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Research Article

Rotational Flocking with Spontaneous Directional Changes

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Revealing the underlying decision-making strategy governing the high-group polarization accompanied by conflicting individual preferences may play a central part in the lives of social animals. Hereby, we construct a structured spin model in accordance with empirical validation, which shows how distinct individual preferences converge from one consensus homeostasis to another lowest-energy equilibrium. To verify the theoretical derivation, we use high-resolution spatiotemporal GPS data of a flock of thirty pigeons and study the dynamical evolution mechanism of systemic spins. Therein, we find successful rotational direction transitions requiring a sufficient number of supporters. A few initiators trigger the phase transition from one equilibrium to another, where the symmetric transient state indicates a diamond hierarchical network being completed by the intermediates and the rear individuals. By further studying the nature, we reveal that decision-making sequences are strongly triggered and influenced by individual positions and the leader-follower relationship. Thus, we can predict which individual is more likely to make the decision before the initial transition moment and who will draw the complete stop. Consequently, the revealed decision-making strategy facilitates a comprehensive understanding of collective behavioral transition.

1. Introduction

Collective movements of natural animal groups are among the most compelling social manifestations in nature. The underlying interindividual interaction principles, decision-making strategies, and the matters triggering transitions from nonequilibrium to a consensus homeostasis have classically attracted considerable attention [1]. A long-standing question is how gregarious animals with conflicting moving preferences affect the flow of information and give group members distinct weights in making decisions. Generally, collective decisions can be dominated by a single despotic leader, can be determined by the influence of hierarchy, or emerge from a shared democratic process [2]. Evidence collected from schooling fish suggests that the process is democratic, with nearest neighbors and the majority shaping overall collective behavior, and uninformed individuals could promote such democratic consensus [3]. In animal groups with obvious hierarchical social structures, such as elephants [4], dolphins [5], and primates [6], however, such democracy may be replaced by despotism. Thus, revealing the decision-making strategy governing the high polarization in collective behavior remains a core challenge for understanding the social complexity of animals. Following the research line, diverse modeling studies have been developed to elucidate complex collective decision-making processes and strategies in animal groups. The fundamental aspects of widely-used models, in common, are that they start with a hypothesis about individual decision-making strategies and then proceed the integration process as an aggregated outcome of collective decision. Such hypotheses about individual decision-making mainly include quorum response [7–9], state-dependent alignment [10–14], assertiveness/submission [15–17], and compromise strategies [2, 18, 19]. These agent-based models adopting various decision-making rules propelling individuals have been sufficiently realistic to reproduce numerous observed phenomena and hence are beneficial for better understanding the system complexity consisting of many self-propelled entities [20, 21].

