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The Functions of Leadership and Followership:

Evolution and Group Dynamics

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Abstract

We suggest that adaptations designed for leadership and followership are the product of selection pressures associated with coordinating behavior with conspecifics. By considering the possibility that adaptive problems faced by our ancestors can be understood as different types of coordination games, we speculate that there might be a number of distinct and distinguishable adaptations associated with equilibrium strategies in these games. This evolutionary perspective might be valuable for integrating diverse research findings across disciplines in the context of the omnipresence of leader/follower dynamics in human and nonhuman groups.

The Functions of Leadership and Followership:

Evolution and Group Dynamics

Anthropologists have identified leadership as a human universal (Boehm, 1999; Brown, 1991). In his analysis of the anthropological evidence for a range of universal human social behaviors, Brown (1991) – using his fictitious Universal People (UP) as a vehicle – says that "[t]he UP have leaders, though they may be ephemeral or situational. The UP admire, or profess to admire, generosity and this is particularly desired in a leader. No leader of the UP ever has complete power lodged in himself alone. UP leaders go beyond the limits of UP reason and morality. Since the UP never have complete democracy, and never have complete autocracy, they always have a de facto oligarchy" (Brown, 1991; p. 138).

This description resonates with the literature in social psychology, which suggests that whenever individuals come together to form a group, a leadership structure quickly emerges (Bass, 1954). However, despite leadership's crucial role in sociality and the enormity of the research directed at understanding it, there exists no overarching theoretical structure that organizes the wealth of thought and empirical evidence gathered on this topic (Chemers, 2000; Yukl, 1989). As Hogan and Kaiser (2005) note "The academic tradition [in the study of leadership] is a collection of dependable empirical nuggets, but it is also a collection of decontextualized facts that do not add up to a persuasive account of leadership" (p. 171). Here, we present a set of ideas grounded in the theory of evolution (Darwin, 1859) in a tentative attempt to integrate the massive body of empirical data into a coherent conceptual framework (for a set of related ideas and a more thorough review, see Van Vugt, in press).

Leadership and Followership in an Evolutionary Framework

Leadership and followership have been defined in a great many ways in the literature (Bass, 1990). Two common construals of leadership are, first, as an individual difference variable (Stogdill, 1974) and, second, the outcome of strategic interactions among rational actors (Hollander, 1985). With deference to the thought that has gone into the research traditions from which these definitions emerge, we introduce here a set of definitions that diverge from these and are, unlike the predecessors, decidedly adaptationist in nature. In particular, we take leadership and follower behaviour to be the product of cognitive adaptations designed to solve adaptive problems humans faced throughout evolutionary history. In this case, these problems are associated with particular features of humans' social and physical environment (Barrett, Dunbar, & Lycett, 2002; Schmitt & Pilcher, 2004; Tooby & Cosmides, 1992).

Leadership is defined here as *design for inducing others to coordinate their actions or goals with that of the individual, the leader, to foster the leader's proximate goals. Followership* is defined as *design to coordinate one's actions or goals with that of another individual -- the leader -- in order to foster the leader's proximate goals*.

There are a few important aspects to these definitions. First, by defining leadership and followership in terms of design, cases in which individuals accidentally coordinate their actions with one other are not included in the definition. For example, a broken down car blocking the road forces other drivers to take a different route, but this is not leadership. The focus on design rather than behaviour correctly excludes "accidental" coordination and emphasizes that evidence for leadership and followership will be in the form of evidence of special design of the associated cognitive adaptations (cf. Tooby & Cosmides, 1996)

Second, rather than being a generic source of social influence like status or prestige (Henrich & Gil-White, 2001), leadership involves specifically the solution to a coordination problem (Bass, 1990; Cartwright & Zander, 1968). To illustrate, by virtue of his contributions, Charles Darwin is a person of esteem, yet it would stretch our definition to suggest that his scientific enterprise was driven by adaptations designed to coordinate others' behaviour.

