The Service-for-Prestige Theory of Leader-Follower Relations: A Review of the Evolutionary Psychology and Anthropology Literatures

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In this chapter we examine leader-follower interaction from the perspective of evolutionary psychology, with the goal of identifying the evolved psychological adaptations that enable humans to be and to follow leaders. We argue that adaptations for leadership and followership both evolved to enable individuals to pursue their own evolved interests in ancestral environments; in other words, leadership and followership are equally genetically "selfish" strategies that ancestral humans pursued in order to survive and reproduce. However, leader-follower relationships vary in the extent to which they promote the interests of the followers versus those of the leader. We suggest that the optimal form of leaderfollower relationship is one that balances the interests of leaders and followers, in an elaborated form of what biologists call "reciprocal altruism" (Trivers 1971). In this mutually beneficial arrangement, leaders provide services to followers in the form of expertise and group organizational skills, and in exchange, followers provide leaders with social prestige. This reciprocity-based form of leadership prevails when leaders and followers possess relatively equal social bargaining power, and when leaders have low power to exploit followers. However, when leaders' exploitative power increases—due, for example, to followers' poor exit options leader-follower relationships are more likely to become based on the leader's ability to inflict harm on (rather than provide benefits to) followers. The theory we present here, then, focuses both on the situations that give rise to the optimal form of reciprocity-based leadership and on the risk factors that cause reciprocity-based leadership to degenerate into coercive leadership. We refer to this theory as the "service-for-prestige" theory of leader-follower relations.

Service-for-prestige shares some predictions with existing evolutionary theories of leadership (Price 2003; Van Vugt, Hogan, and Kaiser 2008; Van Vugt et al. 2008), including the overarching "evolutionary leadership theory" presented by Van Vugt and Ahuja (2010). However, service-for-prestige maintains a uniquely strong focus on the optimal leader-follower relationship as a form of reciprocity, in which leader and followers each incur costs in order to provide benefits for one another, and in which the allocation of prestige to leaders constitutes a collective-action problem for followers. This focus allows service-for-prestige to make some novel predictions, which we discuss throughout the chapter, especially in section 3.

1. EVOLUTIONARY PSYCHOLOGY, RECIPROCITY, AND LEADERSHIP: CORE ASSUMPTIONS

Evolutionary psychology assumes that the brain/mind is composed of a large number of genetically encoded mechanisms that evolved because they helped the individual organism's ancestors to solve adaptive problems (Cosmides and Tooby 2005; Tooby and Cosmides 1992). By adaptive problem, we mean any recurring obstacle to the individual's success in the competition to survive and reproduce (that is, any challenge to the individual's fitness) that existed in the organism's ancestral environments. Evolution solves adaptive problems by endowing individuals with domain-specific, functionally specialized adaptations that are good at solving a particular problem or set of problems but useless for most other tasks. Thus, the pancreas is good at producing insulin but bad at digesting food or filtering blood; opposable thumbs are useful for grasping but not for lactation or sight. A growing body of evidence suggests that this evolutionary design principle of functionally specialized modularity applies to minds as well, including the human mind. For example, people have specialized mate-selection adaptations that are helpful for selecting an appropriate reproductive partner (Buss 1992; Sugiyama 2005) but useless for escaping predators, reading others' emotional states, selecting nutritious food, or avoiding falls from high places.

The large varieties of functionally specialized mental mechanisms that compose our minds were selected because they solved adaptive problems that were chronic and recurrent in human ancestral environ-

170 Michael E. Price and Mark Van Vugt

ments for an evolutionarily relevant length of time (Cosmides and Tooby 2005). We could possess mechanisms that are specialized for leadership and followership, therefore, only if these behaviors solved problems that were present in the types of hunter-gatherer environments in which the vast proportion of human evolution has occurred. The problems that leadership and followership solved for ancestral humans were most likely related to group organization (e.g., solving coordination and collectiveaction problems) and the sharing of expertise; from a cross-species perspective, leader-follower relationships generally evolve as solutions to these problems (King, Johnson, and Van Vugt 2009; Van Vugt and Ahuja 2010). For example, waggle-dancing honeybees share their knowledge about nest site locations in order to guide their followers to a suitable new site; many varieties of fish follow leaders in order to form shoals, which are useful for foraging and protection from predators; in many species (e.g., ravens, elephants), individuals who know the location of food or water lead their groups to these resources; and in primate species such as chimpanzees, alpha males coordinate their group's cooperative actions against predators and rival groups (Boehm 1999; King, Johnson, and Van Vugt 2009; Krause and Ruxton 2002).

Because leadership has evolved to facilitate the sharing of expertise and cooperative group action in so many species, and because humans are adapted for complex cooperative behaviors that require high levels of expertise and coordination (e.g., in coalitions and collective actions; Tooby, Cosmides, and Price 2006), it would not be surprising if humans had evolved adaptations for leadership and followership behaviors. Indeed, the available evidence suggests that the propensity to engage in these behaviors is a universal aspect of human nature: all societies evidence some form of leadership, including the hunter-gatherer and tribal societies that most resemble those of the human evolutionary past (Bass 1990; Brown 1991). In these small-scale, ancestral-type societies, leadership emerges most often to facilitate cooperation in group activities such as hunting, warfare, and moving camp (Service 1966). These were evolutionarily important activities in ancestral environments, because problems of how to acquire sufficient meat, how to prevail in war, and how to camp in a safe and resource-rich location were highly relevant to individual evolutionary fitness (that is, to the individual's ability to survive and reproduce). Selection could therefore have favored leadership and followership behaviors that enabled people to enhance their chances of success in these domains. Throughout this chapter, we make frequent reference to ancestral-type hunter-gatherer societies, because in order to understand how the mind is adapted for leadership and followership, we need to understand the kinds of environments in which these adaptations evolved.

Note that we have so far been considering how leadership and followership benefited the survival and reproduction of individuals. This individual-level perspective on adaptation was popularized by Darwin in the Origin of Species (1859) and remains the standard in behavioral biology. Still, because leaders and followers interact in groups, it might seem reasonable to seek instead a "group selectionist" explanation for the evolution of leadership (or a "multilevel selectionist" explanation, which combines individual, group, and possibly other levels, such as intragenomic and species). In other words, one might propose that psychological adaptations for leadership/followership evolved at least in part because these behaviors produced benefits at the group level (e.g., groups with leaders outcompete groups without leaders [Hogan, 2006]). However, while leadership often does produce group-level benefits, we maintain a focus on ordinary, individual-level adaptations (Williams, 1966). Consideration of all possible selective levels is beyond the scope of this chapter, and we believe that an individual-level focus is an especially productive way of generating insights about the evolution of leadership.

