5 The Nature in Leadership

Evolutionary, Biological, and Social Neuroscience Perspectives

Mark Van Vugt

VU University Amsterdam

University of Oxford

When a honey bee returns to its hive after foraging for nectar, it performs a dance for the other bees. The bee skips around making a figure-eight movement, waggling its abdomen as it does so. In 2005, scientists found out that the dancer is indicating through its moves the location and quality of a foraging site (Riley, Greggers, Smith, Reynolds, & Menzel, 2005). The direction the bee is facing points to the direction of the food source relative to the sun; the duration of the waggle dance represents how far the source lies and its quality. Scientists proved it by setting up artificial food sources and monitoring the behavior of the bees that scrutinized a waggle dance. When the hive was moved 250 meters, the follower bees flew to a site that was 250 meters away from the artificial source, proving that the follower bees were following navigational instructions encoded in the waggle dance. It proved a theory first put forward by the Nobel Prize–winning biologist, Karl von Frisch, in the 1960s. The dancer bee is in fact acting as a leader by scouting out food resources for the hive. The best dancers recruit the most followers, and this interaction produces a very efficient group performance.

AUTHOR'S NOTE: Please address correspondence concerning this chapter to Mark Van Vugt, VU University Amsterdam/University of Oxford, van der Boechorsstraat l, 1081 BT Amsterdam, the Netherlands. e-mail: m.van.vugt@psy.vu.nl.

The waggle dance of the honey bee is one of many leadership and followership displays that take place in the animal kingdom, from the migration patterns of relatively brainless species, such as fish, to food sharing among our brainier primate cousins, the chimpanzees.

Humans are animals too. Although our leadership patterns are, in many ways, more sophisticated than that of our animal relatives, maybe there are lessons to be learned from taking a closer look at the evolutionary history of leadership. In this chapter, I will explain why leadership might have emerged in various social species, such as ours, and what forms it takes. Questions about the origins and evolved functions of leadership are seldom asked by social scientists studying leadership. They tend to be primarily interested in the mechanics of leadership—How does it work?—rather than questions about the nature of leadership.

Yet there is an increasing awareness among leadership theorists of the importance in building a comprehensive theory by integrating knowledge from the natural, biological, and social sciences that all have something interesting to say about leadership (Antonakis, in press; Bennis, 2007; Hogan & Kaiser, 2005). For instance, anthropologists, biologists, cognitive neuroscientists, economists, political scientists, primatologists, psychologists, and zoologists have been studying various aspect of leadership emergence, yet so far, there has been very little cross-fertilization between these areas in developing models and theories of leadership that are consistent with each other (King, Johnson, & Van Vugt, 2009). In addition, social scientists studying leadership have provided many good middle-level theories—such as personality, cognitive, situational, and contingency theories of leadership (for excellent recent reviews, see Avolio, Walumbwa and Weber, 2009; Graen & Uhl-Bien, 1995; Hackman & Wageman, 2007; Yukl, 2006)—yet they are often not very well connected to higher order theories (cf. Bennis, 2007; Van Vugt, Hogan, & Kaiser, 2008).

Evolutionary theory (as I will explain shortly) may provide such an overarching framework that can connect these separate lines of inquiry. Darwin's theory of evolution through natural selection (1871) makes clear that human psychology is ultimately a product of biological evolution—in the same way that our bodies are evolutionary products—consisting of many different traits that evolved because they enabled our ancestors to cope better with the demands of the environments in which they were living.

In this chapter, I will put forward a new theoretical perspective on leadership—evolutionary leadership theory, or ELT—which is guided by the principles of Darwin's evolutionary theory, and explains how our leadership and followership psychology may have been shaped through natural selection pressures. I will define leadership broadly here in terms of a process of influence to achieve coordination between individuals for the pursuit of mutual goals. In this chapter, I will first provide a very brief introduction into evolutionary theory and focus in particular on the growing field of evolutionary psychology. This field applies Darwinian thinking to human psychology and

behavior. Second, I will argue why evolutionary psychology may be particularly relevant for understanding leadership and will address the likely evolved functions of leadership. I will present evidence from across the behavioral sciences—from biology to psychology, and from cognitive neuroscience to game theory—suggesting that leadership and followership may be psychological adaptations—evolved mechanisms—for solving coordination problems between individuals. Much of this research is done by my collaborators and me, who work together in multidisciplinary teams around the world on various aspects of evolutionary leadership theory. Fourth I will put forward a short, speculative natural history of leadership, addressing how leadership may have evolved in small steps from a rather crude device for synchronizing the activities of simple organisms to complex structures able to coordinate the activities of millions of individuals dispersed across space and time. Fifth and finally, I will address some implications of evolutionary leadership theory for developing research on leadership and good leadership practice.

The Evolutionary Psychology of Leadership

Evolutionary leadership theory starts with the recognition that the physiological, neurological, and psychological processes involved in producing human behavior are products of biological evolution. It follows, therefore, that conceptual insights of evolutionary theory, when applied with rigor and care, can produce novel discoveries about human behavior, too (Buss, 2005; Nicholson, 2000; Van Vugt & Schaller, 2008). Charles Darwin is the father of modern evolutionary theory. In his 19th-century voyage on the *Beagle* to the Galapagos Islands, Darwin noted that different species were beautifully adapted to their environments. After much study, he concluded that different species were not created by a divine hand, but they arose as a consequence of their environment. Members of a species displaying certain features—say, a giraffe boasting a long neck—flourished in their environment better than less well-equipped members—short-necked giraffes. A long-necked giraffe would have access to more food (leaves high in the tree tops), and this advantage would give long-necked members a survival advantage. This would result in differential reproduction: Long necks would out-reproduce short necks and, given enough time, long necks would become a universal feature of giraffes. This feature is then referred to as an adaptation. This, Darwin reasoned, explained why creatures seemed so perfectly suited to their environments.

Darwin postulated that natural selection operates via three very simple rules: (1) There is variation in traits between individuals within the same species; (2) some of this variation is heritable (which is why offspring resemble parents); and (3) some of these trait variations give individuals an edge in the competition for resources. These three rules form the backbone of evolutionary theory.

Darwin's insights have been proved right so many times that evolutionary theory is no longer treated as a hypothetical possibility but, rather, as a law

of nature. To understand evolutionary theory, one does not necessarily need to know anything about biology, heritability, or genes. Yet it is good to realize, first, that adaptations (such as the giraffe's neck) are underpinned by genes. Any gene first emerges as a random mutation and usually only spreads through a population if it gives the organism an edge in the competition for resources. Thus, at some point in history, a baby giraffe was born with a spontaneous gene mutation giving him or her a longer neck than the other giraffes. Because this gene produced a giraffe that was better adapted to the environment, this particular gene survived, and over many generations, it has spread through the population such that every giraffe nowadays carries the "long neck" gene—in evolutionary terms, this trait has gone to fixation. It is also important to realize that when evolutionary biologists talk about a "gene for trait X," this is overly simplistic because most traits are underpinned by multiple genes operating in combination. Finally, when evolutionary biologists talk about "traits," they refer to any feature of an organism that is expressed when an organism's genes interact with their environment, including their morphology (such as height and eye color), neurophysiology (such as brain areas, neurotransmitters, and hormones), and behaviors (such as risk taking, sociability, and leadership). Natural selection can operate on any aspect of an organism's design, if it is under the control of genes. For further details on evolutionary theory and biology and evidence for evolution, I refer readers to popular science books written by distinguished evolutionary theorists such as Richard Dawkins (2009) and David Sloan Wilson (2007).

Evolutionary leadership theory is inspired by *evolutionary psychology*, which is a relatively new discipline that applies the principles of evolutionary theoretical biology to human psychology (Barkow, Cosmides, & Tooby, 1992; Buss, 2005; Schaller, Simpson, & Kenrick, 2006). Evolutionary psychology has the potential to integrate theory and research from different branches of psychology and connect it with knowledge from the biological and behavioral sciences to generate a unifying theoretical framework based on the premise of evolutionary theory. Its core tenet is that the human mind is a product of evolution through natural selection: Evolution has shaped the human brain (and its products in terms of hormones and behaviors) in the same way as it has shaped the human body and the bodies and minds of other animals. In effect, this means that humans are viewed as part of the animal kingdom and are subject to the same laws of biology and evolution.

Evolutionary psychology proposes that our brains contain many specialized cognitive mechanisms—or adaptations—that enable humans to solve many different problems affecting their reproductive success (Buss, 2005; Kenrick, Li, & Butner, 2003). For instance, humans likely possess specialized mechanisms for heat regulation, finding food, avoiding predators, searching for mates, face recognition, gossip, reputation, and dealing with strangers. These psychological mechanisms are likely to be functional and domain-specific, in the sense that they are good at solving particular problems and not others (Barrett & Kurzban, 2006). For instance, language is a highly

efficient device for gossiping, but it is probably not so good for arousing positive emotions—laughter probably works much better for this purpose.

It is instructive to think of these mechanisms as evolved if–then decision rules that were selected to produce adaptive behaviors in fitness-relevant situations. An example of an evolved social decision rule would be something like: "Follow an individual whom you trust." (It is easy to see that this is a superior decision rule to that of "follow any individual," and it is therefore more likely to have evolved.) These psychological mechanisms were shaped through natural selection pressures operating in ancestral environments, which means that they may not necessarily produce adaptive behavior in modern environments. For instance, in ancestral times it could have been advantageous to follow a physically strong leader, but in today's society where physical strength matters less, this may not be adaptive anymore—or it may even be maladaptive. This constitutes what we refer to as an "evolutionary mismatch" (Van Vugt, Johnson, Kaiser, & O'Gorman, 2008).

Evolutionary psychology often uses the four questions approach, first coined by Aristotle and then further developed by the Nobel Prize–winning Dutch ethologist Niko Tinbergen (1963) to search for evidence of biological and psychological adaptations. For instance, to the question of why animals have vision, one answer would be that it helps them find food and avoid danger. This is the question about the evolutionary function of vision. An additional question concerns through what particular series of evolutionary steps vision evolved (phylogeny). Other questions concern the mechanics of the eye (form), and even the process of an individual's eyesight across his or her lifespan (ontogeny). The first two questions address the evolutionary explanations for a particular phenomenon (ultimate causes), and the second two address the proximate explanations. Although the answers to these questions are likely very different, they complement each other.

