Tree structures may be the leadership structures employed by group motions exhibiting hierarchy

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Collective behaviors leading to various fascinating movement patterns are believed to be the product of complex interplay among individuals. Previous studies have identified two types of leadership structures in pigeon flocks, i.e., hierarchical networks and reciprocal relationships. However, both of these leadership structures are predicated based on data analysis and lack substantial empirical evidence. Additionally, it is difficult to delineate a direct correspondence between leadership structures and trajectory data for pigeon flocks because birds cannot report their leadership structure. Herein, based on experiments involving volunteers, we found that tree structures may serve as the leadership structures employed by group motions exhibiting hierarchy. In the tree structure, each follower follows its only leader during collective motions, and the single top leader determines the direction of collective motions. By employing the tree structure, we introduced a model for describing collective motions. A method for obtaining the leadership structure through experimental trajectory data was proposed. This strategy was used to analyze flight trajectory data from a pigeon flock and elucidate the pigeons' leadership relationships. Our model can simulate the collective behavior of pigeon flocks, thus accurately replicating the findings of previous experimental studies. The results of this study provide insights regarding the leadership structure in pigeon flocks and have implications for artificial collective systems, e.g., autonomous formation control of multiple unmanned aerial vehicles or unmanned surface vehicles.

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I. INTRODUCTION

The rapid and coherent collective movements of bird flocks containing thousands of individuals is a fascinating display of intelligence and coordination [1]. New monitoring techniques have recently re-ignited scientific interest in this type of collective behavior, allowing for more detailed analysis [2]. Examples include small sensors detecting local movements or physical signs of individuals [3], small high-precision GPS devices providing accurate positional data of individuals in flocks (this can be applied to more meaningful and advanced analysis of collective behaviors) [4–6], high-speed three-dimensional (3D) imaging systems measuring the movements of birds in 3D space [7,8], and video recording equipment obtaining accurate positional data of individual agents [9–12]. With accurate positional data, it is theoretically feasible to understand the behavioral and structural properties of collective behaviors through statistical analysis. Researchers have studied the mechanism governing the emergence of collective behaviors experimentally and theoretically; however, the true mechanism has not been comprehensively elucidated. A fundamental question revolves around whether all individuals of a flock have equal status (i.e., influence the group decision-making equally and obey the same rules) or whether the collective behaviors are decided by one or a few individuals; indeed, there could be another explanation or a more complex mechanism [4,13–18].

Currently, there are two mainstream propositions: (i) all individuals of a flock follow certain rules equally or (ii) collective behaviors of a flock are determined by a small number of leaders [19]. The former is sometimes called the "many wrongs" principle and it stipulates that each individual averages its preferred direction depending on interactions with its neighbors, resulting in a compromise in the choice of direction [20,21]. The latter claims that one or a few leaders may exert a critical influence on the movement decisions of the entire flock [22]. In theory [13], the compromise of all individuals in a flock could lead to better decision-making than the control of one or a few leaders, unless the leader(s) has vastly superior knowledge. This suggests that it may be better to employ a strategy where all individuals compromise for some low-level organisms that cannot grasp certain information [23]. Indeed, experimental and theoretical studies have shown that bacterial colonies adopt the strategy of compromise [11,23,24]. However, for higher-level organisms that can comprehend certain information, such as pigeons, the leadership hypothesis may be more appropriate. For example, the homing performance of a flock of trained pigeons is better than that of the individuals flying alone [25,26]. This indicates that there could be a leadership structure in the pigeon flock, so the individuals that understand the homing information can lead the flock to make a better movement decisions. Recent studies have shown that a well-defined hierarchy among individuals does exist in pigeon flocks in flight [4,5], thus providing strong evidence

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to support the leadership hypothesis. Moreover, hierarchical relationships in pigeon flocks are very stable [27], i.e., once the hierarchy is formed, the individuals in the flock can be quite resistant to change, unless the leaders are misled by external information [28].

