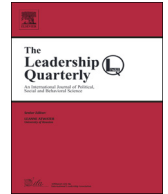




Contents lists available at ScienceDirect

The Leadership Quarterly

journal homepage: www.elsevier.com/locate/leaqua

Leadership in small-scale societies: Some implications for theory, research, and practice

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ARTICLE INFO

Available online xxxx

Editor: Chet Schriesheim

Keywords:

Leadership
Followership
Small-scale society
Evolution
Anthropology

ABSTRACT

Leadership studies concentrate on large-scale societies and organizations with formal hierarchies, large power differences, and diverse membership. Much less is known about leadership in small-scale, homogeneous, and relatively egalitarian societies in which humans have spent most of their existence. We summarize the anthropological literature on leadership from traditional, small-scale societies in terms of (1) the functions and roles of leaders; (2) the traits and behaviors conducive to leader emergence and effectiveness; and (3) the motivations and incentives to assume leadership positions. We address how studies of leadership in small-scale societies inform theory development. By viewing leadership and followership in light of our evolutionary history in small-scale societies, we shed new light on outstanding questions in leadership research and on challenges for leadership practice.

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Introduction

Leadership is a primary mechanism by which groups resolve coordination and motivation problems. We define *leaders* as individuals who have differential influence within a group over the establishment of goals, logistics of coordination, monitoring of effort, and reward or punishment strategies (Bass, 1990; Day & Antonakis, 2012). Leadership can be distributed across multiple group members or concentrated in a single individual, and can range from passive influence to active motivation of followers (Yukl, 2014). However, leadership is not a panacea for organizational problems. Leadership can crowd out cooperation if it is considered illegitimate or if it provokes fear of abuse of power, status envy, or greater competition for rank (Anderson & Brown, 2010). The tension between leadership and dominance – the dark side of leadership – is indicative of a deep evolutionary history of living in groups with dominance hierarchies. In nonhuman primates, dominant individuals use force or threat of force to gain privileged access to food, territory, and mates (Cowlishaw & Dunbar, 1991; de Waal, 1982). Dominance hierarchies also shape human societies, but humans frequently level these hierarchies through collaborations enabling them to form – more or less – voluntary leader–follower relations (Boehm, 1999; Van Vugt, 2006).

It is important to stress that the theories that organize much research in leadership studies (e.g. contingency leadership: Fiedler, 1967; transformational leadership: Bass, 1990; leader–member exchange theory: Graen & Uhl-Bien, 1995) were inspired mainly by observations of leadership in the business, military, and political bureaucracies of modern, industrialized, large-scale societies (LSSs). While leadership is ubiquitous across human societies, leadership tends to be less institutionalized, more egalitarian, and more situational in small-scale societies (SSSs) (Hooper, Kaplan, & Boone, 2010; von Rueden, Gurven, Kaplan, & Stieglitz, 2014a). These societies, in which humans spent more than 95% of their history as a species, are in general characterized by small

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communities, pooling of resources within and across extended families, food production in the absence of significant technology (e.g. foraging), and few formal institutions governing group life.

Can *knowledge about SSSs* inform the study of leadership in large-scale societies? Much leadership in LSSs still occurs informally within households, churches, sports teams, or other community organizations. The face-to-face, spontaneous nature of leader–follower interactions in these contexts is fairly similar to those in which leadership often emerges in SSSs. But the contribution of SSSs to leadership research does not only hinge on descriptive similarity, but rather on its theoretical importance. What we observe of leader–follower relationships in SSSs helps us formulate hypotheses of leadership and followership in *any* context. This is because ethnographically recent SSSs are more representative than LSSs of the range of social environments in which the human mind evolved. By studying leadership within and across modern SSSs, we gain insight into how the minds of leaders and followers in any society operate as they do, including in formal, complex, modern organizations.

