Social animals have to make a multitude of group decisions on a daily basis. At the most basic level, this will involve coordination of activities and travel directions. In groups of insects, birds and fish, much of this ‘coordination’ can be the result of relatively simple interaction patterns among group members. Such systems are self-organizing, and often do not require specific leaders, or followers. However, in more socially complex groups, achieving collective group action—a consensus—may not be accomplished by simple rules alone. Instead, a consensus may be reached by the averaging of preferences (democracy), or by following the choices of specific leaders (despotism). In this mini-review, we discuss the conditions necessary for despotism in animal groups, and focus upon new studies investigating coordinated actions in primates. We ask how specific leaders arise and why others follow them—providing new insight into the mechanisms of effective leadership in groups characterized by strong social relationships.

Introduction

Colonies, schools, flocks, herds and troops—the formation of groups is a universal phenomenon in the Animal Kingdom. Such incredible diversity of sociality has intrigued behavioral and evolutionary biologists, and there is a rich and diverse literature that strives to explain the origins and maintenance of group living. We now know much about the relative costs and benefits of grouping in animals, yet for individuals to maximize the benefits and minimize the costs of grouping, they are required to be at least partially coordinated in their activities and travel directions. At the most fundamental level, this requires that different group members do not undertake such divergent activities as to compromise group cohesion; for example, by initiating a foraging journey while the rest of the group remains at a sleeping site. Group-living animals must therefore co-ordinate to act in unison. Acting in unison can nevertheless be costly to individuals if it requires them to postpone an activity that would be personally more profitable in order to do what the rest of the group is doing. This scenario will be more common in more stable social groups which can be particularly heterogeneous as a consequence of individual variation in dominance, relatedness, internal state and levels of information. In such groups then, coordinated behavior and group cohesion requires individuals to be constantly balancing their desired actions and behaviors with that of their neighbors. Ultimately, it is expected that the resulting cost of such ‘balancing’ will influence an individual’s decision to remain in the group. Where between-individual variation in the timing of activities becomes too large then animals may not be able to reach a consensus on their activities and their coordination breaks down. So how do group-living animals coordinate themselves under such conflicts of interest, and make (group) decisions?

Coordinated Behavior from Simple Rules

Examining the problem of coordinating periods of foraging and resting, models by Rands and colleagues provide a straightforward resolution to the problem of group coordination where individuals’ interests differ. They use a game-theoretic, state-dependent, individual-based approach to model the foraging behavior of a pair of animals. Their models predict that differences in the energetic reserves of the two players spontaneously develop, as a result of stochastic processes, leading them to adopt different behavioral roles. The individual with lower reserves tends to emerge as the leader, since the individual with the higher reserves will always prefer to minimize predation risk by foraging only when the other player is doing so. However, this approach only considers small groups (two animals), and while the effects of the decision rule derived from this model have been explored in larger groups, these studies have not specifically addressed the question of how groups reach a consensus, on the timing of activities and travel directions for example. For this, alternative approaches are needed.

Much of the coordination in the timing of activities and travel directions evident in biological systems can be the result of relatively simple interaction patterns among group members. In such ‘self-organizing systems’ multiple individuals following simple movement rules can produce complex collective behaviours. Such emergent collective behaviors can therefore be explained without invoking complex decision-making abilities at the level of the individual. But whilst self-organizing models can be usefully applied to a variety of group behaviors and in many study systems, such models tend to work best where groups are composed of individuals with identical interests, and which only communicate locally (i.e., between proximate neighbors). Typical examples are decisions made by eusocial insects about choosing a new nest site or by navigating birds about travel routes. For many of the groups that
we see in nature, however, individuals and their interests will differ greatly, as already discussed above.