A hierarchical network [4], which arises from the time delay between movements of different individuals, can describe very complex leadership relationships within the pigeon flock. In this type of leadership relationship, an individual must pay attention to multiple leaders at the same time and make integrated decisions. In addition, a more complex leadership relationship based on such hierarchical networks has been proposed [29]. This suggests that the high synchronization among individuals in the same rank is the result of strong interactions. Some leadership relationships [4,5,29] have been inferred from data, but lack direct evidence because pigeon flocks cannot report the leadership relationships they adopt. Based on the findings of this study, we propose that hierarchical networks [4,5,29] can indicate the presence of hierarchy within the pigeon flock in free or homing flights, but it cannot reflect the direct leadership relationship between a pair of individuals in the flock. To explore this concept, we adopted a strategy to use groups that can artificially set leadership relationships as experimental objects and developed a method to identify the leadership relationship through data analysis. The method can then be extended and applied to derive the leadership relationships of pigeon flocks from experimental data.

The experiments in this study use student volunteers instead of animals to eliminate communication barriers that prevent the establishment or questioning of leadership structures in the group. The findings suggest that tree structures may be the leadership structures employed by group motions exhibiting hierarchy, and we propose a model to describe the collective motions exhibiting hierarchy. We also project that the leadership relationships adopted by pigeon flocks follow tree structures.

II. METHODS

A. Participants and experimental protocols

Twenty-four graduate students participated in the experiments. They were randomly divided equally into three groups of eight, i.e., G^1, G^2, and G^3, and three repeated experiments (G^i_1, G^i_2, G^i_3, $i = 1, 2, 3$) were performed for each group. For example, G^1_2 represents the second experiment with the group G^1. Each group of students jogs under the leadership relationship that we have set up. The leadership relationship requires each individual, except for the top leader, to choose only one leader to follow, and individuals cannot be leaders of one another. The top leader does not have a leader and serves to lead the movement of the flock. The leadership relationship adopts a tree structure, where each individual can only follow its immediate leader.

B. Device and data handling

The movements of the crowds/flocks were recorded using an unmanned aerial vehicle (DJI MAVIC 3 PRO) in the air at 60 Hz. On the video recordings, individuals were tracked with a cursor using the free TRACKER (ver. 5.1.5) software [30]. This established tracks $(x_i, y_i; t_i)$ (see Supplemental Material [31]), where (x_i, y_i) represents the position vector of the individuals at time t_i with the time interval of $\Delta t = 1/20$ s.

C. Directional correlation function

For each pair of individuals ($i \neq j$), the directional correlation function can be expressed as $C_{i,j}(\tau) = \langle \vec{a}_i(t) \cdot \vec{a}_j(t+\tau) \rangle$, where $\langle \cdot \rangle$ denotes the time average [4]. The unit vector $\vec{a}_i$ is the direction of motion of individual i. If $C_{i,j}(\tau)$ reaches its maximum value $C^*_{i,j}$ at τ, then τ is called the directional correlation delay time, denoted as $\tau^*_{i,j}$. A positive $\tau^*_{i,j}$ means that individual i has an effect on the flight direction of the individual j, and a negative $\tau^*_{i,j}$ indicates an effect in the opposite direction. Therefore, we only considered 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.

D. Model

Each individual in groups chooses only one leader to follow, and the leadership structure is similar to that in most experimental protocols. Simulations containing N individuals were carried out in a continuous two-dimensional (2D) space. At time t, the position vector and velocity vector of the individual i ($i = 1, 2, 3, \ldots, N$) can be expressed as $\vec{p}_{i,t}$ and $\vec{v}_{i,t}$, respectively. The time interval Δt is the time between two updates of the positions and directions. The position vector of individual i at time $t + \Delta t$ can be expressed as

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

In addition, the velocity $\vec{v}_{i,t}$ is constructed to have a module $v_{i,t}$ and a direction given by the unit vector $\vec{a}_{i,t}$, i.e., $\vec{v}_{i,t} \equiv v_{i,t}\vec{a}_{i,t}$.

The unit vectors of individuals at time $t + \Delta t$, except for the top leader, can be obtained from the following expressions:

$$\vec{a}_{i,t+\Delta t} = \mathcal{F}(\vec{a}\,'_{i,t+\Delta t}, \sigma W_U),$$
$$\vec{a}\,'_{i,t+\Delta t} = \frac{\vec{a}_{i,t} + \vec{a}_{j,t}}{\| \vec{a}_{i,t} + \vec{a}_{j,t} \|},$$
$$i = 2, 3, 4, \ldots, N, \qquad (2)$$

where $\mathcal{F}(\vec{a}, \theta)$ means to rotate the vector $\vec{a}$ by an angle of 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 individual j at time t, which is the immediate leader of individual i. To ensure that the leaders remain ahead of the corresponding follower(s), the $v_{i,t+\Delta t}$ term can be expressed as follows:

$$v_{i,t+\Delta t} = \tfrac{1}{2} v_c (1 + \mu \vec{b}_{i\sim j,t} \cdot \vec{a}_{i,t}), \qquad (3)$$

where v_c and μ are constants, and $\vec{b}_{i\sim j,t}$ represents the unit vector pointing from i to j.

