The Evolutionary Origins of Leadership and Followership

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Abstract

Drawing upon evolutionary logic, leadership and followership are reconceptualised in terms of two alternative, yet complimentary decision rules aimed at solving coordination problems between two or more individuals. The current paper uses the vast psychological literature on leadership as a database to test evolutionary hypotheses about the adaptive advantages of taking on leader or follower roles. Consistent with hypotheses, leadership correlates with initiative taking, with trait measures of (social) intelligence, with specific task competencies, and with generosity. Our review finds no link between leadership and dominance. Our evolutionary analysis also accounts for reliable age and sex differences in leadership emergence and style. In general, evolutionary theory provides a useful framework for studying leader-follower relations in humans.

The Evolutionary Origins of Leadership and Followership

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. Ancient and modern history is full of examples of individuals who take charge of a group of individuals and lead them, often against the odds, to safety, victory, or prosperity. Examples are military leaders like Alexander the Great, Nelson, and Eisenhower, 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. Furthermore, anthropological evidence suggests that there are no known human societies without some form of leadership (Boehm, 1999; Lewis, 1974). Small group research reveals that a leader-follower structure emerges quickly and spontaneously in most groups, even when a newly formed group sets out to be leaderless (Hemphill, 1961). It seems that whenever two or more individuals need to coordinate their activities, a leader-follower relationship develops quite naturally. This has led various experts to conclude that leadership is a universal human behavior (Bass, 1990; Brown, 1991; Hollander, 1985; Stogdill, 1974).

What about Burns' second claim? Psychological research on leadership contributes a great deal to our understanding of leadership emergence and effectiveness in groups. The latest edition of the *Handbook of Leadership* (Bass, 1990), for example, contains no fewer than 7.500 references to original pieces of research on leadership.

Early research concentrated on the personality correlates of leadership, resulting in a laundry list of traits and motives that reliably distinguish leaders from followers, such as extraversion, ambition, and intelligence – the trait or personality approach to leadership (Bass, 1990). In later research, the emphasis shifted more towards the study of leader functions and leadership styles in light of task demands and the needs of followers – the state or situational approach (Bass, 1990). One archive study into the results of US presidential elections found, for example, that, whenever voters believed the country to be under threat, the more aggressive and conservative candidate was elected by a greater margin (McCann, 1992).

The psychological 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 rather narrowly focused with little integration of findings into unifying theoretical frameworks (Chemers, 2000; Hogan & Kaiser, in press; Hollander, 1985; Hogg, 2001; Yukl, 1989). To quote Chemers's (2000) recent review: "The question remaining is whether a coherent integration of these seemingly disparate findings [on leadership] is possible." (p. 37). Or, as put more bluntly by Hogan & Kaiser (in press): "The academic tradition [on leadership] is a collection of dependable empirical nuggets, but it is also a collection of decontextualized facts that don't add up to a persuasive account of leadership." Furthermore, there is very little cross-fertilization of ideas among the relevant behavioral sciences, including social psychology, organizational psychology, cross-cultural psychology, political science, anthropology, and evolutionary biology.

Evolutionary scientists have also had an enduring interest in leadership. In *Sociobiology: The new synthesis*, the zoologist E. O. Wilson (1975) summarized his discipline's perspective on leadership "When zoologists speak of leadership, they usually mean the simple act of leading other group members during movement from one place to another" (p. 311). Evolutionary anthropologists and primatologists similarly view the locomotion of groups, for example towards new waterholes or hunting grounds, as an essential leader-follower problem (Boehm, 1999; Dunbar, 1983). In addition, they suggest that there is a role for leaders as peace keepers within their groups (De Waal, 1996).

The purpose of this review is twofold. First, we summarize the psychological and evolutionary literatures on leadership and try to synthesize them. The psychological literature contains a great deal of high quality empirical research on leadership emergence, leadership style, dominance, and followership. But, it generally lacks a coherent conceptual framework to unify the wealth of data. In contrast, the evolutionary approach has little experimental data on leadership, but provides a general theoretical framework, which is based on natural selection and adaptation, which can be used to analyze leadership in human groups. Thus, a second purpose of this review is to use the psychological literature as a database for evaluating evolutionary hypotheses about leadership and followership in humans. We should stress that some of these hypotheses might be derived from other frameworks than evolutionary theory. For example, cognitive, social or psychodynamic models of leadership may lead to essentially the same prediction. Yet, these proximate theories of leadership must ultimately also be explained in evolutionary terms in order to be viable; hence, they are no rivals (Buss, 1999).

Definitions and Assumptions

Leadership and followership have been defined in a great many ways in the

psychological literature (see Bass, 1990; Hollander, 1985). For this review, we use

functional definitions of leadership and followership, describing them as design features

of organisms for the purpose of increasing their survival and reproductive chances.

Leadership and followership can thus be seen as behavioral adaptations, designed to

solve specific problems that humans have faced throughout evolutionary history in

dealing with their physical and social environment (Barrett, Dunbar, & Lycett, 2002;

Tooby & Cosmides, 1992; Schmitt & Pilcher, 2004).

Hence, we define *leadership* in terms of a *design to induce others to coordinate*

their actions or goals with the individual's own actions and goals to foster the

individual's goals. There are a few important aspects to consider in this definition. First,

by adopting a functional definition, we exclude cases in which individuals accidentally

induce others to coordinate their activities with them (e.g., an individual who is holding

up others by climbing the stairs very slowly is not showing leadership). Second, rather

than being a generic social influence strategy, like status or prestige, leadership involves

specifically the coordination of a joint activity (Cartwright & Zander, 1968). To illustrate

the difference, by virtue of his scientific contributions, Charles Darwin is a person of

status and influence, but it would be hard to regard him as a leader as he does not

coordinate anyone's actions in a meaningful way. Finally, our definition specifies that

followers (temporarily) adopt the leader's goals. Many psychological definitions assume

that the goals of leaders and followers converge into a single group goal (Chemers, 2001;

Hogan et al., 1994; Hogg, 2001; Hollander, 1985). Yet, from an evolutionary perspective,

this is an unwarranted assumption because organisms are likely to experience frequent

conflicts of interests. Indeed, followers frequently incur a cost by adopting the goals of

the leader. There might, of course, be compensating benefits.

For conceptual clarity, it is important to define and analyze the concept of

followership separately from that of leadership. We define *followership as a design to

coordinate one's actions or goals with that of another individual -- the leader -- that has

the effect of fostering that individual's goals.* In certain respects, the puzzling feature of

leader-follower relationships from an evolutionary perspective is not adaptations for

leadership as there can be obvious reproductive benefits associated with leading (Wilson,

1975). Given what is known about the process of evolution through natural selection, it

might seem odd, however, to find adaptations designed to subordinate oneself to the will

of another individual. Thus, understanding why individuals take on follower roles is of

as much (if not more) theoretical interest as understanding leadership per se. Although

most agree with the dictum that "there can be no leaders without followers" questions

regarding the origins of followership are not normally posed in the psychological

literature (for exceptions, see Bass, 1997; Hogg, 2001; Lord et al., 2001).

<center>Evolutionary Perspectives on Leadership</center>

Anthropological and Nonhuman Evidence for Leadership

Our evolutionary argument rests on the assumption that leadership and

followership are adaptations that have co-evolved in humans because natural selection

favored individuals who enacted these behaviors at the expense of those who did not. If

so, we would expect leader-follower structures to be found recurrently across human

cultures and history. This is backed by anthropological evidence (Boehm, 1999; Brown,

1991; Lewis, 1974; Wright, 2000). Lewis (1974) concluded from a review of numerous band and tribal societies that even when communities do not have institutionalized rulers or elected officials, there are always individuals who are more likely to take a more coordinating role in the group's decision-making -- societies with informal leadership are referred to as "Big man" societies (Chagnon, 1991). In egalitarian hunter-gatherer societies, which are thought to closely resemble human social organization in the Pleistocene (where 95% of human history took place), individuals also differ systematically in their ability to control group activity (Boehm, 1999).

Support for the evolutionary argument would be further strengthened if we were to find examples of leader and follower roles amongst other social species, especially those that are genetically close to us, the nonhuman primates that are likely to have faced similar adaptive problems to early humans (Barrett et al., 2002). Several primate studies have observed differences between individuals in their influence over the group's decision-making process. Among Hamadryas baboons, for example, it is usually an older male that decides which way the group should move by looking or moving a few meters in this direction. Once some other individuals start to move in that direction, the whole troop then follows (Dunbar, 1983; Kummer, 1968). Chimpanzees are known to form leader-follower coalitions in defending their territory against neighboring troops. Boehm (1999) describes an incident when members of one troop spot a rival troop in the distance: "Goblin [the alpha male and 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).

Another form of leadership, observed among both apes and monkeys, is displayed by the so-called control animal (DeWaal, 1996; Wilson, 1975). The control animal – usually the alpha male -- intervenes in aggressive episodes between group members. De Waal (1996) describes it as follows among a chimpanzee colony that he observed in Arnhem Zoo: "On one occasion, 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).

These behavioral patterns resemble leader and follower behaviors in humans, suggesting that similar principles might be at work. It is possible of course that observations among primates are biased by a human-centered view, and that after close scrutiny these patterns turn out to be very different from any form of human leadership. Different selection pressures have shaped the behaviors of primate species in different ways, and humans have many adaptations that make them unique, such as language and sophisticated tool use (Barrett et al, 2002). Nevertheless, these examples suggest that in any group-living species in which members regularly engage in coordinated action, for example, collective foraging or group movement, a pristine form of leader-follower

structure may be found. Hence, we must consider the possibility that the psychology of leadership and followership might have been shaped by selection pressures similar to those that led to adaptations for the behaviors described in the examples.

Evolution, Leadership and Followership

Evolutionary biologists reserve the term leadership for behaviors that determine the type, time, and duration of group activity (Wilson, 1975). In any social species, an important set of adaptive problems is how to coordinate actions to engage in a joint activity. There are obvious benefits to group coordination, such as moving together as a unit, defending against predators or rival groups, and hunting collectively. A critical issue, however, is how group members can be made to act simultaneously and in unity. Our claim is that leadership and followership adaptations may have emerged in humans, and quite possibly in other social species, in order to solve coordination problems in time and place between individuals.

For example, situations would regularly arise where two or more individuals would have to decide between different hunting grounds. If two or more individuals would simultaneously initiate an action, the group would likely break up, and group members would all move into different directions. In this situation, it might pay to wait until one individual would make a move and then follow them to their favorite hunting ground. Similarly, there would frequently be violent episodes within the group, which threatened to undermine group unity and cohesion (Boehm, 1999; Chagnon, 1997). . Again, it would have been beneficial for group members to endorse an individual to break up the fight, who would then emerge as leader.

Thus, our evolutionary analysis indicates that leadership involves two distinct, but closely intertwined adaptive problems, (1) initiating an action, and (2) attracting followers. Followers face a slightly different (and arguably simpler) adaptive problem, that is, if an individual makes a preemptive decision about what to do, they must decide whether or not to subordinate to his preferences.

The evolutionary model assumes that leader follower adaptations need to be extremely fine-tuned in terms of deciding whether, when and with whom to coordinate one's actions (cf. Cosmides & Tooby, 1992). For example, an individual who would follow a conspecific to a waterhole that has dried up, is paying a costly price. There should therefore be selection pressures operating against indiscriminate followership. In the same vein, there should be selection pressures against persisting in a group activity without the support of followers. There are various evolutionary theories about how leader-follower systems might have evolved in humans and how they may have become part of human social behavior. We discuss two of them below.