Whereas LSSs with extensive bureaucracies emerged only ~10,000 years ago with the spread of agriculture, humans have lived in SSSs for ~200,000 years, and our hominid ancestors for several millions of years (Diamond, 1997). With agriculture, populations became larger, denser, and more culturally diverse (Livi-Bacci, 1997), which are properties that tend to increase intra-group conflict and the difficulty of coordination (Johnson, 1982; Olson, 1965; Ostrom, 1990). LSSs that resisted collapse from conflict and coordination failures were those who adopted bureaucracies with multi-tiered, formalized leadership structures to help solve the problems of life in large groups (Johnson, 1982; Richerson & Boyd, 1999; Richerson, Boyd, & Henrich, 2003). Yet the recency of LSSs suggests that much of the evolved decision-making underlying leadership remains tailored to group life in SSSs (Petersen, 2015; Price & Van Vugt, 2014; Spisak, Homan, Grabo, & Van Vugt, 2011; Tooby, Cosmides, & Price, 2006; Van Vugt, Hogan, & Kaiser, 2008a).

Evolutionary approaches to leadership

Our approach to leadership unites an evolutionary perspective – which considers “why” minds evolved as they did – with a proximate perspective – which considers “how” minds operate in present circumstances (Scott-Phillips, Dickins, & West, 2011). Human minds are not blank slates upon which experience is impressed, but are equipped with evolved decision rules – sometimes referred to as cognitive adaptations – that regulate our motivations and beliefs (Pinker, 2002; Tooby & Cosmides, 1992). Evolved decision rules were built by natural selection to solve problems that (1) were recurrent over evolutionary time-scales and (2) had repercussions for our ancestors' reproductive success. The currency in evolution is reproductive success, i.e. representation of genes in subsequent generations. By design, evolved decision rules are often inaccessible to consciousness and highly context sensitive (Kenrick, Li, & Butner, 2003; Tooby & Cosmides, 1992), aligning behavior to changes in reproductive status (Gildersleeve, Haselton, & Fales, 2014), energetic status (Aarøe & Petersen, 2013), social reputation (Sznycer et al., 2012), group structure (Schacht & Borgerhoff Mulder, 2015), or inter-personal and inter-group threats (Gneezy & Fessler, 2011). They shape how we learn (Richerson et al., 2003) and the cultural information we generate and transmit, from art to literature to leadership and religion (Sperber & Hirschfeld, 2004).

An evolutionary perspective is not meant to supplant the theories that currently dominate leadership studies, which describe the mechanisms by which leaders emerge and affect group performance. Rather, an evolutionary perspective can integrate existing theories into a coherent framework, which considers why leadership exists at all and how evolved decision rules contribute to leader emergence and effectiveness in our modern organizations (Van Vugt & Ahuja, 2011). Furthermore, evolutionary theories make novel, testable predictions that can potentially explain previously unexplained phenomena, for example, why leaders are often granted influence well beyond their domain of expertise (see section Leader effectiveness in LSSs).

While evolved decision rules continue to play a role in determining leadership in modern LSSs, an evolutionary perspective suggests they do not necessarily result in optimal decision-making. The “mismatch” hypothesis (Van Vugt, Johnson, Kaiser, & O’Gorman, 2008b) argues that the decisions of followers and leaders are shaped by evolved decision rules designed in the contexts of SSSs, and can be mismatched to the evolutionary novel environments of LSSs. The mismatch hypothesis can explain why, in LSSs, upper body strength shapes people’s abstract political decisions about warfare (Sell, Tooby, & Cosmides, 2009a) and income redistribution (Petersen, Sznycer, Sell, Cosmides, & Tooby, 2013), and why people show preferences for tall, strong and masculine leaders in politics and business (Spisak et al., 2011; Stulp, Buunk, Verhulst, & Pollet, 2013). Such physical cues should be irrelevant in modern societies in which leadership is rarely a physical activity and where leaders derive their legitimacy from formal, often democratic institutions.

We discuss why these and other leader preferences evolved, based on a review of leadership across currently existing SSSs. These small-scale societies vary in their exposure to markets and state-level institutions and are fast disappearing. A few societies still pursue a largely foraging lifestyle in the Amazon, central and eastern Africa, and south-east Asia, and horticulturalists and pastoralists occupy these and other remote regions of the globe. Modern small-scale societies are not “living fossils.” Rather, they enable educated inferences about early humans, and help us develop hypotheses about how leadership developed in the course of human evolution. In this review we describe (1) the functions of leaders in SSSs, (2) the traits and behaviors conducive to leader emergence and effectiveness in SSSs, and (3) the motivations and incentives that drive individuals to lead or follow in SSSs. We then discuss implications for understanding leadership in LSSs, noting similarities and differences between leadership in SSSs and LSSs. This analysis will hopefully stimulate further theory and research development and contribute to understanding leadership practice.