Finally, the definition of followership suggests that there are adaptations designed to cause followers to adopt the goals of the leader. This can be as simple as, for example, following the leader to his or her preferred location. This does not, of course, mean that a follower is not executing a strategy that furthers that organism's ultimate or proximate goals as well. Although many definitions from the psychological literature embody the assumption that the goals of leaders and followers necessarily converge into a single group goal (Chemers, 2000; Hogg, 2001), we include the possibility that organisms can simultaneously pursue multiple proximate goals. By furthering a leader's proximate goals, followers, can be fostering their own as well. This idea is clarified in the discussion of simple two-player coordination games, below.

In certain respects, what is puzzling from an evolutionary perspective is followership. It has been argued that adaptations for striving to lead – to cause others to coordinate their actions with one's goals -- can evolve because there maybe clear advantages associated with leading (Van Vugt, in press). Yet, given what is known about the process of evolution through natural selection, adaptations designed to adopt another organism's goals stand in need of special explanation. Understanding followership adaptations is of as much, if not greater, theoretical interest than those surrounding leadership. It is, then, in some sense surprising that the origins of followership are not normally posed in the social psychological literature (Van Vugt, in press).

An Evolutionary Game Analysis of Leadership

If leadership and followership adaptations evolved for the purpose of solving coordination problems amongst organisms, we should be able to model the evolution of these traits. Evolutionary game theory provides a useful tool (Maynard-Smith, 1982). Evolutionary game theory (sometimes referred to as ESS-strategy) models social interactions as games in which strategies compete in a Darwinian fashion. In evolutionary game theory, the agents are genes which embody strategies that over the course of evolution are tested against alternative strategies and copies of themselves in terms of their fitness. Strategies (genes) spread through a population by virtue of the decision rules they adopt in relevant situations, whereas inferior strategies go extinct, and this is essentially how natural selection operates (Dawkins, 1976). If we can model leadership and followership as alternative strategies in a coordination game then we should be able to examine how well they fare in terms of relative fitness.

The simplest strategic interaction in this context is a coordination game involving two organisms, 1 and 2, who must decide between two alternatives. To make this concrete, consider the case in which the organisms must decide whether to go to waterhole A or B. Each organism is indifferent between the two waterholes, but both prefer to go to the same waterhole as the other. This coordination problem is characteristic of many social species that need to stay close to each other for safety and comfort (E. O. Wilson, 1975). The payoffs structure of this game is depicted in Figure 1. There are four cells in this game, each with two pay-offs representing the fitness outcomes of Player 1 and 2, respectively, given a unique combination of strategies. If 1 and 2 go to Hole A or B together, they receive a pay-off of one unit. If they end up at different holes, they receive a zero pay-off.

Figure 1. Coordinating Leadership

		Player 2	
		Hole A	Hole B
Player 1	Hole A	1,1*	0,0
	Hole B	0,0	1,1*

Figure 1. A simple coordination game in which payoffs (in reproductive success) are for Player 1 and 2 respectively. Equilibria are indicated with asterisks.

Selection will favour adaptations designed to execute equilibrium strategies (Descioli & Kurzban, in press; Maynard Smith, 1982), and this game illustrates how followership adaptations might emerge. If the game is played sequentially, the first player chooses randomly and the second player’s best response is to choose the hole that the first player selected. [1] The game is, in effect, sequential if organisms can signal their intentions to each other through communication; in this case, adaptations can be designed to reach the equilibrium outcomes. This situation selects for followership, whereby it is in the interest of the organism to follow whoever moves first, adopting the goal of the first mover (i.e., which hole to go to), regardless of which hole that individual chooses.

Note that this model makes no commitment regarding certain details of the leader/follower adaptations. In this example, it is easy to imagine that the leader/follower role is adopted facultatively. That is, in some cases, an organism might find itself in a position to be the first mover in such a coordination game, and in other cases, might find itself better off being the follower in such a game. This is consistent with conditional strategies models (West-Eberhard, 2003) which assume that, depending upon the parameter values, leader and follower roles are adopted flexibly by the same organisms.

