Reciprocal relationships in collective flights of homing pigeons

Xiao-Ke Xu,[1,2,*] Graciano Dieck Kattas,[1] and Michael Small[3,†]

[1]*Department of Electronic and Information Engineering, Hong Kong Polytechnic University, Hong Kong*
[2]*School of Communication and Electronic Engineering, Qingdao Technological University, Qingdao 266520, China*
[3]*School of Mathematics and Statistics, University of Western Australia, Crawley, Western Australia 6009, Australia*

Collective motion of bird flocks can be explained via the hypothesis of many wrongs and/or a structured leadership mechanism. In pigeons, previous studies have shown that there is a well-defined hierarchical structure and certain specific individuals occupy more dominant positions, suggesting that leadership by the few individuals drives the behavior of the collective. Conversely, by analyzing the same datasets, we uncover a more egalitarian mechanism. We show that both reciprocal relationships and a stratified hierarchical leadership are important and necessary in the collective movements of pigeon flocks. Rather than birds adopting either exclusive averaging or leadership strategies, our experimental results show that it is an integrated combination of both compromise and leadership which drives the group's movement decisions.

I. INTRODUCTION

The fast coherent movement of flocking birds is a fascinating phenomenon exhibiting apparent intelligence and coordination [1]. New monitoring technologies have meant that this collective behavior has recently attracted renewed interest from scientific and engineering communities, allowing more conclusive analysis to be performed [2,3]. An important open question is whether all members of a flock contribute equally to the collective decision making and follow equivalent rules, or certain individuals have a greater influence on the decisions of the group [3–9].

The proposition that all contribute equally is sometimes referred to as the "many wrongs" principle, and purports that individuals average their preferred directions depending on interaction with their neighbors, leading to a compromise in route choice [10,11]. Conversely, the leadership hypothesis posits that one or a small number of leaders are able to exert a disproportionate influence on the group's movement decisions [12,13]. Both theoretical and experimental arguments predict that the compromise of all members will make more accurate decisions than the leading of one or a small number of individuals, unless leaders have very different and superior information [4]. For example, the homing performance of pretrained pigeons flying as a flock is significantly better than that of these birds released individually [14]. Yet, recent research has shown that time-varying hierarchical decision-making mechanisms do exist during pigeon flights [3,6], giving strength to the leadership hypothesis.

Although new studies show that certain individuals in pigeon flocks are able to exert relatively more influence on the movement decisions of the whole group, only the directed relationship (pointing from the leader to the follower) has been studied [6,7]. In addition to such directed links (representing a leader-follower relationship) selective coordinated behavior may also exist in collective motion, hence mutual relationships must also be examined. For example, in the case of a

perturbation caused by the terrain or a predator, the better strategy for birds would probably be to share the information of all group members to move rapidly to safety regardless of their individual positions within a leadership hierarchy. Such mutual links represent a reciprocal relationship between a pair of pigeons, which appears nonrandomly in real-life directed networks [15,16] and plays a significant role in the evolution of many biological systems [17,18]. We emphasize that the coexistence of compromise and leadership is not a contradiction, but a meaningful supplement to the hierarchical structure of pigeon flocks. The main difference between the work in [6] and ours is as follows: they are concentrating on the leadership aspect, while we are focusing on local interactions (including both directed and reciprocal relationships).

In this paper, we reanalyze experimental high-precision datasets of pigeon flocks to arrive at a more nuanced conclusion about the interactions and decisions in the collective dynamics of birds. Using quantitative methods from statistical physics [6], we find that both outcomes (directed and mutual links) coexist in the same flock flights. The mutual links represent a reciprocal relationship between individuals, which is a useful supplement to the well-defined hierarchical structure. Integrating both directed and reciprocal links, we uncover the complete topology of the network induced by the collective motion of a pigeon flock. Most significantly, our results imply that there is an integrated mechanism of decision-making in pigeon flocks: neither a leadership nor a compromise mechanism is clearly dominant, rather both mechanisms coexist.

