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Evolutionary Origins of Leadership and Followership

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Drawing upon evolutionary logic, leadership is reconceptualized in terms of the outcome of strategic interactions among individuals who are following different, yet complementary decision rules to solve recurrent coordination problems. This article uses the vast psychological literature on leadership as a database to test several evolutionary hypotheses about the origins of leadership and followership in humans. As expected, leadership correlates with initiative taking, trait measures of intelligence, specific task competencies, and several indicators of generosity. The review finds no link between leadership and dominance. The evolutionary analysis accounts for reliable age, health, and sex differences in leadership emergence. In general, evolutionary theory provides a useful, integrative framework for studying leader-follower relationships and generates various novel research hypotheses.

In his influential, award-winning book *Leadership* the political scientist James McGregor Burns wrote that "leadership is one of the most observed and least understood phenomena on earth" (1978, p. 2). There is little argument about the first claim. History is littered with examples of individuals who take charge of a group and lead it, often against the odds, to safety, victory, or prosperity. Examples are military leaders like Alexander the Great, Nelson, and Patton, political leaders like Roosevelt, Nasser, and Mandela, revolutionaries like Mao, Ghandi, and Rosa Luxembourg, business leaders like Ford, Gates, and Branson, and religious leaders like Jesus, Mohammed, and Buddha. Anthropological evidence suggests that there are no known human societies without some form of leadership (Boehm, 1999; Diamond, 1997; Lewis, 1974). Social psychological research reveals that a leader-follower structure emerges spontaneously even when groups set out to be leaderless (~~Bales, 1951;~~ Bass, 1954). It seems that whenever a group of people come together, a leader-follower relationship naturally develops. This has led various experts to conclude that leadership is a universal human behavior (Bass, 1990; Brown, 1991; Hollander, 1985).

What about Burns' second claim? Psychological research on leadership contributes a great deal to our understanding of leadership in groups. The latest edition of the *Handbook of Leadership* (Bass, 1990), for example, contains no fewer than 7,500 references to original articles on leadership. Early research concentrated on the personality correlates of leadership, the so-called trait approach, resulting in a laundry list of traits, needs, and motives that reliably distinguish leaders from nonleaders like power, ambition, extraversion, and intelligence. In later research, the emphasis shifted toward studying leader functions and styles in the light of task demands and the needs of followers, the situational or state approach (Bass, 1990).

The psychological ~~aaa~~literature contains a wealth of empirical findings about leadership and, to a lesser extent, about followership. Yet, it has been suggested that most leadership studies have been narrowly focused with little integration of findings into unifying theoretical frameworks (Chemers, 2000; Hogan & Kaiser, 2005; Hollander, 1985; Yukl, 1989). For example, Chemers (2000) notes rather pessimistically: "The question remaining is whether a coherent integration of these seemingly disparate findings [on leadership] is possible" (p. ~~XXX~~). There is also very little cross-fertilization of ideas about leadership between social and organizational psychology, and other behavioral sciences such as anthropology, political science, economics, zoology, and evolutionary biology.

Evolutionary scientists have had an enduring interest in leadership as well. In *Sociobiology: The New Synthesis*, the zoologist E. O. Wilson (1975) summarized his discipline's perspective on leadership: "When

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zoologists speak of leadership, they usually mean the simple act of leading other group members during movement from one place to another" (p. 311). Many evolutionary researchers indeed view group locomotion, for example toward new waterholes or feeding grounds, as a classic leadership problem (Boehm, 1999; Couzin, Krause, Franks, & Levin, 2005; Lamprecht, 1996). Some also suggest that there is a role for leaders as peace keepers within a group (De Waal, 1996; Wilson, 1975).

The purpose of this review is to synthesize the evolutionary and psychological literatures on leadership. The psychological literature contains many impressive empirical findings on leadership emergence, style, and effectiveness. But this literature generally lacks a coherent conceptual framework to unify the wealth of data. The evolutionary literature on leadership lacks empirical tests, particularly on humans, but it provides a general framework, evolutionary theory, that can be used to understand leadership and generate novel hypotheses. Thus, this review uses the psychological literature as a database for evaluating evolutionary hypotheses about leadership and followership in humans.

Admittedly, some of these hypotheses might be derived from frameworks other than evolutionary theory, for example, psychodynamic (Freud, 1922), cognitive (Lord & Maher, 1991), or social exchange theories of leadership (Hollander, 1985). Yet, a need has been identified for more integrative theories of leadership, because many of the existing psychological models of leadership focus only on a subset of leadership phenomena (Chemers, 2000; Hogan, ~~Hogan, & Curphy~~, 1994). Furthermore, any psychological theory must ultimately turn to evolutionary theory to explain ~~their~~ own assumptions (D. S. Wilson, Near, & Miller, 1996)—for example, why people are driven by sexual instincts. Thus, psychological and evolutionary theories of human behavior offer complementary rather than rival explanations (Barrett, Dunbar, & Lycett, 2002).

Definition, Assumptions, and Outline

Leadership has been defined in a great many ways in the psychological literature. For this review, I define leadership broadly as a process of influence to attain mutual goals (Bass, 1990; Hollander, 1985). Leadership is sometimes regarded as the outcome of a social process in which interacting individuals coordinate their actions to achieve shared goals. According to this notion, leadership cannot be studied without examining the needs and desires of followers. From an evolutionary perspective, it is not surprising why individuals choose to lead given the obvious benefits (Bass, 1990). It is more puzzling why people would voluntarily defer to a leader given what is known about the process of evolution through natural selection. Questions about the origins of followership are not normally posed in the psychological literature, but they are critical in an evolutionary analysis. Similarly, whereas the psychological literature often assumes that the goals of leaders and followers are the same (e.g., Hogg, 2001; Hollander, 1985), an evolutionary perspective suggests that this is an unwarranted assumption. Even members of a highly social species like humans frequently experience conflicts of interest in the pursuit of their goals (Barrett et al., 2002).

Leadership is sometimes described in terms of a quantitative trait. Everyone is capable of leading to some degree, but there are clear individual differences in the propensity to lead. Some researchers have argued that leadership is primarily a function of the situation. Everyone could be a leader in the right conditions (Bass, 1990). By viewing leadership as a strategy of social influence, an evolutionary analysis is consistent with either trait or state explanations of leadership. The empirical literature must decide which of them provides a better account of leadership.

This review is organized as follows. First, I discuss the selection pressures that might have lead to the emergence of leadership and followership in hominid evolutionary history. Next, evidence is examined to support the idea that leadership is designed to solve a particular set of adaptive problems looking at both human and nonhuman evidence. Subsequently, two different theories are presented on the origins of leadership that emerge from evolutionary thinking, a dominance theory and a theory of social coordination. I then use the vast psychological literature to examine the support for each of these theories, relying on data from the empirical literature on leadership, including books (such as the excellent *Handbook of Leadership* by Bass, 1990), chapters, and journal articles that were obtained through searching in PsycINFO (key word: leadership). Finally, I discuss some implications of an evolutionary-based analysis of leadership and offer some directions for further research.

Evolution and Leadership

Evolution, Leadership, and Group Life

Evolutionary biologists reserve the term leadership for behaviors that determine the type, timing, and duration of group activity (Krause & Ruxton, 2002). In any species, an important set of adaptive problems revolves around deciding what to do, when and where to do it. For example, when animals forage they must decide when to forage or rest, when to leave a patch, and which food items to seek. For animals living in social groups, foraging is further complicated by the actions of others. It will normally be safer to forage at the same

time as other group members, favoring some coordination of activity. A critical issue is how group members can reach consensus about the type and timing of group action so that they act together in unity. Usually this can be solved if one individual takes the initiative, and the rest acquiesce and follow. Leader-follower patterns may have emerged in many social species to solve coordination problems such as these.