Because our focus is on the individual level, and because human leader-follower relationships are cooperative interactions that occur between individuals who are not necessarily close genetic kin, our main theoretical tool is a modified version of the leading individual-level evolutionary theory of non-kin cooperation: Trivers's (1971) reciprocal altruism.² In devising reciprocal altruism theory, Trivers realized that if an individual "altruistically" delivers a benefit to a nonrelative (i.e., if the individual incurs a fitness cost in order to benefit the fitness of a nonrelative), then that altruist will be evolutionarily disadvantaged, unless he or she can somehow recoup this fitness cost. Reciprocal altruism theory predicts that altruists will deliver benefits to recipients only for as long as they receive return benefits that compensate them for this altruism. Mutually beneficial exchange can evolve as long as altruists can interact with other altruists (who reciprocate the benefits that they are given), and can avoid interacting with cheaters who fail to reciprocate. If altruists interact too frequently with cheaters instead of with other altruists, cheaters will exploit them to extinction (Henrich 2004).

Traditionally, reciprocal altruism theory has most often been used to explain mutually beneficial exchange that occurs between two individuals. Leader-follower interactions, however, are group interactions, involving exchange between one leader and more than one follower. Efforts

have been made, with varying degrees of success, to extend reciprocal altruism to group interactions (Boyd and Richerson 1988; Price 2003 and 2006a; Takezawa and Price 2010; Tooby, Cosmides, and Price 2006). We acknowledge that important theoretical details about how reciprocal altruism evolves in groups remain to be worked out. In order to clarify that we are using a substantially modified version of Trivers's dyadic reciprocal altruism theory, we use the more general term *reciprocity*, as opposed to *reciprocal altruism*, to describe the kind of leader-follower interaction we have in mind. By *leader-follower reciprocity*, we simply mean that leaders and followers are involved in a mutually beneficial transaction, with each side paying costs in exchange for benefits.

Despite unresolved theoretical issues about the evolution of reciprocity in groups, we propose that reciprocity theory does provide a suitable framework for understanding voluntary, noncoercive leader-follower interactions, that is, interactions in which followers voluntarily follow and leaders voluntarily lead because they feel that they can benefit from doing so. We also believe that by testing some of the predictions made by the theory that voluntary leader-follower interaction is a form of reciprocity, we may make progress toward resolving some lingering theoretical questions about how reciprocity evolves in groups. We say more about these theoretical questions and the predictions that could help to resolve them later in the chapter.

Note that our reciprocity theory bears similarities to existing leadership theories, such as social exchange (Hollander 1992), leader-member exchange (Graen and Uhl-Bein 1995), social identity (Hogg 2001), and charismatic, transactional, and transformational perspectives (Bass 1998; Burns 1978), as they all stress the importance of leader-follower interactions. A notable difference, however, with these theories is that they offer proximate explanations for leadership, such as predictions about whether people will decide to follow a transactional or a transformational leader. In contrast, reciprocity theory deals with the question of why humans have evolved to be attracted to leaders who provide different kinds of services to the group, from tangible rewards such as income and material goods to symbolic rewards such as self-esteem and a positive social identity.

As noted above, leader-follower interactions are not always voluntary; they may also be coercive: followers may comply with a leader's wishes in order to avoid reprisal for noncompliance (French and Raven 1959). The service-for-prestige theory focuses on both voluntary and coercive leader-follower interactions, especially on the conditions that cause

leader-follower interactions to change from being voluntary to coercive. However, we do believe that the voluntary kind are more effective for balancing the interests of leaders and followers, and we focus on this kind first.

2. VOLUNTARY LEADER-FOLLOWER INTERACTION AS SERVICE-FOR-PRESTIGE EXCHANGE

We regard the voluntary leader-follower interaction as a kind of reciprocity in which leaders incur costs in order to provide followers with expertise and solutions to social coordination and collective-action problems, and followers incur costs in order to provide leaders with social status (Price 2003). Social status can result from two general social abilities: the ability to confer benefits on others, which is prestige, and the ability to inflict harm on others, which is dominance (Cheng, Tracy, and Henrich 2010; Henrich and Gil-White 2001; Sell, Tooby, and Cosmides 2009). The voluntary leader-follower interaction can be characterized as a service-for-prestige transaction because followers willingly agree to allocate status to the leader in exchange for the services the leader provides (see Hollander 1992). Again, we stress that these services may vary from instrumental rewards, such as a good salary, to symbolic rewards, such as feeling pride in your group.

If leader-follower interaction is to be seen as reciprocity, then the services provided by leaders and the prestige provided by followers must both be contributions that are costly to provide. The costs of providing leadership seem relatively clear; they could include, for example, making the effort to share one's expertise, risking one's own safety to lead a hunting or war party, investing time and energy in planning company strategy, or incurring the stress of making high-level decisions. The costs of providing prestige ("paying respect") may seem more obscure, because some superficial prestige indicators seem cheap to produce—for example, calling a higher-raking person "sir" and laughing at his jokes. However, allocating prestige is ultimately a costly process because it involves deferring to the interests of prestigious people and taking pains to ensure their well-being, and because it results in a relatively large share of a group's social, material, and reproductive resources being acquired by or flowing to prestigious people. Prestigious people are prestigious because they possess attributes that others value—for example, physical attractiveness, or skill at generating resources, or reliability as a source of useful information—so they are sought after as social partners, and others treat

174 Michael E. Price and Mark Van Vugt

them well in order to retain them as friends and allies. The flow of shared social and material resources in small-scale societies thus tends to move toward high-prestige individuals; therefore, they become relatively more able to attract mates and provision offspring (Betzig 1986; Hagen, Barrett, and Price 2006). The allocation of prestige in these social groups is costly, then, because it ultimately results in prestigious people having superior access to all kinds of resources that could otherwise be consumed by other group members. An analogous situation occurs in modern societies, in which higher-prestige employees are compensated with larger shares of an organization's resources (Day and Antonakis 2011).

In order to elaborate further on the service-for-prestige theory and to specify the predictions that it makes about effective leadership in modern organizations, it is useful to focus more closely on service-for-prestige exchange in the context of the small-scale, ancestral social environments in which it evolved. In section 3, we consider the evolution of leadership in these environments and discuss how this evolutionary history should influence our understanding of leadership and followership in modern contexts.

3. LEADER-FOLLOWER RELATIONS IN ANCESTRAL ENVIRONMENTS AND IMPLICATIONS FOR MODERN ORGANIZATIONS

In order to understand the nature of the cognitive mechanisms that generate leader and follower behaviors in modern environments, we need to understand what adaptive problems these mechanisms evolved to solve in ancestral environments. Although these environments cannot be observed directly, anthropological studies of small-scale societies provide a reasonable approximation of what they were like. This section, therefore, draws heavily on anthropological observations of such societies.