To simulate the collective flights of a pigeon flock, it is necessary to establish a flight trajectory for the top leader. Pigeons exhibit a circlelike flight in free flights [18] and their one-dimensional flight trajectory is like a pseudoperiodic time series [32,33]. Here, we utilized an actual pigeon

TABLE I. τ^* and C^* between different individuals in the experiment G_1^1.

i \ $\tau_{i,j}^*, C_{i,j}^* \backslash j$	**B**	**C**	**D**	**E**	**F**	**G**	**H**
A	1.2 s, 0.96	1.2 s, 0.95	2.1 s, 0.92	2.1 s, 0.93	2.3 s, 0.88	3.4 s, 0.88	3.4 s, 0.89
B		0.0 s, 0.94	1.0 s, 0.91	1.1 s, 0.92	1.3 s, 0.88	2.2 s, 0.88	2.2 s, 0.88
C			1.0 s, 0.91	1.1 s, 0.92	1.1 s, 0.90	2.2 s, 0.88	2.3 s, 0.88
D				0.0 s, 0.90	0.0 s, 0.85	1.3 s, 0.90	1.3 s, 0.85
E					0.0 s, 0.90	1.1 s, 0.86	1.1 s, 0.87
F						1.1 s, 0.82	1.0 s, 0.82
G							0.0 s, 0.82

flight trajectory (see Supplemental Material [31]), which corresponds to the top leader in a free collective flight in Ref. [4]. Because there are no appreciable vertical changes during the free flights of pigeons, these movements can be simulated in a 2D horizontal plane. The projection of the top leader's trajectory on the horizontal plane can be expressed as $\{(x_1, y_1), (x_2, y_2), (x_3, y_3), \ldots\}$.

In all simulations, we supposed that the initial positions of all individuals are randomly distributed in a rectangular area (5 × 5 m). The initial direction of all individuals points in a common direction (specified as horizontal-right in this paper). The following parameters were fixed: $\upsilon_c = 12$ m/s, $\mu = 1.4$, $\sigma = 0.08\pi$, and $\Delta t = 0.2$ s. The dynamic behaviors of pigeon flocks were simulated in a 2D unbounded space.

III. RESULTS

A. Experiments

We instructed the eight volunteers in each of the three groups to employ the leadership relationship illustrated in Fig. 1(a) and allowed the top leader **A** to jog freely. Herein, we take experiment G_1^1 as an example to describe the experimental results. Figure 1(b) shows the movement trajectories of the crowd. We calculated the $\tau^*$and C^* between each pair of individuals from the experimental data (Table I). The use of a previously described method [4] enabled the acquisition of the hierarchical network [Fig. 1(c)] and additional experiments afforded consistent results, i.e., the same hierarchical network. The leadership relationship employed by the crowd [Fig. 1(a)] was clearly not a hierarchical network. Each of the directed edges pointing from the leader to a follower can reflect a connection with a smaller time delay in the hierarchical network (i.e., a connection between adjacent ranks); however, the connections between adjacent ranks may not necessarily be the directed edge pointing from the leader to the corresponding follower. For example, the connection between **B** and **E** in the hierarchical network does not represent the leadership relationship. Moreover, the connections between nonadjacent ranks do not necessarily indicate the leadership relationship either. Thus, the hierarchical networks can only describe the time-delay relationships governing individuals' movements and they cannot elucidate the leadership relationship.

