# Leadership, Followership, and Evolution 

Some Lessons From the Past

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This article analyzes the topic of leadership from an evolutionary perspective and proposes three conclusions that are not part of mainstream theory. First, leading and following are strategies that evolved for solving social coordination problems in ancestral environments, including in particular the problems of group movement, intragroup peacekeeping, and intergroup competition. Second, the relationship between leaders and followers is inherently ambivalent because of the potential for exploitation of followers by leaders. Third, modern organizational structures are sometimes inconsistent with aspects of our evolved leadership psychology, which might explain the alienation and frustration of many citizens and employees. The authors draw several implications of this evolutionary analysis for leadership theory, research, and practice.

Keywords: evolution, leadership, followership, game theory, mismatch hypothesis

Why is leadership important? During times of peace and prosperity, it seems not to matter. However, when politicians start wars, when business leaders gamble with our life savings, and when religious leaders create violent sectarian divides, leadership becomes a matter of life and death.

We know a lot about leadership (Bass, 1990; House \& Aditya, 1997; Yukl, 2006). It is a universal feature of human societies and affects the quality of life of citizens in important ways (Brown, 1991; R. Hogan, Curphy, \& Hogan, 1994). When people are placed in ad hoc laboratory groups, leader-follower structures quickly emerge (Bales, 1951; Mann, 1959; Van Vugt \& De Cremer, 1999). Humans easily recognize leadership potential in others (Lord, DeVader, \& Alliger, 1986). People also romanticize leadership; we often attribute great importance to leaders even when it is not warranted (Hackman \& Wageman, 2007; Meindl, Ehrlich, \& Dukerich, 1985). Leadership is an unavoidable theme in society and arguably the most important problem in the social sciences.

Although the leadership literature is enormous, it lacks an integrative theoretical framework that can make sense of the richness of the data (Chemers, 2000; R. Hogan \& Kaiser, 2005). There are several reasons for this. First, the literature contains many useful mid-level theories that are not very well connected (Bass, 1990; Yukl, 2006).

Second, the literature focuses on leaders and tends to ignore the essential role of followers (Hollander, 1992; Yukl, 2006). Third, research largely concentrates on proximate issues of leadership (e.g., What makes one person a better leader than others?) and rarely considers its ultimate functions (e.g., How did leadership promote survival and reproductive success among our ancestors?) (R. Hogan \& Kaiser, 2005). Finally, there has been little cross-fertilization between psychology and disciplines such as anthropology, economics, neuroscience, biology, and zoology, which also contain important insights about leadership (Bennis, 2007; Van Vugt, 2006).

This article offers a view of leadership inspired by evolutionary theory, which modern scholars increasingly see as essential for understanding social life (Buss, 2005; Lawrence \& Nohria, 2002; McAdams \& Pals, 2006; Nettle, 2006; Schaller, Simpson, \& Kenrick, 2006). We argue first that an evolutionary approach to leadership raises some important new questions. Next we analyze the implications of leader-follower relations in early human and nonhuman societies for theories of leadership. We use (evolutionary) game theory to model the emergence of leadership; this model is followed by a hypothetical account of how leadership developed over four stages of evolutionary history. We conclude with some novel implications of this analysis for leadership theory, research, and practice.

## An Evolutionary Analysis of Leadership

Researchers define leadership in many ways (Stogdill, 1974). We define it broadly in terms of (a) influencing individuals to contribute to group goals and (b) coordinat-

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ing the pursuit of those goals (cf. Bass, 1990; Hollander, 1992; Yukl, 2006). We think pragmatically of leadership as building a team and guiding it to victory (R. Hogan et al., 1994). Leadership is both a resource for groups and an attribute of individuals, but we believe that its primary significance concerns group performance (R. Hogan \& Kaiser, 2005; Kaiser, Hogan, \& Craig, 2008). Given the fitness and reproductive benefits associated with social status (Betzig, 1993; Buss, 2005; Chagnon, 1997), the "selfish-gene" view of evolution (Dawkins, 1976) suggests that everyone should strive to become a leader. From this same perspective it is not obvious why some would voluntarily subordinate themselves. Researchers rarely consider the origins of followership, but the topic is central to an evolutionary analysis.

Although Sigmund Freud, William James, William McDougall, and E. L. Thorndike were enthusiastic Darwinians, evolutionary thinking fell out of favor in mainstream psychology for most of the 20th century (Pinker, 2002). It is now returning in the form of evolutionary psychology. Evolutionary psychology proposes that the mind is composed of mechanisms, called psychological adaptations, that were favored by natural selection because they solved adaptive problems faced by our ancestors. Examples of such mechanisms include mating strategies, cheater detection, status sensitivity, and language (Barkow, Cosmides, \& Tooby, 1992; Buss, 2005; Schaller et al., 2006; cf. Darwin, 1871).

Evolutionary psychologists use Tinbergen's (1963) four functions model to analyze psychological adaptations. This framework first asks about the proximate functions of a mechanism. For leadership we can ask what kind of people make good leaders, a question that interests social, industrial/organizational, and applied
psychologists. The second question concerns ontogenesis: When do leader-follower patterns emerge in the life span? Does developmental history predict leadership propensity? Developmental, personality, and educational psychologists are interested in these issues. The third question concerns phylogenesis: When did leadership emerge in our species, and are there parallels in other species? This question concerns comparative psychologists, anthropologists, and zoologists. Finally, there is the question of the ultimate (evolutionary) functions of a mechanism, a question that interests evolutionary psychologists and biologists: Did leadership promote the survival of our forebearers so that it became part of our evolved psychology?

Each of Tinbergen's (1963) functions analyzes leadership from a different perspective and should be kept distinct. For instance, functional theories assume that leadership involves identifying obstacles between groups and their goals and then finding ways to overcome those obstacles (Hackman \& Walton, 1986; Lord, 1977). These theories offer proximate explanations for why particular leaders are effective in particular circumstances. They can be complemented with an analysis of the functions of leadership in ancestral environments, which may explain why and how the role of leadership evolved in the first place.

## Human Evolution, Group Life, and Leadership

Humans evolved as group-living animals (Baumeister \& Leary, 1995; D. T. Campbell, 1975; Darwin, 1871). The genus Homo is estimated to be about 2.5 million years old, and for most of their existence, hominids lived in small, kin-based bands on the African savannah, adopting a nomadic hunter-gatherer lifestyle. Group living allowed our ancestors to cope with an environment well supplied with predators but poorly supplied with shelter, water, and food (Foley, 1997; E. O. Wilson, 1975). Collective foraging and hunting, food sharing, division of labor, group defenses, and communal parenting provided a buffer against external threats (Kenrick, Li, \& Butner, 2003). The need for collective action raises the question of how individuals in social groups decide what to do and how and when to do it. For example, finding food would require group members to decide on the location and timing of foraging activities (Couzin, Krause, Franks, \& Levin, 2005). Such problems can be solved by a decision-making process in which one individual takes the initiative and provides direction while others acquiesce and follow that direction.