In considering the kinds of environments in which leadership and followership evolved, it is important to keep in mind that although an adaptation must, by definition, successfully solve some adaptive problem in the environments in which it evolves, it may fail to function adaptively in different, novel environments. In other words, an adaptation's adaptiveness in past environments is no guarantee of its adaptiveness in new environments; there may be a *mismatch* between that adaptation and its new environment. Common examples of mismatch are the human tastes for fat, salt, and sugar (Nesse and Williams 1994). In ancestral environments, these substances were nutritionally essential, yet scarce and difficult to obtain, so our ancestors needed to crave them strongly in

order to be motivated to acquire them in sufficient quantities. In modern environments, however, these substances are cheap and easily obtained; as a result, we suffer from maladaptive health consequences, such as obesity, hypertension, and tooth decay. Below we discuss several examples of adaptations for leadership and followership that seem better suited for ancestral conditions than for modern ones (see also Van Vugt et al. 2008).

We also want to emphasize that human psychological adaptations for leadership and followership did not evolve in just one static type of ancestral environment; they evolved across a range of environmental conditions. Under some conditions, leader-follower relations would have been more likely to be based on prestige and reciprocity; under other conditions, they would have been more likely to be based on dominance and coercion. In section 3.1, we discuss implications of the theory that some leader and follower behaviors evolved in the context of reciprocity, and in section 3.2, we consider how variation in ancestral environments would have allowed for leader-follower relations to become more coercive.

3.1. Leader-Follower Relations as a Service-for-Prestige Transaction

3.1.1. In Nomadic Foraging Societies, Followers Decide Whom They Want to Follow

Nomadic foraging (hunter-gatherer) societies are particularly relevant to an understanding of evolved leadership preferences, because these societies approximate the most relevant selective environments for the mental mechanisms that compose the minds of modern humans (Tooby and Cosmides 1992). The most commonly noted aspect of leadership in these societies is that it tends to be informal and based on achievement; any group members can become influential and gain prestige if they happen to have expertise that makes them useful to other people (Fried 1967; Kelly 1995). Leaders in these societies have little coercive power to force others to do what they say; instead, they tend to lead by persuasion and by demonstrating their own expertise to others (Johnson and Earle 1987; Service 1966). Here are a couple of representative anthropological observations: "Nobody ever tells an Eskimo what to do. But some people are smarter than others and can give good advice. They are the leaders" (Chance 1966, 73). An Australian aboriginal man "attracted social prestige only as long as he could validate his status by actual performance" (Meggitt 1960, 250). Because leaders in these societies have relatively lit-

176 Michael E. Price and Mark Van Vugt

tle coercive power, the high regard in which followers hold them appears to be voluntarily conferred prestige (Henrich and Gil-White 2001), which followers grant the leader because they perceive that they benefit from the leaders' shared expertise and organizational abilities (Van Vugt and Ahuja 2010). This prestige in turn benefits the leader: prestigious individuals are highly valued by other people as friends, allies, and mates, and therefore social, material, and reproductive resources tend to flow their way (Sell, Tooby, and Cosmides 2009; Von Rueden, Gurven, and Kaplan 2008).

The observation that leaders in foraging societies achieve their position via public displays of competence can be explained in terms of service-for-prestige theory. Followers provide leaders with prestige in exchange for the group-beneficial expertise and social organization services that leaders provide. A number of studies, conducted in both small-scale and industrialized societies, also support the view that in groups where status can be freely allocated by members, it is allocated to those who have demonstrated their ability to provide benefits to the group (Willer 2009; Anderson and Kilduff 2009). Among the hunter-horticultural Shuar of the Ecuadorian Amazon, for example, people who are perceived as doing the most to help their social group—whether that group be the entire village or a smaller, within-village association—receive the most social status and are preferred as leaders within that group (Price 2003, 2006a, and 2006b). Similar relationships between altruism and social status have been found in industrialized societies in both experimental studies of university students (Hardy and Van Vugt 2006) and field studies of business employees (Flynn 2003). This process of acquiring status via engagement in group-beneficial tasks has been described as "competitive altruism" (Barclay 2004; Hardy and Van Vugt 2006; Roberts 1998), because members compete with one another in order to determine who is most able to benefit the group and therefore most deserving of high social status.

The above evidence suggests that this process of competitive altruism—of followers choosing their own leaders by awarding social status to those who outcompete others in demonstrating leadership ability occurs spontaneously in groups, in all kinds of cultures, whenever followers are allowed to make decisions about whom they want to follow. This process is also, of course, how leaders are supposed to be elected in democratic governments. It appears that, cross-culturally, when given a choice, people prefer to follow leaders whom they have chosen. In contrast, people are less willing to follow leaders who have been imposed on them by some external force (Van Vugt et al. 2004). Results from experimental cooperative groups, for example, show that group members cooperate less when their leaders are selected by experimenters as opposed to when their leaders have volunteered to lead (Rivas and Sutter 2011).

Unfortunately, however, in the vast majority of modern businesses, leaders are imposed on rather than chosen by their followers. The key dynamic of leader-follower reciprocity—of followers freely conferring prestige on leaders in exchange for the services that leaders offer—is thus largely absent in most organizations, which probably results in followers losing motivation to cooperate voluntarily with leaders. Some successful organizations are, however, exceptions to this rule. The best example is W. L. Gore and Associates, which selects its CEO by opening the post up to anyone and allowing employees to nominate candidates (Van Vugt and Ahuja 2010). The philosophy behind this process—"if you attract followers, then you're a leader"—is highly consistent with the notion that people prefer to follow leaders whom they have chosen.

3.1.2. The Preference for Physically Formidable Males as Leaders

The hunter-gatherer activities that most require leadership, especially hunting and warfare, generally require athletic ability, physical strength, aggressive formidability, and skill with weapons. Because of processes in sexual selection (Darwin 1871; Trivers 1972), men are on average betteradapted for such activities. As a result, leaders in small-scale societies tend to be physically formidable males (Van Vugt and Ahuja 2010).

This ancestral need for physically formidable leaders is probably the major reason why a variety of studies have suggested that people tend to prefer male leaders who display cues of health, strength, and height (Judge and Cable 2004; Van Vugt and Ahuja 2010). For females, in contrast, height is not a predictor of leadership emergence (Blaker et al. 2013). Further, a study of West Point graduates revealed that male cadets with more masculine facial appearance—a cue to high testosterone levels and physical formidability—went on to achieve higher-status positions later in their military careers (Mueller and Mazur 1996). Physically attractive leaders are also preferred (Anderson et al. 2001; Van Vugt and Ahuja 2010); the physical traits that people perceive as attractive in others are generally those that would have indicated health and genetic quality in ancestral environments (Grammer et al. 2003).

