ARTICLE

Patterns of group movements in juvenile domestic geese

Amandine Ramseyer · Odile Petit · Bernard Thierry

Abstract We investigated collective movements in a flock of domestic geese (*Anser domesticus*) to test the consistency of group orders and the influence of individual traits and social relationships on movement patterns. The subjects were 20 juvenile females kept in an herbaceous enclosure. Two observers continuously videotaped their movements. Although the positions of individuals might change during moves, the geese tended to hold predictable positions in different movements. We found that geese more reactive to unexpected noises more often held front positions. Moreover, the higher the associativity of a bird as measured by number of neighbors at rest, the more frequent the bird acted as first mover. The analysis did not evidence any influence of dominance status on the positions of geese during progression. In contrast, geese linked by close bonds clustered during progression. The structuring influence of social bonds in collective movements might be a general feature of animals gifted with individual recognition abilities.

Keywords *Anser domesticus* · Movement order · Leadership · Social relationship · Temperament

Introduction

Animals move to exploit the resources of their environment, e.g., to find food patches, resting areas, or breeding sites. In group living species, individuals have to coordinate their moves and maintain group cohesion to keep the advantage of group living—protection from predators, food defense, information exchange, etc. (Alexander 1974; van Schaik 1983; Wrangham 1980; Danchin et al. 2007).

We often lack evidence on the structure of moving groups and about the mechanisms that link individuals and insure group cohesion. In many vertebrates, colonies and communities are no more than aggregates, i.e., individuals do not recognize each other and the composition of groups is variable. Group coordination is likely based on immediate interactions. In schools of fishes, individuals match their moves on the speed and direction of their closest neighbors through the information provided by water displacements (Krause 1993). They also keep interindividual distances through visual cues. When groups change direction, individuals at the head change too.

In other species, individuals form stable groups based on social relationships. Group members know each other and their behavior differs according to relationships with partners. In some species, the most dominant individual consistently leads the group and chooses the direction. In packs of dwarf mongooses (*Helogale parvula*), the alpha female makes all decisions about routes, distances and sites (Rasa 1987). In the mountain gorilla (*Gorilla g. beringei*), the silverback male consistently decides on the moves (Schaller 1963). In other species, several individuals may take part in the process (Kummer 1968; Leca et al. 2003) and kinship bonds may be influential. It is a common finding that subgroups of related females keep their unity within large herds of ungulates (e.g., Estes 1974; Poole and Moss 1989). Moreover, synchronization between familiar individuals may help them influencing other group members. In swans (*Cygnus* sp.), for instance, a couple pulls other birds more effectively when both male and female

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first synchronize their behavior through preflight head and neck movements (Black 1988).

Processes of leadership are little documented in birds. Reports indicate that individuals at the head of the movement may change from one move to another (*Columbia livia*: Wagner 1975; *Cygnus columbianus*: Rees 1987; *Anser indicus*: Lamprecht 1992). In green woodhoopoes (*Phoeniculus purpureus*), dominants initiate flights to a new foraging site more often than subordinates (Radford 2004). No data are available, however, about the stability of movement orders and the positions of group members during progression. Within large flocks, it is reported that family members are together before taking off (*Branta canadensis*: Raveling 1969; *Cygnus* sp.: Black 1988), but nothing is known about the possible role of social relationships during flights and walks. Though stable individual behavioral traits should also play a role, we have no information about the influence of temperament on the dynamics of moves. Nonetheless, in couples of zebra finches (*Taenopygia guttata*), Beauchamp (1999) found that the most active of both birds (as measured in individual tests) reached food sources first.