In the same way, we could ask about the function, phylogeny, form, and ontogeny of leadership to get a complete account of the phenomenon (Van Vugt, Hogan, et al., 2008). For instance, the first question is whether leadership and followership may have been instrumental in fostering the survival and reproduction rates of humans in ancestral environments, such that they became part of our evolved psychology. This question most interests evolutionary-minded biologists and psychologists. The second question is through what series of steps did leadership emerge in humans and other animals, and where were these traits present in a common ancestor (Brosnan, Newton-Fisher, & Van Vugt, 2009). This question most interests biologists, primatologists, and zoologists studying leadership. The third question concerns the mechanics of leadership—How does it work?—and this is what most interests social and industrial/organizational psychologists studying leadership. For instance, what kinds of people make good leaders or followers, and under what conditions is a particular leader style most effective? In terms of proximate mechanisms, we can also examine the neuroscience of leadership, examining what brain regions and hormonal factors are involved in producing leadership and followership

behavior. For instance, individual differences in testosterone underlie the effectiveness of acting as a leader (Josephs, Sellers, Newman, & Metha, 2006), and a leader's punishment of group defectors produces higher activation in the brain reward regions (Fehr & Camerer, 2007).

The final question concerns the developmental aspects of leadership and asks questions such as whether some people are born leaders—given the complexity of this trait, there is unlikely to be a single gene for leadership!—or whether leadership is learned, and whether leadership styles vary as a function of age, experience, and so forth. This most interests developmental and personality psychologists studying leadership (Hogan, 2006; Simonton, 1994).

Each of Tinbergen's four questions analyzes leadership from a different angle, and together they offer a more complete account. Yet these questions should not be confused. Various well-established psychological theories assume, for instance, that leadership involves identifying obstacles between groups and their goals and then finding ways to remove these obstacles (Hackman & Walton, 1986; House, 1971). Such theories offer a proximate explanation for leadership because they identify which particular leaders emerge and are effective in particular situations. For example, a directive leader is more effective when tasks are stressful or ambiguous. These theories can be complemented with questions about the evolved functions of leadership—for instance, How and why did the capacity for directive leadership evolve? Again, it is very important not to confuse these levels of explanations. For instance, if we find that people are attracted to charismatic leadership, we still need to explain why charismatic leadership emerged in the first place and how it evolved. Did it perhaps coevolve with the capacity for language some 100,000 to 200,000 years ago (Van Vugt, 2006)?

The Coevolution of Leadership and the Social Brain

Humans are ultrasocial animals (Baumeister & Leary, 1995; E. O. Wilson, 1975). For most of our history—the genus Homo is approximately between two and two and a half million years old—our ancestors lived on the African savannah in small, highly interdependent, interconnected hunter-gatherer societies that were relatively egalitarian (Richerson & Boyd, 2006). Group living is an adaptation. For many species, group life is a buffer against the perturbations of the natural environment, so this creates selection pressures for mechanisms fostering social interaction and group coordination. Living in groups poses significant challenges, and to deal with these requires relatively big brains.

The social brain hypothesis (Dunbar, 2004; Van Vugt & Kameda, in press) argues that early humans evolved large brains in order to survive and thrive in large, complex social groups. In support of the social brain hypothesis, comparative studies have found a positive correlation between the size of the neocortex (the thinking part of the brain) and group size when comparing

humans with other primates and comparing primates with other mammals (Dunbar, 2004). Humans come out on top, having both a relatively large neocortex and large social network size. From the brain data, the extrapolated maximum social network size for humans is approximately 150 individuals, also known as Dunbar's number. This corresponds roughly to the size of a small community like a neighborhood or religious society, which can be held together through informal social control. Incidentally, 150 is the number of seats in the parliament of the Netherlands—a highly egalitarian country. It is also the median number of recipients on people's Christmas card lists, according to a U.K. study (Hill & Dunbar, 2003).

Early humans may have reaped the benefits of large social networks in terms of getting and sharing food, protection, information sharing, and perhaps communal parenting (Kenrick et al., 2003). Yet, with these benefits also came substantial costs of managing and maintaining large social networks. To reap the benefits and avoid the costs of increasingly large and complex social networks, a host of psychological adaptations likely evolved. Some of these are uniquely human, such as the capacity for language and religion. Other traits were co-opted and served new purposes, such as the capacity for intelligence, laughter, culture, and perhaps leadership.

Why did early humans need leadership? Phylogenetically speaking, perhaps the most ancient leadership problem is group movement (as a nomadic species, early human groups were always on the move). House's (1971) path-goal theory acknowledges this primary function of leadership: Effective leaders clarify the path to help their followers get from where they are to where they want to be, and they make the journey along the path easier by removing roadblocks. Our ancestors needed to move in search of resources, and the risk of predator attacks made it functional to move together as a group (King et al., 2009). But how does a group decide when to go where? This coordination problem can be solved easily by some individuals seizing the initiative and others following in their footsteps. Leadership in group movement has been documented throughout the animal kingdom, from the social insects to fish, birds, and mammals (for a review see King et al., 2009), suggesting that it does not require a lot of brain power A simple decision rule, such as "If one individual moves, I move along," can produce something akin to followership and, by default, leadership. If we assume stable individual differences in adhering to this decision rule—some individuals will always make a first move—it will automatically produce "leaders" and "followers."

Once these rudimentary mechanisms are there, they can easily be co-opted in brainier species to solve a wider range of problems. Evolutionary leadership theory suggests at least six crucial fitness problems in ancestral environments selecting for leadership: (1) finding resources, (2) conflict management, (3) warfare, (4) building alliances, (5) resource distribution, and (6) teaching (Van Vugt & Ahuja, 2010). The first problem concerns exploring resource opportunities, and the honey bee example shows that worker bees take on leadership roles as scouts in pointing the group to explore new foraging sites.

Something akin to scout leaders can be found in hunter-gatherer societies—regarded as models of early human group life (Foley, 1997)—where individuals move around in hunting parties in search of food.

The second problem concerns conflict management and selects for peace leaders. Living in relatively large groups intensifies conflict between individuals. The social lives of our hunter-gatherer ancestors involved constant conflict, and homicide must have been a leading cause of death (Alexander, 1979; Chagnon, 1997; Van Vugt, De Cremer, & Janssen, 2007). Our closest phylogenetic relatives—the great apes: chimpanzees, bonobos, and gorillas—practice peacekeeping. Therefore, we think it was almost surely a feature of early human groups as well (Boehm, 1999; De Waal, 1996). De Waal (1996) describes an instance of peacemaking leadership: "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).

A next set of adaptive problems that our ancestors faced would have been dealing with out-groups, which may have introduced a niche for war and alliance-building leaders (diplomats). In human evolution, increasingly large groups would have competed with one another for scarce resources such as water holes, food, and mates, and this may have induced severe intergroup conflict (Van Vugt et al., 2007). Archaeologists and anthropologists suggest that warfare created a strong selection pressure for the evolution of a range of important group behaviors such as coalitional aggression, altruism, loyalty, and intergroup behavior (Van Vugt & Hart, 2004). Leadership may play a role in coordinating group activities to defeat other groups. In war and in other external threats, it makes sense for groups to defer to a leader (Vroom & Jago, 1978). In traditional societies such as Native American tribes, different chiefs emerge in war or peacetime, depending on the relationship with other tribes (Johnson & Earle, 2000).

The fifth leadership niche concerns the allocation of scarce group resources, such as food and water. For instance, if a large animal is killed, how should the meat be distributed to ensure that everyone gets a share? This problem would have opened up opportunities for an individual to step in as resource allocator. In traditional societies, Big Men leaders emerge to take on these roles (Van Vugt, Hogan, et al., 2008

The final adaptive problem is how to train and socialize individuals to become good group members who contribute to group survival and effectiveness. This requires leaders who can teach newcomers relevant knowledge about the physical and social environment and introduce them to the culture and social norms of a group.

In sum, evolutionary leadership theory (Van Vugt & Ahuja, 2010) assumes that leadership evolved as solutions to distinct coordination problems

involving group movement for foraging (scouts), policing in groups (peacekeepers), organizing attacks against out-groups (war leaders), establishing peaceful alliances with other groups (diplomats), managing the group resources (managers), and socializing newcomers to become productive and loyal group members (teachers).

Successful execution of these leadership and followership roles in each of these domains would have enhanced the reproductive success of individuals and their groups. As a thought experiment, imagine two groups of humans living in the same region and competing for the same resources such as water holes, food, and safe sleeping sites. One group is characterized by internal discord and in-group violence, poor decision making, and poor socialization practices. The second is characterized by relative intragroup harmony, aggression toward out-groups, and good socialization practices. There is no doubt that over time, the second group will prevail and thus the genetic material underlying these adaptive behaviors will spread through the population—maybe via a combination of individual and group selection (D. S. Wilson, Van Vugt, & O'Gorman, 2008)—leading to the fixation of these traits.

Testing Evolutionary Hypotheses About Leadership: Darwin's Toolbox

Evolutionary psychology represents an enormously diverse set of theories, methods, and analytical perspectives (Buss, 2005; Van Vugt & Schaller, 2008). This conceptual and methodological diversity results, in part, from the fact that evolutionary psychology attracts contributions from scientists with an unusually diverse range of scholarly backgrounds—not just scholars with different kinds of training within psychology, but scholars from biology, primatology, zoology, anthropology, economics, political science, and many other academic disciplines. This diversity is a functional response to the high evidentiary standards that attend theories and hypotheses in evolutionary psychology. A truly convincing support for an evolutionary-informed theory or hypothesis about leadership needs to show not only that it is activated in evolutionarily-relevant situations but also that it functions in ways that would have promoted individuals' reproductive interests in ancestral times. The first part is relatively easy. The second part is hard.

Barring the unlikely invention of a time machine, it is impossible to collect behavioral data in ancestral environments or to empirically track the actual evolution of an alleged adaptation. Instead, evolutionary psychologists must rely on a multitude of other, often indirect sources of evidence to build an evolutionary theory of leadership (Schmitt & Pilcher, 2004).

Evolutionary scientists frequently begin with a general theory—often from the core principles of evolutionary biology—that heuristically guides their attention toward potential psychological adaptations. Common theories used by evolutionary psychologists include parental investment theory, inclusive

fitness theory, life-history theory, costly signaling theory, and evolutionary game theory (Gangestad & Simpson, 2007). If a hypothesized adaptation such as leadership flows directly from a theory under the general paradigm of evolution, then evolutionary psychologists can express more confidence in the existence of an adaptation. For instance, a higher parental investment from females leads to the hypothesis that women are interested in sexual partners who can provide resources and that males signal their mate value through achieving high-status positions—because status is linked to resources. This yields testable predictions about leadership, such that (1) women should find male leaders (sexually) more attractive and (2) men should enact leadership behaviors in the presence of (attractive) women. We are currently testing these predictions in our evolutionary social and organizational psychology laboratory (ESOP) at the VU University.