An evolutionary analysis assumes that the emergence of leadership is fine-tuned to specific coordination problems that humans have faced across evolutionary history (cf. Tooby & Cosmides, 1992). Leadership would be unlikely to evolve unless the benefits of group coordination were significant. Furthermore, specific group problems are expected to result in specific types of leadership. For most of hominid history, people lived in seminomadic groups of around 30–50 members that were probably connected to larger social networks (Boyd & Richerson, 2005). These groups periodically had to make decisions about where to move to, for example, to new waterholes, hunting grounds, or sleeping sites (Dunbar, 2004). It would pay for group members to stay together, while moving, to maintain group cohesion. Group decision-making would be facilitated by the emergence of some form of leadership, whereby some individuals persuaded others to follow them in the direction of a preferred waterhole or hunting ground.

Ancestral humans frequently faced threats from other group members, for example, over food, mates, status, and other scarce resources (Chagnon, 1997). There would be frequent violent episodes that threatened to undermine group cohesion by pitting rivals against each other. Here it would benefit group members, especially the weaker ones, to endorse a leader to act as peacekeeper in the group. In addition, confrontations with members of rival groups, for example over the control of waterholes, would also have been common (Alexander, 1987). Again, it might benefit groups to have a leader in place to organize group defense and lead the attack (Diamond, 1997).

Quite possibly, these different adaptive problems might have produced different forms of leadership. For example, in moving toward a new waterhole, one would expect the most experienced and physically fittest group members to lead the group. To maintain or restore peace within a group, fair and impartial leaders might be desirable. Further, intergroup threats might persuade group members to follow a more aggressive leader than what they would normally tolerate in peace time (McCann, 1992).

Anthropological and Nonhuman Evidence for Leadership

The evolutionary argument rests on the assumption that leadership and followership have coevolved in humans, and quite possibly in other social species, because taking on such roles under the right conditions would have been adaptive. Hence, we expect to find examples of leadership everywhere in human history and across cultures. Throughout most of evolutionary history, humans have been organized in small hunter-gatherer societies (Boyd & Richerson, 2005; Dunbar, 2004). Reviews of hunter-gatherer societies suggest that, although they frequently do not have institutionalized rulers or elected officials in place, there are always individuals who are more likely to take a central role in the group's decision-making (Boehm, 1999; Diamond, 1997; Lewis, 1974). Many such societies have a "Big Man" as informal leader, a physically strong, warrior-like figure who exercises a disproportionate influence on group action.

Support for the evolutionary argument would be further strengthened if there were examples of leadership among other social species, especially those that are likely to have faced similar adaptive problems (Schmitt & Pilcher, 2004). Nonhuman primates are known to engage in leader-follower relationships that are very similar to humans. When baboons are moving, for example, an older male takes the initiative by stepping a few meters away from the group in the direction of his preferred destination. Others then move in the same direction, and the whole troop follows (Dunbar, 1983). Essentially, the same pattern has been observed in other nomadic social species, such as deer, buffalo, and migrating birds (Couzin et al., 2005; Krause & Ruxton, 2002).

Examples of leadership have also been found in response to aggression within groups. De Waal (1996) has studied chimpanzee behavior in a captive colony in Arnhem Zoo, and observes on one occasion that

> 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)

Chimpanzees also display leadership in defending their territory. Boehm (1999) describes an incident from Gombe when the members of one group spot a rival group in the distance:

> Goblin [the leader] moves forward quickly to a vantage spot to peer across the valley and Mustard now emulates him. As Goblin (number one), Satan (number two), and Evered (number three) scan the valley, they break off several times to look at one another quickly. After nearly 60 seconds, Goblin suddenly makes his decision and begins to vocalize and display. The entire group, which includes adolescents Freud

> and Beethoven, immediately follows suit and the result is the usual one: Both groups vocalize and display ferociously then slowly retreat into their home ranges. (p. 28)

Because these patterns resemble leader and follower behaviors in humans, it suggests that similar principles might be at work. Admittedly, observations among nonhuman species are biased by a human-centered view, and after close scrutiny they may be very different from any form of human leadership. Different selection pressures have shaped the behaviors of group-living species in many different ways, and humans have many adaptations that make them unique, even among the primates, such as language and sophisticated tool use (Barrett et al., 2002). Nevertheless, it is encouraging to find examples of leader-like patterns among species whose members regularly engage in coordinated activities, for example, to move or feed together, or defend their territory. Hence, there is at least a possibility that the psychology of leadership and followership in humans has a very ancient origin.

Benefits of Leadership and Followership

An evolutionary analysis asserts that there should be benefits associated with a particular trait or behavior to evolve through natural selection (Schmitt & Pilger, 2004). In evolution, an organism's success is ultimately measured in terms of reproductive success, yet there are a host of proximal factors affecting reproductive success such as health, security, and wealth. The benefits for leadership are best documented in the psychological literature.

Positions of leadership are strongly correlated with wealth and other indices of socioeconomic status such as class and education (Switzer, 1975). One study found that leaders of villages in India tended to be higher in caste and have greater land holdings than ordinary villagers (Roy, Jaiswal, & Shankar, 1974). People in leadership positions are also generally healthier and live longer, although the causal direction of this effect is yet unclear (Marmot, 2004). Across many human societies leadership is strongly connected to status—in fact, so much so that the two are often confused in the literature (Bass, 1990). Leaders are held in higher esteem, and their actions are judged as more acceptable even when they break the rules ("The king can do no wrong;" Hollander, 1985). Social psychological studies show that putting participants in a leadership position enhances their mood and optimism (Hardy & Van Vugt, ~~2005~~; Keltner, Gruenfeld, & Anderson, 2003). Finally, research in traditional societies shows a direct link between (male) leadership and reproductive success. Men in leadership positions have, on average, more children and more wives (Betzig, 1986; Chagnon, 1997). Whether this is true for modern society remains to be seen. In a recent study in Canada, Perusse (1993) found that powerful people had more mating opportunities.

It is less obvious what benefits ultimately exist for followers. Not everyone can be a leader, and perhaps these people simply make the best of a bad situation in evolutionary terms (Dawkins, 1976). Yet there might be indirect benefits for followers that derive from their association with good leaders. Various studies show that some leaders produce superior team performances (Hogan, ~~Hogan, &~~ Curphy, 1994). Good leadership increases group morale and satisfaction with group membership (Berkowitz, 1953). Experimental research on social dilemmas shows that leaders enhance group cooperation, thereby producing outcomes that everyone in the group can enjoy (Van Vugt & De Cremer, 1999).

This raises an interesting possibility. Perhaps followership, and consequently, leadership, have been selected for by virtue of their contribution to the success of groups in addition to that of individuals. Multilevel selection theory (Sober & Wilson, 1998) suggests that in principle selection can occur at the level of the gene, the individual organism, and the level of a group of organisms. For group-based adaptations to evolve, there must be between group selection forces at work, which must sometimes be stronger than within group selection forces. At the individual level, followers would generally be expected to do worse than leaders in terms of their reproductive success. Yet, at the group level, followers might fare better than individuals in groups without leaders or poorly functioning leaders. Group selection is a realistic possibility among species like humans that live in groups and frequently face conflicts with other groups (Boyd & Richerson, 2005). Whether it accounts for the evolution of leadership in humans is debatable, but it is a possibility that I examine later on in this review.