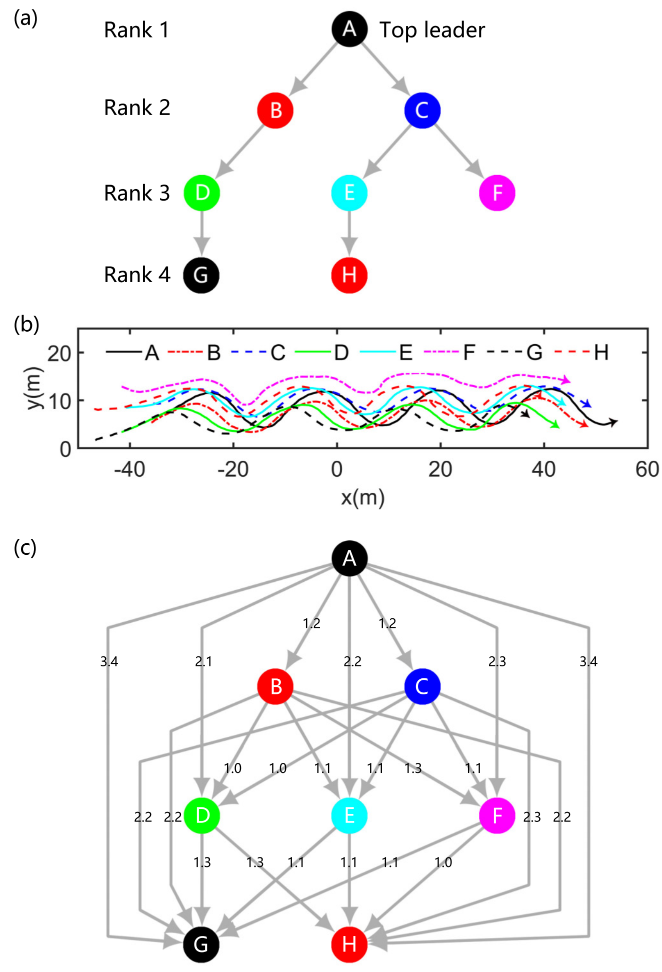

FIG. 1. Hierarchical leadership network generated for experiment G_1^1. (a) The leadership relationship employed in the experiment. For each pairwise comparison, the directed edge points from the leader to the follower. (b) The movement performed by the crowd. Arrows indicate the direction of movement and letters refer to the identities of individuals. See Movies 1 and 2 in the Supplemental Material [31] for a more vivid movement process. (c) Hierarchical network of the crowd for the movement shown in (b). Values on edges show the time delay (in seconds) in the two individuals' movement.

The movements of individuals in the same rank exhibit high synchronization. In Fig. 2(a), synchronized individuals are represented by mutual links (bidirectional connections). For example, Fig. 2(b) shows the difference in angle between two pairs of individuals' directions. Individuals in the same rank maintain a high degree of consistency in terms of direction, whereas individuals in different ranks exhibit significant differences in their direction of movement. Accordingly, the high synchronization of two individuals does not indicate that those pairs with mutual links ($\tau_{i,j}^* = 0$) have strong interactions. Indeed, those pairs with mutual links are completely independent.

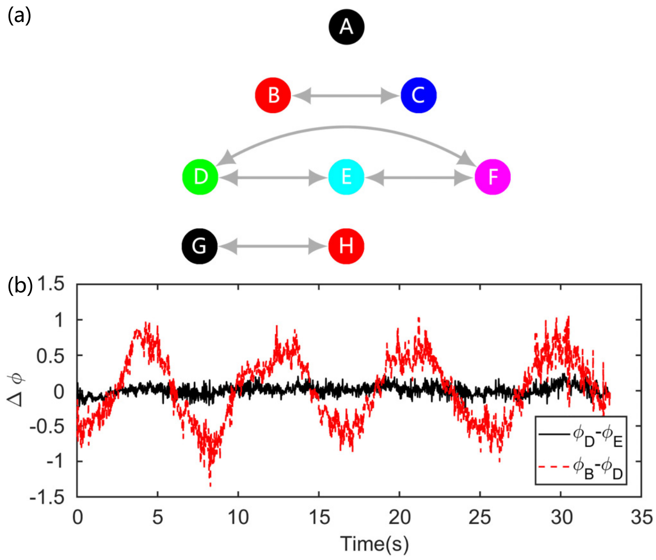

FIG. 2. High synchronization among individuals in experiment G_1^1. (a) Specific synchronization relationships. The pair of individuals connected by the bidirectional arrows exhibit high synchronization. (b) The angle between the directions of movements of individuals. For example, $\phi_{\mathbf{D}}$ represents the angle of the direction of the movement of individual **D**.