Second, evolutionary theorists can apply computer simulations to study the evolution of various group dynamic processes such as leadership and followership. Simulation studies suggest that leadership evolves quicker when the interests of individual agents are aligned, versus conflicting (Van Vugt & Kurzban, 2007). Computer simulations also help in identifying conditions under which democratic leaders produce better results than dictatorial leaders—for instance, when followers have exit options (Van Vugt, Jepson, Hart, & De Cremer, 2004).

Third, experimental methods of behavioral economics and social psychology are also useful in testing evolutionary hypotheses about leadership. The experimental (economics) games method studies interactions between players in games such as the prisoner's dilemma game, the ultimatum game, the dictator game, and the public goods game in which players allocate money. This can produce insights into many questions, for instance, regarding which personality types are more likely to take the lead in games with or without a conflict of interest between players.

Fourth, evidence for any hypothesized leadership and followership adaptation may emerge from recent advances in neuroscience. The nascent field of neuroeconomics applies neuroscience tools to economic games (Fehr & Camerer, 2007). Brain imaging studies, for instance, have the potential to provide data attesting to specific physiological structures associated with specific kinds of social behaviors (Adolphs, 1999). For instance, fMRI research can be used to detect where there is brain activity when leaders successfully coordinate group activities, make fair allocation offers, or punish individuals harming group goals (Fehr & Camerer, 2007). A very recent technique called TMS, or transcranial magnetic simulation, has emerged that disrupts activity in brain areas thought to be responsible for social and economic decisions. This technique has found, for example, that disruption of the left frontal precortex hinders people's ability to build a favorable reputation, with important implications for leadership emergence (Knoch, Schneider, Schunk, Hohmann, & Fehr, 2009).

Hormonal studies can help identify the hormonal correlates of particular leadership or followership experiences. Individual differences in baseline hormone levels, such as testosterone, predict how well individuals perform in high-status positions. Josephs et al., (2006) showed in an experimental study that high-testosterone individuals do better on a complex cognitive task in a high-status position, whereas low-testosterone individuals performed better on this task in a low-status position. In addition, research suggests that when individuals climb up in the hierarchy of their group, their testosterone levels increase to make them look more leader like (Van Vugt, 2006). We expect that the more competitive the organization is in terms of the rewards and stresses on leadership, the higher the rise in testosterone is likely to be. This is currently being tested in our ESOP lab.

Fifth, behavior genetics studies may help to provide an indication of whether leadership emergence has a substantial genetic component. A high heritability index suggests that there may be important individual differences in these traits. Although we are unlikely to find a single gene responsible for leadership, there are some promising results of studies showing that personality differences that systematically relate to leadership emergence (such as extraversion and intelligence) have a substantial heritable component (Ilies, Arvey, & Bouchard, 2006).

Sixth, methods of experimental cognitive psychology are also often used by evolutionary psychologists to find evidence for adaptations. For instance, cognitive experiments have shown that men perform better, on average, on spatial rotation tasks, whereas women perform better, on average, on spatial memory tasks (Buss, 2005). One evolutionary interpretation of this result is that ancestral men—the primary hunters—have evolved these capacities in order to navigate through an unfamiliar terrain and track prey on the move. Ancestral women—the primary gatherers—have evolved greater competencies in remembering locations where fruits and nuts can be collected.

Regarding leadership, cognitive experiments can be used to find out if people have evolved cognitive leadership prototypes about who should lead in particular situations. In our research, we examine if people have automatic associations with leadership when they rate people's faces. We have shown that people prefer a more masculine looking leader during war and a more feminine looking leader during peace (Van Vugt & Spisak, 2008). If these prototypes are cross-cultural and they can be found in children and young adults, then we have strong indication that these prototypes are evolved decision rules rather than learned rules, unlike what is suggested by implicit leadership theory (Lord, De Vader, & Alliger, 1986). Indeed, a recent study found that children as young as 5 years old can pick the winners of political election outcomes based on the faces of the candidates (Antonakis & Dalgas, 2009). Furthermore, there is cross-cultural agreement on what the face of a leader looks like (Berggren, Jordahl, & Poutvarra, 2010), suggesting that these are evolved prototypes.

Seventh, psychological surveys can provide support for evolutionary hypotheses about leadership by examining self-reported data about people's experiences with leadership and followership in the real world. For instance, survey evidence from around the globe reveals that there are some traits that are universally perceived to be associated with good leadership, such as vision, integrity, and trustworthiness (Den Hartog, House, Hanges, Ruiz-Quintanilla, & Dorfman, 1999). In addition, there are traits that are more important considerations in some cultures but not in others, such as a leader's generosity and dominance (Den Hartog et al., 1999). This suggests that some decision rules are relatively biologically fixed, such as "I will only follow a leader I can trust." Yet other rules are more flexible and influenced by culture (such as the rule "follow a generous leader").

In addition, anthropological and ethnographic databases can provide additional evidence for evolutionary hypotheses about leadership, testing the extent to which leadership phenomena are universal across human cultures. This kind of evidence is necessary to differentiate between phenomena that are evolutionary adaptations, and those that are more superficial, culture-specific manifestations. For instance, research on Western and Eastern cultures suggests that whereas the need for leadership is universal, between these cultures, people differ in what they expect from their leaders (Dorfman, Hanges, & Brodbeck, 2004; Hofstede, 1980).

Ninth, cross-species evidence is instrumental in testing speculations about the evolutionary history of any alleged adaptation such as leadership. In both humans and elephants, for instance, older individuals take on leadership positions when there is a knowledge problem—the matriarch elephant takes the lead to a long-forgotten water hole (King et al., 2009). This finding implies that the underlying evolved psychological mechanism or decision rule—follow an older individual when the group does not know where to go—predates the divergence of primates and elephants from their immediate common mammalian ancestor.

When considered in conjunction, the findings from these diverse lines of inquiry can produce new insights into leadership and its evolutionary functions. The utility of an evolutionary approach becomes apparent to just about anyone who seriously employs such an approach. For illustrative purposes, I have made a list of 10 recent empirical findings that have been discovered by biologically inspired research programs on leadership with a diverse methodology, ranging from mathematical models to behavioral and neuroscience studies. Although not one of these findings tells a definitive story about the evolutionary significance of leadership, together they point to the existence of a specialized cognitive machinery for dealing with leadership problems. A growing body of empirical evidence, in other words, shows the generativity of adopting an evolutionary approach to leadership.

1. Mathematical models suggest that in groups in which information is distributed among many individuals, democratic leadership works better than despotic leadership (Conradt & Roper, 2003; Van Vugt, 2009).

2. A laboratory experiment shows that individuals with high testosterone levels perform better on cognitive tasks when assigned to a leadership position, whereas low-testosterone individuals perform better in a followership position (Josephs et al., 2006).

3. A brain imaging study shows that when a follower receives an unfair offer from the leader in an ultimatum game, it elicits brain activity in areas related to emotion (anterior insula), suggesting that emotions play a role in deciding whether to follow a leader or not (Sanfey, 2007).

4. Archival data from traditional societies suggest that despotic leaders, such as emperors and tyrants, have greater reproductive success than democratic leaders (Betzig, 1986).

5. Swarming experiments with humans show that with just a few informed individuals, large groups of individuals can coordinate their activities (Couzin, Krause, Franks, & Levin, 2005).

6. Experiments with capuchin monkeys show that they respond negatively to unfair outcome allocations from (human) experimenters, suggesting an early evolutionary origin of injustice aversion in interacting with leaders (Brosnan, Newton-Fisher, & Van Vugt, 2009).

7. Data from traditional hunter-gatherer societies suggest that they have a host of different devices to keep overbearing leaders in check, such as through gossip, ridicule, exclusion, and assassination (Van Vugt, Hogan, et al., 2008).

8. Survey data show that men in top management positions in Western societies have more sexual liaisons than men in lower ranked functions in the organization (Perusse, 1993).

9. Laboratory experiments show that groups with leaders—who can punish free riders—do much better than groups without leaders; furthermore, groups with a leader achieve the same level of cooperation as groups where everyone can punish (O'Gorman, Henrich, & Van Vugt, 2009; Van Vugt & De Cremer, 1999).

10. When men and women watch someone being punished who has behaved unfairly, there is brain activation in the reward regions of the brain for men only, and this is accompanied by feelings of revenge (Singer et al., 2006).

A Game Theory Analysis of Leadership

Evolutionary scientists sometimes use the tool of game theory to speculate on the evolutionary origins of particular social phenomena. I have done this for leadership and followership, and this has produced a number of interesting insights into the origins and emergence of leadership (Van Vugt, 2006; Van

Vugt, Hogan, et al., 2008). Game theory emerged from the analysis of strategic interactions between combatants in World War II, but it has since become a basic model for studying human choice across the behavioral sciences (Gintis, 2007). Game theory is a helpful tool in identifying under which conditions certain social traits (or strategies) evolve, especially when they are competing with alternative traits (strategies).

For instance, the well-known prisoner's dilemma game has been used to model the evolution of cooperation. This model shows that the dominant strategy—which is the trait that is most likely to evolve—is to defect, resulting in a noncooperative equilibrium. Only by making additional assumptions, such as repeated play (Axelrod, 1984) or reputation-building (Hardy & Van Vugt, 2006), does a cooperative strategy survive.

Leadership and followership can be modeled as (evolved) game strategies, too. Framing leader-follower relations in terms of game theory can test the idea that leadership and followership evolved as two complementary strategies for achieving social coordination (Van Vugt, 2009). Key to leadership is, indeed, the need for coordination. A simple coordination game, depicted in Figure 5.1a, can make clear how leadership evolves. Figure 5.1a depicts a pure coordination game where the players have symmetrical interests. It is best illustrated with an example. (Although we present the simplest dyadic version, this analysis can be easily extended to larger, more complex groups.) Suppose Jamie and Pat are on the African savannah, our ancestral environment. They must choose between two water holes, A or B. For protection against predators, they must move together. Leadership offers a solution. Where do they go? If one of them takes the lead and moves on to his or her preferred choice, the other has no option but follow. It does not matter where they end up, at hole A or hole B, as long as they go together. This coordinating leadership is observed in many group-living animals who are regularly on the move, such as buffaloes, baboons, and humans. It does not require any brain power, just one individual who moves and the other follows. Essentially a dictator can solve this game (Van Vugt, 2009). Figure 5.1a indicates that

Figure 5.1a A Pure Coordination Game

		Pat	
		Hole A	Hole B
Jamie	Hole A	1, 1*	0, 0
	Hole B	0, 0	1, 1*

NOTE: A simple coordination game in which the payoffs are indicated for Jamie and Pat, respectively, within each square. So, if Jamie and Pat choose the same hole, they each get a +1 payoff. The game equilibria are indicated with asterisks. They each get a +1 payoff in reproductive units.

both leaders and followers benefit from coordinated action, and this is why these strategies evolved in tandem (Van Vugt, 2006).