However, although maleness, height, formidability, and attractiveness probably were important aspects of leader performance in the ancestral past, and although these traits are preferred in modern leaders, not all

of them are necessarily associated with better leadership in the present. Could there be a mismatch between any of these traits and modern organizational environments? As noted, these traits were particularly useful in the context of male-dominated coalitional activities such as hunting and warfare—activities that were extraordinarily important matters of life and death in the ancestral past. Hunter-gatherers can acquire high quality protein and other essential nutrients only if their hunters are successful (Tooby and DeVore 1987), and average total mortality rates due to warfare are probably at least twenty times higher in small-scale societies than they were in twentieth-century Western society (Keeley 1996; Bowles 2009). Our modern bias in favor of physically impressive male leaders may be a legacy of our ancestors' need for expertise and coordinated group action in these domains, but this need is reduced in modern business contexts. As a consequence of this bias, followers in modern environments may often overlook qualified female leaders, as well as qualified (but physically unimpressive) male leaders, for reasons that have become largely obsolete (Van Vugt et al. 2008). This mismatch might also be one explanation for why there are persistent negative stereotypes about women leaders.

3.1.3. The Preference for Leaders Who Are Intelligent and Good Communicators

As with traits indicating physical formidability, intelligence and communication skills are also universally valued traits in leaders (Den Hartog et al. 1999; Judge, Colbert, and Ilies 2004), and these preferences make sense in light of the benefits that leaders would have provided followers in the ancestral past (Tooby, Cosmides, and Price 2006; Van Vugt, Hogan and Kaiser 2008). Good communication and oratory skills are essential for social coordination (e.g., communicating plans for a division of labor or for sequences of events in a collective action), and intelligence is related to, for example, good decision making, identifying follower interests and how to achieve them, and effectively communicating plans for group action.

In contrast with traits indicating physical formidability, however, there is probably less of a mismatch between intelligence and communication skills and the job requirements of modern leadership roles. For instance, leadership competence in modern organizations generally does not depend on the ability to wield a spear or physically intimidate your rivals, but it continues to be enhanced by the ability to form a brilliant strategy and communicate it effectively to followers.

Sexual selection and parental investment theory (Trivers 1972) predicts differences in status striving, across all species, based on levels of obligatory parental investment. Because men do not bear the burdens of gestation and lactation, they can reproduce much faster than women can, and they benefit reproductively more than women do from having multiple mates. Thus, to a greater extent than women, men are selected to strive to attract multiple mates, and an important way in which men can acquire mates is by acquiring social status. Status leads to reproductive success for men in small-scale societies, both because it is attractive to women (Ellis 1992), and also because parents in these societies are particularly likely to betroth their daughters to men whom they would like to have as allies, that is, to high-status men (Hart and Pilling 1960; Kelly 1995). As a result, high-status men in these societies have increased mating opportunities, more wives, wives who are more fertile, and more surviving offspring (Betzig 1986; Chagnon 1979 and 1988; Levi-Strauss 1967; review in Von Rueden, Gurven, and Kaplan 2008).

Because men had more to gain reproductively than women did from having high status in ancestral environments (as noted above), they tend to compete more aggressively for status and to desire leadership positions more (Geary 2002; Browne 2006; Croson and Gneezy 2009). It is likely that men emerge more often as leaders in modern organizations not just because followers are biased against women, but also because men (on average) compete for leadership positions more aggressively than do women. However, the fact that men are relatively obsessed with increasing their own status does not necessarily make them better leaders, and could sometimes make them worse ones, if it caused them to focus too much on maintaining their own status at any cost, regardless of whether they are actually leading effectively.

There is one additional aspect of male status-striving and its connection to attracting mates that bears mentioning. Cross-culturally, social status indicates access to social and economic resources, which is much more important as an aspect of male mate-value than as an aspect of female mate-value. In other words, men use status, much more than women do, in order to attract new mates (Ellis 1992; Zeitzen 2008). In contrast, the most important aspects of female attractiveness cross-culturally are fertility indicators such as cues to youth, health, and hormonal status. These sex differences in mate-value make sense from an evolutionary perspective, because they relate to the most important kinds of mating and parental investment that each sex can provide the other: males ben-

efit more from a mate's fertility, and females benefit more from a mate's access to resources (Buss 1992).

These sex differences also have important implications for leadership. They suggest that male leaders will be more likely than female leaders to use their positions in order to attract new mates (particularly, relatively young and attractive mates), and that women will be more likely than men to be attracted to and desire sexual relationships with opposite-sex leaders. These predictions seem consistent with patterns that are now routinely reported in media accounts of political sex scandals, and they probably apply equally well to the sexual behavior of business leaders, although business leaders' behavior is less exposed to public scrutiny than that of politicians. A good business case study is provided by the former CEO of GE, Jack Welch (Stephen Colarelli, personal communication). Welch co-authored Winning (Welch and Welch 2005)—an account of the enormous success and prestige he achieved as a leader—with a woman twenty-four years his junior named Suzy Welch (née Wetlaufer). They began their affair a few years before the book's publication, while Welch was still married to his second wife, who was merely seventeen years his junior (Jones 2002). Thus the title Winning could be seen as something of a double entendre: a high-prestige male leading an organization to victory, while simultaneously "winning" a new, younger wife.

3.1.5. Different Leaders for Different Roles

Because leadership often depends on expertise, and because different people often have expertise in different activities, the best provider of leadership services in one domain is not necessarily the best leader in another domain: for instance, the leader in a hunting expedition might be different than the leader in a political negotiation (Service 1966). That is why leadership is often shared in successful organizations (Wassenaar and Pearce 2011). A particularly vivid anthropological illustration of this principle is the traditional authority system of the Navajo, which included war chiefs who organized war parties, peace chiefs who led nonviolent political interactions, hunt leaders, diviners who diagnosed illnesses, and singers who led ceremonial chants (Shepardson 1963).

Just as the Navajo (and other North American Plains Indians groups) distinguished among several kinds of leaders, members of modern societies prefer different kinds of leaders for different kinds of roles. For example, experimental studies have found that leaders with more masculine male facial appearance (like John McCain) are preferred to lead during wartime, while more feminine-faced leaders (like Barack Obama)

have the edge during peacetime (Little et al. 2006; Spisak et al. 2012); and male leaders are preferred to lead under conditions of intergroup conflict, whereas female leaders are preferred for the resolution of within-group disputes (Van Vugt and Spisak 2008).

Followers' preference for leaders who have shown expertise in a particular activity can sometimes lead them astray in modern environments—another example of a mismatch. In a relatively simple huntergatherer collective action, there is probably little difference between being a skilled participant and being a skilled leader; the task of hunting giraffe, for example, is probably not so different from the task of leading a giraffe-hunting expedition. In the more complex organizations of modern societies, however, the distance between participation and leadership is often more vast. In professional sports such as football (soccer), for example, talented former players are often favored for managerial roles, despite the lack of evidence that better players make better managers (Van Vugt and Ahuja 2010). Managing a football team probably involves skills that are quite different than those required to excel in a particular position on a football team, and the apparently unjustified preference for players as managers may represent a mismatch between our evolved leadership preferences and the demands of leadership roles in complex modern organizations. We should be skeptical of our impulse to assume that someone who has demonstrated superior ability in a particular organizational role is necessarily well-qualified to lead in a different role. Good jockeys don't make good race horses!