**Decision-Making under Conditions of Conflict**

To specifically address the problem of conflicts of interest, Conradt and Roper\(^{32}\) examined consensus decisions: when the members of a group choose between two or more mutually exclusive actions, resulting in a consensus. They specifically addressed the issue of ‘consensus costs’, which are the costs (in terms of reduced fitness) of animals forgoing their own optimal action to comply with the group consensus.\(^{33}\) Thus, if there is a large conflict of interest involved in a consensus decision, the consensus costs will be equally large. They modeled two alternative decision processes. First, decisions may be made in a ‘democratic’ manner, where the average behavior of individuals is adopted. Second, decisions may be made by a single animal or minority of animals in a more ‘despotic’ manner.\(^ {16,32,53}\) Conradt and Roper’s models show that both democratic and despotic decision-making can evolve through, and be maintained by, individual selection.\(^ {16}\) However, they predict that under most conditions the costs to subordinate group members, and to the group as a whole, are considerably higher for despotic than for democratic decisions. As a consequence, they suggest that democratic decisions are more likely to evolve. Conradt and Roper’s models further indicate that democratic decisions can even evolve when groups are heterogeneous in composition; when alternative decision outcomes differ in potential costs and these costs are large; when grouping benefits are marginal; or when groups are close to, or above, optimal size.\(^ {16}\)

So does empirical evidence support these recent models? Tests of consensus decision-making in vertebrate groups have largely concentrated on decisions about travel routes or the timing of activities.\(^ {53}\) Within this body of research, evidence for both democratic and despotic decision-making has been presented, e.g., primates,\(^ {34-37}\) ungulates,\(^ {38-42}\) and birds.\(^ {13,43,44}\) Why despotsim appears at least as often as democracy in nature—contrary to theoretical predictions—remains unclear. In fact, explaining the profusion of despotic decision-making in nature presents us with a significant challenge to our understanding of sociality.

**Understanding Leadership**

New insights into the emergence of despotic group decisions in animal groups may be acquired by understanding how leaders arise and why others follow them. There are conceivably several different types of animal that might emerge as a leader. In eusocial insects, it has been shown that very few individuals within a group may actually possess pertinent information with respect to the decision in hand,\(^ {45,46}\) and thus become crucial to coordinating behavior and the decision process. In vertebrates too, a minority of informed individuals (often elders) are seen to guide entire groups to specific resources. These include golden shiner fish *Notemigonus crysoleucas*,\(^ {47}\) elephants *Loxodonta africana*,\(^ {48}\) ravens *Corvus corax*,\(^ {49}\) and broad-winged hawks *Buteo platypterus*.\(^ {50}\) Specific animals may also lead groups on the basis that they are the hungriest, or because of the feeding benefits they derive from leading groups to food resources.\(^ {51-53}\)

But the incentive or information required to create leaders does not necessarily generate following, and both processes are necessary for effective leadership. Consider long-lived and cognitively complex organisms, like primates, that display intricate social interactions.

These create higher-order properties of groups that can be studied and quantified as dominance hierarchies and social networks.\(^ {5,54}\) Given that such higher-order properties can modify individual behavior, should we expect all individuals to have an ‘equal say’ where group coordination and decision-making is concerned sensu Conradt and Roper?\(^ {32}\) Concerning dominance, high-ranking individuals are known to hold a particularly strong influence over the behaviors of group-mates.\(^ {55,56}\) Where members of families (or matriline) coexist together, specific individuals may also have a larger influence according to the relative number of kin relations (i.e., size of matriline).\(^ {57-59}\) Similarly, given the amount of time invested in social relationships, and the established importance of social networks to individual fitness (for example see Silk et al.\(^ {60}\)), individuals with stronger and/or more social bonds within groups may be in a better position to generate follower behavior. The influence of social relationships can therefore not be ignored, and their critical role has been highlighted by a number of recent studies on primates.

**Looking for Leaders**

Sueur and Petit\(^ {61}\) used network metrics (Fig. 1) to assess what rules may underlie follower behavior in two macaque species: rhesus macaques (*Macaca mulatta*) and Tonkean macaques (*Macaca tonkeana*) living in semi-free-ranging conditions. Rhesus macaques are a highly hierarchical and nepotistic species, whereas Tonkean macaques are often more tolerant and egalitarian in nature.\(^ {62}\) Sueur and Petit examined the organization of group members when joining a movement initiated by a first individual, and found the way macaques joined a movement reflected the two species’ differing social systems. Older and more dominant male rhesus macaques were more often at the front of the movement. In contrast, Tonkean...
macaques exhibited no specific order. Interestingly the researchers also found that rhesus macaques preferred to follow high-ranking or related individuals, whereas Tonkean macaques’ follower behavior reflected only male-female sexual relationships. These observations suggest that dominant rhesus macaques, which were at the front of the movements observed, have an especially strong influence over group-mates behavior, and can be described as leaders that elicit follower behavior.  