Evolutionary game theory (Maynard-Smith, 1982), a special branch of game theory, assumes that game strategies are underpinned by gene alleles that compete with each other in a Darwinian contest. Winning strategies (genes) spread through the population at the cost of inferior ones via the process of natural selection. This simple model suggests that leadership is likely found in any situation (or species) where the benefits of coordination outweigh the costs, which theory is supported by reviews of animal leadership (King et al., 2009).

In nature, there is usually no convergence of interests between players. Indeed, in complex social groups such as where humans live, conflicts are often the rule rather than the exception. How does leadership come about then? The picture is more complicated. I have given an example in Figure 5.1b, a game I have labeled the Leader Game (also known as Battle-of-the-Sexes or Ultimatum Game). Rather than assuming equality of payoffs, Jamie might prefer to move to water hole A, which would give him an outcome of 3, whereas Pat might want to move to water hole B, which would give him a payoff of 3, too. The payoffs of the game suggest that both are still better off moving to the same hole (outcomes of either 1 or 3), yet there is a conflict of interests as to what hole to move to. What are the implications of this for how leadership is negotiated?

First, we should expect leadership will emerge more slowly in situations in which there is a conflict of interest because both individuals have an incentive to take the lead as they profit more from getting to their preferred water hole (van Vugt & Kurzban, 2007). Historically it is true that leaders have enjoyed better health, greater wealth, and more reproductive success than followers (Betzig, 1986; Chagnon, 1997; Perusse, 1993). The imbalance in payoffs between leaders and followers is the cause of constant tension and greater payoff differences create more reluctant followership. It is perhaps not surprising that in human leadership, generosity and fairness are crucial factors in leader endorsement (De Cremer & Van Vugt, 2002; Dorfman et al., 2004; Epitropaki & Martin, 2004).

Figure 5.1b The Leader Game (or Battle-of-the-Sexes)

		Pat	
		Hole A	Hole B
Jamie	Hole A	3, 1*	0, 0
	Hole B	0, 0	1, 3*

NOTE: The Leader Game in which payoffs (in reproductive success) are for Jamie and Pat respectively, within in each square. So if Jamie and Pat go to Hole A, Jamie gets a better payoff (+3) than Pat (+1). Game equilibria are indicated with asterisks.

Second, the game analysis of leadership suggests that leadership across both games should correlate with measures of initiative taking, because the one who moves first is more likely to emerge as leader. In support of this analysis, leadership correlates with various indices of initiative taking, such as boldness, ambition, self-esteem, excitement seeking, and extraversion—all linked to leadership emergence (Judge, Bono, Ilies, & Gerhardt, 2002). Furthermore, more intelligent individuals are better at "reading" the payoff preferences of others and in using fair and collectively sustainable first- and second-move strategies (Burks, Carpenter, Goette, & Rustichini, 2009). Not surprising, studies show consistent links between leadership and general measures of intelligence (with an average correlation of .33 between objectively measured intelligence and leader effectiveness; Judge, Colbert, & Illies, 2004). Links have also been established between leadership and social perceptiveness, indicating that leaders might be superior at responding flexibly to social situations (Kellett, Humphrey, & Sleeth, 2002; Zaccaro, Gilbert, Thor, & Mumford, 1991). Yet it remains to be seen whether leaders are more empathic than nonleaders (Antonakis, Ashkanasy, Dasborough, 2009). A final implication, in comparing the two games, is that when there is greater conflict of interest, personality factors associated with aggression, dominance, and authoritarianism should become relatively more importance because there are incentives to force other individuals to do what you want.

This game analysis also explains the evolution of a diversity of leadership styles and strategies because one strategy may be suited to one situation and another to another situation. A game approach suggests that different leader strategies represent situations with (slightly) different payoff structures, which affect the relationship dynamics between leaders and followers (Van Vugt, 2009). Task leadership is likely to develop as a solution to Figure 5.1a when payoffs for leaders and followers are identical and the leader's task is primarily to coordinate group activity. Relational leadership is most effective when there are noticeable payoff differences and there are opportunities for leaders to exploit and for followers to defect. In this case, the primary task of leaders is to preserve group cohesion (Fiedler, 1967; Van Vugt, 2009).

Payoff differences (Figure 5.1b) account for the distinction between transactional and transformational/charismatic leadership. Transactional leaders appeal to followers' self-interest, by providing them with favorable outcomes in return for support (Bass, 1985; Hollander & Offermann, 1990). Transactional relationships follow the payoff matrix of the Leader Game, where followers are rewarded by leaders, and the higher their rewards the more dedicated followers are. Transformational leaders use charisma and vision to inspire followers beyond their immediate self-interest (Bass, 1985; Burns, 1978). Language seems a prerequisite for this kind of leadership, which suggests that it is uniquely human (charismatic leaders are known to use a lot of metaphors in their speeches; Mio, Riggio, Levin, & Reese, 2005).

Transformational leaders effectively change the game payoffs so that followers do better than their leaders—self-sacrifice is an important aspect of

transformational leadership (De Cremer & Van Knippenberg, 2002). It is also possible, of course, that through clever use of language, charismatic leadership makes followers believe that they are better off—whereas in fact, the leader has the upper hand. Leaders with Dark Triad personalities (a lethal combination of high scores on Machiavellianism, Narcissism, and Psychopathy) have charismatic qualities and may use their appeal to manipulate group members into believing that they have their interests at heart, whereas in reality they pursue only their selfish interests.

The distinction between transactional and transformation leadership is akin to the difference between selfish and servant leadership (Gillet, Cartwright, & Van Vugt, 2010; Greenleaf, 2002). In some situations, an individual may take the lead by moving to the water hole that the other player prefers—Jamie might suggest to Pat to go to Pat's preferred hole. This is essentially servant leadership because doing so contains a sacrifice. This is not unlike what is found in other animals, such as when hyenas share a carcass and one hyena takes the lead in deterring other predators from access to the meat. It is not easy to see how servant leadership could ever evolve, because of the costs of this strategy. Perhaps this has evolved through kin selection, where the self-sacrificial leadership act helps their relatives, or though reciprocal altruism, where the hyenas take turns in taking on this leadership role. In human societies, an alternative payoff is the heroic status that the individual receives in compensation for his or her bravery, which may ultimately produce a payoff.

As an empirical test of this idea, we studied in the lab how groups of four players were able to solve coordination games with varying levels of conflict (much like the example in Figure 5.1b). In this game—where players were anonymous and there was no reputation building—we found evidence for servant leadership. Those who took the lead in the coordination game received a lower payoff than those who moved afterwards. Moreover, leadership in the game was positively associated with a prosocial personality and negatively associated with a selfish personality (Gillet et al., 2010)

Finally, game theory analyses can illuminate the origins of despotic versus democratic leadership. When there is no conflict of interest between players (as in Figure 5.1a), any individual can take the lead, and it does not matter what he or she chooses. Thus, pure coordination problems can be solved by despotic leaders. Yet, in the Leader Game, the payoff differences in the game inevitably cause resentment among players. Once individuals obtain the position of leader, they may be reluctant to give it up (Kipnis, 1972). If followers threaten to defect or revolt, then leaders will have to make concessions to stay in power. They can promise their followers a greater share of outcomes, but followers may (and often do) fear that leaders will not keep their promises. Followers might demand some control over the group's decision making, in order to protect their long-term interests.

In sum, a game theory analysis is helpful in illuminating the evolutionary origins of leadership and different leadership styles. The simplest coordination

game selects for leadership, and this explains why it is common throughout the animal kingdom (King et al., 2009). Any individual who moves first can emerge as the leader, and he or she is effectively a dictator. Leadership is more complicated in situations (or species) in which there is frequent conflict of interest between group members, such as in humans. This selects for a richer variety of leadership styles in which, depending on the conditions, a relational, charismatic, transformational, or servant-style leader emerges to keep large groups of individuals together. We do not know enough yet about the evolution of these different leadership styles and in which situations they emerge, but it seems that language is an important evolved mechanism to support them.

A Brief Natural History of Leadership

Moving away from the evolutionary functions of leadership, what can we say about its phylogeny? How did leadership evolve across evolutionary time, and what can we say about the evolution of leadership in humans and nonhumans? A review of the human and nonhuman leadership literature suggests at least four major transitions in the evolution of leadership (King et al., 2009; Van Vugt, Hogan, et al., 2008): (1) leadership emerged in prehuman species as a mechanism to solve simple group coordination problems, where any individual initiated an action and others followed; (2) leadership was co-opted to foster collective action in situations involving significant conflicts of interest, such as internal peacekeeping, in which dominant or socially important individuals emerged as leaders; (3) dominance was attenuated in early human egalitarian societies, which paved the way for democratic and prestige-based leadership; and (4) the increase in social complexity of societies that took place after the agricultural revolution produced the need for more powerful and formal leaders to manage complex intra- and intergroup relations—the chiefs, kings, presidents, and CEOs—who at best provide important public services and at worst abuse their power to dominate and exploit followers (see Table 5.1). Here, I discuss these different stages briefly (see Van Vugt, Hogan, et al., 2008, for more details on the natural history of leadership).

Stage 1: Animal Leadership

The phylogenetic evidence suggests that cognitive preadaptations for leadership long precede human and nonhuman primates. Simple leader-follower structures for coordinating group movement are observed in various social species, such as the foraging patterns of many insects, the swimming patterns of schools of fish, and the flying patterns of migrating birds. The important issue is that species lacking large brains and complex sociocognitive capacities

Table 5.1 A Natural History of Leadership

Stage	*Time Period*	*Society*	*Group Size*	*Leadership Structure*	*Leader*	*Leader-Follower Relations*
1	> 2.5 million years ago	Pre-human	Variable	Situational	Any individual, often the dominant group member	Situational or hierarchical (nonhuman primates)
2	2.5 million–13,000 years ago	Band, clan, tribe	Dozens to hundreds	Informal, expertise-based	Big man, head man	Egalitarian
3	13,000–250 years ago	Chiefdoms, kingdoms, warlord societies	Thousands	Centralized, hereditary	Chiefs, kings, warlords	Hierarchical
4	250 years ago–present	Nations, states, large businesses	Thousands to millions	Centralized, democratic	Heads of state, CEOs	Hierarchical, but participatory

From M. Van Vugt, R. Hogan, and R. Kaiser. (2008). Leadership, followership, and evolution: Some lessons from the past. *American Psychologist, 63,* 182–196.

can display followership, using a decision rule as simple as "follow the one who moves first." The individual moving first then automatically emerges as the leader.