Evolutionary Theories of Leadership

A review of the evolutionary literature suggests that there are two broad perspectives on the origins of leadership in humans. I discuss the two main theories in the next section, and present evidence from the psychological literature to support or reject each of these hypotheses.

Leadership as Byproduct Dominance

Some evolutionary scientists assert that adaptations for leadership and followership do not exist as such, but that behaviors associated with these roles are simply byproducts of adaptations for dominance and submission (Alexander, 1987; Nicholson, 2000; E. O. Wil-

son, 1975; see also Hollander, 1985). In this view, the occupation of leader and follower roles is explained entirely by the relative positions of individuals in the dominance hierarchy of a group. Dominance hierarchies are the product of competition among group members for scarce resources (Buss, 1999; E. O. Wilson, 1975). Because some individuals are more successful than others in gaining access to these resources, hierarchies emerge in which those at the top of the hierarchy enjoy greater reproductive success than those at the bottom, the notorious pecking order. Highly placed individuals are able to exercise control over group activities, because they are not dependent upon others to achieve their goals. They eat when they are hungry, rest when they are tired, and threaten anyone who annoys them. Low ranked individuals must coordinate their actions with the dominant individual because they offer protection as well as access to other valuable resources, for example, food and mates. Thus, a low ranked individual has no other option but to follow whatever dominant individuals in the group decide to do.

The byproduct dominance theory of leadership is attractive because of its parsimony. It may apply to social species in which it is always the dominant that leads the group, for example, in chasing prey (wolves), in defense against predators (zebras), and in controlling the activities of subordinates (gorillas). Furthermore, it is intuitively appealing because some human leaders are regarded as being dominant, bossy, and controlling (Bass, 1990). Yet this model is unlikely to account for the totality of leadership phenomena in humans. First, human hierarchies are much flatter than those of most other social species, including the nonhuman primates (Boehm, 1999). Moreover, hierarchies in humans are often built upon prestige rather than dominance (Heinrich & Gil-White, 2001). Dominance is made more difficult because many key resources only become available through cooperation, and once they are available, cannot be easily monopolized by one individual, for example, large game hunting (Boehm, 1999). Group members also often have alternatives for following a leader. They can follow a different leader or leave their group entirely (Van Vugt, Hart, Jepson, & De Cremer, 2004). This severely restricts the power and control of one individual over others (Thibaut & Kelley 1959).

Probably most importantly, this theory does not seem to fit very well with the definition of leadership as a "process of influence" and with folk ideas that emphasize persuasion rather than coercion as the main leadership strategy (Hogan, Hogan, & Curphy, 1994). Nevertheless, the possibility should be considered that leadership in humans is nothing more than a byproduct of a drive for dominance, in which the top ranked individual in the group hierarchy controls the type and timing of the social activities. The low ranked individuals can do little else but follow the dominant individual so as to protect their interests.

The Psychological Literature

The byproduct dominance theory leads to a number of predictions about leadership than can be tested using the extant psychological literature. The most obvious prediction is a positive correlation between dominance and leadership ratings, which receives little support in the literature. In a classic review of leadership trait research, Stogdill (1974) found many studies in which leaders and followers did not differ in their scores on dominance, as measured by various personality scales. Leadership also appears to be unrelated to measures of authoritarianism, one's preference for dominance relationships (Christie & Geiss, 1970). In addition, scores on a dominance scale do not predict whether individuals emerge as leaders in a laboratory group task (Kremer & Mack, 1983).

Followers do not generally want to be led by dominant people. Caldwell and Wellman (1926) reported that high school children expressed a preference for teachers who could keep order, but were not bossy. Dominant leaders often induce negative sentiments in groups. In a classic study on leadership in teams of schoolboys, Lewin, Lippitt, and White (1939) demonstrated that there was more anger and less cooperation in teams led by an authoritarian teacher relative to a democratic or laissez-faire teacher. Also, employees are more likely to leave organizations led by dominant managers (Brockner, Tyler, & Cooper-Schneider, 1992), which has been replicated in the laboratory (Van Vugt et al., 2004). Social dilemma research has found that even in a crisis group members do not want to loose their autonomy by appointing a dominant leader, provided there are alternative solutions available (Rutte & Wilke, 1984; Samuelson, 1993; Tyler & DeGoey, 1995; Van Vugt & De Cremer, 1999). Reviewing the evidence, Bass (1990) concludes unequivocally: "Leadership cannot be defined in terms of personal dominance" (p. 68).

The lack of substantial evidence from psychological research for a relationship between leadership and dominance does not necessarily imply that in human evolutionary history these concepts were never correlated. It might be that in ancestral environments, some individuals were indeed able to enforce their decisions upon the rest of the group. Yet if we take research of hunter-gather societies as an indication, then the opposite seems to be true. Boehm (1993) stated in his seminal ethnographic study of 48 hunter-gatherer societies

> simple foragers, complex hunter-gatherers, people living in tribal segmentary systems, and people living in incipient chiefdoms would appear to exhibit a strong set of egalitarian values that express an active distaste

> for too much hierarchy and actively take steps to avoid being seriously dominated. (p. 139)

He then described the way such societies deal with overbearing leaders, for example, by simply disobeying or ridiculing them, leaving the group, and sometimes killing them themselves or allowing others to kill them (Boehm, 1993).

All in all, it seems that in neither modern nor ancestral environments does leadership reliably correlate with dominance. The literature suggests that people do not support dominant leaders, quite possibly because of fears of being exploited by them. It seems that people who have the desire to lead must rely on tactics other than sheer dominance to attract followers.

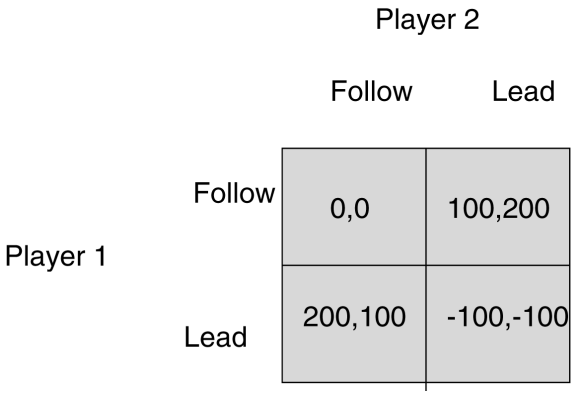

Figure 1. The Game of Leader; within each cell, the first pay-off is for Player 1 and the second for Player 2; pay-offs are in reproductive benefits and costs.

Leadership as Strategy for Social Coordination

An alternative evolutionary theory is that leadership evolved specifically for the purpose of solving coordination problems. Individuals who frequently engage in group activities face a recurrent decision problem. How do they initiate group action while simultaneously maintaining group cohesion? This can be solved if some individuals take the lead and others follow. Thus, leadership and followership are social strategies that have been selected for by virtue of their success in fostering collective action. This adaptive account of leadership is best illustrated by evolutionary game theory.

Evolutionary game theory (Maynard-Smith, 1982), sometimes referred to as "evolutionary stable strategy" or ESS theory, models social interactions as games in which strategies compete with each other in a Darwinian fashion. Evolutionary game theory is like economic game theory, except that 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 relative fitness. Strategies (genes) spread through a population by virtue of the superior decision rules they adopt in relevant situations, whereas inferior strategies become extinct. This process resembles natural selection (Dawkins, 1976). If we can model leadership and followership as different strategies for social interaction, evolutionary game theory can be used to examine how well they fare against alternative strategies as well as each other.