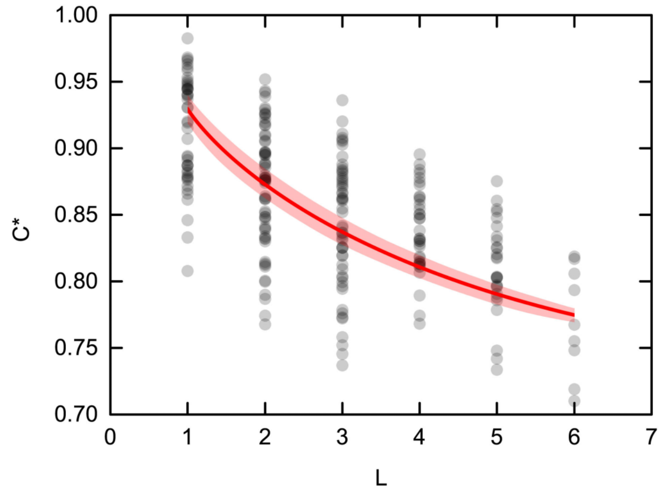

FIG. 3. The correlation coefficient C^* varies with the information distance L. Solid circles represent data points (L, C^*); the red solid line and its semitransparent envelope represent the best fitting line and the 95% confidence interval, respectively.

B. Method for extracting leadership relationship from hierarchical network

The hierarchical network shown in Fig. 1(c) has the same structural characteristics as that of a pigeon flock [4]. In general, individuals at the same level exhibit a high degree of consistency, which is supported by pigeon flight data [29]. Similarly, our experimental data have the same characteristics as the reported pigeon flight data [4]. We propose that the leadership relationship employed by pigeon flocks is a tree structure. Thus, it is desirable to develop a method to derive leadership relationships from the trajectory. The findings presented in Fig. 1 indicate that the leadership relationship can be inferred by eliminating directed edges within the hierarchical network. According to the characteristics of leadership relationships, directed edges only exist between adjacent ranks, and each individual can only be pointed to by one directed edge (except for the top leader). Therefore, to determine the leadership relationship, the directed edges between nonadjacent ranks in the hierarchical network were deleted. Then, we selected the directed edge that represents the leadership relationship from among the directed edges pointing to each individual. The method is described in detail as follows.

First, we introduced the information distance $L_{i,j}$, which reflects the number of edges contained in the shortest path connecting two individuals i and j in the leadership relationship. For example, $L_{\mathbf{M},\mathbf{D}} = 2$ and $L_{\mathbf{D},\mathbf{J}} = 4$. The results show that C^* is negatively correlated with the information distance L (Fig. 3). We proposed the following explanation for this phenomenon: the initial direction information in the flock is emitted by the top leader and is affected by noise during the transmission process; the greater the distance that the information is transferred in the structure of the leadership relationship, the greater the interference. The term $L_{i,j}$ represents the relative distance required for information to reach individuals i and j in the transfer structure, i.e., the structure of the leadership relationship. Therefore, the larger the transmission distance, the smaller the corresponding C^*. This also explains why there is no directed edge between individuals **L** and **C** or individuals **I** and **C** in the hierarchical network [4].

The structural characteristics of the leadership relationships indicate that the information distance L between a certain follower and its immediate leader is equal to 1, which is the minimum value of L. According to the results shown in Fig. 3, among all directed edges pointing to a certain individual between adjacent ranks, the C^* corresponding to the directed edge representing the leadership relationship is likely to reach the maximum value. This maximizes the probability that the directed edge with the largest C^* represents a leadership relationship. For example, as shown in Fig. 1(c), among all directed edges pointing to **G** between rank 3 and rank 4, $C^*_{\mathbf{D},\mathbf{G}}$ has the maximum value (corresponding to the directed edge representing the leadership relationship between **D** and **G**). This analytical approach can be applied to determine the leadership relationship used by a group adopting a hierarchical network.

C. Application and simulation

We applied the developed method to a previously described hierarchical network [4] and obtained the possible leadership relationship employed by the pigeon flock [Fig. 4(a)]. Then the model employed this leadership relationship to simulate the free flight of the pigeon flock. Figure 4(b) shows a one-minute segment of the flock trajectory in the simulation. We calculated the τ^* and C^* between each pair of pigeons from the simulation results (Table II) to elucidate the corresponding hierarchical network [Fig. 4(c)]. The C^* values for the two directed edges pointing from **L** and **I** to **C** are 0.87 and 0.88, respectively. If the directed edges with $C^* \leqslant 0.88$ are ignored, the hierarchical network in Fig. 4(c) is identical to that previously reported [4]. These results confirmed that hierarchical