The present study aimed to analyze the patterns of collective moves in a flock of domestic geese (*Anser domesticus*). Geese exhibit stable differences in behavioral traits, i.e., individuals differ in temperament (Pfeffer et al. 2002; see also Dingemanse and Réale 2005). They engage in long-term pair and family bonds (Lorenz et al. 1978; Lamprecht 1987) and their groups are structured by affiliative bonds among social categories, such as female siblings (Frigerio et al. 2001). There is convergent evidence that their social relationships are based on individual recognition. Early studies showed the occurrence of mutual recognition between parents and offspring (Fischer 1965; Lorenz et al. 1988). Moreover, individuals are able to account for the presence of allies in agonistic interactions and geese support kin-related allies in conflicts (Lorenz et al. 1988; Weiß and Kotrschal 2004; Scheiber et al. 2005). In the wild, adult males and females form reproductive pairs and families that assemble in colonies of some dozens or hundreds individuals. Like in other species of geese, families dominate pairs, which are themselves dominant over single individuals (Raveling 1970; Black and Owen 1986; Lamprecht 1986; Kotrschal et al. 1993).

As geese form social relationships based on social recognition, we predict that their group movements should be structured by social bonds. The study was designed to investigate whether (1) the positions of individuals within moves are not random but ordered according to affinities and/or dominance relationships; (2) group movements are consistently led by the same individuals or whether different individuals may take the lead; (3) the positions of individuals within movements are affected by their temperament characteristics.

Methods

Subjects and environment

The subjects in the study were 20 female domestic geese. They were gathered at hatching and then reared in one group. Each individual was marked with colored rings at both legs and labeled by a letter from the alphabet. The animals were 3 months old at the beginning of the study. They were kept in semi-free ranging conditions in an herbaceous enclosure of 2,630 m^2. The enclosure was composed of different zones, some wooded, others without cover. A pond 5 m in diameter was located at the center of the enclosure. Grains were available ad libitum in three feeding troughs set 30 m from one another and arranged in a triangle. The ground of the enclosure was marked with a grid made of stones placed every 5 m.

Observation methods

The study was carried out for 32 days in August and September 2004 from 9 to 12 a.m. and from 1 to 4 p.m., excluding rainy days and weekends. Two observers continuously videotaped the behaviors of the birds. Each was positioned on the ground within the enclosure so as to monitor half of the enclosure. They did not walk and kept still when the geese were moving. We defined a movement as one or more individuals walking or running for at least 10 m. The first mover was that individual who first took seven steps without making any stops with its head raised. Video records allowed us to accurately count steps. To identify group movements, we arbitrarily required that individuals were no more than 30 m apart from each other before departure and that they were not moving in the 30 s preceding it. To distinguish between two different moves, and recognize the end of a movement, we consistently required that all individuals stop for at least 30 s. In total, 633 movements were recorded, 258 of them involving all the group members. Note that for a proportion of movements, the observers were not able to record either their start or their end. The duration of the fully recorded movements ranged between 52 and 257 s.

One observer (A.R.) recorded the activities of geese using instantaneous sampling (Altmann 1974) every 15 min of observation sessions, yielding 259 scans. She recorded the following behaviors: *resting* (standing with head under wing, or lying with closed eyes and/or head under wing), *monitoring* (standing or lying while holding the neck upright with open eyes), *grooming* (cleaning and smoothing feathers), *foraging* (seeking and consuming vegetals in the field), *locomoting* (walking or running), *eating* (consuming grains provided in troughs), *drinking*, and *swimming*.

To recognize close bonds between individuals, we used proximity at rest. A goose lying down is about 50 cm long. Each time a bird would lie down for resting, the observer (A.R.) would record the identity of neighbors within 50 cm; birds were identified before lying down thanks to their colored rings. A matrix of affinity was built from 182 lying events. Each cell was filled with the number of times an individual was recorded as the neighbor of another.

To measure dominance relationships, the observer (A.R.) collected agonistic interactions using all-occurrence sampling (Altmann 1974). We defined them as an aggression performed by an individual and followed by avoidance or escape of another. We recorded 409 unidirectional interactions.

Video processing

For the movements involving all group members, we determined the position of each goose during movements when they were half-way between departure and arrival points. We used positions to assess the immediate predecessor and follower of each bird and build a matrix in which each cell provided the number of times each individual followed or preceded a given conspecific.