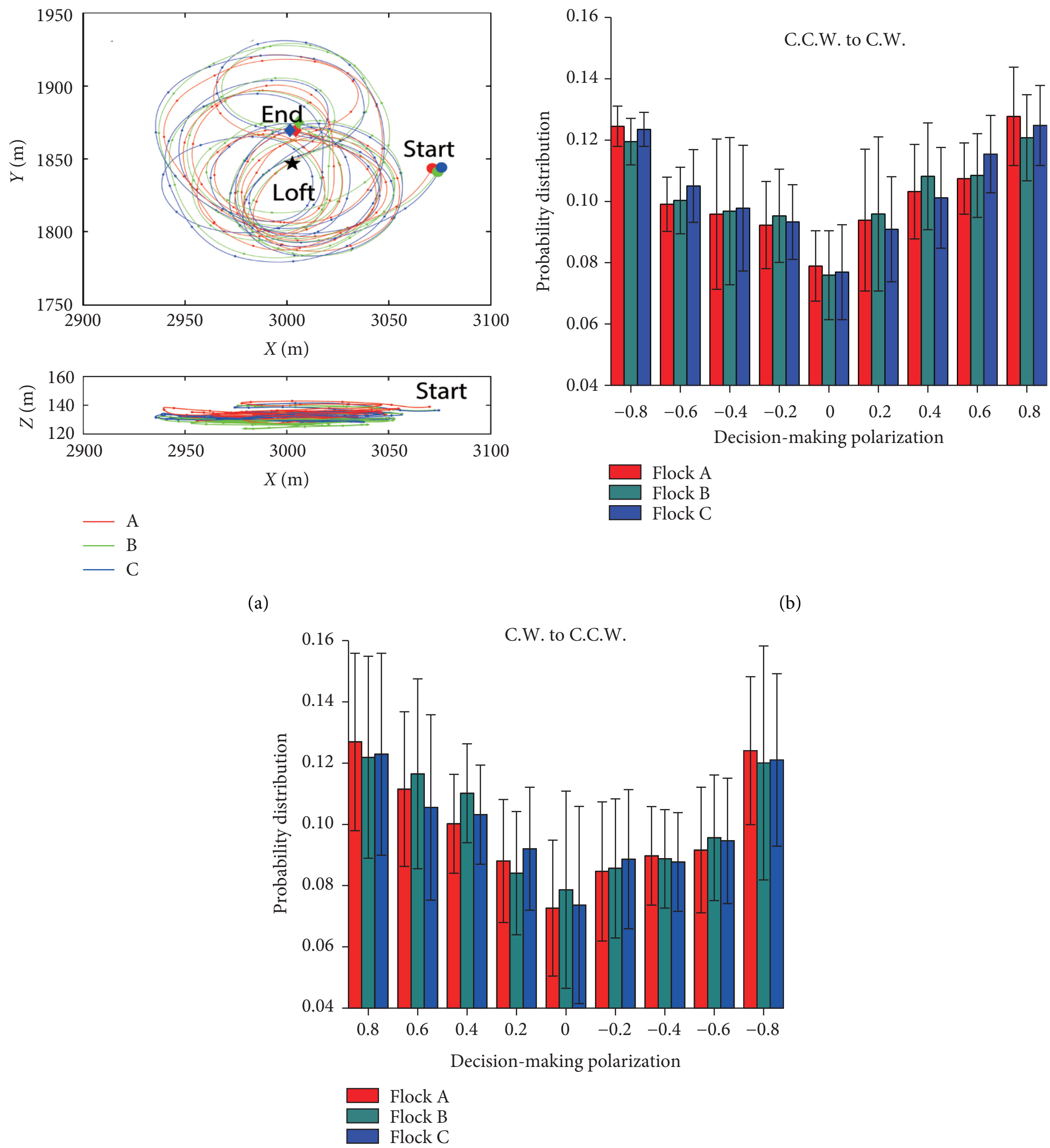
More crucially, in order to deeply ascertain what decision-making strategy is based on for coordinated individuals, empirical study on collective movements and validation of those antecedent types of models are necessary. Recently, Ballerini et al. [22] adopted an image processing method in collecting the data of a huge flock of starlings and proposed a possibility of sharing information that each bird communicated with only a fixed number of topological neighbors, instead of individuals within a specific metric distance as assumed in the celebrated standard Vicsek model [23]. By using another newly emerged technique in collecting experimental data, i.e., GPS tracking device, Nagy et al. [24] revealed a hierarchical leadership structure in small pigeon flocks, which reflects the multilayer leader-follower relationship governing their decision-making process. Such a hierarchical leadership was found independent from the dominance rank in pigeon flocks [25]. In contrast, although the network in dogs [26] constructed from the leader-follower relations is also hierarchical, significant correlations were found between hierarchy and age, dominance rank, trainability, controllability, and aggression measures. Indeed, despotic decision-making is more obvious in the predatory behavior of wolf packs [27]. Previous studies on the mystery of despotism in African elephant herds provided a better sense that dominance rank relationships were transitive within families and highly asymmetrical within dyads, such that older, larger females consistently dominated decision-making of other individuals [28, 29]. An untested hypothesis thus naturally arises that animal groups with higher wisdom are more likely to adopt despotic decision-making strategy.

Hereby, to infer the decision-making strategy, we focus on free flights as shown in Figure 1(a) and carry out a detailed investigation on high spatial-temporal resolution GPS datasets. Therein, three flocks has ten individuals with 30 releases labeled as flocks A, B, and C from [25]. Each release lasts from two to seven minutes. Due to the limitation of the GPS device in z-axis and the average standard deviation of flight altitude in each release being sufficiently small, it suffices to only use the x- and y-axes data for investigation as the previous study [24, 25] did. Subsequently, we construct a structured spin model which shows how distinct individual preferences converge from one consensus homeostasis to another lowest-energy equilibrium. To verify the theoretical derivation, we study the dynamical evolution mechanism of systemic spins. Therein, we find successful transitions requiring a sufficient number of supporters. By further studying the origins, we reveal that decision-making sequences are triggered and influenced strongly by spatial locations and the leader-follower relationship. Thus, we can infer which individual is more likely to make the decision before the transition moment and who will complete the stop.