TABLE II. τ^* and C^* between different individuals.

i \ $\tau^*_{i,j}, C^*_{i,j} \backslash j$	**M**	**G**	**D**	**B**	**H**	**L**	**I**	**C**	**J**
A	0.2 s, 0.97	0.6 s, 0.95	1.2 s, 0.93	1.2 s, 0.94	1.6 s, 0.93	1.6 s, 0.92	1.6 s, 0.91	2.0 s, 0.89	2.0 s, 0.88
M		0.2 s, 0.96	0.6 s, 0.95	0.6 s, 0.94	1.2 s, 0.93	1.2 s, 0.93	1.2 s, 0.92	1.6 s, 0.90	1.6 s, 0.91
G			0.2 s, 0.97	0.2 s, 0.96	0.8 s, 0.93	0.8 s, 0.95	0.8 s, 0.93	1.2 s, 0.92	1.2 s, 0.92
D				0.0 s, 0.95	0.4 s, 0.97	0.4 s, 0.93	0.4 s, 0.92	0.8 s, 0.95	0.8 s, 0.92
B					0.4 s, 0.92	0.4 s, 0.96	0.4 s, 0.97	0.8 s, 0.91	0.8 s, 0.92
H						0.0 s, 0.90	0.0 s, 0.91	0.4 s, 0.96	0.4 s, 0.89
L							0.0 s, 0.96	0.4 s, **0.87**	0.4 s, 0.96
I								0.4 s, **0.88**	0.4 s, 0.93
C									0.0 s, 0.86

networks are not the leadership relationships employed by these groups. Such hierarchical networks can only reflect the time delay of movements between different individuals, which is the result of the follower replicating the leader's movements.

We also examined the synchronization among individuals in the simulation results. The results indicated that individuals with the same rank exhibited high synchronization (Fig. 5). As shown in Fig. 5(a), synchronized individuals are linked by edges. Comparing directional differences among individuals can reveal the degree of synchronization between those individuals. For example, Fig. 5(b) shows the directional information for four pairs of individuals. There are very few differences in direction between individuals **B** and **D** (or **H** and **I**) during flight. However, there are significant differences in the directions of asynchronous individuals, e.g., **A** and **C** (or **M** and **H**). In the described model, there are no interactions between these synchronized individuals. Therefore, this synchronization phenomenon does not originate from the interactions between individuals, but, rather, it is the result of followers copying the flight direction of their common leader.

The simulation results also reveal a negative correlation between the C^* and the information distance L, which is consistent with the experimental results (Fig. 6). We also examined the impact of the noise intensity σ on this negative correlation. As the noise decreases, the difference between C^* values corresponding to different L values also decreases; when there is no noise, the negative correlation disappears. In the developed model, the directional information transmitted from leaders to followers is affected by noise. The information distance L between two individuals is equal to the number of times their information difference is disturbed by noise. The greater the number of disturbances, the smaller the correlation coefficient between the two. These results also support our explanation of Fig. 3.

IV. CONCLUSION AND DISCUSSION

Herein, we demonstrated that tree structures may serve as the leadership structures employed by group motions exhibiting hierarchy. Briefly, each individual except the top leader follows its only leader during collective motions, and the single top leader determines the direction of the group. We recruited student volunteers as study participants to artificially establish leadership relationships and proposed a method for obtaining the leadership relationship based on trajectory data. We also proposed a model to describe collective motions of groups with social hierarchies. As an application, our experiments and simulations provided solid evidence to support the tree structure employed by pigeon flocks.

Our results show that all directed edges between nonadjacent ranks (and some between adjacent ranks) in hierarchical networks [4,5] do not represent leadership relationships, i.e., the previously reported hierarchical networks are not leadership structures. Notably, this article proposes a method for identifying leadership structures from hierarchical networks. Although the tree structure may appear as a simplified version of the hierarchical network in Fig. 4, their significance is completely distinct. The tree structure represents the specific leadership relationship utilized by the group, whereas the hierarchical network does not.