Individual and group survival would also have depended on cooperative effort and group cohesion (Bloom, 2000; Darwin, 1871; Sober \& Wilson, 1998), which are inversely related to group size (Dunbar, 2004; Ingham, Levinger, Graves, \& Peckham, 1974). Anthropological evidence suggests that life in ancestral groups involved constant conflict, and homicide was common (Chagnon, 1997; Knauft, 1987; Wrangham \& Peterson, 1996). The need for peacekeeping created a niche for individuals who, with the support of the group, intervened in conflicts before they

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consumed the rest of the group (Boehm, 1999; de Waal, 1996).

Conflict and warfare between groups was a major force in human evolutionary history (Alexander, 1987; Bloom, 1997; Chagnon, 1997; Diamond, 1997; Keeley, 1996; Van Vugt, De Cremer, \& Janssen, 2007; Wade, 2006; Wrangham \& Peterson, 1996). Intergroup competition may have created pressures for the evolution of a range of groupish traits such as altruism (Axelrod, 1984), empathy (Preston \& de Waal, 2002), morality (de Waal, 1996; Haidt, 2007), social identity (D. T. Campbell, 1965), and perhaps leadership. Darwin (1871, p. 132) noted, "A tribe including many members who . . . were always ready to aid one another, and to sacrifice themselves for the common good, would be victorious over most other tribes, and this would be natural selection." Deferring to a central command enhances group performance during intergroup conflict (Keegan, 1994; Sherif, 1966), creating a role for leadership.

Thus, leadership probably has a long evolutionary history. It may have emerged as a solution to specific group coordination challenges-group movement, intragroup conflict, and intergroup competition are prime candidates. Arguably, individual fitness would be enhanced by living in groups with effective leadership. As a test of Darwin's (1871) observation, imagine two groups of early humans living in the same region and competing for the same resources. One group is characterized by poor group decision making and internal discord. The second is characterized by efficient group decision making and internal cohesion. Over time, the second group will prevail. In this way, psychological mechanisms supporting leadership and followership could eventually spread through a population.

## Adaptations Supporting Leadership and Followership

A computational analysis of the coordination problem provides clues to the cognitive processes needed to support leadership (cf. Cosmides \& Tooby, 1992; Pinker, 2002). The simple decision rule "follow the leader" can be broken down into several components. First, individuals must perceive the need for coordination. In emergencies, people coordinate spontaneously (Argote, 1982), which suggests that humans may have specialized mechanisms for identifying situations requiring coordination. Second, situations in which threats are not obvious (e.g., a slow decline of resources) or are novel (e.g., climate change) require mechanisms that allow people to plan ahead and anticipate new dangers, which suggests a role for general intelligence (Kanazawa, 2004). Third, individuals must decide on a collective course of action-for instance, whether to attack another group-and differing opinions offer a prominent role for leadership. Various specialized decision rules (majority rules, voting procedures, conformity, and minority influence) might have emerged to support this aspect of leadership.

Fourth, once a course of action is identified, it is important to initiate group action. This is facilitated by individual differences in temperament-assertiveness and proactivity on the one hand, and patience, self-control, and acquiescence on the other hand-which ensure that not everyone is likely to make a first move (Ames \& Flynn, 2007; Couzin et al., 2005; Nettle, 2006). A related problem involves identifying individuals worth following because they have the requisite competence and expertise. The solution to this problem requires mechanisms for recognizing leadership potential, which humans possess in abundance (Littlepage, Robinson, \& Reddington, 1997; Lord, Foti, \& DeVader, 1984).

Finally, the problem of maintaining cohesion in large, dispersed groups could be solved by specialized mechanisms for communication, perspective taking, and conflict management. Specific abilities such as theory of mind, empathy, social identity, and language may have played a role in maintaining group cohesion (de Waal, 1996; Haidt, 2006, 2007; Van Vugt \& Schaller, 2008). Also, the capacity for imitation and social learning along with mechanisms that direct attention to higher status individuals would prompt followers to emulate leaders, thereby adding to group identification and cohesion (Chance, 1967; Henrich \& Gil-White, 2001). Punishment of free riders (individuals who benefit from group living without contributing to it) and rule enforcement provide alternative means for maintaining cohesion and are also crucial leadership functions (De Cremer \& Van Vugt, 2002).

Thus, specialized mechanisms for planning, communication, group decision making, competence recognition, social learning, and conflict management would have contributed to the emergence of a specific leadership and followership psychology in humans. It remains to be seen whether these evolved mechanisms were specifically de-

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signed to solve leadership problems or whether they were co-opted for these purposes (cf. Buss, Haselton, Shackelford, Bleske, \& Wakefield, 1998).

## Game Theory Analysis of Leadership

Game theory was devised during World War II to analyze strategic interactions among combatants; it has subsequently become an important method for studying social processes (Gintis, 2007). Evolutionary psychologists use game theory to model social behaviors such as altruism, conformity, and social intelligence (Axelrod, 1984; Schmitt \& Pilcher, 2004; D. S. Wilson, Near, \& Miller, 1996). Leadership and followership can also be modeled, and framing them in terms of game theory does three things. First it suggests the way leadership and followership may have evolved. Second, it requires researchers to consider the perspectives of leaders and followers simultaneously, clarifying the costs and benefits for each. Third, it suggests how individuals whose interests potentially conflict might work together to maximize mutual benefits.

Evolutionary game theory (Maynard-Smith, 1982) views social interaction as a process in which strategies compete in a Darwinian fashion. In these games, the agents embody strategies that are encoded in genes and, over the course of evolution, are tested against alternative strategies and copies of themselves. Genes spread through a population depending on the relative superiority of their associated strategies in evolutionarily relevant situations. By regarding leadership and followership as alternative game strategies, we may be able to tell how well these strategies fare in competition with each other as well as with alternative strategies.

## The Leader Game

The game of leader (Van Vugt \& Kurzban, 2007) can be used to model the leader-follower coordination problem. Table 1 depicts one version of this game, which can be illustrated using an example from our ancestral environment. Note that although we use the simplest case-a dyadic game-the analysis can be easily extended to a coalition of actors or to multiple coalitions (MaynardSmith, 1982). Also note that the payoffs represent units of reproductive success (the currency in evolution). Further, the absolute value of these points matters less than the ranking of preferences across the four game cells.