Leadership as Byproduct Dominance

Some evolutionary biologists assert that leader and follower adaptations do not exist, but are simply byproducts of adaptations for dominance and submission. According to E. O. Wilson (1975), the occupation of leader and follower roles is explained entirely by the relative positions of individuals in the dominance hierarchy of the group. Dominance hierarchies are the result of group members competing for scarce reproductive resources. 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 (i.e., the pecking

order; Murchison, 1935). High ranked individuals can exercise control over group activities because they are not dependent upon others to coordinate their activities with them. They eat when they are hungry, rest when they are tired, and they threaten anyone who annoys them. Low ranked individuals, however, must coordinate their actions with the dominant individual as they offer protection, for example against aggressive ingroup members, as well as access to other valuable resources. Thus, a low ranked individual has no other option but to follow whatever the dominant individual decides to do.

Evaluation

This leadership-as-byproduct dominance model is attractive because of its parsimony. It might apply to various social species in which it is always the dominant individual that leads the group in collective hunting (e.g., wolves), in the defense against predators (e.g., zebras), and in controlling the actions of subordinates (e.g., gorillas; see also Vehrencamp, 1983). This model does not seem to account, however, for the totality of leadership phenomena in humans, however. First, social hierarchies in humans are often much flatter than in other species, including the nonhuman primates (Boehm, 1999). Straightforward dominance is made more difficult, because key resources become available only through the cooperative efforts of several individuals, and, once they are available they cannot be easily monopolized by one individual (e.g., hunting large game).

Second, human groups are quite flexible coalitions (Kurzban, Cosmides & Tooby, 2001). Group members often have alternatives for simply following a leader. They could leave the group or join a collation against the leader (Boehm, 1999; Van Vugt, Hart, Jepson, & De Cremer, 2004). This severely restricts the power of one individual over the other. Third, and possibly most importantly, this model does not seem to fit very well

with both folk ideas and research observations about leadership, which point to the role of persuasion rather than coercion (Hogan et al., 1994).

Nevertheless, we should consider the possibility that leadership and followership in humans is nothing more than a byproduct of a general class of dominance and submission adaptations, whereby the top individual in the hierarchy of the group controls the type and timing of group activities, because he can afford to do so with no or very little regard for what others are doing.

Leadership and Followership as Evolutionary Game Strategies

Another evolutionary perspective on leadership is derived from evolutionary game theory (Maynard-Smith, 1982). Leadership and followership can be conceived of as two complimentary strategies in a game in which two or more individuals must coordinate their actions in order to achieve their goals. Unlike in classic economic game theory, in evolutionary game theory, the outcomes for the actors are measured in terms of the fitness consequences. Hence, we can use evolutionary game theory to compare the fitness benefits of adopting a leader role with a follower role as well as compare how these strategies fare with alternative strategies.

Leadership involves elements of initiative taking, courage and coordination. It is therefore tempting to view leadership and followership as alternative strategies in a coordination game like Leader, which is thought to closely resemble leader-follower relations in the real-world (Rapoport, 1967).[4] Leader is one of several archetypical non-zero games (like the Prisoner's Dilemma and Chicken) in which the interests of actors are partly conflicting and partly overlapping. The pay-off matrix of the game is depicted in Figure 1. The game has two equilibrium points at (B,A) and (A,B). Yet, the natural

outcome of the game is (A,A) – when played simultaneously about 80% of interactions

end up at A,A (Guyer & Rapoport, 1969). A is the strategy that individuals play if they

want to minimize their loss in the game, but as can be seen from the matrix (A,A) is an

inferior outcome for both than either (B,A) or (A,B). Switching to B is a risky strategy,

however. It only pays to switch to B if one can be sure that the other plays A, otherwise

both end up with a deficient outcome (B,B). If player 1 plays B and player 2 plays A,

the first player emerges as the leader and the second player as the follower. In a

sequential game, by playing B, the first player effectively takes the lead and induces

player 2 to follow by coordinating their actions with them. By playing A, the second

player does not get his preferred pay-off, yet it is their best outcome given the

circumstances. Thus, although the game rewards mutual cooperation, there is a

discrepancy in benefits between the two players

Figure 1. The Leader Game

		Player 2	
		A	B
	A	0,0	100,200
Player 1			
	B	200,100	-100,-100

Note. Pay-offs for Player 1 are first and for Player 2 second.

There are many real-world examples of this game. One would be when two

organisms are attacked by a predator. Their best outcome is for one to make a run in a

particular direction (B), and for the other to follow (A). The front runner is obviously in a better position to escape than the follower. Yet, both are better off coordinating their actions in this way than if both start running at the same time yet in a different direction (B.B). Indeed, in that case they would have been better off by not moving at all (A,A). A similar problem emerges when two or more organisms that are resting must decide about when to forage (i.e., they must forage together for protection). If they each choose to forage only when they are hungry, they end up foraging alone (B,B) as it is unlikely that they will both feel hungry at exactly the same time. In that case, they would both be better off waiting (A,A). Their best outcome is to coordinate their activities such that the hungriest individual takes the lead and the not-so-hungry one follows. The hungriest individual gets the largest pay-off in this case.

Computer simulations on the leader game show that with repeated interactions players might develop a turn-taking strategy, alternating between (B,A) and (A,B), in order to maximize their pay-offs (Browning & Colman, 2004). Yet, in the real-world, players are seldom identical in their preferences. For example, some individuals are quicker to react to danger or they get hungry more easily. As a consequence, even slight differences can result in the formation of stable interaction patterns, whereby one individual always emerges as leader and the other always follows.

Evaluation

This game-theoretical model offers a number of testable hypotheses about the emergence of leader-follower structures in humans as long as we are willing to consider the possibility that they are the result of strategic interactions between two (or more) individuals that are trying to maximize their fitness through coordinating their actions to

achieve their goals (e.g., escaping from a predator, foraging). Leader and follower adaptations are likely to be found in social species like humans that frequently encounter situations in which the benefits of group coordination offset the costs that individuals incur by acting alone. Although the benefits of being a follower are generally lower than being the leader, it may nevertheless pay to follow if there is no or very little chance that others will follow you. Moreover, the distribution of benefits of successful group action between leaders and followers are, to some extent, negotiable, and therefore followers might get more than they had expected (Wright, 2000). Finally, there might be indirect benefits for followers. Individuals in groups with a highly developed leader-follower structure might do much better than in groups with a poorly developed leader structure. Hence, follower adaptations may have evolved through group-level selection mechanisms (Sober & Wilson, 1998).

Personality versus situational accounts of leadership

In the psychological literature there are, by and large, two competing theoretical perspectives on the origins of leadership (Bass, 1990; Chemers, 2000; Hollander, 1985; Hogan et al., 1994; Lord & Maher, 1991). Trait models assume that there is a distinct set of personality traits, distinguishing leaders from followers. In contrast, situational theories of leadership emphasize the importance of the decision situation in determining who leads or follows. It might seem that an evolutionary explanation of leadership has more in common with the personality perspective because of a mutual interest in the genetic basis of leadership and followership. Indeed, when psychologists consider evolutionary explanations for human behavior they often assume that the behavior is hardwired, in other words, that it is relatively fixed.

Yet, this assumption is not correct. The evolutionary game model, in particular, suggests that leader and follower roles might be adopted flexibly. Although due to genetic and developmental factors, some individuals might have a stronger inclination to initiate an action or wait, there is presumably a considerable advantage for individuals to be able to take on either of these roles, depending upon the circumstances. For example, it would pay for someone who would not normally be the first to act, to make a move if they are the first one to spot a predator. Particularly in unstable environments in which individuals are confronted with many different threats and opportunities, it pays to be behaviorally flexible. As these were presumably the conditions in which humans lived throughout evolutionary history, there would have been pressures to select for behavioral flexibility (cf. phenotypic plasticity; Cosmides & Tooby, 1992; Wilson et al., 1996). Thus, engaging in both leader and follower roles would have been adaptive for humans as well as the ability to apply these strategies contingent upon specific environmental stimuli.

An evolutionary account of leadership and followership can therefore incorporate both personality and situational theories of leadership. Phenotypic plasticity does not exclude the possibility that genetic factors may influence the likelihood that an individual emerges as leader across a broad spectrum of situations. To the extent that there are personality traits associated with leadership that have a genetic component, we would certainly expect to find heritable differences in the propensity to lead (Bass, 1990). On the population level, these differences may be maintained through what is known as frequency-dependent selection (Frank, 1988; Maynard-Smith, 1982). Frequency dependent selection makes it possible to maintain a mix of different strategies within a

population. If the frequency of traits underlying leadership would increase then the average fitness benefits for leading would decrease – as we have shown in our game-theoretic model, two leaders cannot solve a coordination problem ("too many cooks spoil the broth"). Hence, counterselection forces would kick in to make sure that the ratio of leaders to followers returns to a stable equilibrium in a population.

Summary of Evolutionary Perspective on Leadership

We have provided a general evolutionary framework for thinking about leadership. Our review of the evolutionary literature can be summarized as follows. One possibility is that there are no specific leader and follower adaptations. Behaviors that are generally associated with leadership, such as initiating group movement, simply emerge as byproducts of more universal dominance behavior. Dominant individuals conduct leader-like activities simply because they can afford to do what they want when they want, but subordinates must follow because coordinating with the dominant yields benefits (e.g., in terms of protection).

An alternative view is offered by evolutionary game theory, which views leading and following as the outcome of social interactions between individuals engaged in a coordination game like Leader (Rapoport, 1967). Those that induce others to coordinate their actions with them emerge as leaders. It is possible that these decision rules reflect heritable differences in the propensity for leadership or followership. It is also possible that these strategies are applied rather more flexibly, such that a leader in one situation is not the leader in the other.

These broad ideas can be put to test, using the vast psychological literature on leadership. In addition, we can use evolutionary theory to develop a large number of

specific hypotheses about leadership and followership. For example, leaders should overall benefit more from coordinated actions than do followers. Furthermore, more active and assertive people should be more likely to emerge as leaders because of their impatience. We should also expect to find correlations between leadership and measures of (social) intelligence, because in order to lead an individual must find out and possibly manipulate the pay-offs for others. Leader-follower structures are also more likely to emerge when group coordination is most urgent. Finally, we can evolutionary theory to speculate on how differences in leadership styles may have come about.

Psychological Research on Leadership

To test various evolutionary-based hypotheses regarding leadership and followership, we use the psychological literature as our database. There are a number of excellent, detailed reviews of the leadership literature available, for example, Bass & Stogdill's Handbook of Leadership (Bass, 1990) and articles and book chapters by Chemers (2000), Forsyth (1999), Gibb (1969), Hollander (1985), Hogg (2001), and Lord et al. (2001). We read these reviews as well as the key articles that are referred to in these reviews. In addition, we have done a search in PsycINFO for articles on leadership that have appeared in the last three years (2002-2005), which were not covered in these reviews. We used the term "leadership" as keyword for this search, which resulted in 609 articles. We examined all the abstracts and then read a selection of relevant papers in full, which we added to our database to test our hypotheses about leadership.