II. RESULTS

A. Reciprocal relationships by calculating pairwise correlations

In the past tens of years, it has been a very difficult task to explore the influence of individual members on a fast collective motion at all times. Recently, the advance of global positioning system (GPS) devices allows us to use sophisticated evaluation techniques to mine real flocking data [3]. Employing high-precision GPS in tracking pairs of pigeons, Biro *et al.* found that two birds compromise if they

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*xiaokeeie@gmail.com
†small@ieee.org

have small diversity on directional preferences, while either the pair splits or one of them becomes the leader for a severe conflict [7]. Using lightweight GPS devices and analyzing data concerning leading roles in pairwise correlations, Nagy *et al.* showed a well-defined hierarchy among pigeons belonging to the same flock [6]. In this study, we use the same datasets: 11 free flights and 4 homing flights. More detailed information on the datasets can be obtained from the website for pigeon flocks [19].

To investigate the influence that a given bird's behavior has on the other flock members, the temporal relationship between the flight directions has been evaluated [3,6]. The directional correlation for a pair of pigeons is $C_{ij}(\tau) = \langle \overrightarrow{V}_i(t) \cdot \overrightarrow{V}_j(t + \tau) \rangle$, where $\langle \cdots \rangle$ denotes time average and $\overrightarrow{V}_i(t)$ is the normalized velocity of bird i. When $C_{ij}(\tau)$ obtains its maximum value at the time delay τ_{ij}, τ_{ij} is called the optimal directional delay time. Negative τ_{ij} values mean that the ith bird falls behind the jth bird, which can thus be interpreted as a case of j leading. For each pair, we extract the positive value $\tau_{ij} = -\tau_{ji}$ as a directed edge pointing from the leader to the follower.

If individuals fly together in a flock, they will show a very similar velocity and a high correlation [20]. In a previous study, the authors studied the leader-follower relationship among pairs of pigeons whose directional correlation time delay is nonzero, and such links are directed [6]. The directed link indicates that a following bird tends to consistently copy the directional behavior of particular leading individuals. However, the directional correlation time delay may be near zero, which means a pair of pigeons have a coordinated interaction with one another and there is a mutual (reciprocal) link between them. The frequency distribution of the directional correlation time delay for pairwise pigeons in all collective motions is shown in Fig. 1. Here we select 0.2 s as the time interval of time delay, since the sampling time interval of the original dataset and the resolution of time delay in the previous study [6] are both 0.2 s. The frequency of $\tau = 0$ is the most frequent, meaning
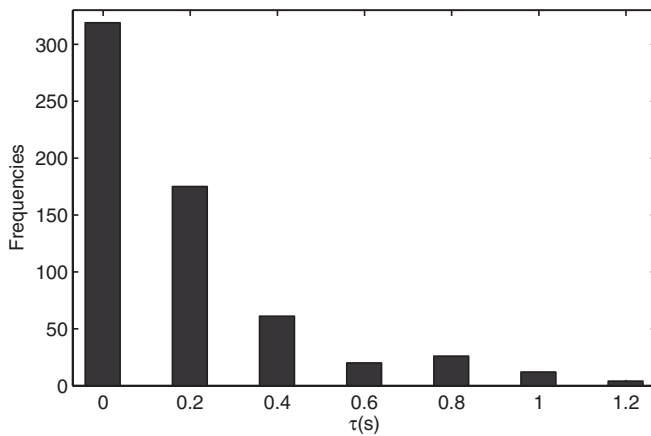

FIG. 1. Histogram for the different values of the directional correlation delay time τ_{ij} between each pair of pigeons in all the flights. When the correlation coefficient reaches the maximum value $C_{ij}(\tau)$ at the time delay τ_{ij}, then τ_{ij} is called the directional correlation delay time and $C_{ij}(\tau)$ is called the maximum correlation coefficient. Here we only consider the conditions of $\tau_{ij} \geqslant 0$.
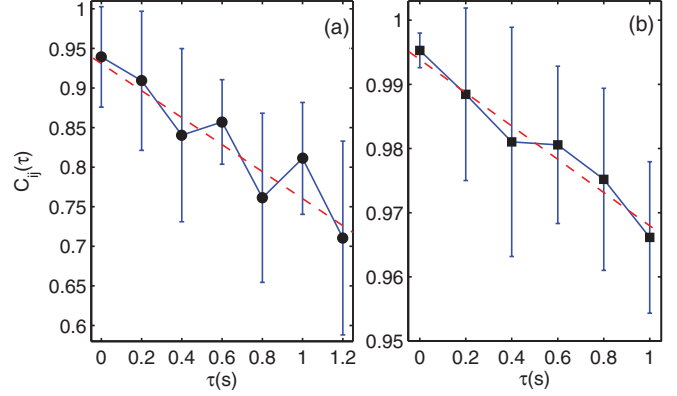