Suppose Pat and Jamie are both dehydrated and that Waterholes A and B contain water. Whichever waterhole they choose, they must travel together for protection. However, Pat prefers Waterhole A-perhaps because he or she knows how to get there-and this advantage gives him or her an outcome of +3 . Jamie prefers Waterhole B-it is closer to his or her family - and this advantage gives him or her an outcome of +3 . The payoffs are such that both Pat and Jamie are better off going to the same waterhole, yet this gives one of them a relative advantage $(+2)$. The asymmetrical payoffs in the leader game make it attractive for players to take the lead. By coordinating on their preferred hole, the leader gets a relatively better payoff than the follower, which may ultimately be paid out in greater reproductive success. Note that this game represents any social coordination problem-for example, where to hunt, whether to fight or take a nap.

The coordinating cells (A, A or B, B; see Table 1) are the equilibrium points of the game, an important concept in game theory (Gintis, 2007). Natural selection will favor adaptations that lead to equilibrium - where neither party can obtain better payoffs by switching strategies-and this is relevant to the emergence of leadership and followership because leadership can lead to equilibrium. If people play the game simultaneously, most pairs fail to coordinate because each will opt for the leader role (Van Vugt \& Kurzban, 2007). However, if they play the game sequentially and one person takes the lead by moving first or indicating a preference (e.g., for Waterhole A), then most

Table 1
The Leader Game

|  | Pat |  |
| :--- | :---: | :---: |
| Jamie | Waterhole A | Waterhole B |
| Waterhole A | $3,1^{*}$ | 0,0 |
| Waterhole B | 0,0 | $1,3^{*}$ |

Note. Payoffs are for Pat and Jamie, respectively; Waterhole A and Waterhole B represent alternative game strategies (underpinned by gene alleles). Game equilibria are indicated with asterisks.
pairs coordinate. ${ }^{1}$ This analysis suggests that in species that frequently encounter coordination problems, adaptations for leadership and followership are likely to emerge. In ancestral humans, these adaptations would have been supported by an increasingly sophisticated cognitive infrastructure involving theory of mind, language, and culture, with implications for the scale, complexity, and style of leadership.

Note that this model makes no assumptions about the design features of leadership and followership adaptations. For instance, leader and follower roles may be adopted flexibly by the same individual because in some cases it pays to be a leader and in others to be a follower. This is consistent with a conditional strategies model (West-Eberhard, 2003), which assumes that organisms adopt strategies based on specific environmental and/or developmental inputs (see also Gangestad \& Simpson, 2000, on strategic pluralism)-for instance, being the firstborn in the family or the tallest in the class might dispose people to assume leadership roles in later life (Simonton, 1994). On the other hand, natural selection may have coded leader and follower strategies in a more static fashion, so that populations reached equilibrium using strategies maintained through frequency-dependent selection (Maynard-Smith, 1982; D. S. Wilson et al., 1996). Such models suggest that populations contain individuals with genotypes predisposing them to either leadership or followership. ${ }^{2}$ As with sex ratios, an increase in the frequency of leader genotypes in a population reduces the payoffs for this strategy-because many would-be leaders compete and fail to coordinatethus selecting against leader genotypes. The distinction between conditional versus pure strategies is analogous to the distinction between situational versus trait theories of leadership (Van Vugt, 2006).

## The Riddle of Following

An important implication of the leader game concerns the origins of followership. Coordinated action serves the interests of both leaders and followers, but the payoffs for leaders are relatively better because they get benefits when others adopt their goals (e.g., status and prestige; Buss, 2005; Henrich \& Gil-White, 2001). Because natural selection is based on relative (rather than absolute) fitness, this seems to make followership puzzling. Perhaps followers simply make the best of a bad situation when they cannot be leaders themselves (Dawkins, 1976). The mind may be designed to evaluate one's relative place in a hierarchy and to evaluate the costs and benefits of competing for higher status. Such a mechanism is implicit in the pecking order phenomenon, first observed in chickens (SchjelderupEbbe, 1935), which promotes stability over conflict in hierarchical social groups. If the calculated costs of competing for status outweigh the benefits, then followership would be a rational choice that would free time and energy for other pursuits (Gangestad \& Simpson, 2000). Perhaps to become leaders themselves someday, followers need to defer to leaders to observe how they lead (Henrich \& Gil-White, 2001). Coordination benefits are also negotia-
ble, and followers can improve their relative benefits if they engage in collective bargaining (Boehm, 1993, 1999).

There is a final intriguing possibility. Although the payoffs for followers may be less than those for leaders, coordination leads to higher aggregate-level payoffs (in Table 1, an aggregate of +4 points vs. 0 points). Thus, groups with an effective leader-follower structure would have higher aggregate fitness. Under the right conditions (discussed in Sober \& Wilson, 1998; D. S. Wilson, Van Vugt, \& O'Gorman, 2008), leadership might create enough variation between groups for natural selection to operate. It is possible that well-led groups are so much better at group hunting, food sharing, and warfare that the relatively lower within-group payoffs for followers are compensated for by between-groups fitness benefits. That is, followers may not be as well off as their leaders, but they are better off than individuals in poorly led groups. ${ }^{3}$ The interplay between individual- and group-level selection pressures yields potentially interesting implications for leadership. Multilevel selection models have provided novel insights into such social traits as culture and morality (Haidt, 2006, 2007; D. S. Wilson et al., 2008).

## A Natural History of Leadership

In this section, we present a hypothetical description of how leadership practices evolved over the course of nonhuman to human primate history. Such scenarios always risk being just-so stories because their key assumptions are difficult to verify. Nonetheless, clues embedded in the relevant literatures can be used to estimate the time frame and structure of social organizations that promoted changes in leadership practices in human societies. We identify four nominal stages (summarized in Table 2).