A previous report [29] claimed that a correlation time delay $\tau_{i,j} = 0$ indicates that a coordinated interaction exists between the pair of pigeons (i and j), and, 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 rank (i.e., $\tau_{i,j} = 0$) will show high synchronization, and the movements of individuals led by a single leader will have larger correlation coefficients. Thus, the strong synchronization phenomenon is not caused by the mutual (reciprocal) link, and the larger correlation

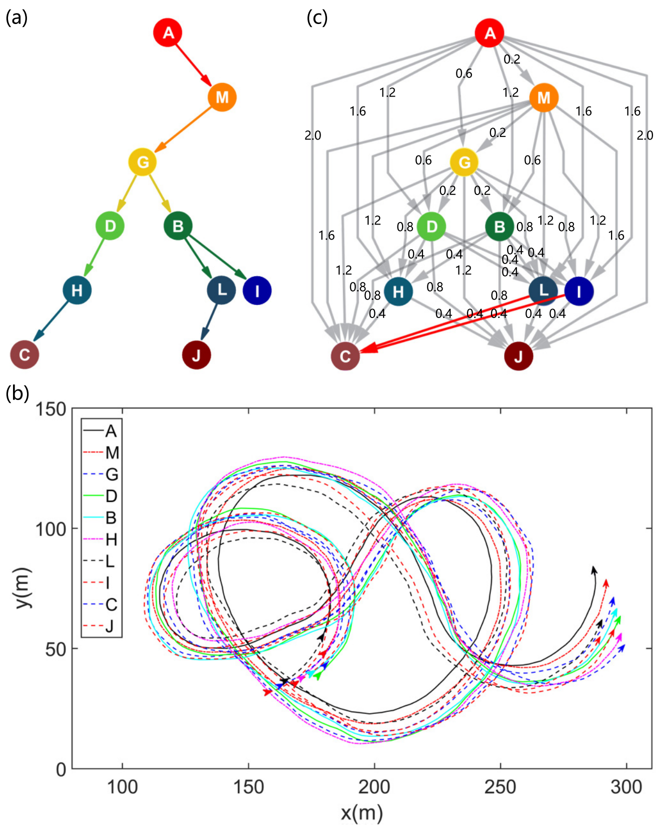

FIG. 4. Hierarchical leadership network generated in the simulation. (a) The leadership relationship employed in the simulation; (b) one-minute segment of the flight performed by the flock. The arrows indicate the direction of movement and the letters refer to the identities of individuals. See Movies 3 and 4 in the Supplemental Material [31] for a more vivid movement process. (c) Hierarchical network of the flock for the movement shown in (b). For each pairwise comparison, the directed edge points from the leader to the follower. Values on edges show the time delay (in seconds) in the two individuals' movement.

coefficient (with $\tau_{i,j} = 0$) is the result of having the same leader.

In terms of form, a tree structure is derived from the removal of specific directed edges within a hierarchical network or a reciprocal network. In a hierarchical or reciprocal network, directed edges may not necessarily carry inherent meaning, but are rather based on the data characteristics they represent. The directed edges in a tree structure hold tangible physical significance, representing the relationship from leader to follower. This conclusion has been substantiated through empirical validation.

In previous self-propelled particle models [34–42], individuals adhered to the principle of equality, wherein there were no leaders or followers. Within these models, individuals exhibit collective motion through basic interactions among themselves. In our recent study [43], we investigated individual visual lateralization. While transient tree leadership structures emerged in the model, they were merely byproducts of spontaneous symmetry breaking in interactions, precluding the establishment of stable and enduring leadership relationships. In this study, we introduced a fixed leadership

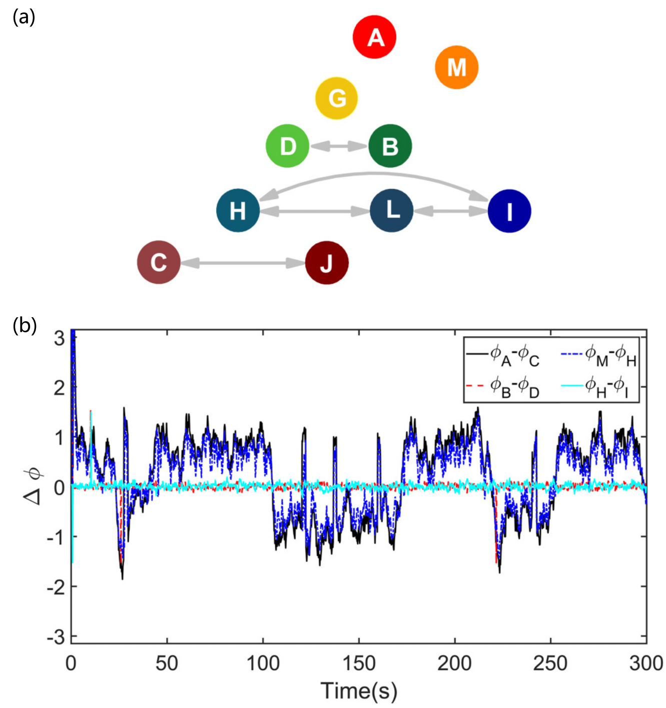

FIG. 5. High synchronization among individuals in the simulation. (a) Specific synchronization relationships. The pair of individuals connected by the bidirectional arrows exhibit high synchronization; (b) the angle between individuals' directions of movement.