Benefits of leadership

Claims:

1. followers benefit from (good) leadership

2. leaders benefit even more

Leadership and Dominance

The evolutionary literature suggests sometimes that leadership is a byproduct of dominance, whereby subordinating individuals follow the highest ranked individual into an activity, because it gives them an opportunity to accomplish their goals (e.g., getting protection). This hypothesis predicts a positive correlation between dominance and leadership in humans, which receives little support in the psychological literature. In Stogdill's (1974) classic review of the leadership literature, he found 11 studies where leaders are indeed more dominant than followers, but in 6 studies they did not differ in their scores on various dominance scales. Leadership is also unrelated to measures of authoritarianism, one's preference for dominance relationships (Christie & Geiss, 1970).

Moreover, individuals do not generally want to be led by dominant individuals. For example, Caldwell & 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 among followers. In a classic study on leadership in boys' teams, Lewin et al., (1939) found that there was more anger and hostility in teams that were led by an authoritarian teacher than teams that were led by a democratic or laissez-faire teacher – although, interestingly, the task performance of these teams did not differ. And, individuals are more likely to leave organizations led by dominant managers (Brockner, Tyler, & Cooper-Schneider, 1992; Van Vugt et al., 2004). Finally, social dilemma research found that, even during a crisis, group members do not want to relinquish full resource control to a leader (Rutte & Wilke, 1984; Samuelson, 1993; Tyler

& DeGoey, 1995; Van Vugt & De Cremer, 1999).   Reviewing the evidence, Bass (1990) concluded that "leadership cannot be defined in terms of personal dominance" (p. 68).

The lack of substantial evidence in psychological research for a relationship between leadership and dominance does not necessarily mean that in human evolutionary history these concepts were never correlated. For example, it might be that in ancestral environments, some individuals were able to enforce their decisions upon the rest of the group. However, if we take the research on hierarchies in modern hunter-gather societies as an indication then the opposite seems to be true. As Boehm (1993; p. 139) concluded in his 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." In order to level the dominance hierarchy, members of these societies would employ different tactics to undermine the decision power of their leaders through ridiculing or disobeying them, and sometimes even through killing an overbearing leader (Boehm, 1993).

All in all, it seems that in neither modern nor ancestral environments is leadership strongly correlated with dominance. The literature suggests that people do not want to coordinate their actions with an overbearing leader, possibly because of the fear of being exploited. In general, it seems that individuals who have the desire to lead must rely on other, more subtle tactics than pure dominance to attract followers.

Leadership and initiative taking

A prediction derived from evolutionary game theory is that individuals will be more likely to emerge as leaders, the more likely they are to take the initiative and undertake a preemptive action in a coordination situation. In contrast, those who wait until someone else is ready to act are more likely to become followers. The psychological literature is generally supportive of 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 further study on the emergence of leadership in student groups, 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).

Research on the "babble" hypothesis provides further support for the relationship between leadership and initiative. There is convincing evidence that those who emerge as leaders are often the ones who have participated most actively in previous group activities, for example, by talking a lot (e.g., Kremer& Mack, 1983; Mullen, Salas, & Driskell, 1989; Sorrentino & Boutillier, 1975). According to one study, quantity of communication is a better predictor of the emergence as leader, whereas the quality of what one says is a better predictor of leadership influence. 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. Whereas the quality of the comments they made influenced perceived differences in competence, influence, and

contribution to group welfare, it was the number of comments made by the confederate that predicted perceived differences in leadership – regardless of how useful these comments were. This is in agreement with our evolutionary game model, because it shows that those who initiate group action are more likely to emerge as leaders, irrespective of the nature of the proposed action.

Other support for this initiative hypothesis of leadership comes from the Ohio leadership studies (Hemphill, 1950). In these classic studies, 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 the initiation of structure. It consisted of activities that facilitated groups to "move" towards their goals (e.g., reducing goal ambiguity, planning and coordinating action, monitoring task progress).

In most studies on the initiative hypothesis, it is difficult to establish the causal direction in the relation between leadership and initiative taking – being appointed as leader may put pressure on individuals to talk a lot (cf. Lord et al., 1991). We know of only one experimental study that has looked into this. Kremer & Mack (1983) showed that pre-emptive behavior by an individual in a coordination game was related to subsequent nomination for leadership in a small task group. Participants first played 100 trials of a Leader game (like the one depicted in Figure 2a) with a simulated other, where by making a pre-emptive move they could improve their and their partner's pay-offs. They were then assigned to a five-person task group and required to solve a number of

group problems. After that, they rated each other on various leadership scales. As predicted, those who were more likely to make a first move in the game subsequently received higher leadership ratings in the group task (this effect, however, was found only for females). It would be important to conduct further experimental research on the initiative-leader emergence effect. For example, would participants be more likely to grant leadership to individuals making a pre-emptive move in a leader game (like Figures 2a and 2b) than in a dominance game (like Figure 3).

Leadership, intelligence, and empathy

The evolutionary game model of leadership also suggests that individuals are more likely to follow leaders who (a) know what goals followers want to achieve, (b) can persuade them of their ability to accomplish these goals, (c) and signal a willingness to share the gains with them (i.e., generosity). There are a number of qualities needed to fulfill these conditions, but presumably an important personality attribute that allows individuals to meet these demands is social intelligence, a person's ability to understand and manage other people, and engage in adaptive social interactions (Kihlstrom & Cantor, 2000). Thus, we would first of all expect a positive, but probably modest correlation between leadership and general measures of intelligence, which is supported by the literature. In Bass' (1990) extensive review, no less than 58 studies are reported, the majority of them (48) finding a positive relationship between intelligence and leadership. The average correlation coefficient across the studies is +.28. Also, in his archive study of the personalities of former US presidents, Simonton (1994) found evidence for superior intellectual abilities among most presidents.

Not surprising, the IQ component that is most strongly associated with leadership is the verbal ability test (Korman, 1968). Given the importance of persuasion, potential leaders must possess superior communication skills and speech fluency to be able to convince others to follow them -- leadership among humans is indeed greatly facilitated by the language capacity. Mathematical, spatial, and logic abilities are, of course, also important in ensuring that followers are persuaded that an individual is capable of leading them to a desired goal. However, as documented in the literature, a large discrepancy between the intelligence of the leader and follower works against the exercise of leadership (Simonton, 1994). This makes intuitive sense as leaders that are relatively more intelligent may have difficulties in communicating their ideas to followers, or their ideas are perhaps too advanced to be accepted by followers (Bass, 1990), which impedes group coordination. In any case, more intelligent individuals are more likely to emerge as leaders, but this relationship is most likely to be curvilinear.

Sometimes it may help aspiring leaders to appear more intelligent than they are, in reality. This way, they can manipulate others into believing that they have a unique ability to accomplish mutual goals, thus turning them into followers. A trait that is frequently associated with this kind of social manipulation is Machiavellian intelligence (Christie & Geis, 1970). Individuals who score high on this trait are no more intelligent than the average individual (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 very competent coalition builders and negotiators (Wilson et al., 1996).

Leadership also involves knowing what followers desire. This requires some degree of empathy, the ability to adopt somebody else's perspective by seeing the world through their eyes (Batson, 1998). As Bass indicated (1960) "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)."

Although there has been a lot of speculation about the relationship between empathy and leadership, the research evidence is mixed. This may have to do with how empathy is measured. For example, various researchers have measured empathy by asking individuals to estimate the percentage of people in a designated population who will endorse items on a personality scale. Leaders should be more accurate in their estimates, due to a higher level of empathy, but the results with this measure have been disappointing (see Bass, 1990). Using more observational measures of empathy – how leaders work with specific members in a group setting – has revealed stronger positive associations between leadership and empathy (Mann, 1959).

Theoretically, however, this positive relationship is not expected to be extremely strong. More empathic leaders perhaps know better what resources followers desire, and are more willing to share these resources with them. Yet, as our evolutionary game model suggests, leadership also involves making a bold, preemptive move to pursue one's own goals at the expense of those of others. Thus, to the extent that empathy involves perspective taking (Batson et al., 1981), we might expect that leaders, on the whole, show more of this trait than followers. However, in terms of their empathic concern, that is, the degree of sympathy and compassion for others, we do not necessarily expect differences

between leaders and followers. These ideas could be tested by studying how individuals

who have been assigned to leader and follower roles behave in a standard empathy-

altruism experiment (Batson, 1998).

Leadership and the probability that others follow

The evolutionary game analysis also delineates that individuals emerge as leaders

if they can ensure that (enough) others follow.   For every leader that has emerged in

human history, there are presumably many more that have tried to become leaders but

failed because of a lack of followership. Our game perspective suggests that following

another individual should be contingent upon perceptions regarding (a) their ability to

accomplish group-relevant goals, and once they have been acquired, (b) their willingness

to share the gains with followers.

Leadership and task competence. There is a long tradition of research showing

that the emergence of leadership in a particular domain correlates with expertise shown 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).

In further support, Stogdill (1974) found that technical and task-relevant skills were

mentioned as important attributes of leaders in nearly every leader survey. Group

members are more willing to follow directions of individuals who have previously

demonstrated task ability (Hollander, 1985).   Moreover, low task ability disqualifies an

individual almost immediately from leadership status (Palmer, 1962). Group members

also process task relevant information quickly. Given enough experience working

together, group members can easily make a rank ordering of each other in terms of task-

specific skills (Littlepage et al., 1997).   Thus, who gets to lead is determined, to some

extent, by followers' expectations about an individual's ability to achieve relevant goals.

But, what about the belief that followers will get a share in the gains?

Leadership and interpersonal competence. The previously discussed Ohio

leadership studies found evidence for a second prototypical leader activity, which can be

summarized in terms of relationship maintenance (Cartwright & Zander, 1968). This

involves actions that enable leaders to maintain positive relationships with others by

listening to them and trying to understand them, being willing to explain decisions to

them, being generally friendly and approachable, and treating them as equals – in other

words, the socio-emotional side of leadership (Lord et al., 1991; Tyler & Lind, 1992).

The importance of these socio-emotional behaviors can be understood from an

evolutionary game theoretical analysis, which delineates that individuals who initiate an

action only emerge as leaders if they ensure that others coordinate their activities with

them. The chances to emerge as leader are greatly enhanced if individuals have an

understanding of what followers want and when they need it. Having a broad range of

social skills greatly contributes to this understanding. For example, Kenny & Zaccoro

(1983) found that that most influential predictor of being perceived as leader was one's

sociability – the ability to accurately perceive the needs and goals of group members –

which, as we have seen before, greatly facilitates group coordination.

Leadership, generosity, and fairness. Furthermore, individuals should be

confident that they will actually benefit if they follow this particular individual and adopt

their goals. Following another organism can be costly, and especially so, if they are

unwilling to share the gains once they have achieved their goals. Thus, we would expect

followership to involve making a judgment not just about an individual's ability to

accomplish group-relevant goals, but also about their willingness to share the benefits. This is presumably another reason why socio-emotional qualities, such as empathy and sociability, are so highly associated with leadership emergence, because they provide followers with valuable information about the prosocial inclination of their leaders.

In support of this, a study measuring satisfaction with cadet leaders found a strong correlation between subordinates' satisfaction and a self-reported measure of the leader's trustworthiness, using Rotter's trust scale (Sgro, Worchel, Pence, & Orban, 1980). In another study, the most important distinction between good and bad supervisors was the amount of support and sympathy subordinates received from them (Konovsky, 1986). Examples of prosocial supervisory behavior involved leniency in personnel decisions, practicing a considerate style, sacrificing personal interests, and spending time and energy to help subordinates – all behaviors containing an element of sharing.

