

RESEARCH ARTICLE

Decision-making in pigeon flocks: a democratic view of leadership

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SUMMARY

When travelling in groups, animals frequently have to make decisions on the direction of travel. These decisions can be based on consensus, when all individuals take part in the decision (i.e. democratic decision; social information), or leadership, when one member or a minority of members make the decision (i.e. despotic decision; personal information). Here we investigated whether decision-making on the navigation of small flocks is based on democratic or despotic decisions. Using individual and flock releases as the experimental approach, we compared the homing performances of homing pigeons that fly singly and in groups of three. Our findings show that although small groups were either governed (i.e. when individuals in the flock had age differences) or not (i.e. when individuals in the flock had the same age) by leaders, with concern to decision-making they were all ruled by democratic decisions. Moreover, the individual homing performances were not associated with leadership. Because true leaders did not assume right away the front position in the flock, we suggest that as in human groups, starting from a central position is more effective as it allows leaders to not only transmit their own information but also to average the tendencies of the other group members. Together, the results highlight the importance of democratic decisions in group decision-making.

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INTRODUCTION

Moving in groups is a widespread behavior across most taxa, from insects to fishes, birds and mammals (Sumpter et al., 2008a). However, when travelling in groups, animals face the problem of how to integrate navigational information from different members of the group. Of particular interest are the mechanisms of information transfer, namely how uninformed individuals recognize those that are best informed (Couzin et al., 2005). The way individuals within a flock negotiate their routes and make their decisions is a fundamental issue in avian navigation. Modelling group decision-making, Conradt and Roper (Conradt and Roper, 2003) proposed that both democratic and despotic decision-making in groups can evolve and be maintained by individual selection. However, under most conditions the costs to subordinate group members, and the group as a whole, are considerably higher for despotism than for democracy. For example, in a situation where all individuals of a group have similar information, the costs to subordinate members are high, as are the costs to a subordinate of following a misinformed leader, when compared with a group decision (i.e. the uncertainty around the information of the leader is higher than the average uncertainty of all individuals' information) (Simons, 2004). Alternatively, when information is dissimilar among individuals or restricted to a few individuals in the group, the costs to subordinate other group members can be minimized by the group taking the most appropriate decision (e.g. during the fall migration, adult birds have outstanding information on the migratory routes compared with first winter birds) (King and Cowlshaw, 2009). It is unclear, therefore, why despotism is as common as democracy in nature

(Conradt and Roper, 2005; King and Cowlshaw, 2009). The coexistence of despotism and democracy in nature is indicated by the occurrence of both well-informed and poorly informed individuals in natural populations.

Leadership is suggested to be common in small groups (e.g. Conradt and Roper, 2003) and could emerge in situations where there is a low cost associated with following a leader, and/or in situations where there is a minority of well-informed individuals, like elders, that possess relevant information about specific resources because of past experience (Conradt and Roper, 2005). However, in the context of animal navigation, little is known about what is needed for a bird to become a leader (for a review, see Biro et al., 2006) or, in the case of leadership, whether leaders ignore social information (i.e. information generated by another members of the group) in favor of their own information (i.e. personal information) or alternatively combine both (Conradt and Roper, 2003; Conradt and Roper, 2005; Conradt and Roper, 2009; Couzin et al., 2005; Dyer et al., 2009; Krause and Ruxton, 2002).

Studying the duality between personal and social information in the decision-making involved in flock navigation is of particular importance in the context of conflicting information. In the present study, using homing pigeons, we investigate the use of personal information (as the vanishing bearing of each individual when flying singly) *versus* the use of social information [as the average of the vanishing bearings (AVB) of each member of the flock when they homed singly] as an approach to study the effect of democratic *versus* despotic decision-making on the navigation of small flocks

(three birds). Pigeons are flock animals with strong group cohesion and therefore the performance of each bird in a flock is affected by the presence of its conspecifics (i.e. the flock acts as a single unit). To address this question, we compare the vanishing bearings of the flocks with the vanishing bearings of the wanders (i.e. the bird that takes the front lead of the flock at the release site) at departure, the leaders at arrival and the non-leaders, and with the AVB obtained when each of the birds was released singly. We predict that in the case of flocks using social information (i.e. information generated by the group), the mean vanishing bearings of the flocks should be indistinguishable from the AVBs. In contrast, if flocks are using the individual information of the leader, then the mean vanishing bearings of the flocks should be indistinguishable from the mean vanishing bearings of the leader. Furthermore, we investigate the effect of differences in age composition of the flocks on the role of different individuals in the navigational decision-making process by comparing flocks with birds of the same age with flocks with birds of different age.