Stage 2: Band and Tribal Leadership

Leadership was further shaped by the unique evolutionary history of humans. The emergence of hominids about 2 to 2.5 million years ago until the end of the last ice age, about 13,000 years ago, and the accompanying growth in brain and social network size had substantial implications for leadership development. During this stage, the Pleistocene era, humans lived in semino-madic hunter-gatherer bands and clans consisting of from 100 to150 closely related individuals (Dunbar, 2004). Modern hunter-gatherers such as the !Kung San of the Kalahari desert and the Aborigines in Northern Australia may provide our best model for human social organization in this stage. The living conditions in this stage are likely to have been fairly egalitarian, as there were no resource surpluses. There were no formally recognized leaders. (There are various anecdotes of White missionaries visiting exotic places and, on encountering the natives, they would ask to be brought to their leader, which bewildered the natives as they did not know the concept of leadership). This period ended with the advent of agriculture some 13,000 years ago.

Stage 3: Chiefs, Kings, and Warlords

It is unlikely that our evolved leadership psychology has changed much since the agricultural period. Yet our social structures have somewhat changed since the agricultural revolution. Agriculture and dependable food supplies enabled groups to settle and populations to grow exponentially. For the first time in our history, communities accumulated surplus resources, and leaders played a key role in their redistribution (Diamond, 1997; Johnson & Earle, 2000). As communities grew, so did the potential for within- and between-group conflict. Leaders acquired extra power to deal with such threats, resulting in more formalized authority structures that paved the way for the first chiefdoms and kingdoms (Betzig, 1986; Johnson & Earle, 2000). In their expanded role, leaders could siphon off resources and use them to create groups of dedicated followers—sometimes by establishing hereditary leadership.

Stage 4: Modern State and Business Leadership

The fourth leadership period corresponds to the beginning of the Industrial Revolution in the 18th century. Communities merged into states and nations, and large businesses developed, all of which had implications for leadership practices. Citizens of states and employees in organizations are relatively free from the predations of their leaders and may defect to other states or organizations. This freedom shifts the balance of power away from leaders and produces conditions more akin, but not equivalent, to the reverse dominance hierarchy of the ancestral period. Although modern bureaucratic arrangements make business sense, they may be constrained by our evolved leadership psychology.

Implications of Evolutionary Leadership Theory for Research and Practice

In this final section, I will note some implications of my evolutionary leadership theory (ELT) for leadership research and practice. Granted some of these implications could be derived from other proximate psychological theories of leadership, for example, path-goal theory, leader–member exchange theory (LMX), and transformational or leadership categorization theories (Avolio et al., 2009; Graen & Uhl-Bien, 1995). Yet, each of these theories must ultimately turn to evolution to explain its own assumptions (e.g., Why do human groups have charismatic leadership? Where do cognitive leadership prototypes come from?). Furthermore, ELT also sheds light on core leadership questions that have not yet been sufficiently addressed in the literature, such as why people follow leaders in the first place; why leadership is consistently linked to intelligence, when leaders prioritize their own needs over the needs

of the group; why there is a consistent preference for tall and healthy looking leaders; and why women CEOs attract so much hostility. Finally, an evolutionary framework also seems to generate a broader variety of practical implications than other theoretical perspectives about the way we should design our organizations in light of the constraints of our evolved leadership psychology.

Why Follow?

First, ELT highlights the importance of studying the origins of followership. The natural psychology of followership is more complicated and interesting than that of leadership, yet it is hardly studied (see chapter 10 of this volume for a follower-centric approach to leadership). ELT suggests that followership evolved in response to specific ancestral coordination problems such as group movement, group defense, internal peacekeeping, and teaching. This implies that followership should emerge more quickly and be more effective in these evolutionarily relevant situations and that there are differences in follower styles.

Although this hypothesis has not been tested explicitly, it is consistent with prior findings. People are more likely to follow a leader under conditions of external threat, such as a natural disaster or bystander emergency situation (Baumeister, Chesner, Senders, & Tice, 1989; Hamblin, 1958). Intergroup conflicts also pave the way for followership and leadership. In the famous Robber Cave experiment, individuals who did not know each other were brought together, and they promptly chose team leaders to represent them (Sherif, 1966). Finally, conformity research suggests that when people are uncertain about what to do, they are more likely to follow the advice of another individual who then effectively becomes the leader. The famous Milgram and Asch experiments demonstrate that followership emerges spontaneously in such situations, even if it is the (morally) wrong option. This implies that our brains are effectively tuned to followership—a heritage of our ancestral past—which is consistent with ELT.

A different implication of ELT is that individuals may not want to follow anyone when they face a relatively evolutionarily new problem (such as global warming) or a simple coordination problem. The latter is consistent with the research on leadership substitutes (Kerr & Jermier, 1978). Exercising leadership outside these adaptive problem domains could even undermine team performance. For instance, highly cohesive groups do less well in performing a routine task with a formally appointed leader (Haslam et al., 1998). An important lesson that emerges from this is that except in certain important and well-defined situations, having a formal leader is both unnecessary and detrimental.

The leadership literature could benefit from adopting an evolutionary approach by studying followership motives in different situations and the personality correlates of good and bad followership (Altemeyer, 1981; Wayne

& Ferris, 1990). Followership styles may be at least as variable and differentiated as leadership styles (Kellerman, 2008). For instance, people may follow a leader with different levels of commitment, from being an indifferent follower to a diehard follower (Kellerman, 2008). In addition, followers' motives may differ in that some people follow because they want to become leaders themselves (apprentices), whereas others follow because they are uncertain (disciples) or simply because they do what they are told by individuals higher up the group hierarchy (subordinates). An evolutionary approach places followership at the forefront of the study of leadership and is a good starting point for developing new followership theory and research (Van Vugt & Ahuja, 2010).

Who Leads? The Savannah Hypothesis of Leadership

A second implication of ELT is that who we get and want as our leaders nowadays is likely to be affected by our ancestral past. Reviewing the literature on both humans and nonhumans, we have found that individual differences in temperament, motivation, dominance, and knowledge—all linked to personality—are consistently associated with leadership emergence across species (King et al., 2009). This makes a lot of sense in light of the evolutionary game analysis of leadership. ELT predicts that first movers in a coordination game will be leaders. A recent meta-analysis indicates that of the Big Five personality dimensions, extraversion (a sign of both temperament and motivation) is most strongly related to leadership emergence ratings (Judge et al., 2002). Other studies report correlations between leadership and such traits as assertiveness, boldness, initiative, need for achievement, proactivity, and risk taking (e.g., Ames & Flynn, 2007; Bass, 1990; House & Aditya, 1997)—all these traits increase the likelihood of being the first to act. In the cognitive domain, knowledgeable people—those who quickly recognize situations requiring coordination—are more likely to become leaders. This explains the reliable relationship between general intelligence and leadership (i.e., average correlation of .33; Burks et al., 2009). Perhaps, across evolutionary time as groups got larger and socially more complex, coordination tasks also became more complicated, and this selected for a higher intelligence, especially in leaders. Thus, we may find that as tasks become more complex—being president of a larger country—intelligence becomes a better predictor of leadership.

Another implication of ELT is that good leaders (those who attract followers) should be perceived as both competent and benevolent because followers want leaders who can acquire resources and then be willing to share them. The first claim is supported by research showing that task expertise correlates with leadership (Bass, 1990) and that low expertise disqualifies individuals from leadership positions (Hollander & Offermann, 1990). Leaders' willingness to share is reflected in such traits as trustworthiness,

fairness, generosity, and self-sacrifice—universally desirable leader attributes (Dorfman et al., 2004; Epitropaki & Martin, 2004; Hardy & Van Vugt, 2006; Lord et al., 1986).

Finally, ELT explains why leadership (still) correlates with such factors as age, height, weight, and health—something not explained by existing leadership theories. Given the risks associated with following the wrong leader, people should prefer leaders who look like they have qualities that at least in ancestral times, would produce benefits. I have labeled this the Savannah Hypothesis of Leadership (Van Vugt & Ahuja, 2010). For instance, in ancestral savannah environments, having specialized knowledge—the location of water holes during a drought, for instance—may have been vital (Boehm, 1999). In baboons and elephants, group movement is also decided by the older, not the most dominant, troop member (King et al., 2009). Older individuals are more likely to have specialized knowledge. This explains why age is correlated with leadership, at least in knowledge domains (such as university professors).

In contrast, when group activities require strength and stamina (group defense in ancestral times, grueling travel schedules in modern business), physical indices such as energy level and health are better predictors of leadership emergence (Nicholson, 2000; Van Vugt, 2006). Modern voters prefer physically fit political candidates (Simonton, 1994). Interestingly, seemingly irrelevant physical factors like height predict leadership status even today (Judge & Cable, 2004). In ancestral times, taller leaders may have been better peacekeepers within groups and more intimidating foes to rival groups.

Consistent with this Savannah hypothesis, ELT suggests that our implicit leadership theories have been shaped through natural selection and that different cognitive prototypes are salient in different evolutionary-relevant situations. As an example, U.S. voters tend to choose hawkish presidents when threatened by war (McCann, 1992) and show an increased preference for charismatic leaders—-and a decreased preference for participative leaders—when reminded of their mortality (Cohen, Solomon, Maxfield, Pyszczynski, & Greenberg, 2004). Similarly, CEO charisma is positively related to organizational effectiveness, but only under conditions when subordinates experience uncertainty (Waldman, Ramirez, House, & Puranam, 2001). Finally, groups prefer a masculine-looking leader when they are in conflict with another group, but they switch to a more feminine-looking leader when they want to establish a peaceful relationship with another group (Spisak & Van Vugt, 2010; Van Vugt & Spisak, 2008).