FIG. 2. (Color online) The values of $C_{ij}(\tau)$ decrease with $\tau_{ij}(s)$ for all the (a) free flights and (b) homing flights. The solid circles (squares) show the mean of $C_{ij}(\tau)$ while the bars show the standard deviation of $C_{ij}(\tau)$.
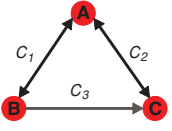
that there are typically many mutual relationships between the pairwise birds in pigeon flocks. Moreover, the result also implies that the perfect hierarchical structure induced by directed links in Ref. [6] may not be adequate to completely explain the collective behavior of pigeon flocks.

Here we hope to explain why a correlation that decays from $\tau = 0$ represents a "mutual link" instead of no interaction in our study. Actually, in some cases of collective motions, a decaying temporal correlation that is maximal at zero lag is evidence that there is no interaction. For example, Katz and collaborators showed that the orientation correlation whose peak is at zero time is significantly lower than that whose peak lies after zero time (Fig. S8A in Ref. [21]). On the contrary, in our study $C_{ij}(\tau)$ at $\tau = 0$ tends to be higher than the values at the large time delay [Fig. 2], which means the strength of mutual links is stronger than that of directed links.

Furthermore, we use multiple effective methods [$C_{ij}(\tau)$, motif, synchronization, and multiscale analysis] to prove the existence of reciprocal interaction as follows. The values of the maximum correlation coefficient $C_{ij}(\tau)$ at the directional correlation time delay τ_{ij} are shown in Fig. 2. The birds' movements under two conditions, free flights and homing flights, are recorded [6]. The pigeon flock makes a circle-like route in free flights; while the group makes less direction turning during homing flights (Fig. S6 in Ref. [6]). Because of the more centralized distribution of turning directions in homing flights, it is easier to obtain a larger $C_{ij}(\tau)$, which results in the values of $C_{ij}(\tau)$ at the same τ_{ij} in homing flights [Fig. 2(b)] being larger than those in free flights [Fig. 2(a)]. In both cases, we can find that $C_{ij}(\tau)$ at the small τ_{ij} tends to be higher than the values at the large time delay. Moreover, when the time delay is zero, the value of $C_{ij}(\tau)$ is the highest, which implies that these mutual links are the most important relationship in the flock and more attention should be paid to such types of links.

Although interaction and correlation are different and their relationship has been extensively discussed [20], using the method of calculating pairwise correlation [6], it is still difficult to determine whether the relationship between a pair of pigeons is a direct interaction or an indirect correlation. Here we develop a simple method to detect whether three links in a

TABLE I. (Color online) Comparison of the values of the maximum correlation coefficient for the three links in the subgraph (motif) structure. C_1, C_2, and C_3 represent the maximum correlation coefficients for the three links, respectively. n is the whole number of the subgraph in all the flights.

Motif	n	$C_1 > C_2$	$C_1 > C_3$	$C_2 > C_3$	$C_1 > C_3$ $C_2 > C_3$
	173	54%	69%	64%	50%

small subgraph (motif) are independent. A motif, defined as a small connected subgraph that recurs in a graph, is the basic functional unit of complex networks [22,23]. A small motif with three nodes in the network induced from each flight are shown in Table I.