2. Results

2.1. Inferring the Decision-Making Strategy. Dynamical equilibrium is an axiomatic concept, which can be seen as no macroscopic change occurs in the system of internal thermodynamic equilibrium. Analogously, in bird flock flights with high polarization, e.g., homing flight of pigeon flocks [30], it is often encountered that the interagent spatial position keeps relatively constant, which can be considered as an equilibrium state. The degree of global ordering in a flock can be measured by the so-called order parameter $\phi = 1/N \sum_{i=1}^{N} \vec{v}_i(t)|/\vec{v}_i(t)\|$, which is employed as a standard index of global order during the study of collective animal behavior [23]. Therein, $\vec{v}_i(t)$ denotes the velocity of bird i in the horizontal plane and N is the total number of individuals in the flock. Apparently, the index ϕ is zero for totally disordered and one for completely synchronized flocks. Furthermore, we introduce the concept of internal angular momentum from quantum mechanics [31], namely, the spin of an individual, $\vec{s}_i = \chi_i \cdot (\vec{v}_i \times d\vec{v}_i/dt)$ [32], with χ_i denoting the moment of inertia of individual i. In this study, we focus on the free flight of pigeon flocks, where individuals hover above their home loft with spontaneous changes of rotational directions. For simplicity, we consider every turning as a part of uniform circular motion without noise and normalize the spin in this study, i.e., $|\vec{s}_i| = |\vec{s}_j| = 1$ for any pair of individuals i and j. Thus, $\vec{s}_i$ is orthogonal to both the velocity and the centripetal acceleration vectors, and its positive and negative normalized values will denote the clockwise (C.W.) and the counterclockwise (C.C.W.) turning by simply using the right-hand screw rule. We then develop the alternative order parameter, namely, $S = 1/N \sum_{i=1}^{N} \vec{s}_i$, which characterizes the collective decision made by the entire flock. Note that S is an indicative vector with the value being equivalent to the summation of $\vec{s}_i$. The value of index S is zero for totally conflicted states with half supporters and half opponents, and $S = \pm 1$ for completely consensus in decision-making in C.W. and C.C.W. turnings, respectively.

As shown in Figures 1(b) and 1(c), we exhibit the probability distributions of the decision-making polarization S. With the reduction and increase of the index values, the entire flock gradually changes the rotational direction from counterclockwise to clockwise and vice versa, respectively. The symmetric probability distribution of S indicates that more individuals change their rotational direction in the medium period, whereas the number of directional switching pigeons reduces gradually in the earlier and later periods. The fitting curves indicate that spontaneous changes of decision on flight directions follow a Gaussian distribution. It provides an evidence how a heterogeneous flock of pigeons with varying stamina can achieve consensus in decision-making of the rotational direction in free flight. An explanation lies in previous numerical studies that every individual has a depletion time which follows a Gaussian distribution. When a pigeon feels tired or just wants to change the rotational direction, but most of the others not, it must compromise unwillingly but with increasingly greater intension to change. Thus, when a sufficient number of willing members have been accumulated to change their rotational direction, they drive the entire flock to switch [33, 34]. Moreover, the distributions of S shown in Figure 1 suggest that pigeon flocks in free flight



(c)

FIGURE 1: Trajectories and the distributions of the systematic spin. (a) Trajectories of ten pigeons in flock A. Each trajectory lies approximately on a plane. (b) Probability distributions of the systematic spin from C.C.W. turning to C.W. turning and (c) the reverse case. It is observed that the spontaneous changes of rotational directions follow a symmetric distribution.

employ a symmetric diamond-shaped structure of decision-making, instead of a pyramid-type leader-follower hierarchical structure [24]. It means that not only the leader initiates the change of rotational direction, there exists a symmetric rear individual completing the transient state to another equilibrium.

Theoretical validation: the distributions of S suggest a symmetric diamond-shaped structure of decision-making, which is in contrast to the previous pyramid-type [24], star-shaped [35], and V-shaped hierarchical structures [36] observed in bird flocks. Note that we normalize the phase transition time T defined as the completing time of a transition from one equilibrium to another, namely, the time from the initiator to the last one changing its direction of spin $(T = 3.25 \pm 1.67\, s)$.