Contingency Approaches of Leadership

Another strength of ELT is that it provides a solid foundation for contingency approaches to leadership by showing that different adaptive ancestral problems elicit different styles of leadership. Extrapolating from hunter-gatherer evidence,

leadership was flexible and, depending on conditions, different leaders emerged—for instance, the best hunter leads the hunting party, the wisest elder resolves internal conflicts the fiercest warrior leads the fight (Van Vugt, Johnson, et al., 2008). An implication is that despite stable individual (and heritable) differences in the likelihood of leadership and followership emergence across situations, these roles can also be adopted more flexibly. Twin research suggests, indeed, that only about 25% of variance in leadership emergence is due to heritable differences in personality (Ilies, Gerhardt, & Le, 2004). In addition, ELT assumes that different leadership styles reflect adaptations to different situations with (slightly) different payoff structures, such as the distinction between task and relational leadership, transformational and transactional leadership, and despotic and democratic leadership.

ELT also accounts for the fact that some leadership attributes are universally valued in leaders (such as integrity and fairness)—they are evolved cognitive prototypes—whereas the importance of other attributes is culturally more variable, as it depends on the specific challenges posed by an organization's physical and social environment (Dorfman et al., 2004; Hofstede, 1980; Richerson & Boyd, 2006). For instance, participative styles prevail in the Netherlands and Australia, where harsh natural conditions forced authorities to share power with citizens, creating a strong egalitarian ethos (cf. Den Hartog et al., 1999). In contrast, more authoritarian leadership styles are found in places in which infectious diseases are prevalent (such as sub-Sahara Africa) and strong social norms, conformity, and punitive measures are necessary to reduce infection risks (Fincher, Thornhill, Murray, & Schaller, 2008).

The Ambivalence Model of Leadership

Another implication of ELT is that it explains when and why leaders prioritize their personal goals above the group goals and what groups can do to prevent this. An evolutionary approach suggests that there are, in fact, two forms of group hierarchies in the animal world. The first is the dominance hierarchy that results from competition for scarce resources, where the strongest and most determined individual prevails and controls group resources and activities (E. O. Wilson, 1975). The second form of hierarchy emerges by consensus when hierarchical structures are perceived to benefit the group. These two forms offer very different accounts of leadership. The dominance model characterizes species in which alpha males control group activities and others are intimidated or forced to acquiesce. The picture is quite different for humans, because our hierarchies are much flatter and are often based on prestige rather than dominance (Henrich & Gil-White, 2001). The evolutionary transition from dominance to prestige-based leadership was pivotal, making it possible for humans to function in highly coordinated, cohesive, and democratic units.

Dominance, however, is part of our primate heritage, and there is always a risk that leaders will try to force followers into submission (Betzig, 1986;

Boehm, 1999; Padilla, Hogan, & Kaiser, 2007). Furthermore, dominance is often taken as a cue for competence (Anderson & Kilduff, 2009). This makes leader–follower relations inherently problematic, and I suggest that these two hierarchies have produced a different set of adaptations. On one hand, there will always be the temptation to dominate for individuals in leadership positions because that is the easiest way to get others to do what you want. Thus, humans should have evolved a leadership psychology with a set of decision rules that should elicit dominance behaviors in appropriate situations (such as when they hold power). On the other hand, we should also have evolved a followership psychology which includes a set of mechanisms, or decision rules, to avoid being dominated and exploited when we follow a leader.

This tension emerging from the conflict of interest between leaders and followers probably created an "arms race" in human evolution between adaptations aimed at enhancing personal power versus reducing the power of others. The anthropological, ethnographic, and psychological literatures reveal several mechanisms that individuals possess to increase their power base. Leaders are known to redistribute resources fairly and generously, and this enhances their influence—these are universally desirable leadership attributes (Brown, 1991; Dorfman et al., 2004). Leaders also sometimes induce external group threats to consolidate their power (Cohen et al., 2004). Leaders sometimes "buy" support through nepotistic and corruptive practices (Altemeyer, 1981), and cronyism is a common strategy for retaining power in both humans and chimpanzees, our closest primate cousin (De Waal, 1982; Gandossy & Sonnenfeld, 2004). Finally, with the advent of language, another powerful tool emerged to enhance power—the invention of ideologies. Throughout history, leaders have used or even created religions to maintain power—for example, the Sun Language religion of Kemal Ataturk—and turned their rule into a hereditary position to benefit their kin, a clear indication of nepotism (Betzig, 1986; Diamond, 1997).

Various antiexploitation devices have evolved in human evolution to ensure that humans were able to benefit from following without being exploited. The first is to accept and endorse authority only in areas where leaders have proven expertise. A second mechanism is language, which allows individuals to gossip about and ridicule those in powerful positions and hold them under public scrutiny. For instance, in hunter-gatherer bands, if a chief misbehaves, he is publicly criticized, and if he tries to give commands, he is often rebuffed (Boehm, 1999).

Shunning exploitative leaders is also a powerful tool to level relationships. Ostracism presumably had severe health and safety consequences for the ostracized in the past, and this is why people still respond negatively to ostracism in the present (Williams & Sommer, 1997) although the consequences nowadays are less severe—people do not die anymore if they are thrown out of their peer group. Another decision rule is to abandon overbearing individuals. Van Vugt et al. (2004) showed that the attrition rates in autocratically led groups are four times greater than in democratically led groups. A final

mechanism to avoid exploitation is homicide. In hunter-gatherer societies, a dominating individual runs the risk of being killed. In the United States, disgruntled citizens have attempted to assassinate 15 of 43 presidents, making it one of the most dangerous jobs in the world.

These leveling mechanisms are critical for the welfare of groups; historical evidence suggests that tyrants and dictators emerge whenever followers are unable to protect themselves against exploitative leaders (Betzig, 1986; Padilla et al., 2007).

The Mismatch Hypothesis

Finally, ELT provides an answer to why modern leadership often fails, by suggesting that there is likely a mismatch between our evolved leadership psychology and the challenges of modern environments. Our leadership psychology evolved over several million years, during which time our ancestors lived among kin in small egalitarian bands in which leadership was informal, consensual, and situational. ELT assumes that this psychology may still affect the way we respond to our leaders, and this sometimes creates a mismatch between our evolved psychology and the requirements of modern leadership. Here are several examples of potential mismatches (Van Vugt, Hogan, et al., 2008; Van Vugt, Johnson, et al., 2008).

First, leadership in the ancestral environment was distributed, democratic, and situational. The individual most qualified for the task at hand had the greatest influence on collective actions. Rarely would one individual make decisions affecting each group member. Yet with bureaucracy, came formal leadership roles in which one individual is responsible for managing all these functions within an organization. We are not adapted to take on so many different formal leadership roles. Few leaders have the right skills to perform a wide array of duties—this is often referred to as leader versatility (i.e., the ability to perform multiple, even competing, roles; Kaiser, Lindberg, & Craig, 2007). This may account for the high failure rate of senior managers, estimated to be about 50% to 60% in modern businesses (Hogan & Kaiser, 2005). It may also explain growing interest in the notion of distributed leadership—the idea that leadership is a process that can be shared because that is closest to our evolutionary leadership prototype.

The current selection process of leaders may create another mismatch. In ancestral times, leaders emerged from the group bottom-up through their skill, personality, or ambition. In modern industrial and bureaucratic organizations, leaders are appointed by managers senior to them in the organizational hierarchy. Pleasing superiors is more important to career success than pleasing subordinates, and this is at odds with our evolved leadership psychology. It is noteworthy that executives are more likely to succeed if subordinates are included in the selection process (Sessa, Kaiser, Taylor, & Campbell, 1998) as predicted by ELT.

The payoff differences between leaders and followers in modern times may also be at odds with our evolved leadership psychology. In ancestral times, there were minimal status and wealth differences, although successful leaders in war or trade may have had greater reproductive success (Chagnon, 1988). In modern business environments, the average salaries for CEOs are almost 200 times the average pay for workers. Research shows that this difference increases the potential for abuse (Kipnis, 1972) and decreases the ability to empathize with subordinates (Galinsky, Magee, Inesi, & Gruenfeld, 2006). The highly asymmetric payoffs for modern business leaders may be at odds with human nature and encourage a kind of management that employees naturally resist.

What about transformational and charismatic leadership? As societies grew in human evolution, there was a niche for leadership in enforcing social norms and fostering social cohesion. The need for such leadership activities is probably even greater today when genetic strangers must work together in large groups and the size of businesses and other kinds of organizations makes group identification difficult. Interestingly, research indicates that transformational leadership works, in part, by influencing followers to identify with the group and by emotionally bonding them (Van Vugt & De Cremer, 1999). Transformational leaders change the way followers see themselves—from self-interested individuals to members of a group—through emphasizing the similarity and shared fate among group members, almost as if they are kin. Transformational leadership may have been necessary to make the leap from small to large interconnected groups in human evolution. Although these individuals are rare in the modern world (Bass, 1985; Burns, 1978), their success suggests that people are naturally attracted to such leaders. We are currently studying whether transformational/charismatic leadership enhances the emotional bonding of individuals to groups and whether their influence works via the release of endorphins and oxytocin among followers.

Another mismatch concerns the scale of modern organizations compared to small hunter-gatherer societies. Interestingly, organizations like Toyota, GoreTex, and Virgin are designed and structured in a way that resembles hunter-gatherer bands. For instance, these companies delegate decision making to managers far down the chain of command, so that the size of functional units approximates that of a hunter-gatherer band (anywhere up to 150 individuals, as predicted by Dunbar's number). Additionally, decentralized decision making is associated with greater employee morale, involvement, and commitment, which in turn are associated with greater productivity, financial results, and customer satisfaction.

Male and Female Leadership Biases

A final potential mismatch is the preference for tall, older, and masculine leaders, which may be another legacy of our evolutionary past (as discussed

under the Savannah hypothesis). The preference for these savannah traits may provide clues about one current social issue, the prejudice against female leadership. Male leadership may have been the norm in ancestral environments—although there must have been a niche for female leaders as peacekeepers (Van Vugt & Spisak, 2008). It remains to be seen—and here is the potential for a mismatch—how beneficial the bias toward male leadership is in organizations that increasingly emphasize interpersonal skills and network building (Eagly & Carli, 2003). Despite many similarities, men and women are biologically somewhat different, and as a result of facing different adaptive problems in ancestral times (e.g., mate choice, parental care, hunting), they have likely evolved different psychologies as well (Geary, 1998). Thus, unlike what social role theorists claim, some sex differences in social behavior are hardwired rather than learned or socialized (Pinker, 2002). Women, on average, have better verbal memory, empathy, and communication skills—presumably as a result of evolutionary selection pressures on females to maintain close social networks for protection and child rearing (Van Vugt, 2006). Women leaders are also more democratic, which is consistent with this peacekeeping hypothesis (Eagly & Carli, 2003), whereas male leaders are more authoritarian and warmongering—human males have evolved a specific warrior psychology to deal with the ancient challenges of intergroup conflict (Van Vugt et al., 2007; Van Vugt & Spisak, 2008).