A recent study by King et al. confirm Sueur and Petit’s prediction that social relationships can have a large influence upon an individual’s ability to act as a leader, and dictate the behavior of group mates. King et al. presented two wild baboon groups with experimental food patches within their home ranges. In the experimental patches, food intake amongst group members was highly skewed so that a minority of (dominant) group members acquired a lot of food, while the majority of (subordinate) group members obtained very little (if any). In contrast, in natural patches, individual food intake was relatively evenly spread across group members. Thus, King et al. predicted that only if dominant individuals were able to act as leaders, and elicit follower behavior from subordinates, would groups choose an experimental over a natural food patch. This is because the majority of group members would incur substantial consensus costs (see above) from this decision. If however, the dominant individuals were unable to dictate group decisions—and act as leaders—then groups were predicted to choose natural patches over experimental patches. Remember that theory predicts that under these circumstances groups should move to the natural patch, which benefits the majority of group members and minimizes overall consensus costs. What King et al. observed was that their baboon groups consistently visited experimental patches in preference to natural patches. What is more, the dominant male consistently led his group to the experimental patches (Fig. 2), and the individuals that followed him most closely were those with whom he shared the strongest social bonds (as indexed by grooming interactions). They also noted that coercion by dominants did not play a role in this choice.

Such leadership behavior is puzzling, because selection is predicted to favor equally shared decisions over dominant decisions under a wide variety of conditions. What Sueur and Petit observed, and King et al. showed experimentally, was that social ties appear key to such patterns of behavior. So why should the desire to follow an individual of high social status be so strong? King et al. suggest that for their baboons, close association with the dominant male may provide females and their dependent offspring with direct fitness benefits, such as increased infant survival and protection from predators. In effect, it is worth experiencing the short-term costs that might ensue from following, because the long-term benefits of association with the leader should outweigh these. Thus far, theoretical models have not considered the importance of social ties in group decision-making and in the emergence of leaders in groups. These recent studies of primates, and observations of other taxa too, e.g., zebra, suggest that this may be a fruitful avenue of investigation in the future.

Outlook

Theoretical developments tackling the topic of leadership and group decision-making have blossomed in recent years, and whilst empirical studies of insects tackling the subject have often matched these developments, work on vertebrate groups has been less productive. There are several reasons for this. One is that it can take many months or even years to investigate the complex aspects of leadership and group decision-making that these theoretical models tackle. Another is that such studies are often limited by small sample sizes (in terms of the number of groups they are able to study), often due to the difficulty of studying vertebrate groups, which may be shy of observers and range over large areas. However, the outlook for future research in this field looks promising. For example, we believe that studies of captive and semi-wild populations can provide enormous scope for investigating the role of certain individuals in group-level behavior. Flack et al. carried out experiments in captive pigtailed macaques, in which high-ranked individuals were temporarily removed. They found that their removal was associated with dramatic reductions in the size and connectivity of social networks, which effectively de-stabilized the social groups. It might well be possible to design similar experiments to investigate the role of certain individuals in maintaining group coordination and directing collective actions. Field-based studies in this subject will now surely advance too, given technological developments. For instance, Global Positioning System (GPS) tracking of individuals...
will allow continuous sampling of multiple individuals' movements in real-time. Combining these data with social network analyses will allow researchers to examine the role of social interactions in shaping the spatial properties of groups and the importance of specific individuals in leading groups to resources in their environment.

What we have learned is that there is a need to understand how social interactions can shape group-level patterns of behavior in vertebrate groups, and how they regulate the basic coordination of multiple individuals. We hope that this mini-review will help stimulate other researchers to explore these issues in a variety of new species and study systems, and we eagerly anticipate their findings.

Acknowledgements
Andrew J. King gratefully acknowledges support from an AXA Postdoctoral Fellowship and a Natural Environment Research Council (NERC) Studentship.

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