If the relationships among the three individuals are independent, the probabilities of $C_1 > C_2$, $C_1 > C_3$, and $C_2 > C_3$ should be about 50%, respectively, while $C_1 > C_3$ along with $C_2 > C_3$ simultaneously should have a probability of 33%. However, we observe that all these relationships (except $C_1 > C_2$) occur significantly more frequently than we would expect (Table I), which means that B and C tend to have a lower correlation than that between A and B, and between A and C. Hence, the correlations among the three individuals are not consistent with three independent events and the directed link between B and C (C_3) can be attributed to the other two high mutual correlations (C_1 and C_2). Again, our result implies that we cannot neglect mutual links or believe that the nodes with such type of relationship do not interact with each other.
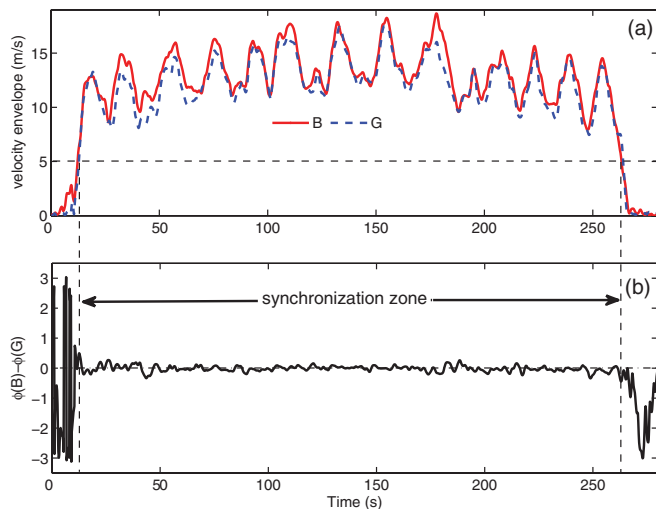

FIG. 3. (Color online) A pair of birds (B and G) in the 11th free flight show a very strong synchronization ($\tau_{ij} = 0$) and correlation [$C_{ij}(\tau) = 0.91$] at the time scale from 10 to 270 s. (a) Velocity envelopes (amplitudes) of B and G, and (b) phase differences between the pair of birds.
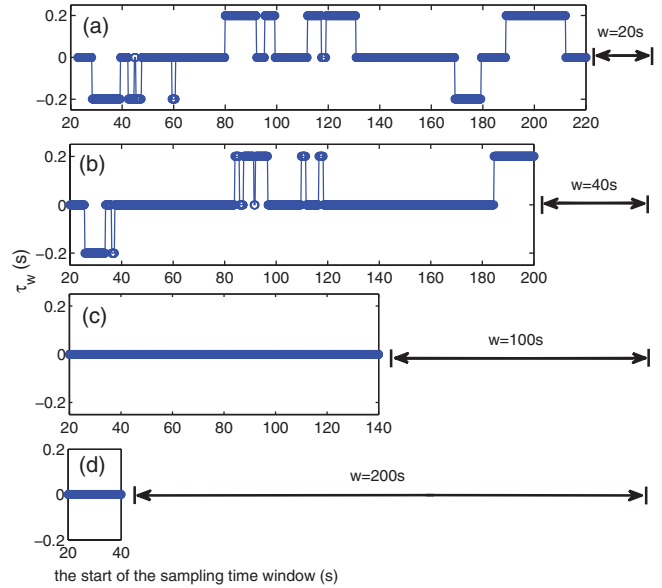

FIG. 4. (Color online) Multiscale pairwise correlation analysis for the different time-window series of B and G in the 11th free flight. When the directional correlation of each time window for a pair of pigeons obtains its maximum value at the time delay τ_w, then τ_w is called the directional correlation delay time of each time window. For the whole trajectories of B and G, the maximum correlation coefficient $C = 0.91$ and the optimal time delay $\tau = 0$. The sampling time interval and the resolution of time delay both are 0.2 s. Because the pigeons make a circle-like flight in free flights and their one-dimensional flight trajectory is like a pseudoperiodic time series [24,25], we select the approximate cycle ($w = 20$ s) as the minimum time window. Pairwise correlation analysis for (a) the time window is 20 s. We only calculate the optimal time delay for the time scale from 20 to 240 s (the strong synchronization segment). The x axis is the start time of the sampling window. When the start time of the sampling window is 20 s, then $\tau_w(t = 20.0)$ is obtained by calculating the directional correlation during the period from 20.0 to 40.0 s. The next value $\tau_w(t = 20.2)$ is obtained from the period between 20.2 and 40.2 s, and so on up to the interval 220.0–240.0 s. (b) The time window is 40 s, (c) the time window is 100 s, and (d) the time window is 200 s.

B. Multiscale analysis of reciprocal links

Although several pioneering researchers have obtained detailed spatiotemporal data on the positions of individuals during group movements, they have not used the data to study the dynamical variation of the relationships within the collective motion [6]. To make clear the spatiotemporal relationship for a pair of mutual-link birds, we show the synchronization of B and G in the 11th free flight (Fig. 3). The high synchronization of two pigeons again provides evidence that those pairs with mutual links ($\tau_{ij} = 0$) are strongly interacting rather than completely independent. The above result implies that the consensus in a real-life bird flock can also be achieved by the neighbor compromise mechanism, if we do not consider they might "copy" the flight direction of their common leader.