It is, by the same token, not implausible that there might be adaptations in which pure strategies are coded in relatively static fashion, with the population reaching an equilibrium of varying frequencies of individuals, each of whom plays a pure strategy, sustained through frequency-dependent selection (Maynard-Smith, 1982; Wilson, Near, & Miller, 1996). This distinction between conditional and pure strategies (the latter maintained via frequency dependent selection) is analogous to the distinction in the psychological literature between state versus trait accounts of leadership (Van Vugt, in press).

A slightly more complex coordination game is depicted in Figure 2. The pay-off structure resembles the game of Leader, one of four classic 2 x 2 games identified by Rapoport (1967). In this game, Players 1 and 2 benefit from going to the same waterhole, but Player 1 benefits more than Player 2 if they go to Hole A. Such an asymmetry in the coordination benefits can derive from any number of causes. For example, Player 1 could know the way to Hole A better than Hole B (Couzin, Krause, Franks, & Levin, 2005). In any case, as in the pure coordination game, both Players prefer to go to the same hole as the other Player. However, each has a preference for a different hole.

Figure 2. Strategic Leadership

		Player 2	
		Hole A	Hole B
Player 1	Hole A	3,1*	0,0
	Hole B	0,0	1,3*

Fig. 2. The Leader Game in which payoffs (in reproductive success) are for Player 1 and 2 respectively. Equilibria are indicated with asterisks.

Unlike the first game, there is now an advantage to being the first mover. By taking the initiative, a Player creates the incentive for the other Player to adopt the first mover's preferred hole. Once the first player has committed to one hole, the follower's best response is to coordinate. The second mover profits from coordination, but not as much as the leader does. Moving first induces an iterated dominance game in which the second mover chooses the best outcome possible given the choice of the first (DeScioli & Kurzban, in press).

As circumstances change, the ability of organisms to take the initiative and move first might vary. However, there might be stable differences between players that might make it more likely that pairs end up at Hole A in a series of interactions over time. For example, there might be individual differences in activity or energy levels, in knowledge, or dominance that might make one individual be more likely to adopt the role of leader versus follower (Couzin et al., 2005).

There is another possibility for the emergence of followership in this situation, suggested by multi-level selection theory (Sober & Wilson, 1998). Although followers do less well than leaders in the Leader Game, it is also clear that aggregate payoffs are higher in the Leader Game when there is coordination. Groups with a leader-follower structure (i.e., where the pair ends up coordinating at the same hole) have higher aggregate fitness (i.e., where the pair ends up at a different hole). Thus, there could, plausibly, be a between-group selection pressure. Under the right conditions – discussed at length elsewhere (Sober & Wilson, 1998) – it is plausible that between group fitness differentials would constitute pressure against which natural selection could act. We take no strong position on this issue, but merely point out that gains from coordination lead to potentially interesting multilevel selection dynamics (see Kurzban & Aktipis, in press, for a brief discussion of finding evidence for the action of multi-level selection).

Finally, consider the game depicted in Figure 3. For Player 1, choosing Hole A is a dominant strategy because the payoffs associated with Hole A are always higher, independent of Player 2's choice. Because of this payoff structure, Player 2 cannot change Player 1's incentive such that Player 1's best response will be to choose hole B. Player 2's best response, therefore, is to "make the best of a bad situation," (Dawkins, 1976), and choose Hole A. In this game, moving first or communicating one's intentions does not matter. The dominant individual (player 1) always emerges as leader and the non-dominant as follower. This kind of leadership matches our definition in the sense that the dominant individual induces the subordinates to adopt the goals of the leader by following them wherever they go.

Figure 3. Leadership and Dominance

		Player 2	
		Hole A	Hole B
Player 1	Hole A	3,1*	2,0
	Hole B	0,0	1,3

Fig. 3. The Dominance Game in which payoffs (in reproductive success) are for Player 1 and 2 respectively. A/A is an equilibrium.

These games are obviously simplified versions of any real world situation, and are intended to give a sense of plausible incentives structures that shaped human cognitive adaptations surrounding leadership and followership. In humans, because of the ability to coordinate actions in groups of larger than size two, leadership can involve multi-party coalitions. In such groups, one individual can lead a group of organisms. The sketch here is intended as a heuristic tool for understanding leadership in dyads. We look forward to additional theoretical work generalizing from groups of size two to groups of size N.