To preserve their position, leaders must continue to award a substantial amount of benefits to followers. A sample of 97 first line supervisors reported spending a significant amount of time per week in helping subordinates, for example, with difficulties at work as well as in their private lives (Kaplan & Cowen, 1981). The link between leadership and sharing is so automatic, that even when individuals are randomly assigned to a leadership role, they show altruism. In one experiment, group members were randomly assigned to occupy a leader (i.e., coordinator) or follower role in a six-person task group. They were then asked for a monetary investment in the group. As predicted, the leaders were much more generous than the followers (Hardy & Van Vugt, 2004). This was confirmed in research on the ultimate bargaining game which showed that allocators (leaders) were more generous to recipients who had exit options (Van Vugt

& Hardy, 2004).   As quite a different example, when individuals were assigned randomly to a leader role, they were more likely to intervene in an emergency – the sudden illness of a group member – than when they were ordinary members (Baumeister, Chesner, Senders, & Tice, 1988).   Finally, from research on hunter-gatherer societies it appears that the failure to share is one of the greatest sins of leaders, often resulting in their disposal by the members of the tribal community (Boehm, 1999).

Quite often, there will be a time delay between moving towards a goal and achieving the goal, and thus, decisions whether to follow or not cannot be based on direct experience with the generosity of a leader. Followers must therefore frequently rely on indirect cues about the cooperative inclination of their leaders. One important cue is derived from the way the leaders treat their followers, while they are moving towards a specified goal. For example, do leaders involve group members in the choice of their goal, and while they are trying to accomplish their goals, are they treated nicely? Research shows that these kind of procedural judgments are important in leader endorsement (Tyler & Lind, 1992).   In light of our analysis, it is not surprising that these judgments are particularly important before followers know what their resource share will be (Van den Bos, Lind, Vermunt, & Wilke, 1997). Furthermore, one would predict that procedural processes become more important when goals are longer-term, less well defined, and more complicated to reach – these are testable propositions.

Situational and personality influences on leadership

There is an ongoing controversy in the psychological literature on personality versus situational models of leadership (Bass, 1990; Chemers, 2000; Hogan et al., 1994). Although trait explanations were common in the early years of leadership research, they

were regarded with some disdain by the following generation of leadership researchers who argued for the importance of situational over personality factors in leader emergence. Unfortunately, there is no systematic research on the heritability of leadership, which could settle the argument. Recent twin studies, however, have shown remarkably strong heritability coefficients of traits that, as we have seen, are empirically correlated with leadership, such as intelligence, empathy, extraversion, ambition, and activity level (e.g., Rushton, Fulkner, Neal, Nias, & Eysenck, 1986; Simonton, 1994). Furthermore, some studies show evidence for a relationship between children's willingness to take on leadership roles and the ambition levels of their parents (Bass, 1960; Klonsky, 1983).

There is stronger evidence for the phenotypic stability of leadership. Correlations between .18 and .63 have been obtained between college leadership and leadership in post-academic positions, such as in business and in the US-Navy (Harell, 1964; Russell et al., 1986). Some studies with college students yield high test-retest reliabilities (with correlations of up to .90) between leadership emergence in the same task groups that were held as much as four months apart (Bass & Norton, 1951). There is also evidence that the same leaders seem to emerge when individuals work in different groups on different tasks (Kenny & Zaccaro, 1983; Zaccaro, Foti, & Kenny, 1991).

For example, Zaccaro, Foti, & Kenny (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, each individual rated themselves and the other group members on the Leader Behavior Description Questionnaire, a standard leadership questionnaire (Stogdill, 1974).

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 behavioral flexibility to be socially receptive to the demands of the task and the group they are leading (Zaccoro et al., 1991). It is indeed quite possible that stability in leadership reflects nothing more than stability in the impressions that followers have about what leadership should be (Lord et al., 1986).

Impressions about what constitutes good leadership may, however, not be entirely inflexible. For example, there is some evidence that systematic changes in leadership occur as a function of age. In children groups between ages 3 and 5, more influence is exercised by children who are more dominant and physically stronger. But, when they grow older, between ages 12 and 15, the more friendly children take over as leaders of informal groups (Barner-Berry, 1982). Also, cultural differences appear to have strong effects on leadership. For example, Hofstede's (1980) 50-country survey of IBM personnel found more evidence for autocratic forms of management in East-Asian and Middle-East countries than in countries in Northern Europe.

Finally, different leaders may emerge when groups face different challenges – e.g., the bullish Winston Churchill only emerged as British Prime-minister when the war with Germany was inevitable, but as soon as the war ended, he was defeated in an election. Corroborating this anecdotal evidence, a more systematic analysis of US-presidential elections found that when the US faced a national crisis, like a war or economic challenge, voters elected a more dominant president (McCann, 1992).

To summarize, the literature shows substantial evidence for a trait component in the emergence of leadership, although this is mainly accounted for by (a) the influence of

very generic personality traits correlating with leadership, such as intelligence, assertiveness, and empathy, and (b) a high degree of stability in impressions from followers. As we have indicated earlier, such stable differences may be maintained through frequency-dependent selection forces (Frank, 1988). Nevertheless, nearly as much variance in leadership emergence is probably accounted for by situational factors, such as (a) cultural differences, (b) the type of threat or opportunity groups are facing, and (c) the developmental stage of followers, thus revealing the importance of behaviorally flexible strategies of leading and following in humans.

Situational Demands on Leadership Emergence

The evolutionary analysis also makes predictions about the situation in which leader-follower relations are most likely to come about. One straightforward prediction from our game models is that leadership is more likely to emerge when the fitness benefits of following another individual are substantial compared to the benefits involved in acting alone. Emergencies and other types of life threats (e.g., fires, wars) are likely candidates for the emergence of leader-follower structures because these situations require that individuals coordinate their activities in order to deal with the threat. The psychological literature supports this. Leadership is more likely to emerge when groups face a crisis (e.g., Baumeister et al., 1988; Hamblin, 1958, Mulder & Stemerding, 1963; Samuelson et al., 1984; Van Vugt & De Cremer, 1999). Furthermore, such situations often pave the way for the emergence of a dominant and aggressive leader (McCann, 1992; Simonton, 1994). This is understandable because such situations create pressures on group members to remain close together as a unit, increasing the need for punitive actions against those who threaten group cohesion (altruistic punishment; Fehr &

Fischbacher, 2003).   Furthermore, in an emergency there is considerable uncertainty among group members, causing any individual with a clearly specified goal to take the initiative.

A specific threat that one might expect to instigate the leader-follower relationship is an intergroup conflict. Surprisingly, to our knowledge, there is no study to date that has examined leadership emergence in direct response to the presence of an outgroup (CHECK THIS). One study has shown experimentally that leaders can strengthen their position in the group by starting a conflict with another group (Rabbie & Bekkers, 1978). Another line of research has looked at preferences for different kinds of leaders in the case of an intergroup competition. Intergroup encounters increase followers' preferences for a highly committed ingroup leader over a leader with stereotypical leadership qualities, such as communication skills (De Cremer & Van Vugt, 2002; Hogg, 2001; Van Vugt & De Cremer, 1999).   In an evolutionary context, these preferences may be explained by the followers' fear that when faced with an intergroup threat, stereotypical leaders may act autonomously and impartially, thereby endangering the welfare of followers.

The evolutionary game models also suggest other possible catalysts for the emergence of leader-follower relations, which could be tested in empirical research. For example, when group size increases and individuals can no longer coordinate their actions through simple coordination rules (like turn-taking), we would expect a stronger preference for leadership (Mullen, Symons, Hu, & Salas, 1989). In addition, leader-follower structures are more likely to the extent that the goal is more valuable, individuals are unable to achieve it on their own, and they can identify an individual in

the group who can lead them towards the goal. These hypotheses could all be tested through careful investigation in the lab and field.

Origins of Different Leadership Styles

There is substantial empirical evidence for the existence of interpersonal and cross-situational differences in how individuals lead, their style of leadership (Bass, 1990). There are a great many ways to describe these variations in leadership style. For the sake of simplicity, they are usually presented in the form of a dichotomy, for example, autocratic versus democratic leadership. How can an evolutionary perspective account for differences in leadership style? Below, we provide a tentative evolutionary account of the emergence of three common distinctions in leadership style.

Task versus relationship orientated leadership. Evolutionary game theory assumes that leadership consists of two distinct, yet intertwined activities, (a) initiating action, and (b) ensuring that others follow. Psychological research has found abundant support for the distinction between these two leadership activities. In the classic Ohio leader studies, for example, researchers developed a list of nine types of behaviors observed in military and organizational leadership and then asked members of various groups to indicate which behaviors their leaders displayed (Cartwright & Zander, 1968; Hemphill, 1950). Through factor-analytic procedures, they were able to extract several prototypical leadership activities. The two most important functions were inititating structure and showing consideration, which closely correspond to the functions we identified by adopting an evolutionary game perspective. In a study among leadership behavior in European school children, Eibl-Eibesfeldt (1980) found evidence for essentially the same two functions.

It is tempting to argue these are two substrategies of leadership and that, depending upon various factors, individuals will either be more focused on making a preemptive move or ensuring that they are being followed. One of the factors determining the strength of these strategies is presumably one's temperament. Task orientated leaders indeed tend to be more aggressive, more goal-directed and achievement-oriented, and better able to tolerate hostility from other individuals than are relationship oriented leaders (Bales, 1958). They are also more autonomous and more likely to be first borns, and they create a greater social distance between themselves and followers (Klebanoff, 1976). Thus, in game theoretical terms, these individuals presumably have a dominant preference for one activity over the other, and are therefore more willing to act independently, making them less concerned about whether others follow (see Figure 2b). Not surprising, task leaders also tend to be more dominant, mature, intelligent, have a higher education, and possess greater relevant expertise than relationship leaders – all these qualities make individuals more prone to act independently (Bass, 1990).

This is not to say that task leaders are more effective than relation leaders. Situational factors are likely to determine how effective each of these styles will be. For example, if it is highly important that others follow, but followers have a very different preference about what to do or where to go then relational qualities in leaders will matter considerably in keeping the group together. Yet, if there is just one viable course of action, like in a crisis or emergency, and everyone knows what to do, then leaders can focus on the task at hand rather than on whether they are being followed. Support for this implication is found in research on Fielder's *contingency model of leadership* (1967,

1978), where they found that leaders with a task orientation perform better under extreme conditions, that is, situations in which everyone either got on so well with each other that they all wanted to do the same thing or situations in which there is only really one option available to the group (e.g., making the deadline for a group project). In contrast, relation leaders performed best when the situation was moderately favorable, and leaders needed to work on their relationships with followers to ensure that they were being followed.

Research on the situational leadership model (Hersey & Blanchard, 1982) is also consistent with these claims. In this model, the effectiveness of task versus relational leadership interacts with the maturity of followers. In their studies, they find that task leaders are most influential when followers are either so inexperienced that they do not what to do -- hence, they will follow any individual with a strong action preference -- or, they are mature enough to understand that they need to coordinate their activities as a group. In contrast, when followers have reached intermediate levels of (job and psychological) maturity, the emphasis for a leader is on getting them to give up their selfish preferences and act together as a group, often by letting them participate in the decision-making process (Hersey, Angelini, & Carakuskany, 1982).

Autocratic versus democratic leadership. In contrast to the above dichotomy, which originates in the distinction between two interrelated aspects of leadership, initiating action and keeping the group together, the difference between autocratic and democratic leadership resides, according to our evolutionary game model, in the power that leaders have to determine the activities of followers. One the autocratic extreme, one individual can dictate others what to do and where to go, which resembles a traditional dominance hierarchy. On the other, democratic extreme, each individual has more or less

an equal say in the group activity. The latter resembles what Boehm (1999) has described as an "inverse" dominance hierarchy, whereby followers effectively control the movements of any individual attempting to dominate the group – evidence for this can be found in most traditional hunter-gatherer societies (Boehm, 1993).