3.1.6. Concerns about In-Group Advantage

Due to the coalitional, political nature of vital leadership tasks in the ancestral past, followers are biased in favor of leaders who belong to their in-group and best represent their in-group interests (Hogg 2001). This orientation emerges most strongly when the in-group is threatened by some external enemy (Van Vugt, Hogan, and Kaiser 2008); at these times followers benefit most from effective leadership and offer the most support and respect for their leader (the "rally effect"). Experimental results suggest that leaders are more likely to start intergroup conflicts when they are more concerned about how their followers assess their leadership ability (Van Vugt and Ahuja 2010). So the rally effect is probably a two-way street: followers gain security from giving their leaders increased support under conditions of intergroup threat, whereas leaders can boost their own status by provoking such conditions or by at least encouraging the impression that such conditions exist (Van Vugt and

182 Michael E. Price and Mark Van Vugt

Ahuja 2010). There is thus the potential for abuse of the rally effect; unscrupulous leaders may exaggerate the extent of an external threat and lead their group into an unnecessary conflict simply because they want to consolidate their power.

On the other hand, there are also relatively innocuous and group-beneficial ways in which the rally effect could be used in organizations. By emphasizing the competitive aspects of an organization's aspirations—for example, by identifying outperformance of a rival group as a key organizational goal—a leader can elicit enhanced cooperation from followers, not just in terms of improved compliance, but in terms of greater overall productivity. Experimental evidence suggests that group members cooperate more and are more productive overall when they perceive that their group is competing with an external group (Van Vugt, De Cremer, and Janssen 2007; McDonald, Navarrete, and Van Vugt 2012). It is important to note, however, that this effect has been observed only among male group members, which suggests that it is an adaptation to conditions of male coalitional violence.

3.1.7. The Preference for "Fair" Leaders

As just noted, conditions of coalitional competition can affect followers' perceptions of leaders. However, such competition does not just occur between two external groups; it can also occur within one group, in the form of within-group factionalization (Hart and Van Vugt 2006). Different factions of a group tend to have different political interests and thus vary in terms of the specific leadership services they require. The result may be a failure of reciprocity, if a leader cannot engage in reciprocity equally effectively with everyone in a group simultaneously because the group is split up into different interest groups. Such factionalization often occurs along kinship lines in small-scale societies (Chagnon 1997), but it can be caused by virtually any kind of coalitional conflict of interest (Hogg 2001), and conflicts between different interest groups (department vs. department, management vs. labor, etc.) can occur in any kinds of organization.

A particularly interesting kind of factionalization occurs when interest groups espouse different fairness norms. An important aspect of leadership in cooperative groups, in both ancestral and modern environments, is overseeing the distribution of resources in ways that seem fair to followers (Den Hartog et al. 1999). Leaders of Northwest Coast communities, for example, were responsible for ensuring that group resources were redistributed in a manner that their followers would perceive as

fair (Fried 1967; Johnson and Earle 1987). Organizational researchers in modern societies have long recognized that employees are deeply concerned about the fairness of such distributive processes (Adams 1963; Ambrose and Arnaud 2005), and studies about leadership preferences suggest that there is a widespread, cross-cultural preference for fair leaders (De Cremer and Van Knippenberg 2004). However, *fair* is a highly ambiguous term. Many different definitions exist, and an evolutionary perspective suggests that different types of people prefer different kinds of fairness. When different factions have different standards of fairness, a leader will have difficulty achieving successful reciprocity with all factions simultaneously.

In terms of distributive justice alone, for example (ignoring other types of organizational justice, such as procedural, interactional, and retributive justice), fairness in groups is often variously defined in terms of equality (all members get the same amount), equity (higher contributors receive more), or need (the needier receive more; see Ambrose and Arnaud 2005). Each of these distribution systems benefits some members more than others. A comparison of equity versus equality, for example, suggests that equity advantages members who are most capable of contributing highly, but disadvantages members who can contribute the least; equality, on the other hand, is good for low contributors who would otherwise be out-competed by high contributors, but is advantage-reducing for higher contributors.

From this perspective, then, a follower's assessment of a leader's fairness should depend on the type of fairness practiced by the leader as well as the characteristics of the follower. Evidence suggests that this perspective is correct: Increased preferences for meritocratic versus equality-based distribution systems, for example, are expressed by individuals in better positions to benefit from meritocracy, such as the highly educated and wealthy (Kunovich and Slomczynski 2007; Ritzman and Tomaskovic-Devey 1992). Further, people who are wealthier or members of ethnic majorities tend to approve more of social inequality, that is, to be relatively high in "social dominance orientation" (Pratto, Sidanius, and Levin 2006). This "condition-dependence" of fairness preferences may often be more comprehensible in terms of ancestral environments than modern ones; for example, men with more muscular upper bodies tend to be more supportive of social inequality (Price et al. 2011) and policies of political aggression (Price et al. 2012; Sell, Tooby, and Cosmides 2009). These preferences were probably adaptive in ancestral environments in which muscularity was an important component of success in resource competition and war, but they seem less useful in modern industrialized societies, in which access to resources and success in war has much more to do with educational and technological attainment than with physical strength.

3.1.8. The Collective Action Problem of Providing Prestige

The most significant theoretical obstacle to regarding voluntary leaderfollower interaction as a service-for-prestige reciprocal transaction is the problem of collective action (Olson 1965). The benefits provided by the leader constitute a kind of public good, as does the leader's motivation to continue to provide them. If increased prestige is what motivates the leader to provide this public good, then the allocation of this prestige is a collective-action problem for the followers (Price 2003). For example, consider a leader who benefits his followers by leading a raid against an enemy tribe or, in a more modern context, leading a hostile takeover of a rival company. The prestige allocated to him in exchange is costly for his followers to provide, because it obligates them to cater to his well-being in a manner that ultimately affords him a relatively large share of the group's social, material, and reproductive resources. In order for the followers to maintain the leader's motivation to provide his services, they must collectively pay these costs of respect. Followers could free ride, and thus gain a fitness advantage over the other followers, if they continued to accept the leader's services while refusing to pay respect (e.g., by not deferring to the leader's interests or by failing to share resources with the leader). Because each individual has the incentive to free ride, the group might not provide enough resources to the leader. Free riders could lose their advantage if they were punished by other followers (Ostrom 1990; Price, Cosmides and Tooby 2002; Price 2005; Yamagishi 1986), but if these punishers were not compensated for their action, they would fall victim to the "second-order free-rider problem" (Boyd and Richerson 1992): their punishment would be altruistic because it would generate benefits for the group, but as only they would pay the costs of punishing, they would be disadvantaged relative to second-order free riders (i.e., relative to followers who paid respect but failed to punish disrespectful followers).