The collective movement of birds, such as during the abrupt splitting of a flock, can instantaneously change. Therefore, we first divide a long time series into many short overlapping
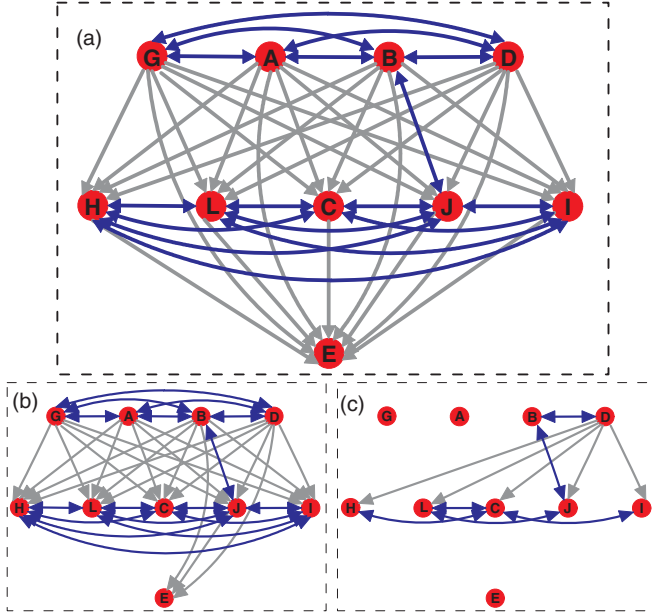
FIG. 5. (Color online) The network topology of the second free flight. If the directional correlation time delay $\tau_{ij} > 0$ and the maximum correlation coefficient $C_{ij}(\tau) > C_{\min}$, we establish a directed link for the network. The light gray arcs represent directed links from leaders to followers. If $\tau_{ij} = 0$ and $C_{ij}(\tau) > C_{\min}$, we build a mutual link. The blue (dark gray) lines are mutual links, which represent a coordinated correlation between a pair of equal pigeons. (a) We construct the network by including only those edges whose maximum correlation values $C_{ij}(\tau)$ are above a given variable minimum, $C_{\min} = 0.5$. E is the follower of all the other individuals. (b) Selecting other thresholds (such as $C_{\min} = 0.9$) to maintain the network connectivity throughout the pigeon flock, also gives similar results. (c) The disconnected network is built by choosing $C_{\min} = 0.99$. Maintaining the network connectivity throughout the flight of the pigeon group is a key issue [27]. Therefore, it is not suitable to select a very high threshold to let the network lose the connectivity for the pigeon group.

segments, and then study the pairwise correlation on each segment. Changing the scale of the time window, we can get the dynamical τ_{ij} for multiple time scales. The variation of the relationship of individuals B and G on multiple time scales in a flight is shown in Fig. 4. Because the pigeons make a circle-like flight in the free flights and their one-dimensional flight trajectory is like a pseudoperiodic time series [24,25], we select the approximate cycle (20 s) as the minimum time window. The relationship between B and G varies fast with time at the small time scale [Fig. 4(a)]. Our result shows that the collective behavior of the birds varies with a short

time scale, and the relationship between a pair of pigeons is time dependent. However, with the time scale increasing, the frequency with which the relationship varies reduces, for the result is an average of a longer time [Figs. 4(b)–4(d)]. Obviously, the longer the time averaging is, the more stable the result of the correlation function becomes.

Recent work has illustrated the group decision rule for homing pigeons: compromise for small conflict and leadership for large [7]. In this study, it is difficult to measure the conflict level among pigeons in each flight. Nevertheless, we find the compromise and leadership both emerge in the *spatial* domain from each dataset by calculating pairwise correlation (Fig. 5 and Table III). However, we do not find the existence of a stable leader-follower relationship between a pair of pigeons throughout all the flights, and this result is different from the findings in Ref. [7]. For example, two pigeons of A and B do not show the same relationships [different sign of $\tau(s)$] in all the flights (Table II). A leads B for three flights, A follows B for five flights, and there is no leadership between them for three flights. That means, considering a very long time scale (e.g., all the flights in this study), there is no single individual always leading a pair of individuals. Actually, A leading B in this flight and then B leading A the next time maybe can be regarded as a general concept of reciprocal behaviors ("You scratch my back, and I'll scratch yours" [18]). The relationship switching among group members supports more flexibility for individuals to respond to external predators [26].