According to our evolutionary game hypothesis, autocratic leadership is more likely to emerge if there are huge fitness benefits associated with synchronizing the group activities such that followers are happy to relinquish some control over their activities to a leader to ensure that the group acts in harmony and deviant individuals can be coerced into following (Figure 3). This implies that we can find evidence for a more coercive leader style in situations in which the benefits of collective action are great. This is supported in the literature on military leadership, an environment in which it can be lethal for groups not to act in unity. For example, in a survey of 30.735 officers in the US – army it was found that leaders were more highly rated to the extent that they established a high level of discipline in their army unit (Penner, Malone, Coughlin, & Herz, 1973). Furthermore, US air force crews who were given training through authoritarian methods performed better than crews who were trained through more democratic methods (Torrance, 1953).

There is historical as well as laboratory evidence, suggesting that dictatorial leaders are particularly likely to emerge during emergencies, when there is a great need for group unity and collective action (Hemphill, 1950; Samuelson et al., 1986). For example, initially leaderless groups were more likely to choose an aggressive leader when they faced an outside threat, and if they had a lenient leader they were more likely to replace him (Firestone, Lichtman, & Colamosca, 1975). Also, when laboratory groups

experienced high stress due to harassment, time and space restrictions, they were more likely to choose the most dominant individual to represent them in negotiations with the experimenter (Lanzetta, 1955). Indeed, as noted by Janis and Mann (1977), when a threat is perceived, it generates the desire for prompt action and leadership becomes centered in one or a few persons who gain increased power to make decisions on behalf of the group.

Our analysis does not imply, however, that autocratic leadership always works better than democratic leadership. On the contrary, in most situations followers are not willing to voluntarily submit to a coercive leader. Generally speaking, this only occurs if there is an urgent need to show group unity. Under conditions in which individuals have many different ways to achieve their goals, we would expect to see a return to a more democratic leader style, where leaders takes the preferences of followers into account before pursuing their goals (Van Vugt et al., 2004).

Transactional versus transformational leadership. A third, more recent distinction in the psychological literature is that between a transactional and transformational leadership style (Bass, 1997; Burns, 1978). Transactional leaders engage in a simple exchange relationship with followers, whereby they reciprocally influence each other in order to get the benefits that each party desires (Hollander, 1985). In contrast, transformational leadership, which uses the power of inspiration, intellectual stimulation, and vision, encourages followers to forego their immediate selfish outcomes in order to adopt the goals of the leader. Transformational leadership is very similar to the classic concept of charismatic leadership (Burns, 1978; Simonton, 1994).

An evolutionary game analysis of these leadership concepts would examine the pay-off structure of the situation in which these two types of leader-follower relations are likely to emerge. The transactional model seems to describe the standard leader-follower situation, whereby two (or more) individuals must act together, but one individual, say Hunter X, has a slightly stronger preference for hunting bison than the other, Hunter Y, has for hunting eland (Figure 2b). By following X, Y gives up his immediate selfish preference, and, in doing so, would expect a pay-off from following X. X acknowledges this and is keen to share the meat with Y. In return, Y encourages X to provide these benefits in the future, and is therefore happy for X to get an additional pay-off by leading him to hunt bison.

In this transaction, both parties can exchange any type of resource with each other as long as they are valuable to both. Anthropological research has established, for example, that in hunter-gatherer societies a good hunter usually receives status and prestige, which enables him to obtain access to other valuable goals, such as better sleeping sites or even mating opportunities (Hawkes, 1993). In further support of this social exchange model of leadership, psychological research has established that followers usually reject leaders who are unable to provide resources, unwilling to share resources, or distribute them unfairly among followers (Hollander, 1985). Of course, leaders are only disposed of if they are held responsible for a failure to share (Lawler & Thompson, 1978). Finally, leaders who are more successful in providing resources generally gain some credits from followers that enables them to occasionally break group rules and norms (cf. idiosyncratic leadership; Hollander, 1964).

A transformational leadership style differs in one unique aspect from a transactional style in that it makes followers actually believe that following the leader in pursing an activity is in their best interest – in game theoretical terms, their dominant preference shifts to that of the leader, hence there is no cost associated with following. Now, there is suddenly no discrepancy between what they wish to do and what the leader wants them to do, resulting in a convergence of actions and goals (see Figures 1a or 1b). In support of this argument, transformational leadership has often been described as bringing a change in individuals' preferences to move them to go beyond their self-interest (Bass, 1997). And, Burns (1978) asserts that "a crucial aspect of this relationship [between leader and led] is the absence of conflict" (p. 244).

Four attributes are seen to be essential for transformational leadership, according to the psychological literature (Bass, 1990; Bass, 1997). First, these leaders must have a clear vision about where they should be going. Second, they should be able to inspire and create enthusiasm in individuals to follow them. Third, they should be intellectually stimulating, encouraging followers to reexamine their values and preferences. And, fourth, they should give personal attention to followers and foster their personal growth and development. All four attributes make it indeed more likely that individuals whole-heartedly adopt their leader's goals as if they are their own. Not surprisingly, a major source of the power of charismatic leaders stems from followers identifying with them, in essence, viewing them as an extension of themselves (Hogg, 2001). Charismatic leaders can sometimes exert such a strong influence on followers that they can persuade them to move ahead of them in pursuing their goals. This enables charismatic leaders often to "lead from the back."

Transformational leadership is most likely to emerge when followers are uncertain about their own preferred action, and are open to persuasion and manipulation by their leaders. For example, children who join cults with charismatic leaders are more likely to be the ones suffering from a low self-esteem – presumably affecting their openness to influence (Freemesser & Kaplan, 1976). Individuals who feel they have lost control over their lives are also more likely to embrace charismatic leadership (Devereux, 1955). Finally, crisis situations (like wars) also contribute to the emergence of charismatic leader-follower relations, presumably because followers want to remain physically or psychologically close to their leader in such situations (Hogg, 2001; McCann, 1992; Tucker, 1968).

In sum, according to our evolutionary game analysis, the main difference between transactional and transformational forms of leadership resides is the fact that, whereas the former is the result of a negotiation process between parties with different preferences (Figure 2a and 2b), the latter emerges when one party – the followers -- voluntarily and enthusiastically adopts the goals of the other party – the leader -- thereby making them their own (Figure 1b).

Leaderless Groups

Evolutionary thinking also suggests that in situations when two or more individuals engage in a joint activity and they have identical preferences for this activity, no stable leader-follower structure will emerge (see Figure 1a). Instead, anyone could find themselves in the position of leader or follower at anyone time, and the distinction between these roles is a largely random affair. 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 to execute. When these substitutes are present, leadership is expected to be of little or no consequence to the outcomes of followers. Which are these substitute variables? One is the activity itself. If the activity is largely predictable – hence, everyone knows what to do and how it should be done -- then a leader structure is unlikely to come about (Comstock & Scott, 1977). Furthermore, in small, cohesive groups (like friendship groups) in which individuals are strongly connected to each other, and there is little or no interpersonal conflict, leadership is also unlikely to emerge. In fact, when such groups perform a task, they often do better by randomly choosing a leader than if they decide to appoint someone (Haslam et al., 1998). In a similar vein, leadership structures do not develop naturally in teams with highly able and highly professional individuals and, in fact, appointing a leader, can be counterproductive (Kerr & Jermier, 1978). Finally, improvements in communication technology can at as a leader substitute, presumably because individuals are able to coordinate their actions by themselves rather than through the appointment of a leader, which as we have indicate can be costly to followers (Sheridan et al., 1984).

Thus, consistent with our evolutionary game model, the emergence of leader-follower is undermined by the presence of factors that increase the likelihood that individuals are able to coordinate their activities in mutual agreement and in the absence of conflict, that is, if they all agree upon where to go, what to do, and how to do it.

Other correlates of leadership: Age, health, and gender.

Age and leadership. Age is related to leadership in a complex manner, according to the psychological literature. Some researchers find a positive correlation between age

and leadership, whereas others find a zero correlation, or sometimes even a negative correlation (Bass, 1990). Could an evolutionary perspective account for these mixed findings? We believe it can. Our analysis suggests that individuals will follow a conspecific only if they are convinced that this individual can lead them towards a desired goal. In ancestral times, some situations required the possession of unique and specialized knowledge, for example, where to find a waterhole that had not yet dried up (Aidar, 1989; Boehm, 1999). Knowledge about where to go would have been more likely to be held by older and experienced individuals, and, thus leading would correlate positively with age. In present times, we can still find evidence for this link between age and leadership in professions that require a considerable amount of specialized knowledge and experience, such as professors and politicians (Caldwell & Wellman, 1926).

In other situations, it would be clear to all what needed to be done, but not how to do it, for example, how to keep the group together on a long journey towards a new waterhole. Those settings would presumably require leaders with a high energy level and stamina, and, in so far as these qualities are more likely to be found among youth, we expect to find a negative rather than positive correlation between age and leadership. This shows the context sensitivity of leader and follower strategies, and it would be interesting to investigate systematically the relationship between age and leadership in further research in different contexts (e.g., business, politics, sports).

Leadership, physique and health. Similarly, individuals are perhaps more keen to folllow an individual towards a desired goal if they have some confidence that the other will actually be able to accomplish that goal. Hence, followers should be sensitive to

cues indicating the health status of potential leaders. Corroborating this hypothesis, there are several studies showing that leaders appear to possess better health than followers -- although the causal direction of this effect is yet unclear (Bass, 1990). Also, there is some anecdotal evidence, suggesting that aspiring leaders must appear healthy and in good shape in order to get elected by followers (Simonton, 1994). Finally, several studies report that a superior physique – a sign of good health -- is one of the main characteristics of leaders (for a review, see Bass, 1990). Cox (1926) found that this was true particularly for military leadership, which is not surprising in light of the demands of this job, especially in war time.

Gender and leadership. Although there has been a dramatic increase in the past decades in the emergence of female leaders across a wide 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 or not in the future fall beyond the scope of the article. We are primarily interested in understanding the possible evolutionary origins of the small, but reliable gender differences that are found in the emergence and execution of leadership.

There are consistent differences between males and females in reproductive strategies, spatial traits, verbal abilities, empathic skills, and a range of other traits and skills (Buss, 1999; Pinker, 2002). Insofar as these traits are meaningfully associated with the emergence of leadership, we should be able to find gender differences. For example, males perform, on average, better at spatial tasks than females. Hence, in mixed sex groups, we would expect males to be more likely to appointed as leaders in activities

requiring such abilities, such as map reading and building houses. Females, on the other hand, have much better verbal skills. They spell better and have a better memory for verbal material. Hence, they are more likely to emerge as leaders in verbal tasks, such as preparing leaflets, and conducting interviews. We know of no research which has looked systematically into sex differences in leadership emergence across different tasks, but it would be an obvious avenue to explore.