Leadership involves elements of initiative, coordination, and direction (Bass, 1990). It is therefore tempting to view leadership as a social strategy in a coordination game like Leader. The Game of Leader is one of several archetypical nonzero sum games, like the Prisoner's Dilemma, Chicken, and Battle of Sexes, in which the interests of actors are partly overlapping and partly conflicting (Rapoport, 1967). The simplest version involves two players, 1 and 2, each with two strategies, say lead or follow. The pay-off matrix of this game is depicted in Figure 1.[1] There are four cells in Figure 1, each with two pay-offs representing fitness outcomes for Player 1 and Player 2, respectively. If both choose follow, they each get a zero pay-off. The players can "solve" the game if one leads and the other follows in which case both obtain a positive outcome, but the leader gets relatively more. Leader, however, is also the riskier strategy, because if both choose to lead, they each receive a negative outcome.[2]

This is not an easy game to play. When two anonymous individuals play this game simultaneously in the laboratory about 75% of players receive a zero pay-off (Guyer & Rapoport, 1976). Following is the strategy that individuals play if they want to get the best (maximum) of their worst (minimum) possible outcome in the game—the so-called maximin strategy. Switching to a leader strategy only pays if one can reasonably expect the other to follow, otherwise both end up with their worst possible outcome. If leaders can somehow communicate their intentions, for example, through verbal or nonverbal signaling it would be easier to solve the game.

The leader-follower combinations in Figure 1 are referred to as the equilibria of the game. This is an im-

[1]For simplicity's sake, we concentrate on a two-person 2 × 2 game to illustrate how leader-follower relationships might emerge. Admittedly, many examples of leadership are found in larger groups. Yet, the logic of the two-person game also applies to the N-person game, where the payoffs for one player are simply replaced by the average pay-offs for the rest of the players (Komorita & Parks, 1994; Luce & Raiffa, 1957).

[2]Here we should note a crucial difference between the Game of Leader and the well-known Battle-of-Sexes game. In Leader, the player who switches from Follower to Leader (the risky alternative) receives the highest pay-off. In Battle-of-Sexes, the player who switches to Leader gives the other player the highest pay-off (provided that the other sticks with Follower). Because of this feature, this game is also known as the Hero game (Rapoport, 1967). Despite some similarities, the concepts of leadership and heroism are therefore not identical and presumably have different evolutionary origins.

portant concept in evolutionary game theory (Maynard-Smith, 1982). Once interactions settle into an equilibrium, they are likely to stay there because neither player obtains a better outcome by switching to a different strategy. This game is thus likely to select for adaptations to execute a mixed leader-follower strategy. Over evolutionary time, we would expect these strategies to become increasingly synchronized and fine-tuned. Populations consisting of exclusively leader or follower strategies would become extinct.

Some evolutionary game theory models predict that all individuals are capable of both leading and following, and that they will choose their strategy flexibly depending on the parameter values (conditional alternative phenotypes; West-Eberhard, 2003). Other models predict a stable mix of leaders and followers in the population that is likely to be maintained through frequency-dependent selection (genetic polymorphisms; Maynard-Smith, 1982; D. S. Wilson et al., 1996). The latter models are particularly interesting because they suggest that a population contains a mixture of leader and follower genotypes. Paralleling the argument for the stability of sex ratios, an increase in the frequency of leaders to followers in a given population will select against the leader strategy, because leaders are more likely to meet each other in which case they do relatively worse than follower strategies (see Figure 1). Thus, selection maintains the ratio of leaders to followers in a population at equilibrium level.

There are many real-life examples of the leader game that might have selected for leader and follower adaptations. For example, how does a group decide when and where to gather food when it must stay together for protection? If individuals decide to forage only when they are hungry, they most likely end up foraging alone because not everyone is hungry at the same time. Hence, their best outcome will be to move when at least one of them is hungry. This person will then get the largest pay-off and emerge as leader, because they determine the timing of group activity. When such differences in energy and food levels vary consistently between people, this results in a stable leadership structure (Couzin et al., 2005). An example of group leadership is when residents from an island community must come to an agreement about investing their collective resources in connecting their island to the mainland when one group prefers to build a boat and the other a bridge. If the boat builders and bridge builders work on their own projects, they end up with either a half-finished boat or half-constructed bridge. So, the two groups must choose between these projects, resulting in one group emerging as project leaders (Insko et al., 1980).

It is not surprising to find evidence for leadership in group-living species like humans because they frequently encounter coordination problems, for example, in food gathering, group mobility, and group defense. According to the game model, coordinated action serves everyone's interest yet the benefits for leaders are frequently higher than for followers. Nevertheless, it might pay to become a follower if, for example, there is little chance for an individual to become a leader. Furthermore, to become leader one day, a person might have to start out as follower and learn the trade (Henrich & Gil-White, 2001). Another intriguing possibility to explain followership from evolutionary game theory is based on group selection. It is clear from the pay-off structure in Figure 1 that individuals in groups with a leader-follower structure fare better than in leaderless groups. Hence, followers might be better off, on average, in groups with leaders although they are less well off than their leaders. This suggests that leadership might be a group-level adaptation that has emerged in human evolutionary history, because between-group selection pressures were sometimes stronger than within-group selection pressures. This argument resembles the group selection logic for the evolution of altruism (Sober & Wilson, 1998).

The Psychological Literature

The evolutionary game analysis offers a number of hypotheses about leadership if we are willing to consider the possibility that leadership and followership have evolved as complementary social strategies to solve coordination problems, whereby one individual initiates an action and others follow. In the following sections, I review the psychological literature in light of these hypotheses.

Leadership and initiative taking. The evolutionary game model suggests first that those inclined to take the initiative are more likely to emerge as leaders in any particular situation. The psychological literature is quite consistent with this claim. A range of traits have been identified that increase the probability for initiating action, which are correlates of leadership. For example, one study among a sample of AT&T executives (Bray & Howard, 1983) found that executives differed from ordinary employees in their activity and energy level, their industriousness, ambition, and readiness to make a decision. In a study on leadership among students, strong positive correlations were found between leadership ratings and self-reported measures of assertiveness, extraversion, spontaneity, and sociability, with a negative correlation between leadership and shyness (Gough, 1984; Judge, Bono, Ilies, & Gerhardt, 2002).

The leader strategy is the bold move in the leader game because the potential costs of this strategy are substantial. I would therefore expect leaders to score higher on measures of boldness and self-confidence, and they do. For example, Andrews (1984) showed among a group of undergraduates that those with high

self-esteem were more likely to emerge as the leaders of their groups. Hemphill and Pepinsky (1955) showed that attempted leadership was higher among participants who were held in high esteem by their group mates. An archive study among the U. S. presidential elections between 1948 and 1984 found that the more optimistic candidates were more likely to win (Zullow, Oettingen, Peterson, & Seligman, 1988). Finally, individuals who show signs of learned helplessness are less likely to take the initiative in social situations (Abramson, Seligman, & Teasdale, 1978).

Research on the so-called babble hypothesis provides further support for the relationship between initiative and leadership. Those who emerge as leaders are often the ones who participate most actively in group activities, for example, by talking a lot (Mullen, Salas, & Driskell, 1989; Sorrentino & Boutillier, 1975). Quantity of communication is a better predictor of leadership emergence, whereas the quality of what one says is a better predictor of leadership effectiveness. Sorrentino and Boutillier (1975) manipulated both the number and quality of comments given by a confederate who was acting as a group member in a group discussion. Although the quality of their comments influenced perceived differences in their competence and influence, the number of their comments predicted perceived differences in leadership, regardless of how useful these comments were.