What are the functions of leaders in SSSs?

SSSs, particularly hunter–gatherers, tend to be *egalitarian*. By “egalitarian”, anthropologists generally mean equal rights and privileges among group members, though women and children tend to have lower status, on average, compared to adult men (Fried, 1967). Both ecological and institutional forces help maintain egalitarianism. In the absence of significant material wealth or storable or predictable food packages, widespread resource sharing emerges to buffer risk in production and creates interdependence among families (Cashdan, 1980; Kaplan & Gurven, 2005; Winterhalder, 1986). To express commitment to sharing, individuals criticize those who brag and successful producers deprecate their own achievements (Lee, 1979). Humility is not optional but is normative. There are also checks on individuals acquiring coercive influence over others. Coalitions of subordinates will ostracize or, more rarely, execute individuals who display dominance (Boehm, 1999).

Yet it is a misconception to believe that egalitarianism and status-leveling pre-empt leadership in SSSs. Leadership emerges informally when there is demand for coordination or conflict resolution. Service (1975) describes the self-effacing, “first among equals” role of leaders in the most egalitarian SSSs, who lack coercive authority but have differential influence over their peer’s opinions and the group consensus-seeking process. Of the !Kung Bushmen of the Kalahari, Shostak (1981) writes: “Each group has individuals whose opinions carry more weight than those of others... These people tend to be more prominent in group discussions, to make their opinions known and their suggestions clear, and to articulate the consensus once it is determined. Despite their lack of formal authority, they function very much as group leaders” (pp. 245). Coordination often occurs in the context of food production. As examples, rabbit drives by the Washoe of eastern California were coordinated by hunt leaders (Lowie, 1948), and whaling among Inuit off the Alaskan coast required coordination among a crew overseen by a captain (Spencer, 1959).

In addition, leadership in SSSs also emerges to manage relations with other groups (war or peace). The majority of ethnographic accounts of war involving small-scale societies include description of informal leadership (Hooper et al., 2010). Inter-group conflict can relax egalitarian norms (which also tends to be true in LSSs). Crow and Omaha war captains exercised authority during warfare that was denied them back in camp (Lowie, 1948), Yanomamo headmen from Venezuela were granted authority during raids that they lacked during other times (Chagnon, 1983), the Nambiquara of Brazil endorsed more authoritarian leadership when under threat of attack by neighboring groups (Price, 1981), and Enga leaders’ influence in highland New Guinea was heightened during periods of conflict while during peace leadership was challenged and frequently changed hands (Meggitt, 1967). However, debate continues surrounding the extent of warfare in modern and Pleistocene foragers (Bowles, 2009; Fry, 2012). Throughout the twentieth century, transition to more formal leadership was common in SSSs, whose members experienced greater motivation to coordinate and quell internal conflict in the face of an encroaching, often exploitative outside world (Lee & Daly, 1999).

The scope of influence granted to leaders in SSSs also fluctuates with group size. Cooperation becomes harder to maintain as group size increases (Boyd & Richerson, 1988; Olson, 1965). The cost of monitoring for free-riding increases, coordination failure is more likely, and conflicts between group members tend to become more frequent (Johnson, 1982; Alberti, 2014). As a result, members of larger groups may afford leaders more power to quell conflict. When the Yahgan of Tierra del Fuego congregated to feast on whale, a leader emerged who coordinated the proceedings and appointed a constable to enforce order (Gusinde, 1937). Plains Indian bands elected a tribal chief to oversee production and to police crime when they aggregated during the summer buffalo hunt; at other times of the year, bands lacked formal leaders (Lowie, 1948). In sum, leadership in SSSs emerges and becomes more prominent as the scale and difficulty of coordination, cooperation and conflict resolution increases (Glowacki & von Rueden, 2015).

Who leads in SSSs?