MATERIALS AND METHODS

Experiments were carried out with homing pigeons (*Columba livia* Gmelin 1789) housed at our lofts (Jorge et al., 2009). A total of 42 homing pigeons that had previous release experience at distances up to 25 km from the loft were used; no training differences existed among individuals (i.e. all pigeons participated in 12 releases at 8 km and nine releases at 25 km from the loft). According to Biro et al. (Biro et al., 2004), after several releases at a same site, pigeons start following highly stereotyped routes.

At the start of the experiments, birds ranged between 8 and 10 months in age (8-month-olds, 32–33 weeks, $N=13$; 9-month-olds, 36–37 weeks, $N=14$; and 10-month-olds, 40–41 weeks, $N=15$). Three familiar release sites were chosen in the cardinal directions, east (261 deg, 7.4 km), south (344 deg, 7.7 km) and west (94 deg, 7.0 km). At each release site, a flock training release was performed before the experimental tests. Flock training releases were performed with all birds and aimed to familiarize pigeons with the new release site before the start of the experimental release tests. Hypothetically, after several releases at one release site, birds could be induced to follow a certain vector bearing. The flock training releases avoid this possible effect in the initial bearings controlling for an individual-induced vector bearing, with all birds being subject to the same group bearing. The experimental tests consisted of: one single release, wherein each bird was released singly, and two flock releases (one with birds from the same age group and another with birds from different age groups). The three experimental tests at each release site were performed on consecutive days (i.e. one test per day). All flocks were composed of three pigeons. The compositions of the three bird flocks were different (i.e. did not include the same individuals) in each of the six flock releases performed (two at each release site; for details see supplementary material Table S1). Because flocks composed of different birds act as different units, we never repeated the composition of a flock. Experimental tests were carried out in the following order: first, a single release; second, a flock release with birds of different ages; third, a flock release with birds of the same age. All releases were carried out under sunny conditions.

Birds were released and their flights were followed according to standard procedures (Jorge et al., 2009). In flock releases, we also recorded wanders at departure and leadership at arrival to the home loft. At departure, the bird responsible for changes in the flying direction of the flock was considered the wander (i.e. the bird that initiates a turn in the flying direction and makes the other ones turn),

whereas at arrival the bird flying at the head of the flock was considered the leader. Wanders and leaders were only recorded when observers were confident of the identity of the bird and its positioning. Moreover, flocks were only considered for analyses if the three birds of the flock arrived together at the home loft.

Directional data were analyzed for each set of releases (individual releases, flock releases, wanders, leaders and non-leaders) and were characterized by the mean vector (direction α_m and length r_m) and the deviation from the home direction (ρ_h). For each release we also calculated the vanishing and homing times. Those parameters were then compared between groups using the non-parametric Mann–Whitney U -test. The effects of age and individual homing performances on leadership was analysed using Fisher's exact test.

To test for the use of personal *versus* social information, the deviations from the home direction of each wander and/or leader and AVB (average of the individual vanishing bearings calculated from the individual vanishing bearings of each one of the three members of the flock when released singly at each release site) were calculated using the vanishing direction of the respective flock as reference. The 95% confidence intervals were used to test whether the different group distributions included the expected direction (Zar, 1999). All circular statistics were calculated using Oriana 3 software (Kovach Computing Services, Anglesey, UK).

RESULTS AND DISCUSSION

From a total of 33 flocks released with pigeons of the same age, we identified 27 wanders at departure and 19 leaders at arrival (Table 1). The results showed that the individual homing performances (i.e. accuracy in determining the home direction, homing time and vanishing time) were not associated with leadership (Table 1). Interestingly, we found that in flocks with birds of different ages ($N=33$ releases, 27 wanders and 18 leaders at arrival; see Table 1), age was an important factor in the determination of the leader of the flock at arrival (Fisher's exact test, $P=0.018$), with older homing pigeons generally leading the flock at arrival (13 out of the 18 leaders recorded) but not at departure (eight out of the 18 leaders recorded). Interestingly, these results suggest that leadership

Table 1. Homing performances of homing pigeons relative to the home direction

	<i>N</i>	Mean vector		Homing performance	
		α (deg)	<i>r</i>	MVT (min:s)	MHT (h:min)
Same age					
Flock	33	-12*	0.81***	2:40	0:09
Wanders	27	29	0.66***	3:01	0:15
Leaders	19	33	0.66***	3:01	0:12
Non-leaders	29	13*	0.70***	2:37	0:15
AVB	31	18	0.90***	–	–
Different ages					
Flock	33	1*	0.81***	2:37	0:08
Wanders	27	29	0.62***	2:33	0:13
Leaders	18	3*	0.64***	3:00	0:14
Non-leaders	32	13*	0.73***	3:03	0:13
AVB	25	19	0.85***	–	–

Mean vanishing vectors are given with number of released units (N), direction (α) and vector length (r).