Collective-action dilemmas of this kind are classic problems in social and psychological science (Ostrom 1990; Yamagishi 1986) as well as in biology (Boyd and Richerson 1988 and 1992; Takezawa and Price 2010), and there is no consensus about the specific nature of the evolutionary processes that may solve them. However, there are a variety of plausible ways in which evolution could overcome first- and second-order free-

rider problems in the context of leader-follower reciprocity (Price 2003). For example, leaders might take it upon themselves to ostracize or punish disrespectful followers (O'Gorman, Henrich, and Van Vugt 2009; Price 2003) or might selectively favor (and thus compensate) followers who paid the costs of ostracizing or punishing the disrespectful member.

We want to avoid becoming overly distracted by this issue of precisely how evolution may have solved collective-action problems in the context of leader-follower reciprocity. However, service-for-prestige theory does make a general, novel prediction on this issue: because a free-rider problem emerges when some followers accept the benefits of leadership without sharing in the costs of paying respect to the leader, it predicts that those who fail to provide respect to a widely respected leader will suffer social consequences. Punishments in small-scale societies typically take the form of informal social sanctions, such as exclusion from reciprocal exchange interactions (Fried 1967), and in both ancestral-type and modern environments, such sanctions may be imposed on disrespectful followers. Among the hunter-horticultural Shuar, for example, the more a follower is perceived as being respectful of a generally well-respected community leader, the more that follower is respected within the community (Price 2003); less respectful followers are themselves respected less. In modern organizations, it is likely that members who disrespect popular leaders are sanctioned by other members through processes of social exclusion, facilitated by gossip (Barkow 1992; Williams 2007), or they may also be punished directly (e.g., fired) by leaders whom they have treated disrespectfully.

It is also worth noting that whereas co-members will regard a member who disrespects a generally popular leader as a kind of free rider, they will regard a member who disrespects a generally *un*popular leader as a kind of hero. A leader who fails to provide the group with valuable leadership services in exchange for prestige will be unpopular, and with such a leader, followers face the problem not of how to allocate prestige collectively, but of how to collectively strip that leader of prestige. A member who disrespects an unpopular leader will usually be making a personal sacrifice by risking retaliation from the leader, and so will be seen by comembers as an altruistic contributor to the public good. If you brave the wrath of an unpopular king, for example, by throwing his tea into the Boston harbor, you become a hero in the eyes of your fellow colonists. Thus, another novel prediction of service-for-prestige is that followers need to solve collective-action problems not just to supply prestige to a good leader but also to deny prestige to a bad one.

186

3.2. Coercive Leadership May Emerge in Large Groups with Few Exit Options

The power of leaders is positively correlated with the extent to which their followers depend on their leadership (Emerson 1962), and the ethnographic record suggests that followers depend on their leaders more in some kinds of small-scale societies than in others. In order to understand human adaptations for leader and follower behavior, it is important to consider in some detail the range of environments in which these adaptations probably evolved and how different environmental conditions would have influenced the likelihood that leadership would be based on dominance and coercion as opposed to prestige and reciprocity.

In general, leadership in small-scale societies is least important in hunter-gatherer societies where residential groups are small (about 20-60 people), population density is low, and nomadic foraging is the way of life (Fried 1967; Johnson and Earle 1987; Marlowe 2011). Nomadic foragers depend on wild resources that usually become depleted locally before residential groups exceed this size. Further, most highly coordinated social activities (e.g., collective actions for hunting or raiding) in these societies involve not the entire residential group but only a few members, usually of a particular sex and age class (Kelly 1995; Price and Johnson 2011). Because social groups in these societies remain relatively small, coordination and collective action problems are fairly simple—group members can relatively easily, for example, organize divisions of labor, plan group tasks, monitor co-member contributions, and sanction low contributors—and therefore strong leadership is less necessary (Tooby, Cosmides, and Price 2006; Hooper, Kaplan, and Boone 2010). Moreover, because of low population density and the ease of moving camp, it is relatively easy for nomadic foragers to leave one group to form a smaller group or join another group. Residential group composition is therefore often in flux, and a "fission-fusion" style of social organization generally prevails, with smaller groups coming together and larger groups breaking apart, depending on local resource availability and the quality of withingroup social relationships (Kelly 1995; Turnbull 1968). Thus, if a leader in this kind of society tries to become too dominant, his power will be limited by the relative ease with which his followers can simply leave his group (cf. Van Vugt et al. 2004). In such societies, then, followers' dependence on leaders is relatively low: they rely less on leaders for the coordination of collective action, and they are relatively free to escape leaders who would seek to exploit them. Not coincidently, members of small nomadic foraging groups express relatively strong distaste for domineering leaders, are particularly wary of letting talented individuals become too full of themselves, and are unlikely to recognize anyone in their group as a formal leader (Lee 1993; Service 1966; Turnbull 1968).

Not all small-scale societies, however, exist in environments that are so conducive to low-power leadership. Leaders become more powerful in hunter-gatherer and tribal societies that have larger residential group sizes, higher population density, and a more sedentary rather than nomadic way of life (Johnson and Earle 1987). Under these conditions, people must cooperate in larger groups, and, as discussed above, coordination and collective-action problems become more difficult in larger groups. Members of larger groups therefore become more reliant on leaders who can solve these problems (Tooby, Cosmides, and Price 2006; Hooper, Kaplan, and Boone 2010). Moreover, because these people have more sedentary lifestyles and live in environments that are more densely populated and hence "socially circumscribed" (i.e., communities are more closely surrounded by neighboring communities [Chagnon 1997]), it becomes more difficult for them to pack up and move to an unoccupied site if their leader becomes too dominant.

Because domesticated food sources allow for increases in residential group sizes, sedentism, and population density, leaders become more important, and leadership becomes more formalized after societies begin practicing agriculture. For example, in hunter-horticultural societies such as the Yanomamö in Venezuela and the Mae Enga in New Guinea, residential groups typically include 100–400 people, population density is high compared to nomadic foraging societies, and leaders are especially valued for their leadership abilities in politics and war. In contrast to the informality of leadership in nomadic foraging societies, these leaders are formally recognized by everyone in the community as headmen (or "big men"; see Chagnon 1997; Johnson and Earle 1987; Meggitt 1977) and are endowed with an enduring political authority. However, the conditions that are conducive to powerful leadership are ultimately related more to resource concentration and the sedentism that it allows than to agriculture per se (Fried 1967). Although Indians in the American Pacific Northwest were non-agricultural, for example, they could maintain villages of 500–800 people and population densities of one or two people per square mile by residing near salmon-rich rivers. Both of these figures are unusually high for hunter-gatherers (Johnson and Earle 1987). Leadership in these societies was much stronger than in nomadic foraging societies, with clearly identified chiefs who advertised their wealth and status in

188

potlatch ceremonies involving the giving away or destruction of material goods. Strong leaders were needed in these societies because it is relatively challenging to organize cooperative labor, intervillage ceremonies, and other kinds of collective action in groups of this size. The military operations of the Nootka, for example, were relatively sophisticated compared to those in smaller-scale band and tribal societies and involved a commander-in-chief and other specialized roles. Processes of resource redistribution also become more complex and formalized in larger groups (Fried 1967; Johnson and Earle 1987).