Age

A cursory review of the correlates of leadership in SSSs suggests that leadership correlates with age. Cross-culturally, older adults often fill leadership roles, in part because they have had more time to accrue task-relevant knowledge (Henrich & Gil-White, 2001; Schniter, Gurven, Kaplan, Wilcox, & Hooper, 2015; Silverman & Maxwell, 1978). Older individuals may also have more wisdom, which can be defined as general knowledge regarding ecological or interpersonal dilemmas and an ability to make appropriate judgments in the face of uncertainty (Baltes & Smith, 1990). Older individuals in SSSs will also have more social support from adult offspring and other kin; individuals with the most kinship ties to other group members tend to hold positions of political influence in SSSs (Chagnon, 1979; Hughes, 1988; Walker et al., 2013). However, older individuals are disfavored as leaders during times of institutional change and rapid informational obsolescence (Maxwell & Silverman, 1970; cf. Spisak, Grabo, Arvey, & Van Vugt, 2014). For example, among the Tsimane horticulturalists of Amazonian Bolivia, middle aged men wield more informal political leadership than older men, due partly to the increasing importance of market-related knowledge for interacting with outside political bodies (von Rueden, Gurven, & Kaplan, 2008). Furthermore, older men are not privileged as leaders when tasks require athleticism or easily acquired skill. For example, even adolescents act as leaders of group fishing events among the Tsimane (von Rueden et al., 2014a).

Verbal skill and religious knowledge

The influence of leaders in SSSs often varies with their religious ties and oratory skills. Headmen among Yokuts of Central California organized festivals, and those shirking contributions to the festivals were inflicted with illness by the medicine-man

(Gayton, 1930). In many Amazonian societies, the headman is also the shaman, which adds to their legitimacy as leaders. In Brazil, Nambiquara leaders with weak social support may seek shamanic power to fortify their position (Price, 1981). The oratory skill of leaders is frequently mentioned in ethnographies of SSSs (e.g. !Kung: Lee, 1979; Semai of Malaysia: Dentan, 1979; Xavante of Brazil: Maybury-Lewis, 1974). Oratory skill may be particularly important for negotiating on the community's behalf with outside political bodies (e.g. Mekranoti: Werner, 1981; Tsimane: von Rueden et al., 2008).

Physical qualities

Success in combat contributes to leadership emergence in more war-like SSSs (Chagnon, 1983; Maybury-Lewis, 1974; Werner, 1982), but even in societies lacking a history of inter-group violence, such as the Tsimane of Bolivia, men who act as leaders during community meetings tend to be stronger and taller than their peers (von Rueden et al., 2008, 2014a). This does not mean leaders emerge by physically intimidating others since attempts to dominate are typically met with resistance, ostracism, or more rarely execution (Boehm, 1999). Instead, group members may prefer leaders with greater stature or strength because this improves cooperation. In two experimental collective action tasks, groups led by more physically formidable Tsimane men were faster to complete the tasks (von Rueden et al., 2014a). When individuals interact face-to-face, larger body size may reduce the effort required by leaders to solicit the joint attention of group members and coordinate action. Larger body size can enable leaders to coordinate punishment of defectors or resolve disputes with less risk of retaliation and with greater efficacy (Glowacki & von Rueden, 2015; von Rueden & Gurven, 2012). Physical strength also signals hunting or other productive abilities, as among the Hadza of Tanzania (Apicella, 2014).

Gender

Women tend to wield less political influence than men in SSSs (Low, 1992; Vandermassen, 2008), which may be due in part to the contribution of body size to leader emergence and effectiveness (Blaker & Van Vugt, 2014). Women's opportunity for leadership in SSSs is also restricted by the sexual division of labor, in which women provide the bulk of direct care for multiple dependent offspring. This limits opportunities for networking beyond the extended family. Furthermore, men and women may differ, on average, in their motivation to build large coalitions in the service of political goals, as a result of different evolved mating strategies (Benenson, 2013; Low, 1992). Nevertheless, women often have a voice in community affairs in SSSs. For example, in Amazonian horticulturalists from Conambo, Ecuador, women gain influence by brokering factional disputes within their village (Bowser & Patton, 2010).