To identify preferential associations between individuals, we additionally analyzed the partnership of subgroups limited to 2–6 birds moving together. Subgroups were defined as sets of individuals moving in the same direction and being more than 30 m apart from the others. We built a matrix of association providing in each cell the number of times when two individuals were present in the same subgroup.

To assess individual differences in temperament, we used two behavioral indices: *Associativity index*: when geese were resting we counted the mean number of neighbors within 50 cm of each individual; the focal bird was identified from its colored rings before lying down. Individual indices were calculated from the sum of ratings over 285 resting periods. *Reactivity index*: when a strong, unexpected noise (car horn) occurred outside the enclosure we measured the response intensity of each individual along a four-grade scale: (1) no reaction; (2) curving the neck; (3) stretching the neck vertically with beak in a horizontal position; (4) stretching the neck vertically with beak above horizontal; individual indices were calculated from the sum of ratings over five events.

Assessment of dominance relationships

We determined dominance relationships from the outcomes of unidirectional agonistic interactions. We used the asymmetry information of the wins and losses of the dyad members. When a bird A won more often from a bird B than B from A, A was recognized dominant to B. We built a dominance matrix in which cells were filled with either 1 (A is dominant to B) or 0 (B is subordinate to A). If A and B had an equal number of wins and losses, their dominance relationships was tied and cells were filled with 0.5. To test the linearity of the hierarchy from the matrix, we calculated the linearity coefficient h' (Appleby 1983) using Matman (Noldus$^{©}$) (de Vries 1995). We found $h' = +0.50$ (NS), revealing that dominance relationships among the group of geese did not follow a linear hierarchy.

Statistical analyses

For analyses, we used Chi-square, Pearson correlation, and multiple linear regression tests. We verified that data were normally distributed using the Ryan-Joiner test. In one case data did not follow a normal distribution (number of times a bird was followed by the entire group), they were successfully normalized using square-root transformation. Matrices were processed with the Kr test for matrix correlations (Hemelrijk 1990a,b; de Vries et al. 1993) using Kendall's rowwise matrix correlation coefficients (τ) and tests of significance based on 10,000 permutations; they were computed using the MatMan software (Noldus$^{©}$). Significance level was set at 0.05.

Results

Locomoting represented 14.7% of the time-budget of geese. Most of the remaining time was devoted to resting (27.3%), grooming (22.2%), and foraging (20.5%). We built a transition matrix built from the activities preceding and following moves. This showed that a majority of movements corresponded to a change in activity (Table 1). For instance, after foraging or eating, geese often moved to the pond to drink, and grooming often followed swimming. A total of 38.9% of movements involved all birds, whereas 38.2% involved only one or two of them. Figure 1 shows that when more than two individuals moved, they generally recruited all group members.

First movers and individual positions

Any goose could be the first mover, but six (A, E, L, M, P, R) were responsible for 77.8% of the movements involving all group members, with two of them (R, L) being at the origin of 37.0% of the movements. Using partial correlation (Pearson tests), we tested the links between three variables for the 20 birds: (1) number of times a bird was first mover—regardless of the number of individuals following it ($n = 139$ departures), (2) percentage of success for an individual to be followed by the whole group ($n = 54$ movements), (3) number of times a bird was in

Table 1 Transition matrix of activities before and after movements

Departure	Arrival						
	Drinking	Foraging	Eating	Resting	Grooming	Swimming	Monitoring
Drinking	0	18	34	2	6	18	0
Foraging	26	10	20	0	2	0	2
Eating	67	21	1	0	6	1	0
Resting	11	2	14	0	0	0	1
Grooming	2	7	5	0	3	7	0
Swimming	0	4	4	0	22	0	1
Monitoring	2	4	2	0	0	2	2

