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The Origins and Evolution of Leadership

Minireview

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How groups of individuals achieve coordination and collective action is an important topic in the natural sciences, but until recently the role of leadership in this process has been largely overlooked. In contrast, leadership is arguably one of the most important themes in the social sciences, permeating all aspects of human social affairs: the election of Barack Obama, the war in Iraq, and the collapse of the banks are all high-profile events that draw our attention to the fundamental role of leadership and followership. Converging ideas and developments in both the natural and social sciences suggest that leadership and followership share common properties across humans and other animals, pointing to ancient roots and evolutionary origins. Here, we draw upon key insights from the animal and human literature to lay the foundation for a new science of leadership inspired by an evolutionary perspective. Identifying the origins of human leadership and followership, as well as which aspects are shared with other animals and which are unique, offers ways of understanding, predicting, and improving leadership today.

Ask a crowd of 200 people to walk around just following the simple rule to stay within an arm's length of one another, and they will form a swirling mass of people moving around an imaginary centre point. Re-run this same experiment, but provide just a handful of individuals a specific target to move towards, while still adhering to the arm's length rule, and this small informed minority will lead the group of naïve individuals to the target — without verbal communication or obvious signalling [1]. This phenomenon is especially striking because the human participants' actions almost exactly correspond to the predictions of computer models designed to explore coordination in animals — such as fish shoals and bird flocks [2]. This suggests that similar coordination rules apply across taxa and highlights the role of a universal feature of animal sociality that is often overlooked: leadership and followership, where one or a few individuals steer the behaviour of many.

In 1947, biologist Warder Clyde Allee proposed that "*The scattered references to leadership in animal groups should be collected and reviewed*" [3]. Yet it has taken more than sixty years for the first review articles on leadership to appear in the animal literature and empirical data are still scarce [1,4]. In contrast, there are many studies on leadership in the social science literature [5,6], but these tend to focus on proximate questions about leadership (e.g., what makes a good leader?) and generally lack insight into the origins and adaptive functions of leadership. As we will demonstrate with examples from the animal and human literature, biological, social and psychological approaches to leadership have much in common and an integrated evolutionary perspective offers a more complete picture as well as a scientific grounding that would advance leadership research across disciplines.

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Games Leaders Play

Key to the emergence of leadership and followership is the need to coordinate. In species where individuals are better off acting and moving together — predominantly as a consequence of social and ecological pressures [7,8] — leader–follower patterns are likely to emerge [1,9,10]. Leader–follower patterns emerge not only during coordinated group movements, but also during other group activities, such as hunting, deterring predators (mobbing), teaching, internal peace-keeping and dealing with other groups.

A simple two-player 'coordination game' illustrates that, in many situations, leadership is almost inevitable (Table 1). Imagine a pair of individuals with two simple goals: one, to stick together for protection, and, two, seek resources such as food patches and waterholes. Two mutually exclusive options are available, patch A or B, and they will get the same pay-off at each one. In this situation, any trait (physical or behavioural) that increases the likelihood of one individual moving first will make them more likely to emerge as the leader, and the other player is left with no option but to follow. Furthermore, if this trait difference between players is stable — for instance, if player 1 is always hungry first — then a stable leader–follower pattern will emerge over time. This two-player game can be easily generalized to a multiple player game where one or a few individuals are able to coordinate a large group [9].

Things get more complicated when we introduce conflict, which is common in most species that form stable social groups. For instance, player 1 prefers food patch A over B and the reverse is true for player 2. In this 'battle of the sexes' game (Table 2), consensus is more difficult to achieve because whichever patch they coordinate on, the players end up with unequal pay-offs. Thus, there is an incentive to be the leader as each player wants to maximise its own pay-off. In the real world, such payoff differences are likely to arise as a result of heterogeneity of interests due to sex, age, size or reproductive status. Research with humans shows that if either the coordination or battle-of-sexes games are played with simultaneous decisions (both players make their decision at the same time), pairs often fail to coordinate. Yet, if played sequentially, they are easily solved, although the conflict over who goes first remains in the latter. Crucially, the greater the payoff difference between the players, the harder it is to achieve coordination [9].

Other game theoretical models such as the 'producer-scrounger' game [11] provide insight into the frequency-dependence of leader and follower behaviours. These models assume that resources (food, mates, or more

Table 1. Pure coordination game where leader and follower roles can be adopted flexibly.