Prosociality

Since group members are wary of exploitation by leaders, trustworthiness, generosity and fairness are integral to leader emergence and effectiveness (von Rueden et al., 2014a). Among Alaskan Inuit, inheritors of boats and whaling gear would not necessarily become captains without attracting a crew via generosity (Rainey, 1947). Across Amazonian societies such as the Tsimane', meat-sharing generosity is an important determinant of coalitional support and political leadership (Levi-Strauss, 1944; Patton, 2005; von Rueden et al., 2008). If not accompanied by obvious signs of humility, generosity can sew distrust rather than affiliation (Lee, 1979; Bliege Bird & Power, 2015). In SSSs with greater access to material wealth and larger population densities, generosity can become highly competitive. In highland New Guinea, individuals known as Big Men acquired leadership through skilled persuasion and calculated generosity with other villagers (Sahlins, 1963). However, their legitimacy as leaders depended less on what their generosity said about their wealth and more on whether they used their influence to benefit the community (Roscoe, 2009). Big Men called in debts and favors to organize grandiose exchanges of pigs and other goods between villages, which functioned to signal their village's competitiveness (Roscoe, 2009). SSSs vary in their degree of egalitarianism, but in general leaders must carefully manage perceptions of their generosity and fairness or risk censure, ostracism, or even execution (Boehm, 1999).

Social networks

Social support from kin and non-kin are paramount to leader emergence and effectiveness in SSSs (Chagnon, 1979; Patton, 2005; von Rueden et al., 2008, 2014a). Emergent leaders tend to be hubs of social networks, in part because this signals their ability to coordinate the consensus-building that is typical of small-scale society politics. Among the !Kung, individuals who excel in healing or hunting are more likely to coordinate enforcement of social norms, because they are valued as social partners by a broad swath of the community (Wiessner, 2005). Among the Tsimane, larger and more skilled Tsimane men accrued more exchange partners and allies over a 4-year period, and increase in exchange partners and allies (but not increase in physical size or skill per se) associated with increased political influence over that same period (von Rueden, 2014). Size and skill may be associated with increased motivation to socialize, as much as they increase one's attractiveness as a social partner. We find evidence among the Tsimane that larger body size calibrates individuals' personalities toward greater extraversion, facilitating the development of broad social connections and pursuit of leadership (von Rueden, Lukaszewski, & Gurven, 2015).

In sum, a motivation to pursue and compete for leadership in SSSs is contingent on the possession of traits that are likely to increase the benefits for followers and lower the costs for individuals of taking on leadership roles in various domains (Lukaszewski & von Rueden, 2015; Tooby et al., 2006).

Benefits for leadership in SSSs

In LSSs, leadership is often rewarded with high salaries and formal privileges (Bass, 1990; Norton & Ariely, 2011). Yet in SSSs, these forms of compensation are typically absent, and leadership may even carry substantial costs. Dispute resolution has the potential to drag leaders' into others' conflicts, and leaders are expected to volunteer for dangerous tasks. For example, Yanomamo headmen take responsibility for patrolling the village perimeter for raiders (Chagnon, 1983). So if psychological motivations for acquiring leadership evolved in the context of SSSs, as we argue, how did leaders benefit to offset these costs? We propose that there are several evolutionary mechanisms by which leaders in SSSs differentially benefit from coordination with followers (see also von Rueden et al., 2014a).

First, leaders may orchestrate collective actions that produce goods more beneficial to themselves and their kin. For example, wealthy Barabaig pastoralists enforce conservation of grazing land because their larger herds stand to benefit the most (Ruttan & Borgerhoff Mulder, 1999). In general, traits are evolutionarily favored to the extent they increase their own reproduction and the reproduction in other individuals of genetically identical traits (Hamilton, 1964). Close kin (e.g. siblings) are most likely to share genetically identical traits, which is why many organisms, including humans, have psychological mechanisms for detecting and transferring benefits to kin.

Second, leaders may claim a fee for their services (Hooper et al., 2010; Smith & Choi, 2007; Gavrilets & Fortunato, 2014), through a greater share of the spoils or through other normatively-prescribed benefits (e.g. rights to polygyny). Such taxation is typical of less egalitarian SSSs with more formalized political leadership. Kwakiutl chiefs manage salmon fisheries and are given a share of followers' production (Boas, 1921), and Chumash chiefs took a percentage of all debt repayments (Hudson & Underhay, 1978). However, coordination failure may mean leaders claim less direct compensation or else face greater losses in reputation and legitimacy. Canoe and net owners among Ponams of Melanesia take more fishing catch than other crew when the catch is large but may forego shares when the catch is small (Carrier & Carrier, 1983). Across SSSs, direct compensation may be a small prize relative to the long-term gains from reciprocity or signaling a cooperative intention (von Rueden et al., 2014a).