Theoretical descriptions of collective motion are widely based on alignment dynamics, namely, each individual tends to keep its direction of motion as close as possible to that of its neighbors. The Vicsek style dynamics of collective motion in a noiseless case is as follows:

$$\vec{v}_i(t+1) = \vec{v}_i(t) + \frac{1}{N_i}\sum_{j\in N_i}\vec{v}_j(t), \quad (1)$$

where the vector v_i is the velocity of individual i and the summation extends over all neighbors j of i. Analogously, we can follow the spirit of the alignment hypothesis and subsequently have the spin dynamics:

$$\vec{s}_i(t+1) = \vec{s}_i(t) + \sum_{j\in N_i} J_{ij}\vec{s}_j(t), \quad (2)$$

where J_{ij} is the interaction strength between two neighboring individuals i and j in the transition state of decision-making. We assume that, in a small pigeon flock, all individuals are mutual neighbors for each other. This dynamics of interaction rules is reminiscent of the classical Heisenberg model, which is formulated in a 3-dimensional lattice, $H = -\sum_{i,j} J_{ij}\vec{s}_i \cdot \vec{s}_j$ with $\vec{s}_i \in \mathbb{R}^3, |\vec{s}_i| = 1$ denoting the normalized spin and $J_{ij} = 1$ only if i and j are neighbors. A common simplification is to assume that all of the nearest neighbors have the same interaction strength, and then $J_{ij} = J$ for all individual pairs i and j. If the spin is one of the two canonical variables, the other would be velocity phase in the internal space of individual i in a uniform circular motion. However, the transient decision-making process definitely cannot be captured according to the simplest Heisenberg model with canonical variables spin and velocity phase.

In a continuous-time case of a flock with N individuals, the Hamiltonian and the update rule (2) can be equivalently derived to the following equations:

$$H = -J\sum_{i,j}\vec{s}_i \cdot \vec{s}_j, \frac{\vec{s}_i(t)}{\mathrm{d}t} = -\frac{\partial H}{\partial \vec{s}_i} = -J\sum_j \vec{s}_j. \quad (3)$$

Hence, each individual changes its decision following a social force $-(\partial H/\partial \vec{s}_i)$, produced by its neighbors. In the transition state of decision-making, it is clear that $S = 1$ evolves to $S = -1$ from consensus C.W. turning to a C.C.W. equilibrium, or the opposite for the reverse case. The total spin $S = \sum_i \vec{s}_i$ is constant for an equilibrium of C.W. or C.C.W turning due to the rotational symmetry, respectively. However, there is no conservation of S in the transition state since we know clearly the variant time-dependent evolution process of S, and we can obtain the following:

$$\frac{\mathrm{d}S}{\mathrm{d}t} = \sum_i \frac{\mathrm{d}\vec{s}_i}{\mathrm{d}t} = -\sum_i \frac{\partial H}{\partial \vec{s}_i} \sim -JN\sum_j \vec{s}_j. \quad (4)$$

Relation (4) contains the theoretical dynamics of S, which indicates that more supporters induce a faster transition of rotational direction change. Hamiltonian equation (3) in this study consists of discrete variables that represent intrinsic properties known as spins of the individuals allowing interaction with neighbors.

2.2. Matters Inducing Decision-Making. To explore the factors inducing the transient symmetric decision-making of pigeon flocks, we investigate the spatial locations of all the individuals. As shown in Figure 2, the sequence of individuals making decision in flock A is significantly influenced by their locations. The average location of the initiator in a transition from a C.C.W. turning to a C.W. turning always plays the leading role at the right front, whereas the followers are linearly distributed from the right front to the left rear (see flocks B, C, and D in Supplementary Materials). Interestingly, the individual who is the last to complete the turning locates symmetrically behind. It leaves the strong impression that the initiator at the cusp makes crucial decision (e.g., escaping natural enemies in the prey), others follow in order, and the protector locating symmetrically behind draws the completing stop.