## Stage 1: Prehuman Leadership

The phylogenetic evidence suggests that preadaptations for leadership precede primates. Simple leader-follower structures for coordinating group movement have been observed in various social species (Bloom, 2000; Boinski \& Garber, 2000; Couzin et al., 2005; E. O. Wilson, 1975). For example, the waggle dance of honeybees recruits other hive members to visit food resources and can be construed as leadership. The foraging patterns of many insects, the swimming patterns of schools of fish, and the flying patterns of migrating birds also resemble leader-follower re-

[^1]Table 2
A Natural History of Leadership

| Stage | Time period | Society | Group size | Leadership structure | Leader | Leader-follower relations |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | $>2.5$ million years ago | Prehuman | Any size | Situational or dominance hierarchy | Any individual or alpha | Democratic or despotic |
| 2 | 2.5 million to 13,000 years ago | Hominid bands, clans, tribes | Dozens to hundreds | Informal, situational, prestige based | Big man, head man | Egalitarian and consensual |
| 3 | 13,000 to 250 years ago | Chiefdoms, kingdoms, warlord societies | Thousands | Formal, centralized, hereditary | Chiefs, kings, warlords | Hierarchical and unilateral |
| 4 | 250 years ago to the present | Nations, states, businesses | Thousands to millions | Strucłural, centralized, democratic | Heads of state, managers, executives | Hierarchical but participatory |

lationships. These examples suggest that species lacking complex cognitive capacities can display follower behavior using a decision rule as simple as "follow the one who moves first."

Group movement guided by leadership is also documented in nonhuman primates. Hamadryas baboons in Ethiopia sleep in large groups on cliffs (Kummer, 1968). They leave the cliffs in the morning to forage in open areas. One individual, usually an adult male, will move a few meters in a particular direction and sometimes the whole group will follow. Sometimes, however, there are no followers, and the would-be leader returns to the group. The bidding starts again until the rest finally choose to follow (Kummer, 1968). This reflects the two key decisions in the leader game: the choice to initiate and the choice to follow.

Chimpanzees, our closest genetic relatives, often display peacekeeping, another response to a coordination problem solved by leadership. The following incident from the Arnhem Zoo chimpanzee colony was reported by de Waal (1996):

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 . . . instead anyone who continued to act received a blow from him. (p. 129)
De Waal (1996) argued that this peacekeeping behavior constituted leadership because it was endorsed by the entire group.

Leadership has also been observed during aggressive encounters between groups of wild chimpanzees (Boehm, 1999; Wrangham \& Peterson, 1996). Boehm (1999) reported a conflict between neighboring chimpanzee groups in Gombe, Tanzania, who met on a borderland in the forest. The alpha male from one group charged the other group and the rest followed him, prompting the other group to retreat into its home range.

These examples support the claim that adaptations for leadership and followership tend to evolve in social species. This does not necessarily explain why leadership evolved in humans; different selection pressures shaped the adaptation of different species, and humans have many unique adaptations (Buss, 2005; Darwin, 1871). Nonetheless, the continuity of evidence across species makes it at least plausible that the selection pressures that gave rise to leadership in nonhumans resemble those in humans.

## Stage 2: Band and Tribal Leadership

It is likely that leadership was further shaped by the unique evolutionary history of humans. One can think about modal patterns of human leadership as evolving through three stages. Each stage represents a change in the scale and complexity of social organization and resource distribution that had implications for the relationship between leaders and followers.

The first (and by far the longest) phase extended from the emergence of early humans around 2.5 million years ago until the end of the last ice age, about 13,000 years ago (Diamond, 1997; Wade, 2006). During this stage, the Pleistocene era, humans lived in semi-nomadic hunter-gatherer bands and clans consisting of 50-150 mostly genetically related individuals (Dunbar, 2004). Experts agree that modern hunter-gatherers-for example, the !Kung San of the Kalahari Desert, the Yanomamo of the Amazon River basin, the Inuit of the Arctic coasts, and the Aborigines in Northern Australia-provide our best model for human social organization in this stage, often referred to as the environment of evolutionary adaptedness (EEA; Bowlby, 1969; Foley, 1997). Extrapolating from hunter-gatherer evidence, we can infer that living conditions in the EEA were fundamentally egalitarian, with no formalized leadership role. The best hunters and warriors, so-called Big Men, exercise disproportionate influence on group decision making, but their power is limited to their domain of expertise and accumulated degree of trust (Boehm, 1999;

Chagnon, 1997; Diamond, 1997). For example, regarding how the Mae Enga in New Guinea make warfare decisions, Meggitt (1977, p. 76) noted,

The men who initiated the conference, or their spokesmen, briefly indicate their view of the clan's position and the action they favor. They may argue that now is the time to launch a full-scale attack on the neighboring clan with the aim of occupying a specific section of its territory. The major Big Man [the leader] then solicits responses from the audience. Ideally, everyone present has a voice and being among his own clansmen can speak with complete freedom. The task of the Big Man at this stage is to ensure that all have a chance to offer their opinions and facts in full and to make no attempt to cut off any but obviously irrelevant speeches.

If the Big Men try to dominate their groups-and they do-they meet fierce resistance from the others, who can collaborate to control them. Dominance hierarchies are the norm in primate groups; for early humans, collaboration among subordinates reversed this dominance hierarchy and resulted in a democratic leadership style that may have existed for nearly 2.5 million years (Boehm, 1993). We believe that the EEA reflects our natural way of thinking about and responding to leadership, and this has implications for modern leadership practice. Modern societies still evaluate leadership against egalitarian "hunter-gatherer" standards such as fairness, integrity, competence, good judgment, generosity, humility, and concern for others, and they regard such attributes as dominance and selfishness as the antithesis of leadership (Den Hartog, House, Hanges, Ruiz-Quintanilla, \& Dorfman, 1999; Dirks \& Ferrin, 2002; Epitropaki \& Martin, 2004; Lord et al., 1984; Nicholson, 2005; Van Vugt, Hart, Jepson, \& De Cremer, 2004).

Homo sapiens emerged roughly 200,000 years ago (Dunbar, 2004); modern humans' increased cognitive capacities supporting theory of mind, language, and culture may have enabled bands to merge into larger tribal struc-tures-likely in response to the pressure of intergroup warfare (Alexander, 1987; Bloom, 1997; Chagnon, 1997; Diamond, 1997; Keeley, 1996; Van Vugt et al., 2007; Wade, 2006; Wrangham \& Peterson, 1996). The new hierarchical authority structures were nonetheless inherently democratic, despite more elaborate social structures and larger groups (Boehm, 1999; Johnson \& Earle, 2000; Richerson \& Boyd, 2006).