Additional support for the initiative hypothesis comes from the Ohio leadership studies (Hemphill, 1950). In this research investigators first developed a list of behaviors observed in military and organizational leaders and then asked members of various groups to indicate how many of these behaviors their leaders displayed. Through a factor analytic procedure they then narrowed down the list of behaviors into a small number of prototypical leader activities. One of the most important leadership behaviors that emerged was *initiation of structure*, consisting of activities that facilitated groups to move toward their goals through planning, coordinating, and monitoring task progress.

In most studies on the initiative hypothesis, it is difficult to establish the causal direction of the effect. For example, being appointed as leaders may well encourage people to seek the initiative (cf. Lord & Maher, 1991). Only one experimental study that I know of has looked into this. Kremer and Mack (1983) showed that people who took the initiative in an experimental version of the leader game were more likely to be nominated as leader during a subsequent group task. Participants first played 100 trials of the leader game with another person who was, in fact, a preprogrammed computer strategy. They were then assigned to a five-person task group and required to solve a number of group problems. After that, the group members rated each other on various leadership scales. As predicted, leadership ratings during the group task were affected by the frequency with which a person adopted a leader strategy in the previous experimental game (this effect was stronger for females).

The evolutionary game hypothesis offers some intriguing suggestions for further research on leadership and initiative taking. For example, what happens if groups contain people who score either all very high or very low on traits associated with initiative taking such as ambition, self-esteem, or extraversion? Leadership should emerge more slowly within such groups. Furthermore, the game analysis shows that leading is the risky game strategy. There should therefore be a correlation in the real-world between leadership and individual measures of risk-taking. To my knowledge, this has not yet been tested.

Leadership and (social) intelligence. The evolutionary game model also suggests that people who are quicker to recognize a situation as a coordination problem, that requires leadership, emerge as leaders more often. Furthermore, they must convince people that following is the best option. From this, I expect that leadership correlates with intelligence, because it helps in identifying coordination problems as well as in coordinating actions of multiple actors. Consistent with this, there are 58 studies reported in Bass' (1990) extant review on leadership and intelligence, and the majority (48) finds a positive relationship between leadership and the score on a standard IQ test. The average correlation coefficient across the studies is +. 28. In an archive study of the personalities of U. S. presidents, Simonton (1994) found evidence for above average intellectual abilities among many former presidents. Finally, in a meta-analytic study, intelligence came out as the trait that followers believed was most consistently linked with leadership (Lord, DeVader, & Alliger, 1986).

Perhaps not surprising, the IQ component most strongly associated with leadership is verbal ability (Korman, 1968). Communication is crucial in coordinating group action, especially when there are goal conflicts, and leaders with good communication skills are therefore at an advantage (Dunbar, 2004). Mathematical and spatial abilities are also important to persuade followers that one has the knowledge and ability to lead them somewhere. Yet, as documented in the literature, a large discrepancy in intelligence between leader and follower works against the execution of leadership, maybe because such individuals have difficulties in giving simple instructions to followers (Bass, 1990; Simonton, 1994).

Sometimes it might help aspiring leaders to appear more intelligent than they really are or to manipulate others into believing that they have a unique ability to accomplish their goals. A trait that is frequently associated with this kind of social manipulation is Machiavellianism (Christie & Geiss, 1970). Individ-

uals who score high on this trait are no more intelligent than the average individual (D. S. Wilson et al., 1996). Yet, in social interactions they often are perceived as more intelligent and attractive by others (Cherulnik, Way, Ames, & Hutto, 1981). As a consequence, they often take on leadership roles in small groups, and they are competent coalition builders and negotiators (D. S. Wilson et al., 1996).

Another crucial attribute in leaders is their *social intelligence*—the ability to understand other people and manage relationships with others (Kihlstrom & Cantor, 2000). Socially intelligent people can figure out what motivates potential followers even if they are not yet aware of it themselves. There is some evidence that leaders have better developed social skills than followers. For example, Kenny and Zaccoro (1983) found that the best predictor of being perceived as leader was one's sociability—the ability to accurately perceive the needs and goals of group members. Leadership is also correlated with measures of nonverbal sensitivity (Hall, Halberstadt, & O'Brien, 1997) and empathy, the ability to put oneself in another's position (Mann, 1959), although this latter effect deserves replication. As Bass (1990) notes

> It is not enough for a leader to know how to get what followers want, or tell them how to get what they want. The leader must be able to know what followers want, when they want it, and what prevents them from getting what they want. (pp. 167–168)

Evidence that leaders are competent. The game analysis suggests that individuals with a unique ability to accomplish a specific group goal are more likely to emerge as leaders in that specific domain; otherwise they simply do not attract followers. In support of this, there is a long tradition of research showing that leadership in a particular domain correlates with expertise in that domain (Aidar, 1989). For example, the successful head of an accounting department is generally held to be a better accountant than his subordinates (Tsui, 1984). Stogdill (1974) found in nearly every leader survey that technical and task-relevant skills were mentioned as important attributes of leaders. Group members are more willing to follow directions of individuals who have previously demonstrated task ability (Hollander, 1985). Low task ability disqualifies an individual almost immediately from leadership status (Palmer, 1962). Group members process task relevant skills quickly. Given some experience working together, group members can easily make a rank ordering of each other in terms of task-specific skills (Littlepage, Robinson, & Reddington, 1997). Thus, leader-follower relationships emerge more quickly if people can identify a person with a specific task competence that they then follow.

Leadership, generosity, and fairness. The game analysis suggests that both leaders and followers benefit from coordinated action, yet leaders benefit relatively more sometimes. How much each party actually gains from collective action is not always clear, and, to some extent, subject to negotiation once the goal is achieved (Diamond, 1997). In theory, as long as the pay-offs for followers exceed those of nonfollowers—anywhere in the range between 0 and 100 units in Figure 1—is it advantageous to follow a leader. Generally, the greater the expected share of the outcomes the more dedicated the followers (Hollander, 1985). Furthermore, people should be reluctant to follow individuals that are unlikely to share with them.

This leads to the general prediction that leadership is correlated with traits and behaviors that signal generosity and fairness. Although there have been no conclusive tests of this idea, there is some indirect support. One reason why socioemotional qualities, such as empathy, predict leadership emergence is perhaps because they provide followers with information about the prosocial inclination of leaders (cf. Batson, 1998). Trustworthiness of a leader is another such trait. A study measuring satisfaction with cadet leaders found a strong correlation between subordinates' satisfaction and a measure of the leader's trustworthiness (Sgro, Worchel, Pence, & Orban, 1980). Another study found that the most important distinction between good and bad supervisors was the amount of help they gave to their workers, for example, in promotion decisions, sharing time and sacrificing personal interests (Konovsky, 1986). Anthropological research also supports the association between generosity and leadership. Reviewing the literature on egalitarian hunter-gatherer societies, Boehm (1999) concludes that leaders get respect by being generous. Leaders who are stingy are sometimes simply disobeyed, replaced, or even killed by the group (Chagnon, 1997).

Experimental research on public good dilemmas provides further support for a link between leadership and generosity. First, group members who invest more into their group are more strongly preferred as group leaders (Hardy & Van Vugt, 2005). Following the saying that "noblesse oblige," a randomly assigned leader also becomes more generous (Hardy & Van Vugt, 2005) and self-sacrificing leaders attract more enthusiastic followers (De Cremer & Van Knippenberg, 2002). As quite a different example, when individuals are assigned randomly to a leader role, they are more likely to intervene in emergencies like the sudden illness of a group member than when they were ordinary members (Baumeister, Chesner, Senders, & Tice, 1988). Finally, when students are unobtrusively primed with words associated with power and leadership (e.g., authority) they become more altruistic toward fellow students (Chen, Lee-Chai, & Bargh, 2001).