The hierarchical leadership structure in small pigeon flocks has been revealed in the previous study [24], which suggests a multilayer leader-follower relationship governing their decision-making process. Furthermore, such a hierarchical leadership was found independent from the dominance rank in pigeon flocks [25]. Since spatial locations and leader-follower relationships are significantly correlated, we subsequently exhibit the distribution of the initiator occupation rate in Figure 3. Compared with the previous study [25] on the dominance rank and the hierarchical leadership structure, it is observed that the initiator occupation rate has no significant correlation with the dominance rank including feeding-queueing and pecking-order ranks. Moreover, it also suggests that age, weight, and sex which are the main factors inducing the dominance rank [25] have no correlation with decision-making sequence in pigeon flocks. However, to our surprise, the individual occupying the highest rate of the initiator position is just the one in the top layer of the hierarchical leadership structure constructed by the time delay in the velocity-velocity correlation [24]. Note that the hierarchical structure in Figure 3 indicates the average leader-follower relationship during the entire free flight. Thus, we may suggest that the leader in the top layer would be the initiator of decision-making and fly in front of the flock in most cases. Therefore, we have established the link among decision-making, spatial location, and hierarchical leadership, and we can infer who would be the initiator of decision-making by the most intuitive spatial distribution in pigeon flocks.

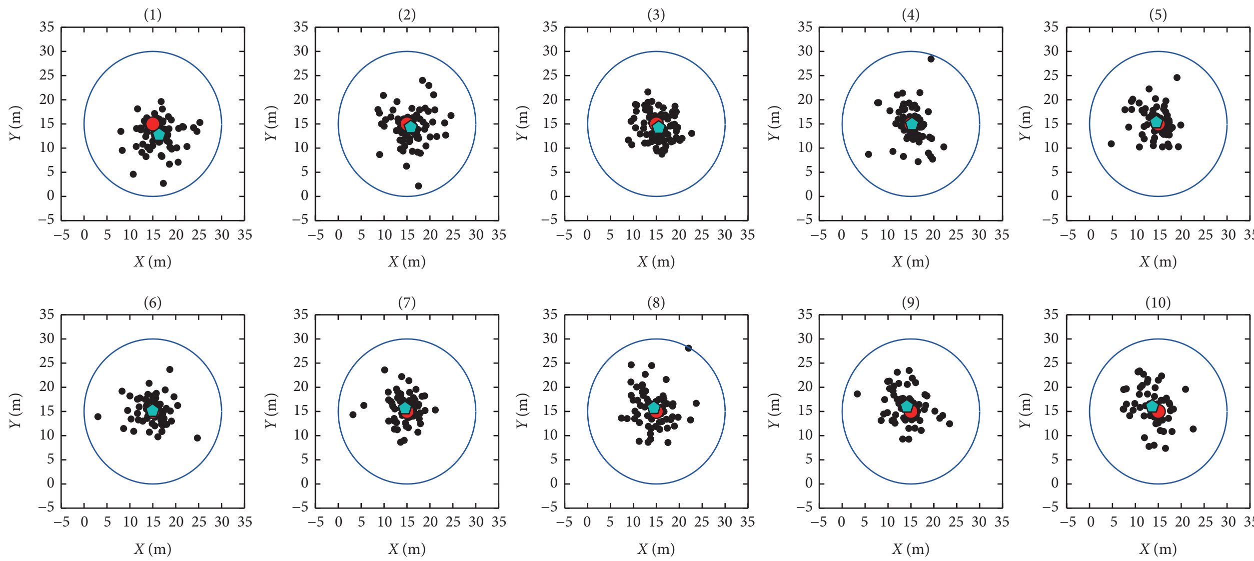


FIGURE 2: Spatial locations of individuals in flock *A* following the decision-making sequence from a C.C.W. turning to a C.W. turning. Numbers 1 to 10 indicate the switching sequence of the individuals. Here, the red point represents the flock center, the blue pentagram means the average center of the focal individual, and the black points denote the relative positions to the center of the individuals.