Men, on average, are also more status and power driven, and therefore they apply earlier to leadership posts. The male bias may be difficult to overcome, especially when the perks and privileges associated with leadership roles are substantial. Because of differences in parental investment, women chose men who were good resource providers and, as a result, men have evolved a stronger status drive. Thus, when leadership comes with status, then men should be more interested in getting such positions. Indeed there is evidence suggesting that when women and men work together on group tasks, the men are quicker to claim leadership roles, even if the women are better qualified (Mezulis, Abramson, Hyde, & Hankin, 2004). In addition, regardless of their talent, men are also more likely to assume leadership roles when being observed by women, perhaps because women prefer status in potential mates. The glass ceiling effect may be a manifestation of this male leadership bias that is rooted in our ancestral past.

Conclusions

Evolutionary leadership theory (ELT) is a new approach to the study of leadership, which connects the diverse lines of research in the social, biological, economic, and cognitive sciences and provides an overarching framework that is consistent, ultimately, with Darwin's evolutionary theory. I have argued why it is important to study the evolutionary origins and functions of leadership. I have shown what evolutionary psychology can contribute to the science of leadership, connecting many old findings and generating many

novel hypotheses and testing them with a diversity of different methodologies, from behavioral genetics to neuroscience and from experimentation to game theory. I hope this new field of enquiry will generate interest from leadership researchers and practitioners who are interested, as I am, in the Nature of Leadership.

Discussion Questions

1. Do nonhuman animals have leadership? If so, how is it different from human leadership?
2. How can neuroscience research contribute to understanding leadership?
3. Does power corrupt? Discuss evidence for or against this claim using insights from evolutionary psychology.
4. Why would there have been a preference for taller leaders in ancestral environments? How would you investigate this?

Supplementary Readings

Antonakis, J., & Dalgas, O. (2009). Predicting elections: Child's play. *Science, 323,* 1183.

Fehr, E., & Camerer, C. (2007). Social neuroeconomics: The neural circuitry of social preferences. *Trends in Cognitive Sciences, 11,* 419–427.

King, A. J., Johnson, D. D. P., & Van Vugt, M. (2009). The origins and evolution of leadership. *Current Biology, 19,* R911–R916.

Van Vugt, M., & Ahuja, A. (2010). *Naturally selected: Why some people lead, why others follow, and why it matters.* London: Profile

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., Hogan, R., & Kaiser, R. (2008). Leadership, followership, and evolution: Some lessons from the past. *American Psychologist, 63,* 182–196.

References

Adolphs, R. (1999). Social cognition and the human brain. *Trends in Cognitive Sciences, 3,* 469–479.

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

Altemeyer, B. (1981). *Right-wing authoritarianism.* Winnipeg, Canada: University of Manitoba Press.

Ames, D. R., & Flynn, F. J. (2007). What breaks a leader? The curvilinear relation between assertiveness and leadership. *Journal of Personality and Social Psychology, 92,* 307–324.

Anderson, C., & Kilduff, G. J. 2009. Why do dominant personalities attain influence in face-to-face groups? The competence-signaling effects of trait dominance. *Journal of Personality and Social Psychology, 96,* 491–503.

Antonakis, J. (in press). Predictors of leadership: The usual suspects and the suspect traits. In A. Bryman, D. Collinson, K. Grint, B. Jackson, & M. Uhl-Bien, *Sage Handbook of Leadership*. Thousand Oaks, CA: Sage.

Antonakis, J., Ashkanasy, N. M., & Dasborough, M. (2009). Does leadership need emotional intelligence? *The Leadership Quarterly, 20,* 247–261.

Antonakis, J., & Dalgas, O. (2009). Predicting elections: Child's play. *Science, 323,* 1183.

Avolio, B., Walumbwa, F. O., & Weber, T. J. (2009). Leadership: Current theories, research, and future directions. *Annual Review of Psychology, 60,* 421–449.

Axelrod, R. (1984). *The evolution of cooperation.* New York: Basic Books.

Barkow, J., Cosmides, L., & Tooby, J. (1992). *The adapted mind: Evolutionary psychology and the generation of culture.* New York: Oxford University Press.

Barrett, H. C., & Kurzban, R. (2006). Modularity in cognition: Framing the debate. *Psychological Review, 113,* 628–647.

Bass, B. M. (1985). *Leadership and performance beyond expectations.* New York: Free Press.

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

Baumeister, R. F., Chesner, S. P., Senders, P. S., & Tice, D. M. (1989). Who's in charge here? Group leaders do lend help in emergencies. *Personality and Social Psychology Bulletin, 14,* 17–22.

Baumeister, R. F., & Leary, M. (1995). The need to belong: Desire for interpersonal attachments as a fundamental human motivation. *Psychological Bulletin, 117,* 497–529.

Bennis, W. (2007). The challenges of leadership in the modern world. *American Psychologist, 62,* 2–5.

Berggren, N., Jordahl, H., & Poutvaara, P. (2010). The looks of a winner: Beauty and electoral success. *Journal of Public Economics, 94,* 8–15.

Betzig, L. (1986). *Despotism and differential reproduction: A Darwinian view of history.* New York: Aldine.

Boehm, C. (1999). *Hierarchy in the forest.* London: Harvard University Press.

Brosnan, S. F., Newton-Fisher, N. E., & Van Vugt, M. (2009). A melding of minds: When primatology meets personality and social psychology. *Personality and Social Psychology Review, 13, 129–147.*

Brown, D. (1991). *Human universals.* Boston: McGraw-Hill.

Burks, S. V., Carpenter, J. P., Goette, L., & Rustichini, A. (2009). Cognitive skills affect economic preferences, strategic behavior, and job attachment. *Proceedings of the National Academy of Sciences, 106,* 7745–7750.

Burns, J. M. (1978). *Leadership.* New York: Harper & Row.

Buss, D. M. (2005). *Handbook of evolutionary psychology.* Hoboken, NJ: John Wiley.

Chagnon, N. A. (1988). Life histories, blood revenge, and warfare in a tribal population. *Science, 239,* 985–992.

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

Cohen, F., Solomon, S., Maxfield, M., Pyszcynski, T., & Greenberg, J. (2004). Fatal attraction: The effects of mortality salience on evaluations of charismatic, task-oriented, and relationship-oriented leaders. *Psychological Science, 15,* 846–851.

Conradt, L., & Roper, T. (2003). Group decision-making in animals. *Nature, 421,* 155–158.

Couzin, I. D., Krause, J., Franks, N. R., & Levin, S. A. (2005). Effective leadership and decision-making in animal groups on the move. *Nature, 433,* 513–516.

Darwin, C. (1871). *The descent of man*. London: Appleton & Co.

Dawkins, R. (2009). *The greatest show on earth: The evidence for evolution*. New York: Free Press.

De Cremer, D., & van Knippenberg, D. (2002). How do leaders promote cooperation? The effects of charisma and procedural fairness. *Journal of Applied Psychology, 87,* 858–866.

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.

Den Hartog, D. N., House, R. J., Hanges, P. J., Ruiz-Quintanilla, S.A., & Dorfman, P. W. (1999). Culture-specific and cross-culturally generalizable implicit leadership theories: A longitudinal investigation. *The Leadership Quarterly, 10,* 219–256.

De Waal, F. B. M. (1982). *Chimpanzee politics: Power and sex among apes*. New York: Harper & Row.

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

Diamond, J. (1997). *Guns, germs, and steel*. London: Vintage.

Dorfman, P. W., Hanges, P. J., & Brodbeck, F. C. (2004). Leadership and cultural variation: The identification of culturally endorsed leadership profiles. In R. J. House, P. J. Hanges, M. Javidan, P. W. Dorfman, & V. Gupta (Eds.), *Culture, leadership, and organizations: The GLOBE study of 62 societies* (pp. 669–719). Thousand Oaks, CA: Sage.

Dunbar, R. I. M. (2004). *Grooming, gossip, and the evolution of language*. London: Faber & Faber.

Eagly, A. H., & Carli, L. L. (2003). The female leadership advantage: An evaluation of the evidence. *The Leadership Quarterly, 14,* 807–834.

Epitropaki, O., & Martin, R. (2004). Implicit leadership theories in applied settings: Factor structure, generalizability, and stability over time. *Journal of Applied Psychology, 89,* 293–310.

Fehr, E., & Camerer, C. (2007). Social neuroeconomics: The neural circuitry of social preferences. *Trends in Cognitive Sciences, 11,* 419–427.

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

Fincher, C., Thornhill, R., Murray, D., & Schaller, M. (2008). Pathogen prevalence predicts human cross-cultural variability in individualism/collectivism. *Proceedings of the Royal Society B, 275,* 1279–1285.

Foley, R. A. (1997). The adaptive legacy of human evolution: A search for the environment of evolutionary adaptedness. *Evolutionary Anthropology, 4,* 194–203.

Galinsky, A. D., Magee, J. C., Inesi, M. E., & Gruenfeld, D. H. (2006). Power and perspectives not taken. *Psychological Science, 17,* 1068–1077.

Gandossey, R., & Sonnenfeld, J. A. (2004). *Leadership and governance from the inside out*. London: Wiley.

Gangestad, S., & Simpson, J. A. (2007). *The evolution of the mind*. New York: Guilford.

Geary, D. (1998). *Male/female: The evolution of human sex differences*. Washington, DC: APA Press.

Gillet, J., Cartwright, E., & Van Vugt, M. (2010). Selfish or servant leadership? Leadership personalities in coordination games. *Personality and Individual Differences.* doi:10.1016/j.paid.2010.06.003

Gintis, H. (2007). A framework for unifying the behavioral sciences. *Behavioral and Brain Sciences, 30,* 1–16.

Graen, G. B., & Uhl-Bien, M. (1995). Development of leader-member exchange (LMX) theory of leadership over 25 years: Applying a multi-level domain perspective. *The Leadership Quarterly, 6,* 219–247.

Greenleaf, R. (2002). *Servant leadership.* Google Books.

Hackman, J. R., & Wageman, R. (2007). Asking the right questions about leadership. *American Psychologist, 62,* 43–47.