Ultimate bargaining research shows that fairness, another prosocial trait, is important in leader's allocation decisions (Fehr & Fischbacher, 2003). In the ultimatum game, which is effectively a sequential leader game, one individual is assigned to the role of leader and the other to follower. The leader proposes to divide a sum of money (say $10) between themselves in a certain way. The follower either accepts the offer, in which case each gets what the leader has proposed, or rejects the offer, in which case neither of them gets anything. In theory, followers should accept anything above $0 because that is what they get when they reject the offer. In practice, followers reject any offer below $2 with a very high probability. As a result, most leaders propose $4 and $5 to followers, an indication that leaders are trying to be fair (Fehr & Fischbacher, 2003).

In the real-world, there will often be a time delay between the emergence of leadership in groups and goal achievement. In deciding who to follow, people must therefore often rely on indirect signals of generosity. One important cue is the way that leaders treat followers, while they are moving toward a specified goal. For example, do leaders consult followers while they are pursuing their goals, and do they treat them nicely and respectfully? Research shows that such procedural fairness judgments are an important factor in leadership endorsement (De Cremer & Van Knippenberg, 2002; Tyler & Lind, 1992; Van Vugt & De Cremer, 1999). In light of the relevant game analysis, it is not surprising that procedural fairness is particularly important when the benefits of group actions are uncertain (Van den Bos, Lind, Vermunt, & Wilke, 1997). Thus, procedural fairness concerns should be more important when the group goals are long-term rather than immediate, when the pay-offs for followers are variable and uncertain, and when the leader is new and has not yet developed an altruistic reputation. These are testable propositions.

Leadership emerges in response to threats and opportunities. The evolutionary game analysis also makes predictions in which situations leader-follower relations are likely to develop. A straightforward prediction from this model is that leadership does not emerge unless the benefits of coordinated action are substantial (i.e., the pay-offs in the leader-follower cells of Figure 1). Natural disasters such as droughts, hurricanes, and earthquakes, as well as social threats such as wars and rebellions, are likely candidates for the development of leadership because these situations require urgent group action and mobilization. The psychological literature supports this idea. Leadership develops more quickly in emergency situations (Baumeister et al., 1988; Hamblin, 1958; Mulder & Stemerding, 1963; Samuelson et al., 1984; Van Vugt & De Cremer, 1999). Furthermore, crises often pave the way for directive and sometimes coercive leaders who can enforce group unity if it is needed (Samuelson et al., 1984; Simon & Guetzkow, 1955; Van Vugt & De Cremer, 1999; cf. McCann, 1992). Followers might accept a more autocratic style leadership in a crisis because the costs of being in a noncohesive group are likely to be substantial.

This might be especially so when groups are in competition with other groups (Alexander, 1987; Sober & Wilson, 1998). In intergroup settings, groups with leaders are expected to do better than groups without leaders. In the famous Robber Cave experiment, one of the first activities within each of the competing groups of schoolboys was to elect a team leader (Sherif, 1966). Another study shows that leaders sometimes strengthen their position in the group by starting a conflict with another group (Rabbie & Bekkers, 1978). Intergroup encounters presumably also determine the type of leadership that emerges. Intergroup rivalries increase the desire for prototypical group leaders who by virtue of their similarity with other group members could act as a unifying force (De Cremer & Van Vugt, 2002; Hogg, 2001).

Leaderless groups. Sometimes leadership might not emerge at all, according to the evolutionary game analysis. If groups face a relatively simple coordination problem, and there is little or no conflict between the group members, a stable leadership structure might not emerge and leadership might be ephemeral. This hypothesis is supported, by and large, in the psychological literature on leadership substitutes (Kerr & Jermier, 1978). Substitutes for leadership are variables that make leadership either unnecessary or impossible. What are these substitute variables? One is the activity itself. If the activity is predictable—hence, everyone knows what to do and how it should be done—then leadership is unlikely (Comstock & Scott, 1977). Small and cohesive units with overlapping goals between members, like a friendship group, also lack the necessity for centralized coordination. Often, these groups actually do better without a leader, because power differences between members undermine group cohesion (Haslam et al., 1998; Kerr & Jermier, 1978). Finally, improvements in technology like telephone or the Internet could render leadership unnecessary because individuals can communicate with each other directly without central coordination (Wright, 2000).

Summary

To summarize, the psychological literature offers some support for the idea that leadership and followership are complementary strategies specialized in solving coordination problems. Leadership involves initiative taking and maintaining group cohesion, whereas followership involves deciding who to follow,

when, and where to. Most of the evidence comes from studies that were not designed to test an evolutionary game model, therefore they are not definitive tests. Future empirical studies should be based explicitly on an evolutionary game framework to examine leadership emergence when people adopt different strategies to solve coordination problems.

Other Correlates of Leadership: Age, Health, and Gender

Evolutionary theory can be used to generate a large number of specific hypotheses about correlates of leadership such as age, health, and gender. I conclude this review of the psychological literature by framing some of these hypotheses and reviewing relevant data.

Age and leadership. Age relates to leadership in a complicated way, according to the psychological literature. Some research finds a positive correlation between age and leadership, whereas others find a zero or negative correlation (Bass, 1990). Could an evolutionary perspective account for these mixed findings? People should only defer to a leader who is likely to achieve mutual goals. In ancestral environments, some situations required the possession of unique and specialized knowledge, for example, where to find a waterhole that has not yet dried up (Barrett et al., 2002; Boehm, 1999). Knowledge about where to go would have been more likely to be held by older and experienced individuals, and, thus leading is expected to correlate positively with age in this domain. In the present time, evidence for this link between age and leadership can still be found in professions that require a considerable amount of specialized knowledge and experience, such as in science, politics, and arts (Caldwell & Wellman, 1926).

In other situations, the group goals might be clear yet difficult to accomplish. For example, intergroup struggles presumably require leaders with considerable strength, energy, and stamina. Insofar as these qualities deteriorate with age, I would not expect a positive correlation between age and leadership. The military, athletics, and some competitive business environments might be examples. Thus, the age-leadership relationship might be quite context specific and it would be interesting to investigate this relationship more systematically.

Health. Earlier I have indicated that in the real-world there is often a delay between the decision to follow someone and the actual benefits received. This implies that followers should be very sensitive to cues about whether leaders are capable of delivering future benefits. The health of potential leaders might provide a reliable indication. There are several studies showing that leaders possess better health than followers (Bass, 1990; Marmot, 2004). The causal direction of this effect is still unclear. Several studies suggest that a superior physique, a sign of good health, correlates with leadership (Bass, 1990). Cox (1926) found that this is particularly true for military leadership. Leadership also correlates with a favorable waist-to-hip ratio, a reliable indicator of health and genetic fitness (Campbell, Simpson, Stewart, & Manning, 2002). Finally, archival evidence shows that aspiring political leaders such as U. S. presidential candidates must appear healthy and in good shape to get elected (Simonton, 1994).

Gender. Finally, although there has been a dramatic recent increase in female leadership in a range of organizational settings, from business management to education, science, and government, male leadership is still the norm in most societies (Eagly & Carli, 2003). Predictions about whether this is likely to change, fall beyond the scope of the article. Here I am interested in the possible evolutionary origins of gender differences in leadership. There are reliable differences between males and females across a range of traits and behaviors that might explain sex differences in leadership (Buss, 1999; Pinker, 2002). For example, females possess, on average, better verbal memory and communication skills. Hence, they should be more likely to emerge as leaders in situations in which these skills are important. I know of no research that has looked systematically at sex differences in leadership emergence across different tasks, but it would be an obvious avenue to explore.