## Stage 3: Chiefs, Kings, and Warlords

Our evolved leadership psychology may not have changed fundamentally since the EEA, but our social structures changed dramatically beginning with the development of agriculture at the end of the last ice age some 13,000 years ago. Agriculture and dependable food supplies enabled groups to settle and populations to grow exponentially. For the first time in human history, communities accumulated surplus resources, and leaders played a key role in their redistribution (Diamond, 1997; Johnson \& Earle, 2000). As communities grew, so did the potential for within- and between-groups conflict. Leaders acquired extra power to deal with such threats, which resulted in more formalized
authority structures that paved the way for the first chiefdoms and kingdoms (Betzig, 1993; Johnson \& Earle, 2000). In their expanded role, leaders could siphon off resources and use them to create groups of dedicated followers, the cultural elite (Padilla, Hogan, \& Kaiser, 2007), and sometimes they established hereditary leadership. The payoff for leaders increased substantially during this period, attracting shrewd, resourceful individuals to these positions for selfish reasons that are reflected in these leaders' astonishing relative reproductive success (Betzig, 1993). ${ }^{4}$ In contrast to hunter-gatherers, families in settled communities found it difficult to move away from or defend themselves against these exploitative leaders.

The inevitability of intergroup conflict led to the rise of warlords and soldier classes, tough, aggressive men who built coalitions of followers united in the common purpose of extracting resources by force. Warlord societies are the norm in preindustrialized societies such as medieval France (Johnson \& Earle, 2000). A substantial proportion of modern humanity, including those living in parts of Asia and much of Africa, the Middle East, and South America, still live under these oppressive conditions (Transparency International, 2005). When centralized governments break down, warlords inevitably emerge (e.g., Iraq or Afghanistan). Warlords are leaders-they have followers whose loyalty is predicated on the possibility of gaining resources, privilege, and prestige in the new regime (Padilla et al., 2007). Warlords use their power to dominate resources and advance their personal interests, agendas that conflict with our evolved leadership psychology.

## Stage 4: State and Business Leadership

The fourth leadership period corresponds roughly to the beginning of the Industrial Revolution some 250 years ago. Communities merged into states and nations, and large businesses developed, all of which had implications for leadership practices. Citizens of states and employees in organizations are relatively free from the predations of their leaders and may defect to other states or organizations. This freedom shifts the balance of power away from leaders and produces conditions more akin, but not equivalent, to the reverse dominance hierarchy of the EEA (Boehm, 1993). In the early stages of the Industrial Revolution, however, and in developing economies today, workers were almost slaves. Class warfare is real, but in the developed world it is moderated and its effects are muted compared with the situation in parts of the world still dominated by warlords (Transparency International, 2005). Modern academic discussions of leadership almost exclusively concern social arrangements in the industrialized world (Wielkiewicz \& Stelzner, 2005).

Although modern bureaucratic arrangements make business sense, they may be constrained by our evolved leadership psychology. Human beings are not fungible;

[^2]certain social arrangements are more compatible with human nature than others. For example, large organizations seem to perform better when organized in units roughly the size of hunter-gatherer groups with minimal status distinctions between superiors and subordinates (Nicholson, 2000). Leadership practice should consider these constraints.

## Summary

Cognitive preadaptations for leadership-for example, solutions to simple coordination problems-probably evolved long before humans. Leadership became more refined during the EEA in response to challenges associated with the growing size and complexity of groups and the inevitability of conflict both within and between groups. The development of cognitive capacities-notably language, theory of mind, and culture-facilitated large-scale leadership. Hunter-gatherer data suggest that leadership in the EEA was consensual, democratic, and transitory. The formalized leadership structures that emerged after the agricultural revolution are novel and potentially conflict with our evolved leadership psychology. The Industrial Revolution helped free people from tyrannical warlords, but the scale, complexity, and form of contemporary organizations pose novel challenges to our innate leadership psychology.

## Implications of an Evolutionary Analysis for Leadership Theory and Practice

In this final section, we note implications of the foregoing discussion for leadership theory, research, and practice. Some of these implications can be derived from other models of leadership, for example, psychodynamic or social exchange theories. Yet, any proximate theory of leadership must ultimately turn to evolution to explain its own assumptions (e.g., why people are driven by sexual instincts or motivated by fair outcomes). Moreover, an evolutionary framework seems to generate a wider variety of implications than other theoretical perspectives, as well as some unique implications.

## Understanding Followership

The leadership literature overwhelmingly focuses on the people in charge (cf. Hollander, 1992; Kaiser et al., 2008), but an evolutionary view highlights the importance of followership. The psychology of followership is more complicated and interesting than that of leadership. First, most people are followers, so there is, in principle, more to talk about. Second, and more interesting, it is not obvious why people agree to subordinate themselves when this may put them at an evolutionary disadvantage (Dawkins, 1976). We suggest that followership emerged in response to specific ancestral problems that were best solved through collective effort coordinated by a leader-follower structure that enhanced individual and group survival. This implies that leader-follower patterns will emerge more quickly and
effectively in circumstances that mirror adaptive problems (e.g., internal group conflict, external threats).

This hypothesis has not been tested explicitly; however, it is consistent with prior findings. People are more likely to follow under conditions of threat-for example, during natural disasters or intergroup conflicts (Baumeister, Chesner, Senders, \& Tice, 1989; Hamblin, 1958). Van Vugt and De Cremer (1999) showed that leaderless groups negotiate internal conflicts less effectively in times of crises. In the famous Robbers' Cave experiment, when faced with team competition, the two groups of schoolboys promptly chose team leaders (Sherif, 1966). Followers also prefer different leaders depending on the problem they face. U.S. voters tend to choose hawkish presidents when threatened by war (McCann, 1992) and to show an increased preference for charismatic leaders and a decreased preference for participative leaders when reminded of their mortality (Cohen, Solomon, Maxfield, Pyszczynski, \& Greenberg, 2004). Similarly, CEO charisma is positively related to organizational effectiveness only under conditions of environmental uncertainty (Waldman, Ramirez, House, \& Puranam, 2001).

Another implication of our analysis is that leadership may be unnecessary and even resented when people face relatively simple or routine coordination problems. This is consistent with the literature on substitutes for leadership (Kerr \& Jermier, 1978) and self-managing teams (Morgeson, 2005); exercising unneeded leadership can actually undermine team performance (Haslam et al., 1998). Here lies an important leadership lesson: Except for certain well-defined situations, people will perform better if they are left alone.

The leadership literature could benefit by the addition of studies investigating follower motives in different situations, the personality correlates of good followers, and the ways in which followers influence leaders (cf. Altemeyer, 1981; Hollander \& Offermann, 1990; Wayne \& Ferris, 1990). We predict that followership styles are at least as variable and differentiated as leadership styles (cf. Boccialetti, 1995). An evolutionary view of leadership emphasizes followership and is a promising perspective for theory and research on followers.