As indicated by our evolutionary game analysis, leadership involves two interrelated activities, initiating an action, and ensuring others follow. Psychological research reveals that males are, on average, more assertive and self-confident, they have a stronger need for status, and are more willing to take risks (Bass, 1990; Buss, 1999). As a result, they should be quicker to take the initiative in a newly formed group, thereby emerging as leader. This is supported by research, showing that in mixed sex groups men much more often emerge as leaders (Aries, 1976). Even in dyads, where a dispositionally submissive male is paired with a dominant female, the male is more likely to take the lead. Males are particularly likely to engage in leader actions if they know that they are observed by females, presumably because leadership is associated with status (Campbell et al., 2002)

Yet, as indicated in our analysis, the probability to emerge as leader increases if one can ensure that others follow. When this aspect is important, female leadership is more likely both to emerge and to succeed. Because of their superior empathic skills, they should be better at figuring out which goals followers wish to pursue, and with a superior verbal ability, they should be better at persuading them to follow. Not surprisingly, researchers obtain small, but consistent differences between males and

females in leadership style, with female leaders using a more open, democratic leader style -- with the emphasis on encouraging followership -- whereas male leaders are more dominant and autocratic -- with a greater emphasis on initiative taking and coercion (Eagly & Johnson, 1990). This leads to the hypothesis that in situations in which there is heterogeneity in the goals and preferences of group members (e.g., an intragroup conflict), a female leader is more likely to emerge in order to restore group unity. In contrast, in situations in which the group goals are very clear (e.g., an intergroup rivalry), a male leader is more likely to emerge – a testable hypothesis.

Furthermore, an evolutionary analysis can also make predictions about the different leader-follower structures emerging in male or female groups. Anthropological and primate research suggests that interactions between males often consist of short-term alliances, whereby one male cooperates with another male in gaining access to a resource, yet once the resource has been obtained, they compete with each other over its ownership (DeWaal, 1986; Kelly, 1995). This suggests that leader-follower relations among males can quickly convert into a struggle for dominance, and, as a consequence, such relations are inherently unstable. In contrast, female coalitions are often cemented between genetic relatives, and, as a consequence, the leader-follower structure is more stable with an emphasis on sharing, rather than one party trying to monopolize the resource (as amongst males). Thus, we would expect female leader-follower relationships to be more cooperative and stable than their male counterparts. This hypothesis could be tested by comparing organizations employing predominantly males (the army) with organizations employing predominantly females (nurseries). In the latter,

there should be fewer changes in the hierarchy, fewer conflicts between management and staff, and greater cooperation.

An evolutionary perspective also argues that leader and follower strategies will be used flexibly within the same gender. For example, it has been found that female leaders entering traditionally men dominated occupations tend to adopt a more controlling and autocratic leadership style – they mimic the dominant style of males (Eagly & Carli, 2003). This is especially likely if their subordinate is male and they anticipate a dominance struggle once they have accomplished their mutual goals. Similarly, a male manager with many female staff may start to act in a more democratic manner, and be more willing to share than when his staff is predominantly male. The latter hypothesis awaits further investigation.

Thus, although there may be reliable gender differences in leadership emergence and style of leadership, the use of these strategies is still highly context dependent. Depending upon the context, adopting a particular leader (or follower) strategy may yield greater relative fitness benefits to individuals involved.

Resistance Against Leaders and Leadership Succession

Finally, our evolutionary approach delineates that there are frequent tensions in the interests of leaders and their followers. In terms of fitness payoffs, leaders are better off if, once they have accomplished a goal with the help of followers, they keep as much of the benefits to themselves as they can get away with. In contrast, it is in the interest of followers to ensure that leaders share as much as possible with them. If a resource is difficult to divide (e.g., getting a promotion), this poses a problem, which is likely to undermine any leader-follower structure. Really the only solution is a promise for the

future ("I will ensure that you get promoted next time, if you support me in this one"). If resources are divisible, there is likely to be continuous monitoring from followers of the actions of leaders to ensure that they are generous. In this regard, it is not surprising that social attention in groups is often targeted at leaders and other high status individuals who have control over valuable resources (Depret & Fiske, 1999).

Constant monitoring is costly, but can be beneficial. Research has shown that leaders will extract benefits from followers if they think that they can get away with it, adding credence to the saying "Power corrupts and absolute power corrupts absolutely." In an experimental test of this idea, Kipnis (1972) asked students to supervise other students, confederates of the experimenter, working on a task. The confederates always had the same performance. But the supervisors varied in the power they had over them. In one condition, supervisors could punish and reward workers for not doing enough, whereas in the other condition they could only send a persuasive message. As predicted, supervisors in the first condition used more punishments, although the students performed equally well.

To ensure that leaders continue to provide benefits, followers can use the ultimate sanction to replace their leader. In his research on traditional hunter-gatherers societies, Boehm (1993) found that bands got rid of extremely selfish, arrogant, or overaggressive leaders by replacing them, or sometimes even by killing them. Usually, however, groups could keep the selfish impulses of their leaders under control by using a mixture of ridicule, gossip, and disobedience. Future research into these strategies is necessary for understanding how leaders and followers resolve tensions in their often ambivalent relationship.

Discussion

The aim of this review is to start a constructive dialogue between two scientific disciplines that have studied and thought about leadership, evolutionary biology and social psychology, but that have hardly influenced each other. Evolutionary scientists have begun to theorize about leadership and dominance, based on the principles of natural selection and adaptation, but this tradition has been generally lacking in empirical research (Buss, 1999). In contrast, social psychologists have gathered a wealth of highly reliable results on leadership through large scale surveys and controlled experiments, but their research lacks an overarching theoretical framework that can make sense of the richness of data (Bass, 1990; Hollander, 1985). If anything, we hope that this review will be read by both evolutionary scientists and psychologists who have an interest in leadership and followership, and will give momentum to a more integrated research agenda.

Reviewing the psychological literature, Bass (1990, p. 11) notes that "there are as many different definitions of leadership as there are persons who have attempted to define it." This cannot be an ideal situation for a serious scientific enterprise. Using insights from evolutionary theory, we have offered a functional definition of leadership that, in our view, captures the essence of the leader-follower relationship in terms of a strategy to induce others (i.e., the followers) to coordinate their actions or goals to accomplish the goals of the leader. This definition brings conceptual clarity in what leadership is (and what it is not). Leadership involves coordinating a group activity instead of being a generic social influence strategy (like status or esteem). Leadership involves getting other organisms to temporarily adopt the leader's goals rather than

pursuing their own goals. This delineates that there is likely to be an ambivalent relationship between leaders and followers and that leadership only emerges under special circumstances in which individuals believe (rightly or wrongly) that there are substantial benefits associated with following another individual, which are offsetting the costs.

Evolutionary Perspective on Leadership

We have offered two general evolutionary perspectives on the emergence of leader-follower relations. The first, which is based on the animal and primate literatures (Boehm, 1999; E.O. Wilson, 1975), suggests that leadership and followership are mere byproducts of adaptations for dominance and submission. Dominant individuals may undertake leadership activities, like determining the direction of group movement or intervening in conflict, either because the fitness costs for them are negligible (e.g., they move when they are hungry), to preserve the existing group hierarchy (e.g., dominants intervene in conflicts which undermine group cohesion; DeWaal, 1996) and/or they may use leadership as a costly signal (McAndrew, 2002). This leads to the prediction that leadership correlates with measures of dominance, which receives little or not support in the psychological literature. Leaders do not score higher on dominance scales than do followers. Furthermore, followers are reluctant to endorse dominating leaders and, if individuals threaten to become dominant, followers engage in various tactics to undermine the power of the leader (e.g., exiting, sabotage). The literature suggests that there is probably one exception to this general aversion of dominant leaders. If there is an extreme danger to the group, such as an immediate intergroup conflict, then followers

may accept a coercive leader, possibly to coerce non-complying individuals into following, thus cementing group unity.

The second theoretical framework is based on evolutionary game theory (Maynard-Smith, 1982). A game-theoretical analysis treats the distinction between leaders and followers as the outcome of strategies that individuals play in coordination games (like the classic leader game), particularly sequential games with asymmetrical pay-offs. Strategies that are successful can spread through the population via either genetic or cultural evolution at the expense of those that are not successful. Viewed in this way, taking the lead has obvious advantages in dictating one's preferred action to others, but there are also costs involved in terms of sharing the benefits of coordinated action with those who follow. Similarly, followership entails both costs – giving up one's preferred action and running the risk to be exploited by the leader – as well as benefits in, for example, not having to make a risky preemptive move.

There are a number of hypotheses emanating from an evolutionary game analysis that we have put to test using the psychological literature as database. For example, as predicted by these game models, leadership correlates with personality and behavioral variables that are predictive of initiative taking (e.g., ambition, extraversion). Although leadership correlates moderately with general intelligence, it correlates strongly with measures of verbal ability, social intelligence, and empathy – traits that increase the capacity to understand the goals and intentions of potential followers. Finally, the probability to emerge as leader is enhanced when individuals show evidence of being generous as well as task-specific and interpersonal competencies. It should be noted that the support is largely based on research that did not set out from a game theoretical

perspective (but see Kremer & Mack, 1983). More controlled empirical tests of these predictions are desperately needed and we have offered many suggestions for further research in this review.

Although our game-theoretical framework seems to be a sensible way of looking at leader-follower relationships, it only begins to address the diversity in these strategies. We have already addressed how subtle differences in the pay-off structure may give rise to the emergence of autocratic versus democratic leadership, task versus relation leadership, and even to charismatic leadership. We have also addressed how particular situations may suppress the emergence of leader-follower relationships. Finally, we have looked at how particular settings may be conducive to the emergence of male or female leadership. At some point, sound experimental tests are needed to compare the success of these different leader strategies within any given context to see which ones are more likely to be successful.

Psychology, Evolution, and Leadership

The evolutionary perspective challenges some traditional conceptions on leadership, and may be criticized on various grounds. A criticism that we deem to be unfair is that an evolutionary perspective would imply genetic determinism. Although there are likely to be differences in the propensity to leads or follow based on very general, partly innate dispositions, such as temperament and intelligence, whether they result in reliable distinctions between leaders and followers is highly contextually dependent. For example, followers may not generally endorse aggressive, dominating individuals as leaders, except if they believe they can secure an intergroup victory for them, enabling each to profit from their leadership (Boehm, 1999; McCann, 1992).

Similarly, even in groups with all highly ambitious and assertive individuals, a leadership structure develops if the situation requires it (Bass, 1990). Thus, evolutionary theory offers very much an interactionistic perspective on leadership emergence, arguing that, within certain boundaries, leader and follower strategies can be used flexibly by the same individuals when they are confronted with different coordination challenges with different social interaction partners.

A fair concern is whether an evolutionary game model makes fundamentally different predictions about leadership emergence than other theories do. In principle, any theory that assumes that individuals follow strategies so as to maximize their benefits and minimize their costs in social interactions could have made the same predictions, including classical game theory (Luce & Raiffa, 1957), and its psychological counterpart, social exchange theory (Hollander, 1985). Yet, these models do not generally address where these strategies originate from or how they develop over time. In addition, most psychological theories of leadership are built around a particular leadership phenomenon, such as transformational leadership, and are therefore less suitable as a generic theory of leadership.