Psychological studies show that, on average, males are more assertive, self-confident, and risk taking (Buss, 1999; Mezulis, Abramson, Hyde, & Hankin, 2004). Hence, they should be quicker to seize the initiative in newly formed groups, and they do: In mixed sex groups, men emerge as leaders more often (Aries, 1976). Men are also more likely to take on a leadership role if they are being observed by women, presumably because leadership is associated with status rewards (Campbell et al., 2002), and male status is more strongly associated with reproductive success (Buss, 1999; Perusse, 1993).

Evolutionary thinking might also explain differences in leadership style in male versus female groups. Anthropological and primate research suggests that hierarchies form much quicker in male than in female groups (Boehm, 1999; De Waal, 1996; Kelly, 1995). Female coalitions, which are often cemented between genetic relatives, tend to be more egalitarian. Thus, leader-follower relationships are expected to emerge more rapidly in groups of men, and these relationships are predicted to be more hierarchical and less stable over time. These hypotheses could be tested by comparing leadership emergence in same-sex groups in both the laboratory and the field. Corroborating these

differences, meta-analytic research shows that female leaders tend to exercise a more democratic and egalitarian leadership style, whereas male leaders tend to be more autocratic and controlling (Eagly & Johnson, 1990).

Finally, an evolutionary account does not imply that gender differences in leadership style are somehow "set in stone." On the contrary, the main argument emerging from an evolutionary game analysis is that it pays to be behaviorally flexible. For example, it has been found that female leaders entering a traditionally male dominated occupation adopt a more controlling and autocratic leadership style—they mimic the dominant style of males (Eagly & Carli, 2003). Similarly, a male manager might adopt a more egalitarian and participative style among a predominantly female staff. These hypotheses await further investigation.

Evolution and the Debate Between Personality and Situational Accounts of Leadership

In the psychological literature there are by and large two rival perspectives on the origins of leadership (Bass, 1990; Chemers, 2000; Hogan et al., 1994; Hollander, 1985; Lord & Maher, 1991). Personality or trait models assume that there is a distinct set of personality traits reliably distinguishing leaders from nonleaders or followers. In contrast, situational or state theories of leadership emphasize the importance of the decision situation in determining who gets to be leader. At first glance, it seems that an evolutionary account of leadership has more in common with the personality perspective, because of a mutual interest in genetic influences on leadership. When psychologists consider evolutionary explanations for human behavior, they often assume that the behavior is genetically fixed and therefore relatively inflexible (Kenrick & Simpson, 1997).

This is a wrong assumption. An evolutionary account can incorporate both trait and state models of leadership, and the psychological literature must ultimately decide which of these perspectives is supported by the data. In general, natural selection will favor some degree of behavioral flexibility particularly in rapidly changing environments (phenotypic plasticity; Tooby & Cosmides, 1992; West-Eberhard, 2003). For a large part of evolutionary history, humans have lived in relatively fluid and complex social environments that would have selected for phenotypic plasticity (Dunbar, 2004). Although genetic and developmental differences might make some individuals more likely to emerge as leaders or followers, there would be considerable advantage if people could adopt either of these roles flexibly. For example, even a very shy person should be able to lead a group to safety if they were being attacked by a rival group, and he was the first to notice the danger.

As stated earlier, the psychological literature must tell us whether leadership and followership primarily reflect a difference in traits or states between individuals. If these behaviors are relatively fixed, it could be that genetic differences in the propensity to lead are maintained through frequency-dependent selection (Maynard-Smith, 1982). Frequency dependent selection makes it possible to maintain a mixture of different strategies within the same population. If the frequency of leader strategies increases in a given population then the fitness benefit of this strategy decreases. The game theory model (Figure 1) clearly shows that when two leaders meet, they do worse in a coordination problem than when a leader meets a follower (cf. "too many cooks spoil the broth"). Thus, negative selection forces would ensure that the ratio of leader to follower genotypes remains stable in the population over time.

The Psychological Literature

The psychological literature provides support for both trait and state influences on leadership emergence, suggesting that leadership is neither completely genetically fixed nor phenotypically flexible. To determine the genetic heritability of leadership traits, one can look at the data from twin research. These studies show substantial heritability coefficients of traits predicting leadership such as intelligence, empathy, extraversion, and ambition (Ilies, Gerhardt, & Le, 2004; Rushton, Fulkner, Neal, Nias, & Eysenck, 1986).[3] In addition, children's desire to take on leadership roles is contingent upon the ambition levels of parents (Bass, 1960; Klonsky, 1983). [3]

There is also some evidence for the phenotypic stability of leadership. Correlations between .18 and .63 have been obtained between displaying leadership at college and taking on leadership positions later in life, for example, in business and in the army (~~Harell, 1964;~~ Russell, Mattson, Devlin, & Altwater, 1986). Studies with college students have yielded high test-retest reliabilities (with correlations of up to .90) between leadership emergence in task groups that were held as much as four months apart (Bass & Norton, 1951).

[3]It must be noted that heritability does not imply that there are specific genes coding for leadership. It is more likely that leadership and other complex social traits are influenced by multiple genes that each play a small role in producing differences in a particular trait (Plomin & Colledge, 2001). This means that the trait is distributed quantitatively within a population. Furthermore, some of these genes are likely to have a very generic influence on the manifestation of leadership. For example, inheriting a slightly taller build might increase the likelihood of adopting the leader phenotype (cf. Bass, 1990). Finally, heritability does not imply genetic determinism (Kenrick & Simpson, 1997). Environmental and developmental factors are likely to determine the phenotypic expression of genetic traits associated with leadership (West-Eberhard, 2003).

There is also evidence that the same leaders emerge when individuals work in different groups on different tasks (Kenny & Zaccaro, 1983; Zaccaro, Foti, & Kenny, 1991). Zaccaro et al. (1991) placed individuals in three-person groups with rotating membership, working on four different tasks, each requiring a different leader skill (persuasion, initiating action, consideration, and production). After each task, people rated themselves and each other on the Leader Behavior Description Questionnaire. This study found that as much as 59% of the variance in leadership ratings across the tasks was trait-based, leading to the conclusion that what sets leaders apart from followers is their flexibility to be socially receptive to the demands of the task and the group they are leading (Zaccoro et al., 1991). Thus, it seems that leadership is at least partly influenced by traits with a substantial genetic component, although this does not imply that there are gene-specific traits for leadership.

Yet other research suggests that leadership emergence is phenotypically more flexible. For example, systematic changes in leadership appear as a function of age. In children between ages 3 and 8, more influence is exercised by the physically strongest and more dominant children, but between ages 12 and 15 the more friendly children take over as group leaders (Barner-Berry, 1982). Cultural differences also appear to have strong effects on leadership. For example, Hofstede's (1980) 50-country survey of IBM personnel found more evidence for autocratic style managers in East-Asia and the Middle-East than in countries in Northern Europe and the United States. It is also likely that different leaders emerge when groups face different challenges (Fiedler, 1967). The bullish Winston Churchill became prime-minister of Britain only when World War II had started; yet as soon as the war ended, his party was defeated in a general election. An archival analysis of U. S.-presidential elections found that when voters believed the United States was facing an internal or external crisis, they opted for a more aggressive and conservative president (McCann, 1992).

To summarize, the literature shows evidence for a trait component in leadership, which is mainly accounted for by the influence of some very generic personality traits that appear to have a substantial genetic component. As indicated before, such stable trait differences between individuals may be maintained through frequency-dependent selection forces (Maynard-Smith, 1982). Nevertheless, as much of the variance in leadership is probably accounted for by situational factors such as followers' needs and the type of group threat. It is possible that leadership reflects a trait in some individuals and reflects a state in others, thus, within the same population there might be individuals with genotype-specific leader or follower traits as well as individuals with flexible genotypes who could take on either of these roles depending upon particular environmental conditions (West-Eberhard, 2003).