## Who Shall Lead?

Our analysis explains why certain individual differences are consistently associated with leadership. The leader game predicts that first movers in coordination situations are most likely to become leaders, and this prediction is borne out in the literature. A recent meta-analysis indicated that of the Big Five personality dimensions, extraversion is the most highly related to leadership emergence and effectiveness ratings (Judge, Bono, Ilies, \& Gerhardt, 2002). Moreover, the ambition component of extraversion, rather than the sociability component, accounts for this relationship (cf. J. Hogan \& Holland, 2003): Primary studies report correlations between leadership and such narrower band dimensions as assertiveness, boldness, initiative, need for achievement, proactivity, and risk taking (e.g., Ames \& Flynn, 2007; Bass, 1990; House \& Aditya, 1997), which all
increase the propensity to move first. In the cognitive domain, people who quickly recognize that situations require coordination are more likely to become leaders. This might explain the relationship between general intelligence and leadership (Judge, Ilies, \& Colbert, 2004) and why intelligence is a universally desired characteristic of leaders (Den Hartog et al., 1999; Lord et al., 1986). We expect that as coordination tasks become more complex, cognitive factors will become a better predictor of leadership (cf. Jacques, 1989).

Our analysis also suggests that an ability to estimate the payoffs for followers is necessary for leaders to be influential. This would explain the empirical links between leadership and social intelligence, political skill, empathy, perspective taking, and nonverbal sensitivity (R. Hogan \& Hogan, 2002; Kellett, Humphrey, \& Sleeth, 2002; Zaccaro, Gilbert, Thor, \& Mumford, 1991). Bass (1990) noted, "The leader must be able to know what followers want, when they want it, and what prevents them from getting what they want" (p. 168). This also suggests that the more complex the group, the more socially astute the leader needs to be.

Another implication of our analysis is that good leaders should be perceived as both competent and benevolent because followers want leaders who can acquire resources and then are willing to share them. The first claim is supported by research showing that task expertise correlates with leadership (Bass, 1990) and that low expertise disqualifies individuals from leadership positions (Hollander \& Offermann, 1990). Leaders' willingness to share is reflected in such traits as trustworthiness, fairness, generosity, and self-sacrifice-universally desirable leader attributes (Den Hartog et al., 1999; Dirks \& Ferrin, 2002; Epitropaki \& Martin, 2004; Hardy \& Van Vugt, 2006; Lord et al., 1984; Nicholson, 2005).

Finally, an evolutionary analysis explains why leadership correlates with such factors as age, height, weight, and health-something not explained by existing leadership theory. Given the risks associated with following, people should prefer leaders who can benefit the group. In ancestral environments, having specialized knowledgethe location of waterholes during a drought, for instancemay have been vital (Boehm, 1999). Older individuals are more likely to have specialized knowledge, and age should therefore be correlated with leadership. Group movement in nomadic species-for example, baboons and ele-phants-is often decided by the older, not the most dominant, troop member (Dunbar, 2004). Today, age and leadership are related in roles that require specialized knowledge, for example, directors on governing boards of public corporations (Gandossy \& Sonnenfeld, 2004). When group activities require strength and stamina (group defense in ancestral times, grueling travel schedules in modern business), physical indices such as energy level and health should correlate with leadership (D. P. Campbell, 2002; Nicholson, 2000; Van Vugt, 2006). Not surprisingly, modern voters prefer physically fit political candidates (Simonton, 1994). It is interesting that seemingly irrelevant physical factors like height predict leadership status today
(Judge \& Cable, 2004). In ancestral times, taller leaders may have been more effective peacekeepers within groups and more intimidating foes to rival groups.

## Situational Accounts of Leadership

Our evolutionary model provides deeper insight into situational theories of leadership. Although there are individual differences in leadership propensity (Ilies, Gerhardt, \& Le; 2004; Judge et al., 2002), distributed leadership was probably advantageous in ancestral environments (e.g., the best hunter leads the hunting party, the wisest elder resolves internal conflicts, the fiercest warrior leads the fight; see Boehm, 1999). This suggests that leadership and followership are flexible strategies elicited by the interaction between certain evolved decision rules and specific environmental inputs (cf. Gangestad \& Simpson, 2000). Consider the distinction between task- and people-oriented leadership (Bass, 1990; Yukl, 2006). Our model suggests that task leadership emerges when the interests of leaders and followers converge, for example, when both parties prefer Waterhole A and the decision is how to get there. Peopleoriented leadership should emerge when interests diverge and leaders must persuade people to follow them. This logic provides an explanation for proximate models of leadership such as Fiedler's (1967) contingency theory and House's (1971) path-goal theory.

Vroom's prescriptive model of when to apply autocratic (hierarchical) versus more participative (egalitarian) decision-making styles (Vroom \& Jago, 1978) can be similarly understood. In emergencies, the interests of leaders and followers converge, and followers readily defer to the decisions of a single individual (Guetzkow \& Simon, 1955; Keegan, 1994). However, when the interests of leaders and followers diverge, leaders must encourage participation to ensure acceptance of the decision. Consequently, leadership styles can vary somewhat between organizations, nations, and cultures depending on the specific challenges of their physical and social environments (Hofstede, 1980; Van De Vliert, 2006), and these differences can be transmitted culturally from one generation to the next (Richerson \& Boyd, 2006). Participative styles prevail in the Netherlands and Australia, where harsh natural conditions forced authorities to share power with citizens, creating a strong egalitarian ethos (cf. Den Hartog et al., 1999). Economists have recently used game theory to model the origins of modern democracy versus dictatorship and reached essentially the same conclusion: Democracies emerge when authorities must make concessions to avoid losing power (Acemoglu \& Robinson, 2006).

## The Role of Dominance

Our analysis suggests that there are two forms of group hierarchies. The first is the dominance hierarchy that results from competition for scarce resources, in which the strongest and most determined individual prevails and controls group resources and activities (Schjelderup-Ebbe, 1935; E. O. Wilson, 1975). The second form of hierarchy emerges by consensus when hierarchical structures are perceived to benefit the group. These two forms offer very
different accounts of leadership. The dominance model characterizes species in which alpha males control group activities and others are intimidated or forced to acquiesce. However, human hierarchies are much flatter and often based on prestige rather than dominance (Henrich \& GilWhite, 2001). The emergence of prestige-based hierarchies was pivotal and probably increased our capacity to function in highly coordinated units.