		Player 2	
		Lead	Follow
Player 1	Lead	0, 0	1, 1
	Follow	1, 1	0, 0

generally, information) can be acquired by two alternative tactics: individuals can invest effort in searching for their own resources — the producer/leader tactic, or exploit the resources that have become available from the leaders' efforts — the scrounger/follower tactic. Models assume that the use of each tactic is frequency dependent. That is, scroungers do well when they are rare, because they have the opportunity to exploit the efforts of a large number of producers. However, as the number of scroungers increase, they must compete for the resources made available by a diminishing number of producers. Thus, the solution to the game is a stable equilibrium frequency of each tactic, and individuals should adjust their behaviour according to what others are doing. In other words, if there are many followers, an individual should take the lead, since it will pay to do so. Despite the generality of the producer-scrounger game, it has seldom been applied to understanding the emergence of leader–follower behaviour, and we encourage more researchers to consider this well-developed framework to understand the evolution and prevalence of leadership in humans and other animals, e.g. [12].

Who Leads?

Across species, individuals are more likely to emerge as leaders if they have a particular morphological, physiological, or behavioural trait increasing their propensity to act first in coordination problems.

Motivation

First, those individuals most in need of a particular resource are more likely to be the leader. Rands *et al.* [13] developed state-dependent individual-based models predicting that for pairs of foraging individuals the one with the lower energy resources spontaneously emerges as a leader and thus coordinates foraging. This is supported in empirical research. Food-deprived fish take the front position in shoals where they have a stronger influence on movement direction as they maintain a larger inter-social distance [14], and females in energetically demanding reproductive states often assume the leading positions in e.g. zebras [15], lemurs [16] and gibbons [17]. More mechanistic models of coordinated action in larger groups suggest that specific individuals — for whom reaching a particular destination is crucial or group cohesion is least important — can direct group movement patterns [18]. Similarly, leadership in humans is often determined by whoever has the greatest incentive to move or the one who is least concerned about the interests of others. Indeed, leadership correlates strongly with both ambition and autonomy traits [9].

Table 2. Coordination with conflict where one individual has to 'persuade' the other to follow if the pair is to remain together.

		Player 2	
		Lead	Follow
Player 1	Lead	0, 0	2, 1
	Follow	1, 2	0, 0

Temperament

Correlations between leadership and temperament are well documented in the animal and human literature. Intraspecific differences in temperament (or personality) have traditionally been assumed to be non-adaptive variation surrounding adaptive population-average behaviours. However, it is argued that such personality differences may reflect stable phenotypic or even genotypic variation [19]. In a recent experiment in which pairs of sticklebacks coordinated their foraging excursions to a food patch, personality differences were crucial for achieving coordination. Bold fish emerged as leaders and shy fish emerged as followers, and these differences were enhanced by social feedback, that is, bold leaders inspired faithful followership, and shy followers facilitated effective leadership [20]. A review of the human literature shows that extraversion correlates highest with leadership emergence, and this trait — an indication of boldness — has a substantial heritable component [21]. Furthermore, experiments show that the most talkative member of a group often becomes the group's leader, more or less regardless of the quality of their inputs — this is referred to as the 'babble effect'. The consistent correlation between leadership and personality across taxa suggests the intriguing possibility that personality differences are maintained in populations because they foster social coordination.

Dominance

In species with dominance hierarchies, dominant individuals often take on leadership roles. Gorillas [22] and wolves [23] are commonly cited examples for leadership being correlated with dominance. Despite these correlations, in many cases dominant individuals lead not because they enforce followership. Instead, dominants operate more autonomously (given their superior body size, or access to resources) and are in a better position to elicit followership since they hold a particularly strong influence over the behaviours of group-mates and have an established importance within social networks [24]. A study with wild baboons supports this, showing that alpha-males consistently lead groups to specific food sources where the most individuals in the group get little or no food, but at which the alpha-leader enjoys a hearty meal because he can monopolise the food source [25]. This constitutes a situation in which there is a conflict of interests and one would expect individuals to be reluctant followers. However, leaders did not incite following through coercion or punishment, instead, close followership was correlated with strong grooming relationships, that is, the alpha-males' close 'friends' followed most dependably. Similarly, correlations between leadership and dominance are also present in humans, although dominance is usually measured in terms of social status rather than by the result of agonistic interaction [26]. The fact that human males score higher in dominance and self-confidence assessments than females in psychological surveys may help to explain why male leadership is (still) the norm in most human societies [27].