The dark side of the increased power acquired by leaders in larger and more socially circumscribed communities is that their status can become less based on their ability to help and more on their ability to threaten or hurt their followers (Padilla, Hogan, and Kaiser 2007). In a mutually beneficial, reciprocal relationship between equally powerful partners, a main incentive to pay the costs of treating one's partner well is to avoid motivating him to exit the relationship. As followers become more dependent on leaders for the organization of collective action and less capable of leaving their residential group, they become less powerful relative to their leaders. Leaders thus lose their incentive to behave altruistically toward their followers and gain more ability to harm them by excluding them from the benefits of group membership. Thus, with increases in group size and population density, leader-follower relationships become more likely to be based on dominance than on reciprocity and prestige, and more likely to be coercive instead of voluntary. For example, the practice of slavery is rare in the ethnographic record of band and tribal societies, but it was widespread among the relatively large and socially circumscribed Pacific Northwest Coast communities mentioned above. The enslavement of war captives was practiced all along the Northwest Coast, and slaves probably constituted 7–15% of the population in a typical community (Kelly 1995).

3.2.1. Low Tolerance for Unnecessary Leaders

According to the service-for-prestige theory, when leadership is based on reciprocity, followers receive the benefits of the leader's expertise and group organizational skills; when leadership is based on coercion, however, these benefits need not be present. The theory predicts, therefore, that the human mind has evolved to desire and actively seek out leadership only when the benefits that leadership offers—the leader's expertise and group organizational skills—are actually required by group mem-

bers. In group situations where strong leadership is not really necessary, members tend be unenthusiastic and mistrustful of those who try to lead (Haslam and Platow 2001). People understand intuitively that leaders benefit personally from the prestige that being a leader entails, so people who attempt to claim this prestige without offering any real services in return are rightfully regarded with suspicion.

As a result of this low tolerance for superfluous, self-serving leadership, we would expect people to be less enthusiastic about leaders when they are members of smaller groups, because the lack of challenging social coordination problems in small groups tends to render leaders unnecessary. The presence of leaders will thus more likely be resented and undermine group performance in smaller groups (Van Vugt, Hogan, and Kaiser 2008). Similarly, aspiring leaders who have no beneficial expertise but act as though they do will be resented by potential followers as self-serving and arrogant. Kerr and Jermier (1978), in their "substitutes for leadership" theory, have identified a number of additional factors that may render leadership unnecessary in order for work to get done within an organization. For example, leaders are less required by employees who have a high degree of professional expertise; for tasks that are unambiguous, routine, or intrinsically satisfying; and in situations where the allocation of organizational rewards is not under the control of the leader.

But whereas aspiring leaders will be relatively disliked in groups where they are superfluous, leaders will be sought and embraced in groups where they can really offer benefits to followers. The lesson here for managers is that, although leadership often is a vital aspect of group success, it can undermine success in groups where it is not really needed. Managers should therefore avoid appointing leaders in groups unless it is clear that the other members of the group perceive that the services of that particular leader would contribute significantly to group performance.

3.2.2. The Preference for Leaders with Personality Traits Associated with Altruistic. Pro-group Orientation Rather Than Dominance and Selfishness

The service-for-prestige theory suggests that followers benefited more in ancestral environments from reciprocal leadership as opposed to coercive leadership. Therefore, the minds of followers should be sensitive to cues indicating that a leader is likely to behave in a reciprocal, pro-group manner as opposed to being dominant and narrowly self-serving. Crosscultural data suggests that followers universally do prefer leaders who are altruistic and competent enough to act in ways that benefit followers

190

(Van Vugt, Hogan, and Kaiser 2008). The GLOBE list of universally valued leadership traits (Den Hartog et al. 1999) suggests that across sixtyone cultures, people prefer leaders who show signs of being *willing* and *able* to provide altruistic benefits to followers. This willingness takes the form of an altruistic disposition (e.g., trustworthiness, fairness), and this ability takes the form of possessing group-beneficial skills (e.g., intelligence, competence). By the same token, followers express universal aversion to traits associated with coercive, self-serving leadership (e.g., dominance, selfishness).

Along similar lines, in a review of the literature on leadership and personality, Hogan and Kaiser (2005) mention modesty, humility, integrity, decisiveness, competence, and vision as the most important traits of successful leaders. Integrity is described as "keeping one's word, fulfilling one's promises, not playing favorites, and not taking advantage of one's situation" (173). In other words, integrity is essentially trustworthiness, which is a key characteristic that one should seek in a reciprocal partner. Modesty and humility are also cues to a prosocial personality that is oriented toward consideration of others and not just of one's self. Decisiveness, competence, and vision are all involved with the benefits that good leaders provide to followers. Taken together, then, all of these traits have to do with a leader's willingness (modesty, humility, integrity) and ability (decisiveness, competence, vision) to act as a reliable and valuable reciprocal partner.

Leaders are reviled for being selfish (or in the language of reciprocity, for "cheating") if they control group actions or resources in a manner that benefits themselves while injuring followers (Tooby, Cosmides, and Price 2006). The salary of a typical modern business leader is astronomically high compared to that of the average worker, and economic inequality in these organizations is far more severe than could ever occur in a huntergatherer society (Smith et al. 2010). Workers in these organizations may perceive their leaders to be hoarding the group's resources for their own selfish interests—a behavior that followers are probably adapted to distrust and resent (Van Vugt, Hogan, and Kaiser 2008).

To some extent, service-for-prestige theory is similar to servant leadership theory (Gillet, Cartwright, and Van Vugt 2011; Greenleaf 2002) in terms of the predictions it makes about which leader characteristics followers will prefer. Both theories emphasize that followers prefer leaders whose personal traits orient them toward promoting the welfare and interests of their followers, often at a large personal cost to themselves. Service-for prestige differs from servant leadership theory, however (as we

discuss in more detail below), in that it sees this concern with follower welfare as one side of a mutually beneficial leader-follower transaction, in which the costs borne by each side are reciprocated by the other.

3.2.3. Leaders Are More Likely to Exploit Followers Who Lack Exit Options

According to service-for-prestige, leaders may benefit (at the expense of followers) by adopting a more coercive leadership style when they can get away with it, because leading via coercion saves them the costs of having to deliver benefits to followers. In small-scale societies, leadership tends to become less reciprocal and more coercive in environments in which, because of high population density and resource concentration, followers are less able to exit groups in which coercive leaders have gained control. Similarly, it has long been suggested that in modern organizations and states, when members have fewer exit options, leadership tends to be less responsive and more autocratic (Hirschman 1970). If, on the other hand, leaders attempt to adopt a coercive leadership style when their followers *do* possess good exit options, then their leadership days will likely be numbered. In experimental research by Van Vugt et al. (2004), members were more likely to flee from groups led by autocratic leaders than from groups led by democratic leaders.