$n = 324$ movements for which both departure and arrival were recorded. Movements could involve 1–20 individuals
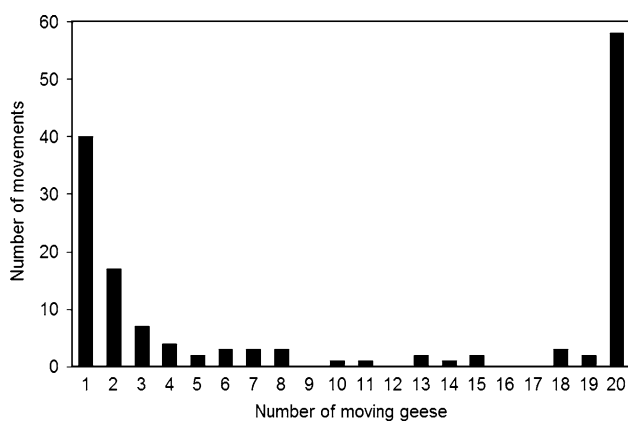
Fig. 1 Number of movements recorded as a function of the number of geese involved

first position during movement ($n = 68$ orders). The results showed that the first two variables were highly correlated ($r = +0.90$, $P < 0.001$), whereas other correlation coefficients did not reach statistical significance (1/3: $r = +0.26$, NS; 2/3: $r = -0.33$, NS).

To know whether the positions of individuals were similar from one movement to another, we tested rank correlations during movements involving all geese. We attributed to each of them a position from 1 to 20 and establish movement orders. Orders were randomly distributed into two series to calculate two mean orders. We then tested the correlation between these two orders. This procedure was run five times to check the robustness of the results through different drawings. The results showed that mean orders were significantly correlated (1st drawing 1: $r = +0.61$, $P < 0.01$; 2nd: $+0.70$, $P < 0.01$; 3rd: $+0.77$, $P < 0.001$; 4s: $+0.82$, $P < 0.001$; 5th: $+0.82$, $P < 0.0001$; $n = 48$ movements).

To know whether some individuals regularly held similar positions, we compared the number of times each individual was found in the first three positions and in other positions. We produced contingency tables and then compared observed and expected numbers using the Chi-square test. When distributions were significantly different, we then calculated partitioned Chi-square values for each

individual that was in the first-three positions for more than one quarter of the total number of movements. We found that geese held preferential positions during movement ($\chi^2 = 63.3$, $P < 0.001$). Chi-square tests showed that three individuals were more often in the first three positions than in any other position (goose R: $\chi^2 = 25.5$, $P < 0.001$; S: $\chi^2 = 9.33$, $P < 0.002$; L: $\chi^2 = 7.1$, $P = 0.008$).

Social relationships

To assess the influence of dominance relationships on the positions of individuals, we tested the correlation between the matrix of unidirectional conflicts and the matrix of succession of the 20 geese. The Kr test did not yield a statistically significant correlation ($\tau_{rw} = +0.05$, NS).

To test the influence of social bonds on the positions of individuals, we performed partial correlation analyses between three matrices: matrix of succession, matrix of association in subgroups and matrix of affinity at rest. Using partial Kr tests, we found that the three matrices were significantly pairwise correlated (succession/affinity: $\tau_{rwXY,Z} = +0.25$, $P < 0.001$; association/affinity: $\tau_{rwXY,Z} = +0.32$, $P < 0.0001$; succession/association: $\tau_{rwXY,Z} = +0.35$, $P < 0.001$).

Behavioral traits

We used multiple regression analyses to assess whether the behavioral traits of geese could account for their role as first mover or their position during movement ($n = 20$). We first verified that there was no colinearity between associativity and reactivity indices. Regression analyses produced significant r^2 (Table 2). The associativity index explained the role of individuals as first movers, and the reactivity index explained their position during movement (Table 2).