C. Coexistence of compromise and leadership

We have shown that mutual links are ubiquitous and important in collective flights, so it is necessary to investigate whether the conclusion that certain leaders are able to exert more influence on the group's movement decisions still holds [3,6]. We construct a flight network by including only those links whose maximum correlation values $C_{ij}(\tau)$ are above a given variable minimum, $C_{\min} = 0.5$ [Fig. 5(a)]. Here E is the follower of all the other individuals. Selecting different thresholds in a suitable range ($C_{\min} \in [0.5 - 0.95]$) to maintain the network connectivity gives similar results [Fig. 5(b)]. In such a network the nodes represent individual birds, while the links (arcs) denote inferred relations between their movements. If $C_{ij}(\tau) > C_{\min}$ and $\tau_{ij} > 0$, we build a directed link pointing from the leader i to the follower j. While if $C_{ij}(\tau) > C_{\min}$ and $\tau_{ij} = 0$, we generate a mutual link for the pair of pigeons. Hence we have two types of links in the network induced from the collective movement of a pigeon flock: directed and mutual links.

If we consider only directed links, a well-defined hierarchical structure is evident. On the other hand, considering only

TABLE II. The correlation delay time $\tau(s)$ and the corresponding correlation coefficient $C(\tau)$ between A and B in all the flights. FF means free flight and HF means homing flight. Here "−" represents that the individual did not attend the flight, so we have no data for analyzing its behavior.

Flight	FF1	FF2	FF3	FF4	FF5	FF6	FF7	FF8	FF9	FF10	FF11	HF1	HF2	HF3	HF4
$\tau(s)$	−	0	−0.4	0	1.0	−	0	−	0.2	−0.2	−0.6	−	−0.2	0.2	−0.2
$C(\tau)$	−	0.98	0.75	0.88	0.86	−	0.95	−	0.73	0.84	0.84	−	0.99	1.00	0.98

TABLE III. Summary of the statistics in each free and homing flight performed by subjects. $L^{\leftrightarrow}$ is the number of mutual links, L is the total number of links, l is the ratio of the number of links pointing in both directions $L^{\leftrightarrow}$ to the total number of links L: $l = \frac{L^{\leftrightarrow}}{L}$ [15], m is the number of loop of size 3, $N^{\leftrightarrow}$ is the number of pigeons with the reciprocal relationship, N is the total number of pigeons in the flight, D is the serial number of the individuals without reciprocal links to others, and R is the ranks of D in each flight. "$-$" indicates that the individual did not attend the flight, so we have no data for analyzing its behavior.

Flight	FF1	FF2	FF3	FF4	FF5	FF6	FF7	FF8	FF9	FF10	FF11	HF1	HF2	HF3	HF4
$L^{\leftrightarrow}$	16	34	20	14	14	24	44	42	14	36	26	20	12	22	14
L	34	62	31	32	52	34	50	49	35	54	58	55	42	39	43
l	0.47	0.55	0.65	0.44	0.27	0.71	0.88	0.86	0.40	0.67	0.45	0.36	0.29	0.56	0.33
m	16	35	17	16	8	29	79	70	8	56	41	32	13	25	9
$N^{\leftrightarrow}$	7	9	7	9	7	8	7	8	7	8	9	7	8	6	7
N	8	10	7	9	10	8	7	8	8	9	10	10	9	8	9
D	H	E	$-$	$-$	A,M,G	$-$	$-$	$-$	I	M	A	A,D,I	G	C,L	A,G
R	8	10	$-$	$-$	1,2,3	$-$	$-$	$-$	8	9	10	1,3,5	9	7,8	2,9

mutual links, we find that most individuals share an equal structure and the individuals with reciprocal links form many loops. Finally, when we take all the links into account, the topological structure is very complex because not only are many directed links contained within the hierarchical structure but also many reciprocal links form a large range of equal relationships. Instead of showing birds exclusively adopting either an averaging or a leadership strategy, our experimental analysis demonstrates that there is an integrated mechanism between compromise and leadership.