Evolutionary game theory can offer an 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 adaptations that have emerged in human evolutionary history in order for two or more individuals with often conflicting interests to engage in joint action, it provides the foundation for more proximal psychological models of leadership. For example, our model can account for the consistent personality differences associated with leadership, such as ambition,

extraversion, and intelligence. It also accounts for the relatively stable impressions that followers hold about what constitute leadership attributes, such as honesty, trustworthiness, and competence – the leader prototypes – thus offering the underpinnings for cognitive models of leadership (Lord & Maher, 1991). At the same time, it provides clues as to why these prototypes may sometimes change, for example, in the presence of an acute intergroup competition, thus supporting more recently developed social identity models of leadership (Hogg, 2001). The evolutionary game model also accounts for the existence of different leadership styles, such as task versus relation styles, autocratic versus democratic styles, by assuming that they derive from subtle differences in the pay-off structure for the individuals involved. Finally, it makes predictions about when these styles are likely to be more or less effective that are generally upheld by research on contingency models of leadership (Chemers, 2000; Fiedler, 1967; Vroom & Jago, 1978).

In addition, the evolutionary framework suggests various new directions for research on leadership. One straightforward prediction is that leadership emerges more slowly in groups in which there is a need for coordination but there is a pronounced conflict of interests between the group members. This can be easily tested in the laboratory by letting individuals play coordination games with or without conflict. Another prediction, which could be tested in the laboratory, is that leadership emerges more slowly with an increase in group size because there will be fewer opportunities for one individual to take the initiative. Furthermore, experimental game research could study the emergence of different leadership styles, for example, by testing the idea that autocratic leaders (who can dictate group action and punish deviants) are more likely to

be endorsed in case of an intergroup rivalry (for a suitable procedure, see Hogg, 2001; Van Vugt et al., 2004). Finally, a combination of lab and field studies could examine the hypothesized link between leadership and empathy. If, as the evolutionary perspective suggests, taking the perspective of other individuals is an important leadership quality, then we should expect leaders to score higher on this trait than followers. Finally, and perhaps as a more general point, future research could benefit from multi-disciplinary efforts between psychologists, anthropologists, and animal biologists interested in the study of leadership.

Before closing, we should note an important, but inevitable limitation of our review. The psychological literature on leadership is so vast and dispersed across many subdisciplines that it was not possible for us to read or review all the relevant empirical and theoretical papers. We concentrated on reading the major reviews of the leadership literature, such as Bass & Stogdill's Handbook (Bass, 1990) -- containing no fewer than 7.500 references -- Hollander's chapter in the Handbook of Social Psychology (1985), and Chemers' review article in Group Dynamics (2000). We then read the articles that were cited in these outlets, as well as some post 2002 articles, that we deemed relevant to our review. Despite our efforts to ensure a representative review, we are pretty sure that we have omitted important materials, and would like to apologize in advance for this.

The main aim of this review was to start a constructive dialogue between two scientific communities that have studied leadership for many decades, but have evolved rather independently from each other. Evolutionary scientists study leadership from a unified theoretical framework based on adaptation and natural selection. Yet, this tradition generally lacks empirical research, and what research there is, often has

insufficient methodological rigor (e.g., case studies on primate or hunter-gatherer groups).   In psychology, in contrast, there is a vast empirical literature on leadership, which has a high degree of precision and control yet lacks a coherent theoretical framework that can fit the disparate findings.   We hope to have shown that an evolutionary approach can strengthen the scientific study of leadership and set the agenda for future leadership research.

References

Aidar, J. (1989). *Great leaders.* Guilford: Talbot press

Alcock, J. (1998). *Animal behavior: An evolutionary approach* (6th edition).

Sunderland, Mass: Sinauer.

Alexander, R. D (1979). *Darwinism and human affairs.* Seattle: University of

Washington.

Aries, C. (1976). Interaction patterns and themes of male, female and mixed groups.

Small Group Behavior, 7, 7-18.

Bales, R. F. (1958). Task roles and social roles in problem solving groups. In

E. Maccoby et al. (Eds.), *Readings in social psychology,* New York: Holt,

Rinerat, & Wilson.

Barner-Berry, C. (1982). An ethological study of leadership succession. *Ethology and*

Sociobiology, 3, 199-207.

Barrett, L., Dunbar, R., & Lycett, J. (2002). *Human evolutionary psychology.* London:

Palgrave

Bass, B. M. (1960). *Leadership, psychology and organizational behavior.* New York:

Harper.

Bass, B. M. (1990). *Bass and Stogdill's Handbook of leadership: Theory, research, and managerial applications* (3rd edition). New York: Free Press.

Bass, B. M. (1997). Does the transactional-transformational leadership paradigm transcend organizational and national boundaries. *American Psychologist, 52,* 130-139

Bass, B. M. & Norton, F. M (1951). Group size and leaderless discussions. *Journal of Applied Psychology, 35,* 397-400.

Batson, C. D. (1998). Altruism and prosocial behavior. In D. Gilbert, S. Fiske, & G. Lindzey, *Handbook of Social Psychology* (pp. 282-316). New York: McGraw-Hill

Batson, C. D., Duncan, B. D., Ackerman, P., Buckley, T., & Birch, K. (1981). Is empathic emotion a source of altruistic motivation? *Journal of Personality and Social Psychology, 40,* 290-302.

Baumeister, Chesner, Senders, & Tice, 1988

Boehm, C. (1993). Egalitarian society and reverse dominance hierarchy. *Current Anthropology, 34,* 227-254.

Boehm, C. (1999). *Hierarchy of the Forest.* London: Harvard

Bray, D. W., & Howard, A. (1983). The AT&T longitudinal studies of managers. In K. Shaiel (Ed.), *Longitudinal studies of adult psychological development.* New York: Guilford Press.

Brockner, J., Tyler, T., & Cooper-Schneider, R. (1992). The influence of prior commitment to an institution on reactions to perceived injustice: The higher they

are, the harder they fall. *Administrative Science Quarterly, 37,* 241-261.

Brown, D. (1991). Human Universals. xxxx

Browning, L, & Colman, A. M. (2004). Evolution of coordinated alternating reciprocity

in repeated dyadic games. *Journal of Theoretical Biology, 229,* 549-557.

Burns, J. M. (178). *Leadership.* New York: Harper & Row.

Buss, D. M. (1999). *Evolutionary psychology*. London: Allyn & Bacon.

Caldwell, O. W. & Wellman, B. (1926). Characteristics of school leaders. Journal of

Educational research, 14, 1-15.

Campbell. L. T. et al., 2002 Human nature

Cartwright, D., & Zander, A. (1968). *Group dynamics – research and theory.*

Evanston, Il: Row Peterson.

Chagnon, N. A. (1997). *Yanomamo.* London: Wadsworth

Chemers, M. M. (2000). Leadership research and theory: A functional integration.

Group Dynamics. 4, 37-43.

Cherulnik, P. D., Way, J. H., Ames, S. & Hutto, D. B. (1981). Impression of high and

low Machiavellian men. *Journal of Personality, 49,* 388-400.

Christie, R. & Geiss, F. L. (1970). *Studies in Machiavellianism.* New York:

Academic Press.

Comstock, D. E., & Scott, W. R. (1977). Technology and structure of subunits:

Distinguishing individual and work efforts. *Administrative Science Quarterly, 22,*

177-202

Cosmides, L., & Tooby, J. (1992). Cognitive adaptations for social exchange.

In J. Barkow et al., *The adapted mind: Evolutionary psychology and the*

generation of culture (pp. 163-28). New York: Oxford University Press.

De Cremer, D., & Van Vugt, M. (2002). Intra and intergroup dynamics of leadership in social dilemmas: A relational model of cooperation. *Journal of Experimental Social Psychology, 38,* 126-136.

Depret, E. & Fiske, S. T. (1999). Perceiving the powerful: Intriguing individuals versus threatening groups. *Journal of Experimental Social Psychology, 35,* 461-480.

Devereux, G. (1955). Charismatic leadership and crisis. In W. Muenstberger and S. Axelrod (Eds.), *Psychoanalysis and the Social Sciences.* New York: International University Press.

De Waal., F. (1996). *Good natured: The origins of right and wrong in humans and other animals.* Cambridge, MA: Harvard University Press.

Dunbar, R. I. M. (1983). Structure of gelada baboon reproductive units: Integration at the Group level. *Zeitschrift fur Tierpsychologie, 63,* 265-282.

Eagly, A. H., & Johnson, B. T. (1990). Gender and leadership style: A meta-analysis. *Psychological Bulletin, 108,* 233-256.

Eagly, A., H. & Carli, 2003).

Fehr, E., & Fischbacher, U. (2003). The nature of human altruism. *Nature, 425,* 785-791.

Fiedler, F. E. (1967). *A theory of leadership effectiveness.* New York: McGraw-Hill.

Fiedler, F. (178). The contingency model and the dynamics of leadership processes. In L. Berkowitz (Ed.), *Advances in Experimental social psychology: Vol. 11.* New York; Academic Press.

Firestone, I. J., Lichtman, C., & Colamosca, J. V. (1975).   Leader effectiveness and

leadership conferral as determinants of helping in a medical emergency. *Journal of Personality and Social Psychology, 31,* 243-248.

Forsyth, D. R. (1999). *Group dynamics*. London: Wadsworth.

Frank, R. (1988). *Passions within reason.* New York: Norton.

Freemesser, G, F., & Kaplan, H. B. (1976). Self-attitudes and deviant behavior: the case of charismatic religious movement. *Journal of Youth and Adolescence, 5,* 1-9

Gibb, C. A. (1969). Leadership. In G. Lindzey, & E. Aronson (Eds.), *Handbook of Social Psychology: Vol. 4.* Reading, MA: Addison-Wesley.

Gintis, H. (2000). *Game theory evolving.* Princeton, NJ: Princeton University Press.

Gough, H. G. (1984). A managerial potential scale for the California Psychology Inventory. *Journal of Applied Psychology, 69,* 233-240.

Guyer & Rapoport (1969).

Hamblin, R. L. (1958). Leadership and crises. *Sociometry, 21,* 322-335.

Hardy, C., & Van Vugt, M (2005). Giving fro glory: The altruism-status relationship. Unpublished manuscript, University of Kent

Harrell, T. W., Burnham, L. E., Hunt, R. S., & lee, H. E. (1964). *Reliability and intercorrelations for thirteen leadership criteria.* Stanford, CA: Stanford University.

Haslam, A., McGarthy, C., Brown, P., Eggins, R., Morrison, B., & Reynolds, K. (1998). Inspecting the emperor's clothes: Evidence that random selection of leaders can enhance group performance. *Group Dynamics, 2,* 168-184.

Hawkes, K. (1993). Why hunter-gatherers work: an ancient version of the problem of public goods. *Current Anthropology, 34,* 341-361.

*Heinsohn, R., & Packer, C. (1995). Complex cooperative strategies in group territorial

African lions. *Science, 269,* 1260-1262

Hemphill, J. K. (1950). *Leader behavior description.* Columbus: Ohio State University

Hemphill, J. K. (1961). Why people attempt to lead. In L. Petrullo& B. Bass (Eds.),

Leadership and interpersonal behavior. New York: Holt, Rinehart& Winston.

Hersey, P., & Blanchard, K. H. (1982). Leadership style; Attitudes and behaviors.

Training and Development Journal, 36, 50-52.

Hersey, P., Angelini, A. L., & Carakushansky, S. (1982). The impact of situational

leadership and classroom structure on learning effectiveness. *Groups and*

Organization Studies, 7, 216-224.

Hogan, R., Curphy, G. J., & Hogan J. (1994). What we know about leadership.

American Psychologist, 49, 493-504.

Hogan & Kaiser. (in press)

Hogg, M. A. (2001). A social identity theory of leadership.

Personality and Social Psychology Review, 5, 184-200.

Hollander, E. P. (1985). Leadership and power. In G. Lindzey & E. Aronson (Eds.),

The handbook of social psychology (pp. 485-537). New York: Random House.