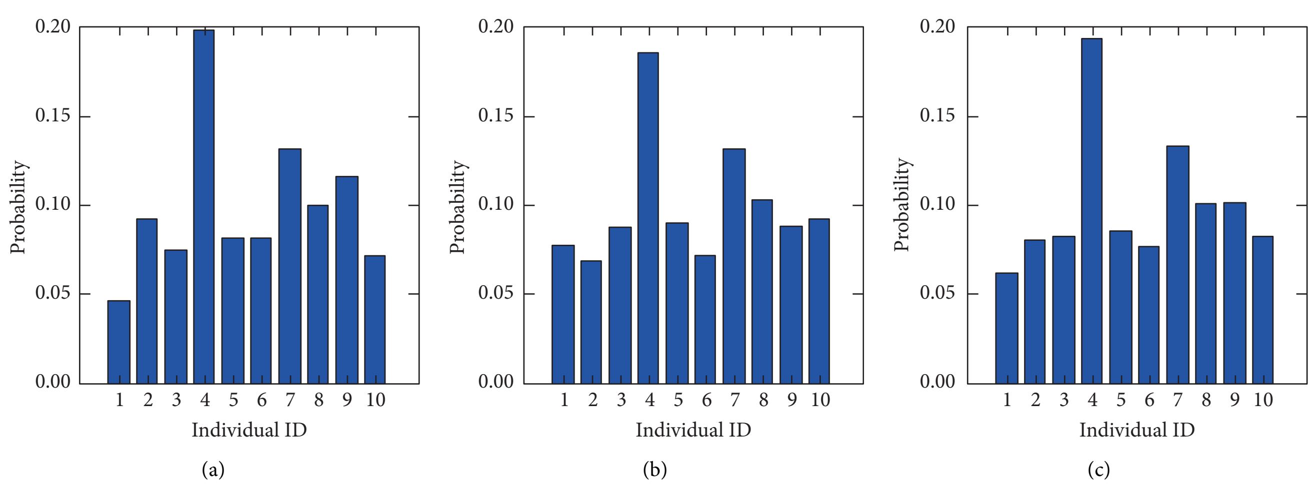


FIGURE 3: Probability distributions of the initiator occupation rate. (a) From C.W. to C.C.W. (b) From C.C.W. to C.W. (c) Average probability distribution of the initiator occupation rate.

3. Discussion and Conclusion

Besides focusing on the appealing behavioral characteristics of collective movements, e.g., consensus and other specific patterns, it is crucial to explore the mechanisms and dynamics of decision-making processes at the individual level. Classically, collective decision-making is viewed as the outcome of the leader-follower relationship among individuals, but how decisions are taken is still an under-investigated question. The hierarchical or centralized control model has been challenged by recent theoretical and experimental findings, which suggest that leadership can be more distributed. Moreover, self-organized processes can account for collective movements in many different species, even in those that are characterized by high cognitive complexity.

Hereby, to infer the decision-making strategy, we focus on free flights and carry out a detailed investigation on comprehensive datasets of four pigeon flocks with different flock numbers. We construct a minimally structured spin model in accordance with the maximum entropy method, which shows how distinct individual preferences converge from one consensus homeostasis to another lowest-energy equilibrium. To verify the theoretical derivation, we study the dynamical evolution mechanism of systemic spins denoting group decision, and we find that, in addition to foreseeable compromise of a small quantity of initiators, successful transitions require a sufficient number of supporters. A few initiators trigger the phase transition from one equilibrium to another, where the symmetric transient state indicating the hierarchical network is completed by the intermediates and the rear individual. This observation of the diamond-shaped decision-making structure is different from typical pyramid-type, star-shaped, and V-shaped hierarchical structures observed in bird flocks.

To reveal the origins of the symmetric decision-making of pigeon flocks, we find that decision sequences are triggered and influenced strongly by spatial locations and the leader-follower relationship, rather than dominance rank. This would not be surprising since the hierarchical leadership patterns observed in bird flocks arise from an anonymous, self-organizing mechanism related to individual differences in flight speed. Leaders learned more effectively during free flights, and a possible explanation is that faster birds flying in front of the flock have no choice but to make decisions, whereas the slower followers are able to rely on social information. The enhanced learning by leaders would be expected to reinforce a particular direction of information transfer through the flock. However, the revealed symmetric decision-making strategy implies that other individuals except the initiator are not equivalent followers. The most special follower is the one flying in the rear, which leaves us the strong impression that it acts as a protector responding the initiator. This is due to the fact that the head and the tail would be the vital part when pigeon flocks are facing the predators. To sum up, we have established the link among decision-making, spatial locations, and hierarchical leadership structure, which allows us to predict which individual is more likely to make the decision before the transition moment and who will complete the transition.

Data Availability

The data used to support the findings of this study are available from the corresponding author upon request.

Conflicts of Interest

The authors declare no conflicts of interest.

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