Nonetheless, dominance is part of our primate heritage, and there is always a risk that leaders will try to coerce followers (Betzig, 1993; Boehm, 1993; Padilla et al., 2007). This makes leader-follower relations inherently ambivalent. There are at least two forces reinforcing this ambivalence. First, many with leadership aspirations do not become leaders (R. Hogan, 2006, chap. 5). Accession to leadership is a Darwinian process; through a series of events influenced by circumstances and luck, one person prevails. The losers join the ranks of the followers and scheme to gain power in the future. Second, dominance facilitates leadership functions such as enforcing rules within the group and presenting a formidable opposition to enemies during warfare. Yet dominant leaders can also bully their own group for personal gain; obviously, followers do not want to be exploited and must find ways to protect their interests. Anthropological data show that in most societies, people fiercely resist domination and often band together to curb the power of their leaders (Boehm, 1993).

This tension probably created an evolutionary "arms race" between the strategies of leaders and followers to gain control. The ethnographic and psychological literatures reveal several decision rules that leaders use to increase power. For instance, leaders can redistribute resources fairly and generously-this is a universally desired leadership attribute (Brown, 1991; Den Hartog et al., 1999; Hardy \& Van Vugt, 2006; Tyler \& Lind, 1992). Leaders can use an external group threat to consolidate their power (Cohen et al., 2004; Padilla et al., 2007). Leaders can also "buy" support through bribery-some followers will collude with authoritarian leaders if the price is right (Altemeyer, 1981; Padilla et al., 2007). Nepotism and cronyism are also common strategies for retaining power in humans (Gandossy \& Sonnenfeld, 2004) and chimpanzees (de Waal, 1982). Finally, leaders can impose ideologies to justify their privileged position. Throughout history, leaders have used religion to maintain power-for example, the "divine" right of kings-and turned their rule into a hereditary position to benefit their offspring (Betzig, 1993; Diamond, 1997; Johnson \& Earle, 2000).

Various decision rules may have evolved to enable individuals to benefit from followership without being exploited by leaders. Boehm $(1993,1999)$ described several such "leveling mechanisms." One is to accept leadership only in areas where leaders have expertise. A second mechanism is to use gossip, ridicule, elections, and other forms of public scrutiny to control leaders. In hunter-gatherer bands, if a chief misbehaves, he is publicly criticized, and if he tries to give commands, he is often rebuffed (Freeman, 1970, cited in Boehm, 1999). Overbearing leaders can also
simply be disobeyed. Freeman (1970, cited in Boehm, 1999) reported that followers ignore Philippine chiefs who issue commands rather than suggestions. Disobedience is effective because leaders are sanctioned without being replaced, which could disrupt and weaken the group. Reluctant followers can also ostracize exploitative leaders. Ostracism usually has severe consequences for the ostracized (Bloom, 1997; Williams \& Sommer, 1997). Moore (1972, cited in Boehm, 1999) reported that when an aggressive tribal leader starts a feud without group support, the other tribesmen can declare him no longer one of their own and allow rival groups to kill him with impunity. Followers can also desert despotic leaders. Van Vugt et al. (2004) found that attrition rates were four times greater in autocratically led groups than in democratically led groups. Finally, followers can overthrow or even kill an overbearing leader. These leveling mechanisms are critical for the welfare of followers and groups. Historical evidence suggests that tyrants and dictators emerge whenever followers are unable to protect themselves against exploitative leaders (Betzig, 1993; Padilla et al., 2007).

## The Mismatch Hypothesis

Climate surveys routinely show that $60 \%-70 \%$ of employees in most organizations report that the most stressful aspect of their jobs is their immediate boss (R. Hogan, 2006, chap. 6). Further, the failure rate of managers in corporate America is $50 \%$ (R. Hogan \& Kaiser, 2005). These findings raise the possibility that there may be a mismatch between the evolved leadership psychology of humans and the practice of leadership in the modern world (Van Vugt, Johnson, Kaiser, \& O'Gorman, in press). ${ }^{5}$ Our leadership psychology evolved over two million plus years, during which time people lived in small, kin-based egalitarian bands in which leadership was informal, consensual, and situational. This psychology may still affect the way we respond to leaders. The challenge for modern organizations is either to work with or work around the limitations of this psychology.

Situational versus structural leadership. Leadership in the ancestral environment was fluid, distributed, and situational. The individual most qualified for the task at hand had the greatest influence on collective actions. Rarely would one individual coordinate all group activity and make all group decisions. However, with bureaucracy and formal leadership roles, one individual-the leader-is responsible for managing all these functions (Weber, 1947). Accordingly, leadership versatility-the ability to perform multiple, even competing, leadership roles-is highly associated with executive effectiveness (Kaiser, Lindberg, \& Craig, 2007; Kaplan \& Kaiser, 2006). However, few leaders have the range of skills needed to perform a wide array of such duties (Kaiser \& Kaplan, 2007;

[^3]Lombardo \& Eichinger, 2000). This may account for the high failure rate of senior managers. It may also explain recent interest in the notion of distributed leadership-the idea that leadership is a process that can be shared (Gronn, 2002; Pearce \& Conger, 2003).

Relative power. Boehm's $(1993,1999)$ concept of the reverse dominance hierarchy suggests that the power of ancestral leaders derived from legitimization from followers (cf. Hollander, 1992). In modern industrial and bureaucratic organizations, however, leaders are appointed by and accountable to managers senior to them in the organizational hierarchy, and subordinates have little power to sanction their bosses. Modern organizational ethnographers report that most managers implicitly understand that pleasing superiors is more important to career success than is pleasing subordinates (Sayles, 1993). This may be one source of the alienation and disengagement felt by today's workforce. It is noteworthy that executives are more likely to succeed if subordinates are included in the selection process (Sessa, Kaiser, Taylor, \& Campbell, 1998).

In the EEA, there were minimal status distinctions between leaders and followers (Boehm, 1999; Nicholson, 2005). However, in modern American corporations, average salaries for CEOs are 179 times the average pay for workers ("Business Bigwigs," 2007). Research shows that power increases the potential for abuse (Kipnis, 1972) and decreases the ability to empathize with subordinates (Galinski, Magee, Inesi, \& Gruenfeld, 2006). The highly asymmetric payoffs for modern business leaders may encourage a kind of leadership that followers naturally resent.

