close or very far away. This is consistent with the findings of this paper.

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- [35] See Supplemental Material at [URL will be inserted by publisher] for Movie 1 and the documents named “Supplementary Information”, “Directional correlation delay time” and “Maximum value of C ”. Movie 1 shows the flight process of a pigeon flock containing 40 individuals; the “Supplementary Information” document contains the Supplementary Methods and Supplementary Figures; the documents “Directional correlation delay time” and “Maximum value of C ” are the data used in the main text.
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