Knowledge

Finally, having some unique knowledge or expertise increases the likelihood of an individual emerging as leader

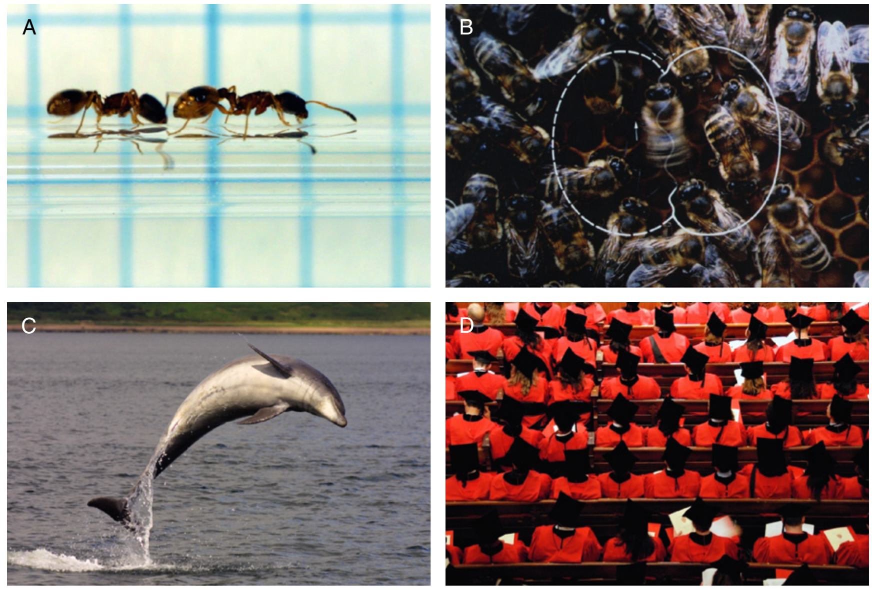

Figure 1. Follow me: What are the mechanisms?

(A) Tandem running in ants, the ant on the left is following the other to a known food source, and is led via tactile communication. Image courtesy of Tom Richardson and Nigel Franks. (B) Honey bee 'waggle' dance (indicated by the white lines) signalling the location and quality of potential nest sites to colony members. Image courtesy of Jürgen Tautz and Marco Kleinhenz. (C) Side-flop display by an informed lead dolphin, used to coordinate shifts in activity patterns in group-mates. Image courtesy of Susan and David Lusseau. (D) Graduation ceremony at Harvard University, led by music, hierarchical costumes, a myriad of signals, and ritualised ceremony. Image courtesy of Dominic Johnson.

and attracting an enthusiastic following. In golden shiner fish [28] and ravens [29], individuals with superior information can guide groups to attractive resources, elephant herds appear to benefit from old females' memories of distant waterholes during droughts [30], and broad-winged hawks line-up behind their elders during migration [31]. Research on humans also shows that age correlates with leadership in domains that require considerable specialised knowledge and training, but not in domains that require risk-taking and physical bravery [9]. Moreover, humans are extremely good at estimating the expertise of other individuals even in newly formed groups and knowledgeable individuals often emerge as group leaders [12].

How to Lead

So far, we have described who leads groups, but how do they do so? On the one hand, leadership can be entirely passive and occur as a consequence of the emergent properties of the group. For instance, where individuals possess pertinent information, they need not necessarily actively communicate this knowledge to group-mates to assume leadership roles. Instead, leadership can emerge simply as a function of information differences among members when individuals apply simple and local heuristics such as: 'move away from very nearby neighbours', 'adopt the same direction as those that are close by', and 'avoid becoming isolated' [2,32]. Moreover, for sufficiently large groups only a very small proportion of informed leaders is needed to achieve close to maximal accuracy [1,2]. Such *laissez-faire* leadership is perhaps most common in large homogenous groups, such as insect swarms, fish schools, bird flocks and human crowds, where individuals have little or no significant conflict of interest [33]. However, where conflict does occur, theoretical models and experiments with human crowds predict these groups to almost always decide in favour of the majority preference. Thus, if only a few leaders possess valuable information in the first place, just one more informed leader can have a decisive role in the collective action of the entire group [1,2].

On the other hand, mechanisms can involve active leadership, where potential leaders explicitly signal their intention to group-mates, who can choose to follow, or not. This, too, can occur at a local scale, that is, between local neighbours. In ants (*Temnothorax albipennis*), individuals who have learnt the route to feeding sites use 'tandem running' to lead another ant from the nest to food — with signals between the pair of ants controlling both the speed and course of the run (Figure 1A) [34]. In migrating honeybee colonies, leaders play a role in a two-part process that involves deciding where to go, and then guiding the swarm to the selected site. Specifically, lead individuals (scouts) recruit followers using 'dances' that inform proximate colony members on the location of new nest sites (Figure 1B) [35,36]. However, as there are likely to be costs associated with increasing the proportion of informed individuals (specifically, costs in terms of time: as a result of recruiting followers via dancing, and learning navigation skills), only about 5% of the bees participate in deciding where to go. Rising body temperature of the bees and vibration signals then stimulate the swarm to become airborne, and the leading scouts guide the colony to the chosen site [36].