In business contexts, the temptations of leaders to resort to a leader-ship style based on dominance rather than reciprocity should increase when employees are less able or willing to leave their jobs because, for instance, the labor market is bad, or because they will not consider relocating geographically in order to work somewhere else. This prediction of a positive relationship between the quality of leadership and the availability of follower exit options has apparently not been tested explicitly in a business setting. There is evidence, however, that employees with better exit options tend to receive a greater share of organizational rewards, a phenomenon known as "rational selective exploitation" [Rusbult et al. 1988]). Nevertheless, the logic behind the prediction is compelling enough to send a clear message to members of modern organizations: when exit options are few, workers and management ought to be more vigilant to ensure that leadership does not become based on coercion as opposed to reciprocity.

The lack of exit options also makes followers more vulnerable to exploitation by leaders with truly antisocial personalities. When followers have no bargaining power to demand a leader-follower relationship based on reciprocity, it creates a niche for leaders who feel no real responsibility to provide benefits to followers and are motivated to lead by the benefits

they can obtain through selfish exploitation of the position. Such toxic leadership may be exhibited by people who score highly on one or more of the "dark triad" traits of Machiavellianism, narcissism, and psychopathy (Paulhus and Williams 2002; Van Vugt and Ahuja 2010).

4. DISCUSSION AND CONCLUSION

The service-for-prestige theory, as presented in sections 3.1 and 3.2, suggests that from an evolutionary psychological perspective, followers and leaders would have faced different kinds of adaptive problems in ancestral environments. In the range of ecological and social environments experienced by our hunter-gatherer ancestors, follower fitness would have benefited more when leader-follower interactions were based on reciprocity as opposed to coercion. Therefore, followers' leadership preferences should be seen as solutions to the adaptive problems of how to encourage leadership services from those who display essential expertise and group organizational skills, and how to avoid leaders who lack these skills or whose interactions with followers more resemble exploitation than exchange. Leaders, on the other hand, would have faced the primary adaptive problem of how to acquire social status in the least costly manner. In small, nomadic foraging groups, the relatively equally powerful negotiating positions of followers and leaders meant that prestige, freely conferred by followers in exchange for leadership services, was the form of status that leaders could most efficiently acquire. In environments in which followers were more dependent on leaders, however, dominancebased status—status based on a leader's ability to harm followers—would often have been cheaper for leaders than prestige, because it would have saved them the costs of producing benefits for followers.

The service-for-prestige theory does not capture all aspects of leader-follower interaction that are relevant from an evolutionary perspective. For one thing, as noted, service-for-prestige focuses on only one level (the individual level) in a selective process that may also involve other levels (Wilson, Van Vugt, and O'Gorman 2008). Further, it may not satisfactorily account for the process by which leadership emerges evolutionarily in the first place, which could have more to do with leadership's role in solving coordination problems between organisms (Van Vugt and Kurzban 2007; Van Vugt, Hogan, and Kaiser 2008) than with its role in being one side of a service-for-prestige transaction.

There are also existing, well-known, non-evolutionary theories of leadership that have important attributes in common with service-for-

prestige. For example, leader-member exchange theory (LMX; Graen and Uhl-Bien 1995) suggests that the quality of leadership is heavily influenced by the quality of the exchange relationship between the leader and individual subordinates, and servant leadership theory (Gillet, Cartwright, and Van Vugt 2011; Greenleaf 2002) emphasizes that good leaders are altruistic, compassionate people whose influence rests on their moral authority and ability to provide benefits to followers rather than their dominance. While service-for-prestige shares some predictions with these theories, it also makes some novel predictions, because it sees both leadership and followership as individually adaptive strategies, and because it sees the leader's altruism and the follower's delivery of prestige as two kinds of costly contributions in an exchange transaction. Thus, unlike servant leadership theory, service-for-prestige sees leadership as "altruism" that ultimately profits leaders (as well as followers), and unlike LMX, service-for-prestige focuses not on general aspects of relationship quality but on how evolution designed both leaders and followers to maximize their own fitness benefits and minimize their own fitness costs in their interactions with one another. Unlike either servant leadership theory or LMX, service-for-prestige focuses not just on the conditions under which leaders will be most likely to provide benefits for followers, but also on the conditions under which leaders will be most likely to exploit and coerce followers. Finally, service-for-prestige focuses not just on the material rewards flowing from leaders to followers but also on the symbolic benefits of leadership—for instance, cohesion and identity benefits. In that respect, service-for-prestige has as much in common with transformational leadership models as with transactional models of leadership (Bass 1998). Service-for-prestige is mute about the nature of the service offered to followers, as long as the service ultimately contributed to follower fitness in the ancestral past. For instance, charisma may be an indicator of the prestige awarded to a leader who makes costly contributions to help the group.

In conclusion, the service-for-prestige theory does not claim that either kind of leader-follower relationship—reciprocity or coercion—is more "natural" or more consistent with evolutionary design. People are adapted for both reciprocal and coercive leader-follower interactions. However, it is clear that of the two kinds of relationships, reciprocity involves the greater degree of mutual benefit between leaders and followers. Unlike coercion, reciprocity allows followers to act on their leader preferences and award prestige to group members who, via their ability to benefit the group, are worthy of leadership roles. Reciprocity is also the relationship that is more closely associated with what most would con-

sider to be "good" leadership, that is, leadership that genuinely helps followers achieve their shared goals, as opposed to leadership that primarily serves the leader's narrow self-interest. Coercion is more likely to result in corrupt and exploitative leadership by leaders who strive to maintain their status via their ability to harm instead of to help.

Notes

- 1. Although Darwin usually focused on individual-level adaptation, he does speculate in *The Descent of Man, and Selection in Relation to Sex* (1871) about how human morality may have evolved as a group-level adaptation. While there has been considerable controversy about the importance of biological adaptation at levels above the individual, such as the group or species (Williams 1966), most adaptationist analyses continue to maintain an individual-level focus. However, our focus on individual fitness should be not interpreted as a rejection of multilevel selection theory (Wilson and Wilson 2007). We acknowledge that selection can operate simultaneously on multiple levels, including intragenomic, individual, and group levels; indeed, one of us has suggested that multilevel selection may explain some important aspects of leadership (Wilson, Van Vugt, and O'Gorman 2008).
- 2. A distinct theory, Hamilton's (1964) kin selection, is the leading explanation for cooperation among close genetic kin. According to this theory, a gene situated in one individual can cause its own replication, and thus gain an evolutionary advantage, if it can somehow benefit exact copies of itself that exist in other individuals. The gene accomplishes this goal by causing the individual in whom it is situated to behave altruistically toward other individuals who are likely to carry the same gene, that is, toward close genetic kin. This theory thus predicts that altruism will be relatively likely to evolve between genetic kin, especially very close kin (e.g., siblings). Kin-selection theory has been tested and supported in a vast variety of species and was popularized by Dawkins (1976) in his best-selling book *The Selfish Gene*.

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- 196 Michael E. Price and Mark Van Vugt

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