Non-Human Evidence for Leadership

Evolutionary biologists have historically reserved the term leadership for behaviours that determine the type, timing, and duration of group activity (E. O. Wilson, 1975). In any species an important set of adaptive problems revolve around deciding what to do, when, and where. For animals living in social groups, a further complication is the presence of conspecifics. As mentioned above, it is often safer to move together as a unit, forage as part of a group, and sleep at a communal site. This favours some coordination of activity (Krause & Ruxton, 2002). This problem could be solved by one or several individuals taking the initiative and others in the group to acquiesce and follow. These sorts of problems are likely to have paved the way for the emergence of leadership and followership in many social species, including humans.

There are many examples of putative leadership in the animal behaviour literature. The waggle-dance of the honey bee that recruits hive members to visit food resources has been construed as a kind of leadership; the aerial formations of certain bird species and the swimming patterns of schools of fish are also often cited as examples of leader-follower patterns (Couzin et al., 2005; Krause & Ruxton, 2002; Lamprecht, 1996).

Because individuals hold different preferences about the type and timing of group activities, some individuals stand to benefit more than others from group coordination, and therefore have an incentive to get others to adopt their preferences. Further, individuals' preferences are likely to differ systematically. For example, some organisms might simply consume more energy and digest their food more quickly. Because they get hungry sooner, they decide the timing of the group movement, inducing others to follow them (Couzin et al., 2005).

Leading by taking the initiative is not automatically going to be effective, as the game being played is not always as simple as the ones sketched above. An interesting example is found among the nomadic Hamadryas baboons (Kummer, 1968). When they decide upon which sleeping site to move to on a given night, one individual might make a move in a particular direction. Sometimes they are followed by the rest, but sometimes they are not, in which case they are forced to return to the group and the decision processes is repeated. Individual recognition makes it possible that some individuals are more likely to be followed, based on such factors as age and knowledge.

Dominant individuals also sometimes take on leadership functions in groups. De Waal (1996) observed an example when the dominant (alpha) male in a troop of chimpanzees that he studied at Arnhem Zoo intervened in a fight: “A quarrel between Mama and Spin got out of hand and ended in fighting and biting. Numerous apes rushed up to the two warring females and joined in the fray. A huge knot of fighting, screaming apes rolled around in the sand, until Luit [the alpha male] leapt in and literally beat them apart. He did not choose sides in the conflict, like others; instead anyone who continued to act received a blow from him” (p. 129).

Boehm (1999) observed an instance of leadership displayed by the alpha male in the chimpanzee colony at Gombe. When members of this colony encountered the members of a different troop, the alpha charged towards them and the rest followed his example, until the enemy slowly retreated into their home range. Finally, there is evidence for dominant leadership among other social mammals (lions and wolves), suggesting that dominant individuals emerge as leaders more frequently in chasing prey or chasing away intruders (Heinsohn & Packer, 1995; E. O. Wilson, 1975). In these instances, dominant individuals make the first move in initiating group action. Once a leader commits to a course of action, the best move on the part of others is to follow (see Fig 3, above).

Leadership in Humans

Obviously, selection pressures that created leadership in other social species might not be the same as those observed in humans (cf. Kurzban & Leary, 2001). The above analysis suggests that in humans, the concept of “leadership” might be best understood as a constellation of adaptations designed to solve two qualitatively different types of group problems.

Coordinating Leadership

In some cases, individuals are playing relatively simple coordination games. That is, people care less about which specific action is taken than about coordinating on one action. Such cases require coordination and, hence, a coordinating leader. Real world examples have been discussed at length by Schelling (1960).