Discussion

The aim of this review was to start a constructive dialogue between two scientific disciplines, evolutionary biology and social psychology, that have studied leadership but that have hardly influenced each other. Evolutionary scientists theorize about the origins of leadership, based on the principles of natural selection and adaptation, but this tradition is generally lacking in empirical research. In contrast, social psychologists have gathered a wealth of highly reliable results on leadership through surveys and experiments, but their research lacks an overarching theoretical framework that can make sense of the richness of these data. I hope this review will be read by both evolutionary scientists and psychologists interested in leadership and followership, and give momentum to a more integrated research agenda.

Evolutionary Perspectives on Leadership

I have offered two general evolutionary perspectives on the emergence of leader-follower relationships. The first, which is based on the animal and primate literatures (E. O. Wilson, 1975), suggests that leadership and followership are mere byproducts of adaptations for dominance and submission. Dominant individuals undertake leader-like activities because the costs are negligible to them, for example, they move when they are hungry. This led to the prediction that leadership correlates with measures of dominance, which received very little support in the psychological literature.

The second theoretical framework is based on evolutionary game theory (Maynard-Smith, 1982). A game-theoretical analysis views leadership and followership as complementary social strategies in coordination situations. Strategies spread through the population by virtue of their fitness benefits on organisms adopting these strategies. Viewed in this way, leadership has evolved as social strategy because it was superior to alternative strategies in solving coordination problems. Leadership involves taking the initiative and attracting followers. There are a number of hypotheses emanating from this evolutionary game analysis that were put to test using the psychological literature as database.

Leadership, for example, correlates with traits and actions that encourage initiative taking, such as ambition, boldness, self-esteem, and extraversion. Leadership correlates with general intelligence, reflecting an ability to identify a coordination problem and organize

group coordination. Leadership also correlates with competence, fairness, and generosity, qualities that might persuade followers to give up their preferred strategy. The support for these predictions is largely based on research, which did not set out from a game theoretical model (for some exceptions, De Cremer & Van Knippenberg, 2002; Kremer & Mack, 1983; Van Vugt & De Cremer, 1999). A more controlled test of many of the predictions is needed, and various suggestions have been offered throughout this review. Although a game-theoretical framework is a sensible way of looking at the origins of leadership, it only begins to address the diversity and complexity in this phenomenon. For example, I have addressed why particular coordination situations facilitate or suppress the emergence of leadership. It has also been explained how leadership might vary as a function of differences in age, health, and gender. Future tests of these ideas are obviously needed.

Psychology, Evolution, and Leadership

The evolutionary perspective challenges some traditional conceptions on leadership and could be criticized on various grounds. A criticism that is deemed to be unfair is that an evolutionary perspective implies genetic determinism. Although there are heritable genetic differences in the propensity for leadership, based on very general personality traits like extraversion and intelligence, who leads is still highly context dependent. For example, an immediate group crisis might pave the way for an autocratic leader whom followers would not normally tolerate (Boehm, 1999; McCann, 1992). Similarly, in groups of introverts a leadership structure would still be expected to develop albeit more slowly. Thus, evolutionary theory is very much consistent with an interactionistic perspective on leadership (Fiedler, 1967; Hogan et al., 1994; Hollander, 1985).

Another concern is whether an evolutionary game model makes fundamentally different predictions about leadership than other theories. In principle, any theory that assumes that individuals are designed to reap the benefits from group action and coordination could make the same predictions, including economic game theory (Luce & Raiffa, 1957) or its psychological equivalent, social exchange theory (Hollander, 1985; Thibaut & Kelley, 1959). Yet, these models must ultimately address where these inclinations originate from, which only evolutionary theory can (Tooby & Cosmides, 1992; D. S. Wilson et al., 1996). Most other psychological theories of leadership are built around a particular leadership phenomenon such as transformational (Bass, 1997) or intergroup leadership (Hogg, 2001) and are therefore less suitable as a generic theory of leadership.

Conclusions, Implications, and Future Research Directions

Evolutionary theory offers a much needed integrative framework in which it is possible to understand the wealth of disparate theories and findings in the psychological literature on leadership. By viewing leadership and followership as products of adaptations that have emerged in human evolutionary history to facilitate group action, it provides the foundation for more proximal, social-psychological models of leadership. Evolutionary theory accounts for the existence of personality differences in leadership on the basis of traits like ambition, extraversion, and intelligence. It accounts for the relatively stable impressions that followers hold about leadership, such as intelligence, health, and generosity, thus offering the underpinnings for cognitive models of leadership (Lord & Maher, 1991). At the same time, it provides clues as to why these stereotypical impressions might sometimes change, for example, in the presence of an acute intergroup threat (Hogg, 2001).

The evolutionary framework suggests various new directions for research on leadership. One straightforward prediction is that leadership emerges more quickly when groups are under threat, consist of people inclined to take initiatives (extraverts, risk-takers, people with high self-esteem), and when there is little or no difference in pay-offs between individuals. This can be tested in the laboratory by letting individuals play different variants of the leader game in small groups. These studies could also investigate the emergence of different leadership styles in response to different group threats such as an intergroup conflict or within-group aggression (for a suitable procedure, see Van Vugt et al., 2004). More research is also needed to study the interplay between genetic and environmental influences on leadership. My review suggests that leadership is neither a completely flexible nor fixed trait. Twin studies might be useful to obtain heritability estimates of traits that predict leadership (but see Footnote 3). Research should also look at environmental factors that might trigger people to adopt leader or follower phenotypes, for example, birth-order, relative age in peer group, and socialization processes (West-Eberhard, 2003).

More studies are needed to examine the link between leadership and such factors as self-esteem, empathy, risk-taking, and generosity. If these qualities are predictive of leadership then leaders are expected to score higher on these traits. More research is also needed to study the benefits of leadership for groups. Although the benefits of leading are fairly obvious, it is yet unclear what profits there are for followers. Some evolutionary models suggest that leadership is a group-level adaptation (Sober & Wilson, 1998). To test this, we need to show that communities with good

leaders generally do better than communities with poorly functioning leaders or no leaders at all, perhaps by inspecting organizational performance data or the economic records of countries. This review also suggests that leadership and dominance are different evolutionary pathways to obtaining status (cf. Henrich & Gil-White, 2001). It would be interesting to examine why in some groups status hierarchies are built around dominance and in others around leadership. The importance of group cooperation presumably influences the emergence of status through personal contributions to the welfare of the group, for example, in the form of leadership. Finally, perhaps as a more general point, future research could benefit from multidisciplinary research efforts between psychologists, anthropologists, biologists, and zoologists interested in the study of leadership. An evolutionary perspective naturally lends itself to multidisciplinary study.

Before closing, an important, but inevitable limitation of this review should be noted. The psychological literature on leadership is so vast and dispersed across so many subdisciplines that it was not possible for me to read or review all the books, chapters, and articles in the field. I concentrated on reading the major reviews of the leadership literature as well as many influential empirical articles. Despite efforts to ensure a representative review, I am ~~pretty~~ sure that I have omitted important materials.

The main aim of this review was to start a constructive dialogue between two scientific communities, psychology and evolutionary science, that have studied leadership for many decades, but unfortunately have evolved quite independently. I hope to have shown that an evolutionary approach can strengthen the scientific study of leadership, and provide profitable new directions in leadership research.

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