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Non-human Leadership

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Synonyms

Collective action; Flocking; Leading; Swarming

Definitions

Leadership occurs when an individual or subset of individuals within a social group or aggregation has a disproportional influence on the behavioral outcomes of conspecific members within the group regardless of how this effect is achieved.

Introduction

Leadership is ubiquitous within animal societies, occurring when one individual or subset of individuals, the leader(s), exert(s) a disproportional influence on the behaviors of others (followers; Smith et al. 2016). Leaders emerge in non-human groups or aggregations of animals regardless of the how this influence is achieved (Smith et al. 2016). Within non-human animals, most research has focused on collective movements during groups travel (e.g., Reyonds 1987; Boinski and Garber 2000). More recently, the concept of leadership has been extended to also explain collection action within the domains of foraging, conflict resolution and between-group conflicts (Smith et al. 2016). Here, I synthesize what is known about leadership in non-human societies by providing a brief overview of seminal work within domain of group travel and recent developments in this domain of leadership, discussing the ways that leadership permeates into other domains within non-human animals, and then comparing these patterns of leadership in non-human societies to those in human societies.

Collective Movements During Group Travel

Collective movement occurs when two or more individuals maintain spatial proximity while travelling together to a new location (Petit and Bon 2010). Pioneering studies on collective behavior set out to understand the basic rules explaining coordinated, large-scale patterns of movements by aggregations comprised of hundreds of insects, fishes, starlings or hooved migratory animals traveling together in a seemingly coordinated manner. Whereas it was once hypothesized that such aggregations might rely upon a centralized authority, seminal work by Reynolds (1987) proposed an alternative model suggesting that instead complex patterns of swarming, shoaling (schooling), flocking and herding behaviors may

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be explained by patterns of localized leadership and followership. This parsimonious mathematical model relies upon the following simple rules by which individuals adjust their movements based on information gathered from their local neighbors' movements and positions. For example, flocks of birds coordinate collective movements by following three simple rules: velocity matching, flock centering and collision avoidance. Flocking therefore emerges when an individual bird (follower): (i) matches the speed of nearby flockmates (localized leaders), (ii) maintains close spatial proximity to nearby flockmates, and (iii) avoids colliding into nearby flockmates. These powerful insights have prompted a large body of research confirming these patterns and this model is the most-widely accepted view of how leaders emerge in these contexts. For example, desert locust nymphs (*Schistocerca gregaria*) also rapidly transition from disordered movements to form large swarms comprised of coordinated movement patterns during marching behavior (Buhl et al. 2006).

Extensive studies documenting how and why non-human vertebrates travel in groups suggests that socially-complex mammals also follow simple rules (Boinski and Garber 2000). That is, as in other gregarious animals, social carnivores, birds, and primates living in closed social groups also seem to adhere to simple rules to navigate group travel from one location to another; these group-living animals often accrue individual fitness benefits, such as reduced predation risk, group acquisition of shared resources and group defense against neighboring social groups from following leaders (Boinski and Garber 2000).

Group travel that requires all group-mates to choose between collectively moving to a new location and remaining together in their current location represents a 'consensus decision' (Conradt and Roper 2005). Because travel decisions often have fitness consequences for all participants, leaders may emerge to resolve consensus decisions that impose conflicts of interest (consensus costs) requiring all members to settle on a single direction, timing or destination of group travel (Conradt and Roper 2005). For groups in which only a few individuals have pertinent information, such as about the location of a food source or a migratory route, patterns of leadership often emerge even in the absence of signaling by leaders, without any active coercion on the part of the leader, and even when followers lack information about which individuals possess information (Couzin et al. 2005; Smith et al. 2015). Importantly, Couzin et al. (2005) showed that only a small proportion of the informed individuals (leaders) are required to lead during collective movement.

Although pioneering models of leadership based on short-term studies in non-human mammalian societies indicated that one or few dominant individuals may consistently occupy leadership roles, more recent work drawing from long-term studies based on recognizable individuals suggests that leadership roles tend to be flexible and shared within groups (Smith et al. 2015). Specifically, Smith et al. (2015) joined others in showing that attribute-based leadership is the most common pattern among mammals, with an individual's motivational state, sex, relative social status and age class at the time of group travel profoundly shaping his/her leadership (or followership) during the group travel (Smith et al. 2015).