Our data analysis shows that mutual (reciprocal) links, representing coordinated correlations between a pair of individuals, are dense and important in pigeon flocks. A traditional way of quantifying the reciprocity is to compute the ratio of the number of links pointing in both directions $L^{\leftrightarrow}$ to the total number of links L [15]: $l = \frac{L^{\leftrightarrow}}{L}$. In general, the reciprocity of real-life directed networks ranges between the two extremes of a purely directed one ($l = 0$, such as citation networks, where recent papers can cite less recent ones while the opposite cannot occur) and of a purely bidirectional one ($l = 1$, such as the Internet, where information always travels both ways along computer cables) [16]. The value of l for a real network lies between the above two extremes. As is shown in Table III, there are many mutual links and the reciprocal coefficient l is very high in each network of the homing and free flights. Moreover, the high frequency of loops (the size of 3) m shows that not only reciprocal relationships exist between two individuals but also such type of transitivity [28,29] can be extended to three or a larger number of individuals.

The number of individuals with reciprocal links and the entire number of individuals in a flight have been listed in Table III, and we find that there are very few pigeons having no reciprocal links. Furthermore, we list the ranks of individuals without reciprocal links, and we find such pigeons tend to be pure leaders or followers when observing their ranks in the group, like E in Fig. 5. Therefore, a reasonable conclusion is that the individual whose position is the head or tail of the flock has a stronger tendency to have a directed relationship with others. In contrast, the individuals in the middle of the group tend to have a reciprocal correlation with their neighbors. We emphasize that the hierarchical structure of pigeon flocks in the previous study [6] does not imply that there are no mutual correlations: they simply concentrate on the leadership

aspect. Our findings show that both the many wrongs and leadership mechanisms coexist in collective motion. Within and between distinct strata, the hierarchical structure likely dominates long-term decisions such as navigation objectives of the whole flock, while the mutual interactions characterize local behavioral rules that are essential to maintain flock cohesion and alignment.

III. CONCLUSION AND DISCUSSION

Our study indicates the balance between compromise and leadership for the organized flight of pigeons. Reciprocal links represent a mutual correlation between a pair of individuals. Note that our result is not contradictory to the previous conclusion that there is a hierarchical structure in pigeon flocks [6], instead it is a meaningful supplement. Our results show that the many wrongs and leadership mechanisms can coexist in a collective motion. Hence, the dichotomy between these two mechanisms is false, at least for the flocking flight of pigeons.

Our work also has significant meaning for modeling the collective motion of animals. If a pigeon flock only has a hierarchical structure, it means that the local interaction mechanism of previous models [30,31] may not be adequate for simulating the group flights of homing pigeons (lacking the leadership), despite the interaction rule being dependent on the metric distance [31–33] or the topological distance [34,35]. However, our work suggests that the local interaction relationships (including directed and mutual links) are sufficient to characterize cohesive motion of pigeon flocks. Our results are helpful to providing a comprehensive picture of collective dynamic behavior in animal group movement and unifying both the interaction mechanisms observed in experimental data and theoretical models of coherent behavior.

We hypothesize that the integrated mechanism between compromise and leadership also brings more advantage to both the individuals and the whole system to cope with external perturbations (e.g., predatory threat and food source). Individuals of the same species come together to form a group because a compact flock has more advantages to react to environmental perturbations than separate individuals [14,36,37]. Any external perturbation for flocking movement is likely to directly cause a change of velocity (direction,

magnitude, or both) for a small subset of birds that first detect the perturbation. Such localized changes can be transmitted to the whole flock to produce a collective response as if being of one mind [38], making the whole group both very flexible and responsive. Conversely, if there is only a hierarchical structure in pigeon flocks, the followers cannot transmit any external signals to the leaders, so the whole group is not so sensitive to environmental perturbations. The sensitivity of the whole group can evolve and strengthen if the group members have a local interaction mechanism among them [39]. In particular, reciprocal links allow individuals to interact with their neighbors and supply a useful way for the followers to convey information to the leaders.

It needs to be noted that calculating pairwise correlation and even the methods in Refs. [6,7] can be regarded as dividing a large-scale complex system (such as a fish school [37,40]) into multiple local subsystems (a pair of subjects). In future work, an extension of the pairwise correlation method based on the holism of complex systems [41] for analyzing these trajectory data should be developed to more accurately determine how one individual is simultaneously affected by the others.

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