Discussion

The analysis of the orders showed that group movements were structured. Although the positions of individuals

Table 2 Relationships between behavioral indices and role of individuals as first movers or position of individuals in group movements (multiple regression analysis, $n = 20$ subjects)

Variable	F ratio (df 2, 17)	Adjusted R^2	Standardized coefficient (β value)	P-value
Role as first mover	3.44	0.20		0.056
Associativity			+0.46	0.047
Reactivity			+0.16	0.465
Position during movement	4.56	0.27		0.014
Associativity			−0.19	0.377
Reactivity			−0.50	0.026

might change during moves, geese tended to hold predictable positions in different movements involving all females. We found that some birds were regularly in the first three positions of the flock. It is worth noting that two of the three individuals most often seen in the first three positions (R and L) were also those liable to recruit the whole group when acting as first movers. Until now, succession orders based on reliable individual positions had been reported in mammals only. In cattle, individuals consistently occupy the same positions (*Bos indicus*: Reinhardt 1983; *Bos taurus*: Dumont et al. 2005). In many species, some individuals or categories of individuals are repeatedly found at the head of moving groups (Schaller 1963; Rhine and Westlund 1981; Boinski 2000; Holekamp et al. 2000). Although the latter are commonly labeled as 'leaders', an individual may also lead others either by 'pushing' or 'herding' them (Kummer 1968; Leyhausen 1971; Waring 1983). In geese, there was no indication that some individuals pushed others, i.e., that their behavior prompted others to move away. Authors often do not distinguish between first movers and those individuals that took the head during the move (Dumont et al. 2005). In the present study, we found no relationship between moving first and holding the first position during group progression.

The analysis did not evidence any influence of dominance relationships on the positions of geese during progression. In barnacle geese (*Branta leucopsis*) at foraging, Stahl et al. (2001) report that dominance affected group foraging and resource defense; dominant individuals preferentially hold central positions, while subordinates remained in peripheral positions. Similar effects were found in brown capuchins (*Cebus apella*) (Janson 1990). The group movements here studied in geese are quite different from the context of foraging, however. Among mammals the study of group movements brought different conclusions according to species. Dominant adult males progressed more often frontward and subordinate ones rearward in savanna baboons (*Papio cynocephalus*) (Rhine and Westlund 1981) whereas no relation appeared between dominance and travel positions in zebus (*Bos indicus*) (Reinhardt 1983). It should be added that clear differences in dominance ranks are observed in flocks of wild geese of

mixed gender and mating status (Raveling 1970). Further works are needed to test the influence of dominance on individual positions during collective movements and flights in free-roaming geese.

Geese linked by close bonds clustered during group movements. Individuals found together at rest frequently moved in close positions. Moreover, they often traveled in the same subgroups. Such results are consistent with family take-off in wild barnacles and swans (Raveling 1969; Black 1988). Close proximity between related individuals seems also to occur during progression in mammals, but that remains poorly documented (e.g., in sheep: Scott 1945). In the present study, partial correlation tests further showed that the succession order of geese remains correlated to association in subgroups when the effect of affinity at rest was controlled. This indicates that factors other than affinity are responsible for the pattern of group movements.

We found that some individual traits predicted positions. More reactive geese more often held front positions during movement; it could be that their higher responsiveness drove them to the head once the group was on the move. Besides, the higher the associativity of a bird as measured by number of neighbors at rest, the more frequent the bird acted as first mover. Such a result may look counter-intuitive at first; we might have expected that first movers were more independent individuals. As previously reported, the most frequent first movers were those birds better able to initiate group movements. It could be that the latter were more successful owing to their numerous social bonds. Interestingly, Reinhardt and Reinhardt (1981) similarly report that the main leader in a herd of zebus was the cow displaying the greatest diversity of partners at grazing.

In many bird colonies, moves and flights are basically anonymous, that is, interindividual coordination lies on local cues (e.g., de Schutter 1997). In contrast, geese displayed consistency in their moves. The structuring influence of social bonds in collective movements might be a general feature of animals gifted with individual recognition abilities. The present conclusions are drawn from one flock of juvenile domestic geese. Future studies should check whether they still hold for flocks of birds structured

by family bonds and differences in mating status. It could be that the assemblies found in some species of birds are composed of subgroups of individuals that remain cohesive during flights owing to their social bonds. Investigating the balance between the role of single individuals and subgroups would allow specifying the effectiveness and energetic costs of the processes underlying group movements.

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