Small, homogeneous groups versus large, heterogeneous groups. The small hunter-gatherer societies of our ancestral past were essentially extended families. Members knew each other, understood their interdependencies, and had a genetic investment in one another's fate (Dunbar, 2004; Hamilton, 1963). These groups were held together by kinship and norms of reciprocity and fairness, which require that individuals depend on others for cooperation and return the favor in kind (Trivers, 1971). Leaders played a role in enforcing these norms by punishing cheaters and free riders. The need for such leadership activities is probably greater today, when organizational members are unrelated and the size of corporations makes identification with the group difficult. It is interesting that social identity research indicates that transformational leadership works by influencing followers to identify with the group and to internalize group aspirations (Shamir, House, \& Arthur, 1993; Van Knippenberg, Van Knippenberg, De Cremer, \& Hogg, 2004; Van Vugt \& De Cremer, 1999). Transformational leaders change the way followers see themselves-from self-interested individuals to members of a larger group, almost as if they are kin-by modeling collective commitment, emphasizing the similarity of group members, and reinforcing collective goals, shared values, and common interests. However, transformational leaders are the exception, not the rule, in the modern world (Bass, 1985; Burns, 1978).

Modern citizens may feel more alienated and discon-
nected from their employers and other social organizations since the Industrial Revolution (Durkheim, 1897). Arendt (1951) suggested that these feelings of alienation promote apathy and make followers feel powerless to influence social institutions, including leadership. Arendt further argued that the alienation and indifference felt by citizens paved the way for the totalitarian regimes that swept into power in Germany, Russia, and Italy in the early 20th century.

Effective organizations such as Toyota, GoreTex, and Virgin are designed and structured in a way that resembles hunter-gatherer bands. For instance, these companies delegate decision making to managers far down the chain of command so that the size of functional units approximates that of a hunter-gatherer band (50-150 individuals; Dunbar, 2004; Nicholson, 2000). In addition, decentralized forms of organizing are associated with greater employee morale, involvement, and commitment (Likert, 1967), which in turn are associated with greater productivity, financial results, and customer satisfaction (Harter, Schmidt, \& Hayes, 2002).

Leadership prototypes. The ancestral environment may have shaped our leadership prototypes (Lord et al., 1984) so that we have a natural preference for persons who match these implicitly desired characteristics. Evolved prototypes can be inferred from characteristics that are both prominent among hunter-gatherer Big Men and endorsed across industrial societies. We have already discussed the importance of certain physiological traits such as height. Strong candidates for psychological leader traits include integrity-good leaders are trustworthy; per-sistence-good leaders are models of steadiness in the face of adversity; humility - good leaders are modest and put the good of the group ahead of personal ambitions; com-petence-good leaders are resources for their groups; de-cisiveness- good leaders make timely and defensible decisions, especially under trying conditions; and finally, vision-good leaders are inspiring (Den Hartog et al., 1999; Epitropaki \& Martin, 2004; Hogan \& Kaiser, 2005; Lord et al., 1984; Nicholson, 2005). It is striking to note how so-called "derailed" executives-bright, ambitious, and talented managers who nonetheless fail-are often described as lacking these very characteristics (cf. Bentz, 1985; McCall \& Lombardo, 1983).

Another apparent prototype may provide clues to a controversial modern social issue, that of leadership and gender. Male leadership was the norm in ancestral envi-ronments-although there has always been a niche for female peacekeepers among primates (de Waal, 1996) and humans (Van Vugt, 2008)—and male leadership continues to be the norm today (Eagly \& Karau, 2002; Heilman, 2001; Schein, 1973). It remains to be seen how beneficial the male leadership bias is in a global economy that emphasizes interpersonal skills and network building (Eagly \& Carli, 2003). There is evidence that women have better empathy and communication skills than men (Van Vugt, 2006) and that women are more likely to adopt a democratic leadership style (Eagly \& Johnson, 1990). Nonetheless, the male bias may be difficult to overcome. Research
indicates that when women and men work together on group tasks, the men are quicker to claim leadership roles-even when the women are better qualified (Mezulis, Abramson, Hyde, \& Hankin, 2004). An intergroup threat automatically activates a preference for male leadership (Little, Burriss, Jones, \& Roberts, 2007; Van Vugt, 2008). Regardless of talent, men are also more likely to assume leadership roles when being observed by women, perhaps because women prefer status in potential mates (Buss, 2005; Jensen-Campbell, Graziano, \& West, 1995). Women are also penalized for excelling at stereotypically masculine tasks such as leadership (Eagly \& Karau, 2002; Heilman, 2001). Finally, there is consistent but subtle bias in the way executives-including those who espouse diversity-evaluate women leaders (Lyons \& McArthur, 2007). It is possible that the "glass ceiling" is a vestige of our ancestral past that requires more than sociostructural and policylevel solutions.

## Conclusion

Leadership is a crucial but often misunderstood topic. Much of the misunderstanding comes from the tendency to think about leadership only in terms of the people in charge (R. Hogan et al., 1994; Kaiser et al., 2008). In this article we have analyzed leadership from an evolutionary perspective and suggested three conclusions that are not part of the conventional wisdom. The first is that leadership cannot be studied apart from followership and that an adequate account of the leadership process must consider the psychology of followers. Second, the goals of leaders and followers do not always converge, a fact that creates a fundamental ambivalence in the relationship between leaders and followers. Third, 2.5 million years of living in small egalitarian communities shaped the way we respond to leadership today. We are often required to defer to people in leadership roles whose behavior is markedly inconsistent with qualities important in ancestral leadership. This may lead to frustration, alienation, and efforts to change leaders, jobs, or careers. If we want to know why leadership sometimes fails in modern society, we should consult the lessons from our past.

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[^1]:    ${ }^{1}$ Yet, the greater the asymmetry in payoffs, the longer it takes to establish coordination (Van Vugt \& Kurzban, 2007).
    ${ }^{2}$ Arvey and colleagues have conducted twin studies and estimate that about a third of the variance in holding a professional leadership job is due to genetic factors, which provides partial support for frequency-dependent selection (Arvey, Rotundo, Johnson, Zhang, \& McGue, 2006; Arvey, Zhang, Avolio, \& Kreuger, 2007).
    ${ }^{3}$ Evolutionary models demonstrate that leadership substantially increases variability in outcomes between groups (Richerson \& Boyd, 2006). For instance, technological innovation, education, and quality of life are far greater for citizens in modern democracies than for those in dictatorships, totalitarian regimes, and corrupt societies (Bloom, 1997; Diamond, 1997; Lawrence \& Nohria, 2002; Transparency International, 2005).

[^2]:    ${ }^{4}$ For example, population geneticists estimate that $8 \%$ of the men living in southern Asia today are descended from the warlord Genghis Khan (Xue et al., 2005; also reported in Wade, 2006).

[^3]:    ${ }^{5}$ Mismatch is an evolution-informed concept that refers to the fact that traits that were adaptive in ancestral environments might no longer produce adaptive behaviors in modern environments, especially when these environments dramatically differ, as is the case with those of modern humans.