Hackman, J. R., & Walton, R. E. (1986). Leading groups in organizations. In P. S. Goodman (Ed.), *Designing effective work groups* (pp. 72–119). San Francisco: Jossey-Bass.

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

Hardy, C., & Van Vugt, M. (2006). Nice guys finish first: The competitive altruism hypothesis. *Personality and Social Psychology Bulletin, 32,* 1402–1413.

Haslam, A., McGarty, 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.

Henrich, J., & Gil-White, F. (2001). The evolution of prestige: Freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior, 22,* 165–196.

Hill, R. A., & Dunbar, R. (2003). Social network size in humans. *Human Nature, 14,* 53–72.

Hofstede, G. (1980). *Culture's consequences: International differences in work-related values.* Beverly Hills, CA: Sage.

Hogan, R. (2006). *Personality and the fate of organizations.* Hillsdale, NJ: Lawrence Erlbaum.

Hogan, R., & Kaiser, R. (2005). What we know about leadership. *Review of General Psychology, 9,* 169–180.

Hollander, E. P., & Offermann, L. (1990). Power and leadership in organizations: Relationships in transition. *American Psychologist, 45,* 179–189.

House, R. J. (1971). A path-goal theory of leader effectiveness. *Administrative Science Quarterly, 16,* 321–339.

House, R. J., & Aditya, R. N. (1997). The social scientific study of leadership: Quo vadis? *Journal of Management, 23,* 409–473.

Ilies, R., Arvey, R., & Bouchard, T. (2006). Darwinism, behavioral genetics, and organizational behavior: A review and agenda for future research. *Journal of Organizational Behavior, 27,* 121–141.

Ilies, R., Gerhardt, M., & Le, H. (2004). Individual differences in leadership emergence: Integrating meta-analytic findings and behavior genetics estimates. *International Journal of Selection and Assessment, 12,* 207–219.

Josephs, R. A., Sellers, J. G., Newman, M. L., & Metha, P. (2006). The mismatch effect: When testosterone and status are at odds. *Journal of Personality and Social Psychology, 90,* 999–1013.

Johnson, A. W., & Earle, T. (2000). *The evolution of human societies.* Stanford, CA: Stanford University Press.

Judge, T. A., Bono, J., Ilies, R., & Gerhardt, M. (2002). Personality and leadership: A qualitative and quantitative review. *Journal of Applied Psychology, 87,* 765–780.

Judge, T. A., & Cable, D. M. (2004). The effect of physical height on workplace success and income: A preliminary test of a theoretical model. *Journal of Applied Psychology, 89,* 428–441.

Judge, T. A., Colbert, A. E., & Ilies, R. (2004). Intelligence and leadership: A quantitative review and test of theoretical propositions. *Journal of Applied Psychology, 89,* 542–552.

Kaiser, R., Lindberg, J., & Craig, S. (2007). Assessing the flexibility of managers: A comparison of methods. *International Journal of Selection and Assessment, 16,* 40–55.

Kellerman, B. (2008). *Followership*. Boston: Harvard Business School Press.

Kellett, J. B., Humphrey, R. H., & Sleeth, R. G. (2002). Empathy and complex task performance: Two routes to leadership. *The Leadership Quarterly, 13,* 523–544.

Kenrick, D., Li, N. P., & Butner, J. (2003). Dynamical evolutionary psychology: Individual decision rules and emergent social norms. *Psychological Review, 110,* 3–28.

Kerr, S., & Jermier, J. (1978). Substitutes for leadership: Their meaning and measurement. *Organizational Behavior and Human Performance, 22,* 374–403.

King, A. J., Johnson, D. D. P., & Van Vugt, M. (2009). The origins and evolution of leadership. *Current Biology, 19,* R911–R916.

Kipnis, D. (1972). Does power corrupt? *Journal of Personality and Social Psychology, 24,* 33–41.

Knoch, D., Schneider, F., Schunk, D., Hohmann, M., & Fehr, E. (2009). Disrupting the prefrontal cortex diminishes the human ability to build a good reputation. *Proceedings of the National Academy of Sciences of the United States of America, 106,* 20895–20899.

Lord, R. G., De Vader, 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.

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

Mezulis, A., Abramson, L., Hyde, J. S., & Hankin, B. L. (2004). Is there a universal positivity bias in attributions? A meta-analytic review of individual, developmental, and cultural differences in the self-serving attributional bias. *Psychological Bulletin, 130,* 711–746.

McCann, S. J. H. (1992). Alternative formulas to predict the greatness of U. S. presidents: Personological, situational, and zeitgeist factors. *Journal of Personality and Social Psychology, 62,* 469–479.

Mio, J. S., Riggio, R. E., Levin, S., & Reese, R. (2005). Presidential leadership and charisma: The effects of metaphor. *The Leadership Quarterly, 16,* 287–294.

Nicholson, N. (2000). *Managing the human animal*. New York: Thomson.

O'Gorman, R. O., Henrich, J., & Van Vugt, M. (2009). Constraining free-riding in public goods games: Designated solitary punishers can sustain human cooperation. *Proceedings of Royal Society B, 276,* 323–329.

Padilla, A., Hogan, R., & Kaiser, R. B. (2007). The toxic triangle: Destructive leaders, vulnerable followers, and conducive environments. *The Leadership Quarterly, 18,* 176–194.

Perusse, D. (1993). Cultural and reproductive success in industrial societies: Testing the relationship at the proximate and ultimate levels. *Behavioral and Brain Sciences, 16,* 267–322.

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

Richerson, P. J., & Boyd, R. (2006). *Not by genes alone: How culture transformed human evolution.* Chicago: Chicago University Press.

Riley, J. R., Greggers, U., Smith, A., Reynolds, D., & Menzel, R. (2005). The flight paths of honey bees recruited by the waggle dance. *Nature, 435,* 205–207.

Sanfey, A. (2007). Social decision making: Insights from game theory and neuroscience. *Science, 318,* 598–602.

Schaller, M., Simpson, J., & Kenrick, D. (2006). *Evolution and social psychology.* London: Psychology Press.

Schmitt, D. P., & Pilcher, J. J. (2004). Evaluating evidence of psychological adaptation: How do we know one when we see one? *Psychological Science, 15,* 643–649.

Sessa, V. I., Kaiser, R., Taylor, J. K., & Campbell, R. J. (1998). *Executive selection.* Greensboro, NC: Center for Creative Leadership.

Sherif, M. (1966). *In common predicament.* Boston: Houghton Mifflin.

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

Singer, T., Seymour, B., O'Doherty, J. P., Stephan, K. E., Dolan, R. J., & Frith, C. D. (2006). Empathic neural responses are modulated by the perceived fairness of others. *Nature, 439,* 466–469.

Spisak, B., & van Vugt, M. (2010). *Face masculinity and femininity as predictors of electoral success.* Unpublished manuscript.

Tinbergen, N. (1963). On the aims and methods in ethology. *Zeitschrift for Tierpsychology, 20,* 410–433.

Van Vugt, M. (2006). The evolutionary origins of leadership and followership. *Personality and Social Psychology Review, 10,* 354–372.

Van Vugt, M. (2009). Despotism, democracy, and the evolutionary dynamics of leadership and followership. *American Psychologist, 64,* 54–56.

Van Vugt, M., & Ahuja, A. (2010) *Naturally selected: Why some people lead, why others follow, and why it matters.* London: Profile.

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., De Cremer, D., & Janssen, D. (2007). Gender differences in cooperation and competition: The male warrior hypothesis. *Psychological Science, 18,* 19–23.

Van Vugt, M., & Hart, C. M. (2004). Social identity as social glue: The origins of group loyalty. *Journal of Personality and Social Psychology, 86,* 585–598.

Van Vugt, M., Hogan, R., & Kaiser, R. (2008). Leadership, followership, and evolution: Some lessons from the past. *American Psychologist, 63,* 182–196.

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.

Van Vugt, M., Johnson, D., Kaiser, R., & O'Gorman, R. (2008). Evolution and the social psychology of leadership: The mismatch hypothesis. In J. B. Ciulla (Set Ed.) and C. R. Hoyt, G. R. Goethals, & D. R. Forsyth (Vol. Eds.), *Leadership at the crossroads: Vol. 1. Leadership and psychology* (pp. 267–282). London: Praeger.

Van Vugt, M., & Kameda, T. (in press). Evolutionary approaches to group dynamics. In J. Levine (Ed.), *Handbook of group processes*. London: Sage.

Van Vugt, M., & Kurzban, R. K. (2007). Cognitive and social adaptations for leadership and followership: Evolutionary game theory and group dynamics. In J. Forgas, W. von Hippel, & M. Haselton (Eds.), *Sydney Symposium of Social Psychology: Vol. 9. The evolution of the social mind: Evolutionary psychology and social cognition* (pp. 229–244). London: Psychology Press.

Van Vugt, M., & Schaller, M. (2008). Evolutionary perspectives on group dynamics: An introduction. *Group Dynamics, 12,* 1–6.

Van Vugt, M., & Spisak, B. R. (2008). Sex differences in leadership emergence during competitions within and between groups. *Psychological Science, 19,* 854–858.

Vroom, V. H., & Jago, A. G. (1978). On the validity of the Vroom-Yetton model. *Journal of Applied Psychology, 63,* 151–162.

Waldman, D. A., Ramirez, G. G., House, R. J., & Puranam, P. (2001). Does leadership matter? CEO leadership attributes and profitability under conditions of perceived environmental uncertainty. *Academy of Management Journal, 44,* 134–143.

Wayne, S. J., & Ferris, G. R. (1990). Influence tactics, affect and exchange quality in supervisor-subordinate interactions: A laboratory experiment and field study. *Journal of Applied Psychology, 75,* 487–499.

Williams, K. D., & Sommer, K. L. (1997). Social ostracism by co-workers: Does rejection lead to loafing or compensation? *Personality and Social Psychology Bulletin, 61,* 570–581.

Wilson, D. S. (2007). *Evolution for everyone*. New York: Delta.

Wilson, D. S., Van Vugt, M., & O'Gorman, R. (2008). Multilevel selection theory and major evolutionary transitions: Implications for psychological science. *Current Directions in Psychological Science, 17,* 6–9.

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

Yukl, G. A. (2006). *Leadership in organizations* (6th ed.). Englewood Cliffs, NJ: Prentice Hall.

Zaccaro, S. J., Gilbert, J. A., Thor, K. K., & Mumford, M. D. (1991). Leadership and social intelligence: Linking social perceptiveness and behavioral flexibility to leader effectiveness. *The Leadership Quarterly, 2,* 317–342.