This type of leadership ties well with the literature on task-orientated leadership, which is the most common form of leadership displayed in human groups (Cartwright & Zander, 1968; Hemphill, 1950). Task leaders display activities to promote task completion, such as the coordination of group activities, assignment of subtasks, and performance monitoring (Fiedler, 1967). Leadership as coordination is also seen in highly cohesive groups in which members have very similar preferences. Cohesive groups actually do better with a randomly changing leader than a permanent leader, presumably because structural leadership creates power differences between members, which undermines group cohesion (Haslam et al., 1998; Hogg, 2001). Finally, in pure coordination problems, groups might choose one individual to make a decision on behalf of the entire group, paving the way for a highly directive, autocratic leader (cf. Peterson, 1997).

Interestingly, in pure coordination situations, leadership does not have to be granted to a person. Groups might converge on a coordination point by all following the same social norm (e.g., driving on the left; wearing a tie) or adhering to the same vision (e.g., religion, political belief). Again, Schelling (1960) is an excellent source for discussions of problems of this type.

Strategic Leadership

Strategic leadership emerges when one individual can change the payoffs of others' actions so that they are induced to assume the leader's proximate goals, even if these do not, globally, maximize the follower's outcomes. Figure 2 illustrates such a case: In such situations, there is an incentive for individuals to move first and seize the initiative.

Real world examples are not always so clean. Clearly, there are cases in which potential followers must be persuaded that coordinating on the leader’s goal is more beneficial than not doing so (e.g., Bass, 1990). This idea touches the broad literature on relational-style leadership. Relational leaders’ primary concern is to build up a good relation with followers (Cartwright & Zander, 1968; Hemphill, 1950). One form of persuasion is to be fair and generous to followers so that they expect to get what they have been promised (Boehm, 1999; Tyler & Lind, 1992). A third strategy is to develop a unique skill or competency that attracts followers. Apparently, members of task groups are very good at recognizing the strengths and weaknesses of each other (Littlepage et al., 1997). In these cases, potential followers are persuaded about the benefits of relevant choices; this stands in contrast to purely coordinating leadership, in which a leader need not worry about persuasion as it is to others’ advantage to coordinate on the selected act.

The concept of strategic leadership is of potential value in understanding interesting correlations between leadership and traits like ambition, intelligence, extraversion, sociability, empathy, and Machiavellianism (Van Vugt, in press). To emerge as leaders, individuals must think and behave strategically to influence potential followers. Having the ability to put oneself in other people’s shoes (empathy) as well as having excellent communication skills (sociability) fosters leadership. Research suggests that leadership in ad-hoc groups is granted to the most talkative group member, regardless of what they have to say (the babble hypothesis; Sorentino & Boutillier, 1975). Also, coming across as intelligent – Machiavellianists are particularly good at this (Wilson et al., 1996) -- might persuade others to give up their preferred option, following the leader instead.

Of course, not all forms of strategic interactions are equal. One way to change potential followers' payoffs is to use coercion or the threat of coercion. It is not clear the extent to which pure coercion is used as strategic leadership in humans. To achieve important adaptive goals, such as food gathering and self-protection, humans depend upon other humans (Kenrick, Li, & Butner, 2003). Human leaders often cannot achieve their goals without the voluntary support of followers. Further, comparative research suggests that human hierarchies – particularly in non-industrialized societies – are often much flatter than the nonhuman primates, where examples of dominant leadership have been obtained (Boehm, 1999; De Waal, 1996). In human, if followers disagree with their leaders, they have strategies to deal with them (Boehm, 1999). Humans also form unusually large coalitions (Dunbar, 2004), which makes it difficult for anyone individual to dominate an entire group.

The psychological literature suggests that there is a weak correlation between dominance and leadership in humans (Van Vugt, in press). It seems that people do not want to be dominated by others. If they are, they either form a coalition to turn against their leader (Boehm, 1999) or simply leave the group (Van Vugt et al., 2004). The importance of cooperation, combined with the availability of exit and voice strategies thus prevents leaders from turning into dictators (cf. Vehrencamp, 1983). This is not to say that leaders are not tempted to dominate followers. One might expect that there would be a tendency in leaders to try to dominate followers (Van Vugt & Hogan, 2005). However, this is likely to be counteracted by subversive tactics among followers (Boehm, 1999). In short, while there is no doubt that human history is replete with modern examples of coercive strategic leadership, it is not clear the extent to which this has been typical of human social groupings.