AVB, average of the vanishing bearings; MHT, median homing time; MVT, median vanishing time.

Asterisks at α -values indicate that the 95% confidence interval of the mean vector includes the home direction, whereas asterisks at r -values indicate significance by the Rayleigh test (*** $P<0.001$).

needs some time after release to be established and therefore the determination of flock leaders is best performed during flock arrival to the home loft. Moreover, we did not find any differences between the homing performances of the two types of flocks (Mann–Whitney U -test, $P > 0.05$).

During the process of the establishment of leadership in flock flying, age is frequently mentioned as a clue for the determination of leaders (Benvenuti and Baldaccini, 1985), especially between juveniles and adults. Nevertheless, small differences in age, in the order of a few months, are not expected to influence leadership. Surprisingly, we found that at least in young homing pigeons, those small differences in age are in fact enough to influence leadership in small flocks. An age effect in decision-making, i.e. a rule to follow the bird that is oldest and thus has more experience, would be particularly important in migratory species. Migration is challenging for young birds undertaking their first journey and there is good evidence that juvenile birds have a less-developed navigational ability compared with experienced birds (Drury and Keith, 1962; McLaren, 1981; Moore, 1984; Wiltshcko and Wiltshcko, 2003). Previous studies have shown that in their first journey, young birds follow a predetermined vector program (Mouritsen and Larsen, 1998; Wiltshcko and Wiltshcko, 2003) but lack experience, and they do not have the flexibility to use different cues or account for wind drift effects as do experienced individuals (Mouritsen and Larsen, 1998; Reilly and Reilly, 2009). So a tendency of juveniles to follow an older bird when flying in a group would be highly adaptative not only to juveniles that can avoid their own orientation errors, but also to adults if there is a cost associated with obtaining consensus decisions (Conradt and Roper, 2005; Sumpter et al., 2008a).

Because wanders were not the best-performing individuals (Table 1), we analyzed which information flocks may have used at the release sites to determine the homeward direction (personal information of the leader *versus* social information of the group, AVB). To analyze the use of personal *versus* social information, we plotted the deviations of the vanishing bearings from the home direction of the individuals that were wanders (leaders at departure), the individuals that were leaders at arrival, the individuals that were non-leaders, and the AVB, relative to the mean home deviation of the respective flocks (Fig. 1). The results showed that in flocks with birds of the same age (Fig. 1A), the mean vanishing bearing of non-leader individuals (green circles) was indistinguishable from the mean vanishing bearing of the flocks (i.e. the 95% confidence intervals encompass the flock direction; Fig. 1A). Moreover, the mean vanishing bearings of both wanders (blue circles) and leaders (red circles) were significantly distinct from the mean vanishing bearing of the flocks, whereas that of the AVB (black circles) was in an intermediate position, although distinct from the mean direction of the flocks (Fig. 1A). In flocks with birds of different ages, a completely different picture arises, and although the non-leader individuals (green circles) were still indistinguishable from the mean vanishing bearing of the flocks, the closest approach was the mean vanishing bearings of the leaders (red circles) and the AVB (black circles), all of which were indistinguishable from the mean vanishing direction of the flocks (Fig. 1B). Interestingly, in groups of birds with different ages, wanders (blue circles) were the only ones that significantly deviated from the flock mean vanishing bearing, like the finding with birds of similar ages.

In the broad sense of group decision-making, two related questions arise in the determination of the goal direction: (1) who makes the decision and (2) what type of information is used? Our findings suggest that the navigation of small flocks may be governed by leadership depending on the age structure of the flock (Fig. 1).

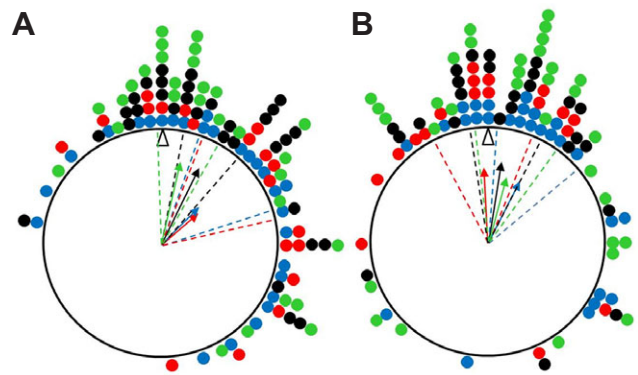


Fig. 1. Influence of personal *versus* social information on the flock's initial orientation when composed of homing pigeons of (A) the same age and (B) different ages. Orientation of wanders (personal information, blue symbols), leaders at arrival (personal information, red symbols), the average of the vanishing bearings (AVB; social information, black symbols) and non-leaders (personal information, green symbols) are shown relative to the flocks. Solid symbols plotted outside the edge of the circular diagrams are the individual vanishing directions of the different individuals (red, blue and green symbols) and the mean vanishing directions of AVB (black symbols). To test which information was being processed by flocks at the release sites, here we reference the mean vanishing bearings of all groups to the mean vanishing bearing of the flocks. Therefore, the white triangle at the top edge of each diagram indicates the mean direction of the flocks. Dashed lines are the 95% confidence intervals. Vectors radiating out from the center of each diagram are the mean vectors of each experimental group plotted as deviations from controls.