Collective Acquisition and Distribution of Food

Although most research to date focuses on leadership during collection movements, leaders also emerge within the acquisition and distribution of foraging (Smith et al. 2016). Most notably, leaders emerge in gregarious species, such as in the social carnivores (carnivorans) when individuals cooperate to acquire energy-rich food items that they would be unable to capture or locate on their own. For example, female elders within groups of African lions, Verreaux's safakas (*Propithecus verreauxi*), killer whales (*Orcinus orca*) and spotted hyenas all typically enlist more followers than do young, naïve individuals in collective foraging presumably because they possess the greatest local knowledge (reviewed by Smith et al. 2015). Orcas are noteworthy because postreproductive (menopausal) female resident killer whales lead collective foraging efforts in search of salmon, particularly when food is in low abundance and to promote the survival of their sons who lack local ecological knowledge (Brent et al. 2015). Following the acquisition of food, leadership roles vary widely across taxa. For example, even within carnivorans, lionesses equally distribute food within their egalitarian societies whereas high-ranking adult females control priority of access to food resources within their female-dominated societies (see: Smith et al. 2016). Nonetheless, as in the context of collective movements, leadership also appears to be attribute-based. That is, to the extent to which it has been investigated, those individuals with local knowledge tend to emerge as leaders within the foraging domain.

Leadership During Within and Between-Group Conflicts

Lastly, as in human societies, non-human leaders often emerge to settle or win conflicts within or between groups (de Waal 1990). Because conflict is potentially costly to individuals, natural selection favors mechanisms, such as the emergence of leaders, that mediate conflict resolution within groups (de Waal 1990). Moreover, because the outcomes of between-group competition often have large fitness consequences for members of a social groups, such as determining the size of a territory containing key resources, natural selection often favors those individuals who join forces during between-group conflicts. Both during conflict resolution within groups and during warfare associated with between-group conflicts, leadership roles in mammalian societies are much more concentrated (less shared) and leaders exert more power than in contexts when conspecifics are simply traveling from one area to another or engaged in collective foraging (Smith et al. 2016). Future studies are needed to elucidate whether this pattern extends to other taxa beyond mammals.

Within these conflict domains, leadership roles also tend to be occupied consistently by one or a few dominant individuals who exert the most power within their societies. For example, among non-human primates, high-ranking apes and monkeys most often take the lead in resolving within-group conflicts through reconciliation; dominants often lead in consoling their former opponents after fights (De Waal 1990). Within spotted hyenas (*Crocuta crocuta*), high-ranking adult females also emerge as leaders, tending to emerge most often at front lines of between-group conflicts and to intervene most often during within-group conflicts (Smith et al. 2016).

Conclusions

Overall, despite the enormous range of taxa across the animal kingdom for which individuals emerge as leaders, common rules appear to explain patterns of leadership within and across leadership domains. Together, studies of collective movements indicate that attribute-based leadership is often shared within groups or aggregations and that patterns on non-human leadership is best explained by simple rules requiring localized decision-making and only a few informed leaders. Thus, despite the enormous disparities in the scales over which animals collectively move and the vast differences in presumed cognitive abilities across taxa, similar rules appear to explain collective movement decisions, suggesting that general principles may underlie leadership during collective movements.

Although most research to date has focused on leadership during collective movements, leaders emerge across multiple domains within loose aggregations of animals and close social groups ranging from insect swarms to pods of killer whales. Leaders disproportionally influence the collective behaviors of others, determining the direction of travel, foraging decisions and the outcomes of conflicts within and between groups. Synthesis of current data suggests that leadership roles are particularly flexible during group movements, as dictated by current state variables such as age and reproductive status, but that leadership roles are least shared and leaders wield the most power in contexts involving resource acquisition.

Indeed, preliminary data suggest that this is also the case for small-scale societies of humans as well (Smith et al. 2016). Moving forward, workers should draw upon the comparative framework of Smith et al. (2016) to evaluate the generalizability of these patterns of human and non-human leadership across the domains of group movement, food acquisition, within-group conflict mediation and between-group interactions. Within an evolutionary framework, workers studying leadership more broadly will gain new insights about the importance and universal principles of leadership that together give rise to collective behaviors in gregarious species of animals, including ourselves.

Cross-References

- ▶ Coalition Leaders
- ▶ Coalitional Hunting
- ▶ Coalitional Relationships
- ▶ Cooperation
- ▶ Cooperation Among Fishes
- ▶ Cooperation Among Non-chimpanzee
- ▶ Cooperation Among Non-human Primates
- ▶ Cooperation Among Non-humans
- ▶ Cooperation Among Non-primate Mammals
- ▶ Cooperation and Social Cognition
- ▶ Cooperation in Social Carnivores
- ▶ Cooperation in Social Insects
- ▶ Cooperation Varies with Genetic Relatedness
- ▶ Cooperative Alliances, Cooperative Coalitions
- ▶ Cooperative Foraging
- ▶ Cooperative Hunting
- ▶ Division of Labor
- ▶ Dominance Hierarchy
- ▶ Group Level
- ▶ Non-human Primates
- ▶ The Evolution of Cooperation
- ▶ The Evolution of Human Sociality
- ▶ Warfare
- ▶ War Raids
- ▶ Within-Group

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