Discussion

In this chapter, we have offered an evolutionary perspective on leadership. To understand leadership, it is important to ask the previous question surrounding why individuals might have come to be designed to follow a leader. In particular, we suggested that followership adaptations emerged in order to reap the benefits of coordination in response to problems that many group-living species face.

Evolutionary Game Analysis

Our analysis of leadership heavily relied on evolutionary game theory. The evolutionary game analysis enabled us to model the evolution of leader and follower traits through identifying problems (games) that could be solved through leadership. Without attempting to be exhaustive, our analysis identified two basic forms of leadership, coordinating and strategic leadership. We first reviewed the animal literature and found some support for this distinction. Subsequently, we reviewed the human (psychological) literature to illuminate some of the conditions under which each of these leader types might develop.

Leadership and Cognition

We can offer a few speculations to make concrete our ideas surrounding the cognitive adaptations designed for leadership and followership. First, it seems plausible that there are specialized mechanisms designed to identify situations as coordination problems. It is not clear, as yet, what these adaptations would look like, but certainly such skills might look like facets of what has come to be understood under the broad umbrella of intelligence (Dunbar, 2004). Not surprisingly, psychological research shows that leadership is consistently linked with intelligence (Van Vugt, in press).

Along similar lines, coordination is tightly bound to the ability to predict others' actions. This is tightly bound to belief/desire-psychology, or what Dennett (1987) has termed the Intentional Stance. Of course, the broad literature on theory of mind and, obviously, language, are relevant for understanding how humans came to coordinate actions (Dunbar, 2004). Consistent with this interpretation, leadership is correlated with measures of empathy, verbal ability, and social skills (Van Vugt, in press).

Finally, leader-follower relationships would benefit if people are able to recognize those in the group with a particular skill, ability, or piece of information that could help them achieve a desired goal such as solving a coordination problem. Perhaps this is the underlying reason why task ability is considered to be highly important for qualifying as leader (Palmer, 1960). Furthermore, given enough experience working together, people can easily rank each other in terms of skills and knowledge (Littlepage et al., 1997).

Implications

One implication of the approach sketched here is that leadership is tightly bound to the need to coordinate. To the extent that individuals are able to determine when they are in such a context, one would expect leader/follower adaptations to be differentially activated. Second, the distinction we draw in terms of types of leadership implies that different types of leadership might be more appropriate under different conditions. Pure coordination games should be solved best by coordinating leaders while other types of games might be better suited to strategic leadership, as illustrated by the example of chimpanzees. As a corollary to this, our analysis suggests that an individual's style of leadership – whether oriented toward coordinating or strategic – might be a crucial determinant of the success of groups and their members (Sober & Wilson, 1998).

Our analysis suggests various new directions for research on leadership. One straightforward prediction is that leadership emerges more quickly when groups are under threat and there is an urgent need for coordination. Studies could also investigate the emergence of different forms of leadership in response to different kinds of threats such as an intergroup conflict or intragroup aggression (for a suitable experimental procedure, see Van Vugt et al., 2004). More research is needed to study the benefits of leadership for groups. Multi-level selection theory suggests that leadership might have evolved as group-level adaptation (Sober & Wilson, 1998). One way to test this idea is to show that groups with a functioning leader-follower structure fare better than groups without this structure. Perhaps more generally, the leadership field could benefit from developing a more integrated research agenda involving efforts from many behavioural science disciplines. Evolutionary thinking naturally lends itself to developing this agenda.

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Footnote

[1] In the one-shot simultaneous version of this game, there are equilibria in pure strategies in which each chooses the same hole and an additional equilibrium in mixed strategies in which each player chooses each watering hole with probability .5. In the third equilibrium, they reach the non-zero payoffs only half the time. For standard game theoretical discussions, which typically do not include sequential play, see Rapoport (1967). We use these games, and include the possibility of sequential play, simply to illustrate our broader points about leadership and followership.