structure into multiple self-propelled particle models, enabling the simulation of group behavior with hierarchical differentiation.

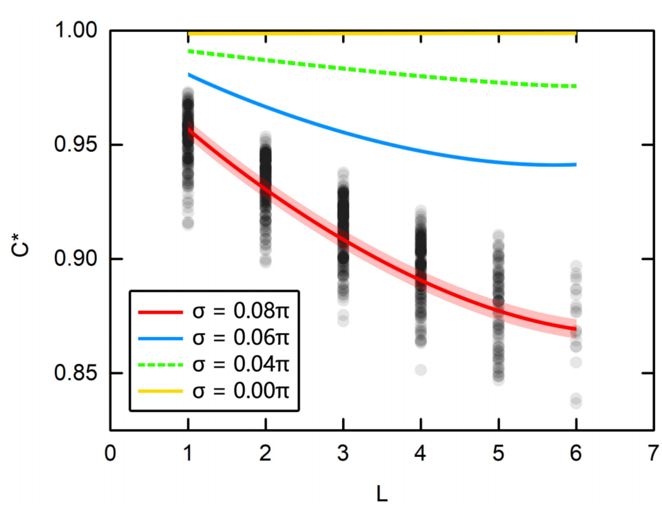

FIG. 6. The correlation coefficient C^* varies with the information distance L with different σ. Solid circles represent data points (L, C^*) with the parameter $\sigma = 0.08\pi$, and the red solid line and its semitransparent envelope represent the best-fit line and its 95% confidence interval. The blue solid line, green dotted line, and yellow solid line are the fitting lines for the results corresponding to $\sigma = 0.06\pi$, 0.04π, and 0.00, respectively. Each group of experiments comprises 20 independent experiments.

Previous studies [44,45] measured the head movements of pigeons during paired flights and observed that birds can attenuate their head movements to pay closer attention to the other individual(s). Interestingly, birds can attenuate their head movements to a greater degree as the size of the flock increases, most likely to improve their visual tracking abilities [3]. According to previous reports [4,5,29], birds will also enhance their head movements in a larger flock to focus on more individuals. These findings clearly contradict the experimental studies.

A comparison of our simulated and experimental data revealed that the tree structure governs the flight formations of pigeon flocks, whereas the compromise mechanism (interactions among individuals, e.g., repulsion to prevent collisions between individuals, the attraction to prevent individuals from moving away from the flock, and the polarization force to ensure a consistent direction) is not supported.

The intermittent interactions (e.g., alignment, polarization forces) between each pair of individuals during a pigeon flock flight do not need to be determined at every moment [18]. This mechanism can help reduce the information processing and/or communication requirements, thereby reducing the costs of the intragroup communication and the energy of information processing and communication [18]. The present study showed that the leadership structure is more straightforward than previously reported and, therefore, it is possible to save more energy used for information processing and communication. Consequently, applying the leadership structure to control the autonomous formations of unmanned vehicles can save energy for the entire system.

Birds have strong anticollision abilities and can effectively avoid collisions even when flying in a narrow space [46]. Therefore, during flights of pigeon flocks, the individuals may not consider the interaction forces (attraction and repulsion) between individuals unless the individuals are very close or very far away.

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[31] See Supplemental Material at http://link.aps.org/supplemental/10.1103/PhysRevResearch.6.043058 for the experimental data, the trajectory data utilized by the top leader in the simulation, and the following movies: Movie 1 shows the movement process of volunteers in experiment G_1^1. Movie 2 shows the pattern recognition results of individuals' movements in experiment G_1^1. Movie 3 illustrates the simulation results from a mobile perspective, showcasing the changes in individual relative positions during the collective flight. Movie 4 illustrates the simulation results from a stationary perspective, showcasing the trajectories of all individuals during the collective flight.

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