Explicit signalling and active leadership can also operate at a global scale, via communication with all group members. Ravens with information about the location of high quality food sources can direct individuals from roosting sites through a series of acrobatic display flights [29], whilst knowledgeable dolphins precipitate shifts in the behaviour of the entire group through visual displays (Figure 1C) [37]. In non-human primates, there too is an abundance of vocal and visual signals used by aspiring leaders to initiate group movement, e.g. [38]. Global communication signals are very well developed in humans, with facial expressions, gestures, rituals, and complex language serving to synchronize group activity and transmit desires or demands [39]. Group leaders, such as priests, politicians, soldiers or conductors, use a variety of signals to foster group coordination (Figure 1D) [40].

In the case of active leadership, followers need to agree with leaders to achieve coordinated group action [32,41]. In some species followers accept the decision of a specific individual on a regular basis (despotism); while in others almost any individual can, in principle, elicit followership (democracy). In each case, individuals must agree with leaders on a particular course of action if conflict is to be avoided; in the case of democratic leadership, this can be achieved via a majority vote, or when a threshold number of followers agree with a potential leader's proposal [41]. How leadership is distributed in social species may affect the selection pressures on individuals [42,43], their contributions to coordination and cooperation activities [44,45], the structure of social groups [46] and the dynamics of populations [24]. In fact, there is considerable debate as to whether human groups are essentially democratic and egalitarian or despotic and hierarchical given that the former is more common among hunter-gatherer societies while the latter is evident throughout recent history [47–49].

The Role of Leaders in Cooperation

The evolution of cooperation remains a puzzle because collective action can be easily undermined by free-riders, individuals who reap the benefits from others' efforts without contributing anything themselves [45]. It is unclear how cooperation can evolve without some facilitating mechanism. One potential solution to the free-rider problem is punishment. However, because punishment is itself a costly act, a credible threat of punishment is well-established, both theoretically and empirically, as an effective method of achieving cooperation because it increases the costs of free-riding [50]. A major debate remains about who carries out the punishments.

Several authors have resorted to cultural or group selection explanations [51]. But, one possibility that has not yet been considered in the cooperation literature is that specific individual leaders may be willing to bear the costs of punishment in return for access to status, resources or reproduction. Indeed, high levels of cooperation can be achieved with just one designated individual acting as a sole arbiter of punishment [52] (Figure 2). This is striking for two reasons. Not only can a single individual promote high levels of cooperation, but when punishment is restricted to a leader, all individuals do better because fewer group-mates suffer the costs of administering punishment [53].

This solution is supported by observations of primate groups in which dominant individuals often play a central role in organizing group action but unlike our examples so far, they achieve this via top-down leadership. Alpha-male chimpanzees and male hamadryas baboon harem leaders play a disproportionate role in peacemaking and conflict resolution, exacting direct costs on those who fail to cooperate [54,55], and the temporary removal of high-ranked pigtailed macaques has been shown to de-stablise groups [56]. Leadership, therefore, represents a simple solution to the problem of collective action [57], and may play a central role in the evolution of human cooperation but one that has been largely overlooked in the cooperation literature.

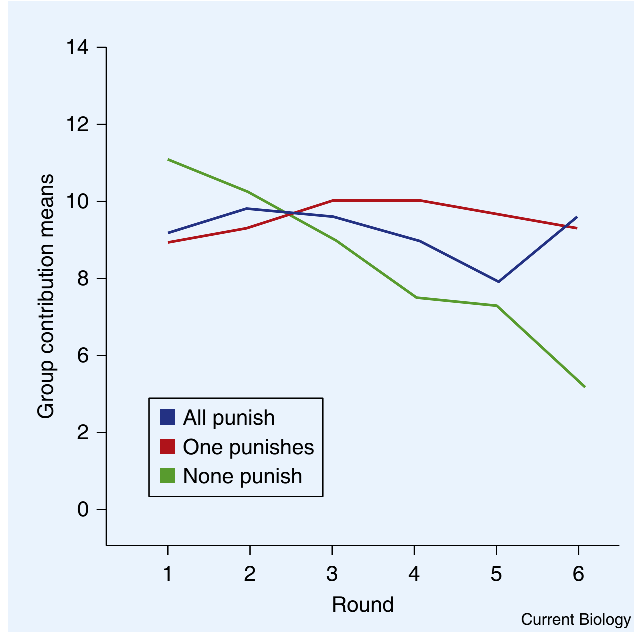

Figure 2. Solving the free-rider problem through leadership.