Hollander, E. P. & Julian, J. W. (1969). Contemporary trends in the analysis of

leadership processes. *Psychological Bulletin, 71,* 387-397.

Hofstede G. (1980). *Culture's consequence: International differences in work related*

values. Beverly Hills: Sage.

Janis, I. L., & Mann, L. (1977). *Decision making: A psychological analysis of conflict,*

choice, and commitment. New York: Free University Press.

Kaplan, E. M., & Cowen, E. L. (1981). Interpersonal helping behavior of industrial

foremen. *Journal of Applied Psychology, 66,* 633-638.

Kelly, R. (1995). *The foraging spectrum: Diversity in hunter-gatherer lifeways.*

Washington, D. C: Smithsonian Institution Press.

Kenny, D. A., & Zaccoro, S. J. (1983). An estimate of variance due to traits in

leadership. *Journal of Applied Psychology, 68,* 678-685.

Kerr, S., & Jermier, J. (1978). Substitutes for leadership: Their meaning and

measurement. *Organizational Behavior and Human Performance, 22,* 374-403.

Kihlstrom, J. F., & Cantor, N (2000). Social intelligence. In R. Sternberg (Ed.),

Handbook of intelligence (pp. 359-379). Cambridge, UK: Cambridge University

press.

Kipnis, D. (1972). Does power corrupt? *Journal of Personality and Social Psychology,*

24, 33-41.

Klebanoff, H. E. (1976). Leadership: An investigation of distribution in task oriented

small groups. *Dissertation Abstracts Internationals, 36,* 3614.

Klonsky, B. G. (1983). The socialization and development of leadership ability.

Genetic Psychology Monographs, 108, 95-135.

Konovsky, M. A. (1986). *Antecedents and consequences of informal leader helping*

behaviour: A structural equation modelling approach. Doctoral dissertation.

Indiana University, Bloomington.

Korman, A. K. (1968). The prediction of managerial performance: A review.

Personnel Psychology, 21, 295-322.

Kremer, J., & Mack, D. (1983). Pre-emptive game behavior and the emergence of

leadership. *British Journal of Social Psychology, 22,* 19-26.

Kummer, H. (1968). *Social organization of Hamadryas baboons.* Basel and New York: S. Karger.

Kurzban, R., K, Cosmides, L., & Tooby, J. (2001) xxxx

Kurzban, R. K., & Leary, M (2001). Evolutionary origins of stigmatization: The functions of social exclusion. *Psychological Bulletin, 127,* 187-208.

Lamprecht, J. (1996). What makes an individual the leader of its group? An evolutionary concept of distance regulation and leadership. *Social Sciences Information, 35,* 595-617.

Lanzetta, J. T. (1955). Group behavior under stress. *Human Relations, 8,* 29-52.

Lawler, E., J., & Thompson, M. E. 9178). Impact of a leader's responsibility for inequity on subordinate revolts. *Social Psychology Quarterly, 41,* 264-268.

Lewin, K., Lippitt, R., & White, R. (1939). Patterns of aggressive behaviour in experimentally created social climates. *Journal of Social Psychology, 10,* 271-299.

Lewis, H., (1974). *Leaders and followers: Some anthropological perspectives.* Reading, MA: Addison-Wesley

Littlepage, G. E., Robinson, W., Reddington, K. (1997). Effects of task experience and group experience on group performance, member ability, and recognition of expertise. *Organizational Behavior and Human Decision processes, 69*, 133-147.

Lord, R. G. (1977). Functional leadership behaviour: Measurement and relation to social power and leadership perceptions. *Administrative Science Quarterly, 22,* 114-133.

Lord, R. G, DeVader, C. L, & Alliger, G. M. (1986). A meta-analysis of the relation

    between personality traits and leadership perceptions: An application of validity

    generalization procedures. *Journal of Applied Psychology, 71,* 402-410.

Lord, R. G. & Maher, K. J. (1991). *Leadership and information processing: Linking*

    perceptions and performance. Boston: Unwin Hyman.

Luce, R.D., & Raiffa, H. (1957). *Games and decisions: Introduction and critical survey.*

    London: John Wiley and Sons.

Mann, R. D. (1959). A review of the relationships between personality and performance

    in small groups. *Psychological Bulletin, 56,* 241-270.

Maynard-Smith, J. (1982). *Evolution and the theory of games.* Cambridge, UK:

    Cambridge University Press.

Maynard-Smith, J., & Price, G. (1973). The logic of animal conflict. *Nature, 246,*

    15-18.

McAndrew, F. T. (2002). New evolutionary perspectives on altruism: Multi-level

    selection and costly signaling theories. *Current Directions in Psychological*

    Science, 11, 79-82.

McCann, S. J. H. (1992). Alternative formulas to predict the greatness of U. S.

    presidents: Personologial, situational, and Zeitgeist factors. *Journal of*

    Personality and Social Psychology, 62, 469-479.

Meggitt, M. (1977). *Blood is their argument.* Palo Alto, CA: Mayfield Press.

Mulder, M., & Stemerding, A. (1963). Threat, attraction to group, and need for strong

    leadership. *Human Relations, 16,* 317-334.

Mullen, B., Salas, E., & Driskell, J. E. (1989). Salience, motivation, and artifact as

contributions to the relation between participation rate and leadership. *Journal of Experimental Social Psychology, 25,* 545-559.;

Murchison, C. (1935). The experimental measurement of a social hierarchy in Gallus Domesticus. *Journal of General Psychology, 12,* 3-39.

Palmer, G. J. (1962). Task ability and effective leadership. *Psychological Reports, 10,* 863-866.

Penner, D. D., Malone, D. M., Coughlin, T. M., & Herz, J. (1973*). Satisfaction with U.S. Army leadership.* U.S. Army War College, Leadership Monograph Series, 2.

Pinker, S. (2002). *The blank slate.* Penguin Classics.

*Prins, H. H. T. (1996). *Ecology and behaviour of the African buffalo. Social inequality and decision making.* Chapman & Hall, London.

Rabbie & Bekkers, 1978

Rapoport, A. (1967). Exploiter, leader, hero, and martyr: the four archetypes of the 2x2 game. *Behavioral Science, 12,* 81-84.

Rushton, J. P., Fulkner, D. W., Neal, M. C., Nias, D. K. B., & Eysenck, H. W. (1986).

Altruism and aggression: The heritability of individual differences. *Journal of Personality and Social Psychology, 50,* 1192-1198.

Russell, C. J., Mattson, J., Devlin, S. E., & Altwater, D. (1986). *Predictive validity of biodata items generated from retrospective life experience essays.* Paper, Society for Industrial and Organizational psychology, Chicago.

Rutte, C.G., & Wilke, H.A.M. (1984). Social dilemmas and leadership. *European Journal of Social Psychology, 14,* 105-121.

Samuelson, C.D. (1993). A multi-attribute approach to structural change in resource

dilemmas. *Organisational Behaviour and Human Decision Processes, 55,* 298-324.

Samuelson, C.D., & Messick, D.M. (1986). Inequities in access to and use of shared resources in social dilemmas. *Journal of Personality and Social Psychology, 51,* 960-967.

Schmitt, D. P., & Pilcher, J. J. (2004). Evaluating evidence of psychological adaptation. *Psychological Science, 15,* 643-649.

Sgro, J. A., Worchel, P., Pence, E. C., & Orban, J. A. (1980). Perceived leader behaviour as a function of the leader's interpersonal trust orientation. *Academy of Management Journal, 23,* 161-165.

Sheridan, J., Vredenburgh, D., & Abelson, M. (1984). Contextual model of leadership influence in hospital units. *Academy of Management Journal, 27,* 57-78.

Sidanius, J. & Pratto, F. (1999*). Social dominance: An intergroup theory of social hierarchy and oppression.* New York: Cambridge University Press.

Simonton, D. K. (1994). *Greatness: Who makes history and why?* New York: Guilford.

Sober & Wilson (1998).

Sorrentino, R. M., & Boutillier, R. G. (1975). The effect of quantity and quality of verbal interaction on ratings of leadership ability. *Journal of Experimental Social Psychology, 11,* 403-411

Stogdill, R. M. (1974). *Handbook of leadership* (1st edition). New York: Free Press.

Torrance, E. P. (1953). Methods of conducting critiques of group problem solving performance. *Journal of Applied Psychology, 37,* 394-398.

Tsui, A. S. (1984). A role set analysis of managerial reputation. *Organizational*

Behavior and Human Performance, 34, 64-96.

Tucker, R. G. (1968). The theory of charismatic leadership. *Daedalus, 97,* 731-756.

Tyler, T. R., & Lind, E. A. (1992). A relational model of authority in groups.

In M. Zanna (Ed.), *Advances in experimental social psychology*

(Vol. 25, pp. 115-191). New York: Academic Press.

Van den Bos, K., Lind, E. A., Vermunt, R., & Wilke (1997). How do I judge my

outcome when I don't know the outcome of others? The psychology of the fair

process effect. *Journal of Personality and Social Psychology, 72,* 1034-1046.

Van Vugt, M., & De Cremer, D. (1999). Leadership in social dilemmas: The effects of

group identification on collective actions to provide public goods. *Journal of*

Personality and Social Psychology, 76, 587-599.

Van Vugt, M., Jepson, S. F., Hart, C. M., & De Cremer, D. (2004). Autocratic

leadership in social dilemmas: A threat to group stability. *Journal of*

Experimental Social Psychology, 40, 1-13.

Vehrencamp, S. L. (1983). A model for the evoluti9on of despotic versus egalitarian

societies. *Animal Behavior, 31,* 667-682.

Vroom, V. H., & Jago, A. G. (1978). On the validity of the Vroom-Yetton model.

Journal of Applied Psychology, 63, 151-162.

Wilson, D. S., Near, D. & Miller, R. R. (1996). Machiavellianism: A synthesis of the

evolutionary and psychological literatures. *Psychological Bulletin, 119,* 285-299.

Wilson , E. O. (1975). *Sociobiology: The new synthesis.* Harvard, MA:

Harvard University Press.

Wright, R. (2000). Nonzero

Yukl, G. A. (1989). *Leadership in organizations.* Englewood Cliffs, NJ: Prentice Hall.

Zaccaro, S. J., Foti, R. J., & Kenny, D. A. (1991). Selfmonitoring and trait-based

variance in leadership: An investigation of leader flexibility across multiple

group situations. *Journal of Applied Psychology, 76,* 308-315.

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Footnotes

[1] For the sake of simplicity, we concentrate on a two-person 2x2 game in order to illustrate how leader-follower relationships may 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, whereby the payoffs for one player are replaced by an average of the pay-offs for all group members (Luce & Raiffa, 1957).

[2] Sequential games are probably the rule rather than the exception in real-world situations. Yet, most research on experimental games, including the Prisoner's Dilemma, assumes for convenience purposes that players are making a simultaneous choice. We believe that this is an unnecessary restriction, which undermines the validity of much gaming research (ROB, ANY REFERENCE).

[3] Formally, sequential games ought to be represented in a decision tree rather than in a 2x2 matrix. Because most readers will be more familiar with the 2x2 matrices, we have decided to stick with them.

[4] The leader game is a variant of the better known Battle-of-Sexes game (Luce & Raiffa, 1957). There is a slight distinction in the pay-offs between the two games in that in Leader the individual who makes the preemptive move gets a higher pay-off, whereas in Battle-of-Sexes the individual who waits gets a larger pay-off (Browning & Colman, 2004)