With regard to the type of information used, the data show that all groups are using social information (Fig. 1B) and, therefore, leadership in small flocks of homing pigeons is ruled by democratic decisions (Conradt and Roper, 2005). Furthermore, we only found evidence of consistency for leadership at home arrival, which suggests that the emergence of leaders does not occur immediately after release and requires a certain amount of time to develop. The analysis of decision-making and collective behavior in humans suggests that the best start position for a leader in order to pass on their own information is a central position in the group (Dyer et al., 2009). Also, one can hypothesize that in order for the leader to incorporate information from all other group members (social information), it will be best if the leader starts from a central position in the group. However, models on information transfer in animal groups have suggested that, after a certain time, consensus decisions are made even when uninformed members did not recognize the informed ones (Couzin et al., 2005; King and Cowlshaw, 2009). Our findings showed that in small groups, the personal information of the leader and the social information of the group overlap much of the time (Fig. 1B), suggesting that leaders have taken into account the information generated by the group when making their decisions and have therefore ruled by democratic decisions. Moreover, in groups where leaders could not be defined, the bearings of the followers when released singly were the best predictor of the group (i.e. flock of three) vanishing bearings (Fig. 1A). This behavior suggests that when leadership is not an option to govern a group, the birds who take the lead most of the time are paying attention to those who follow (Conradt and Roper, 2005; King and Cowlshaw, 2009). As a result of this behavior, followers can influence the movements of the incidental leaders (i.e. birds that fly in the head of the group) either by alternating in the lead or as has been shown in pairs of fishes that solve their conflicts by making

turns and forcing the leaders to change their directions (Harcourt et al., 2010; Sumpter et al., 2008b). These findings are clearly in contradiction with the general definitions of democracy or leadership in animals (for review, see Biro et al., 2006; Conrad and Roper, 2003; King and Cowlshaw, 2009). In leadership, the leader is assumed to use their own personal information and therefore to make despotic decisions. However, our results showed that leaders can also use social information generated by the group and thus make democratic decisions, as has been suggested in human leadership (Gill, 2006; Grint, 1997). In a recent paper, King and Cowlshaw (King and Cowlshaw, 2009) raised the question, why is despotism as common as democracy in nature, even though this form of social organization is more costly (see Introduction)? An answer to this question can be found if we consider that in those despotic systems based on leadership, the leader minimizes the costs of leadership by incorporating social information and therefore by making democratic decisions.

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Table S1. Flock assignment of each bird by release site and flock age composition

Flock	Same age			Different ages		
	8W	8S	8E	8W	8S	8E
1	A01	A01	A01	A01	A01	A01
	A02	A04	A06	B10	B11	B07
	A03	A05	A07	C01	C08	C03
2	A04	A02	A04	A04	A02	A04
	A06	A06	A10	B01	B03	B11
	A08	A10	A11	C04	C07	C08
3	A05	A03	A03	A05	A05	A05
	A07	A07	A05	B04	B01	B03
	A10	A08	A09	C05	C01	C07
4	A09	A11	A02	A11	A11	A11
	A11	A13	A08	B05	B04	B01
	A12	A14	A13	C13	C04	C01
5	B01	B01	B01	A02	A02	A02
	B02	B04	B06	B02	B05	B04
	B03	B05	B07	C02	C05	C04
6	B04	B06	B04	A06	A06	A06
	B06	B09	B08	B06	B02	B08
	B08	B10	B11	C06	C13	C11
7	B05	B03	B03	A10	A10	A10
	B07	B07	B05	B09	B06	B10
	B09	B08	B10	C09	C02	C13
8	C01	C01	C01	A09	A09	A09
	C02	C04	C06	B03	B09	B06
	C03	C05	C07	C12	C06	C02
9	C04	C02	C04	A03	A03	A03
	C06	C06	C09	B08	B10	B09
	C08	C09	C10	C03	C09	C06
10	C05	C03	C03	A08	A08	A08
	C07	C07	C11	B07	B08	B02
	C09	C08	C12	C08	C12	C09
11	C10	C10	C02	A07	A07	A07
	C12	C11	C08	B11	B07	B05
	C13	C13	C13	C07	C03	C12

Birds' IDs are as follows: A##, 10 months old; B##, 9 months old; C##, 8 months old.