The graphs show results of an experiment in which human participants (n = 136) played a standard public goods game (in groups of 4 players) that precisely replicated that of Fehr and Gachter [51] (each subject was allocated an endowment of 20 monetary units for each round, of which they could invest any amount into a group fund and retain the remainder; each monetary unit invested in the group fund yielded a payoff of 0.5 monetary units). In each round, groups were randomly re-formed so that participants did not know with whom they were playing and their decisions were anonymous. The first stage consisted of six rounds of a standard public goods game (not shown). In the second stage (shown in the figure) there were three groups: 'None punish' (blue line) was a standard public goods game; In 'All punish' (red line), individuals could simultaneously make deductions from each other by paying a fee, drawn from their earnings for that round, up to a maximum of 10 MUs per punished member; 'One punishes' (green line) was the same as 'all punish' except that just one group member was randomly selected to be the designated punisher in each round. The striking result is that a single punisher was able to maintain almost same level of cooperation as everyone punishing in Fehr and Gachter's [51] famous experiment. Y-axis depicts mean contribution of monetary investments to group fund by participants. Figure adapted from [52].

The Evolutionary Origins of Leadership

The role of leadership in solving both coordination and collective action problems involving varying degrees of conflict allows us to speculate about the scale and importance of leadership in human evolution. Human leaders not only initiate group action but also motivate, plan, organise, direct, monitor, and punish to achieve group action. They may lead democratically or despotically, from the front or from the back, and lead small or very large groups. How do we account for the unparalleled scale and complexity of human leadership? Although there are phylogenetic consistencies between human and non-human leadership, the expansion of the human brain and the associated increase in human group size has created a unique selection environment for human leadership [10]. A review of the human and nonhuman leadership literatures suggests at least five major transitions in the evolution of human leadership: (1) leadership emerged in pre-human species as a mechanism to solve simple group coordination problems where any individual initiated an action and others followed [13,18]; (2) leadership was co-opted to foster collective action in situations involving significant conflicts of interest such as internal peacekeeping in which dominant or socially important individuals emerged as leaders [9,10]; (3) dominance was attenuated in early human egalitarian societies which paved the way for democratic and prestige-based leadership facilitating group coordination [47]; (4) the increase in human group size selected for powerful social-cognitive mechanisms, such as theory of mind and language, providing new opportunities for leaders to attract followers through manipulation and persuasion [58,59]; (5) the increase in social complexity of societies that took place after the agricultural revolution produced the need for more powerful and formal leaders to manage complex intra- and intergroup relations — the chiefs, kings, presidents, and CEOs — who at best provide important public services and at worst abuse their position of power to dominate and exploit followers [60].

How to Utilise Leadership Research

Today, human societies continue to rely heavily on political, economic, military, professional, and religious leaders to function effectively. Yet the consistently high rate of leadership failure — managerial incompetence accounts for 60–75% of business failures in corporate America [61] — suggests that new approaches may be useful in understanding when and why human leadership succeeds or fails.

First, research into the fundamental principles behind leadership and followership can be used to craft effective leadership practices. Evolution has fashioned these principles over many million years of trial and error, and we should take account of Nature's own lessons on what works best in different contexts. For instance, coordination and cooperation do not necessarily need to be imposed from above. Individuals can willingly take on leading and following roles and self-organize, given the right incentives and environment. Second, future research offers the opportunity to ground the complex (even apparently mystical) social phenomenon of leadership and followership in science. We can use empirical observation, theoretical models, neuroscience, experimental psychology, and genetics to reverse engineer the ingredients of good leadership. Third, exploring the development, proximate mechanisms and adaptive functions of leadership and followership may reveal practical advice for profiling, recruitment, selection, and management. Finally, a cross-taxa examination, and an evolutionary perspective on leadership can identify potential "mismatches" between how evolved mechanisms of leadership map onto our relatively novel social environment [10]. For example, modern human leadership still correlates with age, sex, height, and weight even though there is little evidence that these attributes still matter in today's world — perhaps a hangover from our evolutionary past [12]. The lens of evolution highlights where our adaptations for leadership will dovetail with contemporary challenges, and where they will go awry, thereby offering practical goals for effective leadership in the modern world.

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