Third, leadership may induce *reciprocity* in other currencies including food, childcare, or political support (service-for-prestige theory; Price & van Vugt, 2014). These reciprocated benefits may accrue principally during times of need, such as conflict or food shortage whereby leadership acts as a form of insurance (Boone & Kessler, 1999). In support of this argument, only Tsimane men who ranked in the top 25% of political leadership reported receiving food aid from non-kin following an episode of crop loss (von Rueden, 2014). Since the benefits leaders provide are often public goods, the service-for-prestige theory entails that group members can free-ride by not contributing to collective action, not rewarding leaders, and not punishing group members who fail to reward leaders. This leads to the prediction that followers will experience punitive sentiment toward other group members who fail to reciprocate with effective leaders. Among the Shuar of the Ecuadorian Amazon, group members who lack respect for popular leaders are themselves disrespected (Price, 2003).

Fourth and finally, effective leadership may act as a hard-to-fake signal of personal qualities, which motivates community members to reward leaders with sex, alliance, or deference (Gintis, Smith, & Bowles, 2001). For example, Meriam turtle hunt leaders give away most of their catch to neighbors or at feasts, not with expectation of reciprocity but to demonstrate their qualities to potential mates and political allies (Smith, Bliege Bird, & Bird, 2003).

Via these mechanisms, leaders in SSSs may receive compensation for the costs they incur taking on these roles. Indeed, men's leadership and social status in SSSs are positively associated with various indicators of reproductive success such as number of mates and surviving offspring (von Rueden, Gurven, & Kaplan, 2011; von Rueden, 2014). While reproductive disparities between leaders and followers are on average small in SSSs, such differences can nevertheless generate natural selection on traits that facilitate and motivate leadership (Lukaszewski & von Rueden, 2015). This does not entail that some individuals have "leadership genes" while others lack them. Rather, motivations to pursue leadership (and the dependence of these motivations on individuals' traits and the situations they find themselves in) are an evolved component of our shared human psychology.

Contributions and implications of SSS leadership

Study of the functions, determinants, and rewards of leadership in SSSs has tremendous importance in its own right, since SSSs encompass the majority of human societies over our history, and those remaining benefit from outside political assistance as they and their leadership navigate the forces of globalization. However, our principal aim is to communicate the theoretical importance of leadership in SSSs for the interpretation and prediction of leader and follower behavior in LSSs. As we argued in the Introduction, studying leadership in ethnographically recent SSSs is an invaluable tool for modeling the evolution of our leader and follower psychologies. The challenges of life in ancestral SSSs structured the evolution of psychological decision rules that continue to operate in modern contexts, including in large bureaucracies and formal institutions in which leaders and followers may never meet. Occasionally, these decision rules are *mismatched* to modern environments especially when the latter have changed rapidly (Tooby & Cosmides, 1992), resulting in sub-optimal or seemingly irrational decision-making by followers and leaders (van Vugt et al., 2008b). In the sections that follow, we describe the emergence of leadership in LSSs in light of this

evolutionary perspective, focusing on leaders' personality, physical size, and social networks. We then describe leader effectiveness in LSSs, with attention to leaders' skills, integrity, procedural fairness, and the structure of organizations. Finally, we discuss why leaders may care more about relative versus absolute social status.

Leader emergence in LSSs

Personality

In modern organizations, individuals who are narcissistic or over-confident are often selected as leaders (Brunell et al., 2008; Judge & Bono, 2000; Paunonen, Lonqvist, Verkasalo, Leikas, & Nissinen, 2006; Reuben, Rey-Biel, Sapienza, & Zingales, 2012), despite null or even negative consequences for groups (Brunell et al., 2008; Campbell, Bush, Brunell, & Shelton, 2005; Maccoby, 2007; Malmendier & Tate, 2005). This may be indicative of evolved leader preferences mismatching with the evolutionary novel conditions of modern LSSs. In LSSs, individuals switch jobs or institutional affiliations with increasing frequency, and are often newcomers in their social groups. In these contexts, over-confident and narcissistic leaders – because they are also often persuasive, charming and sociable (Brunell et al., 2008) – can at least initially be mistaken for competent and agreeable leaders. In large organizations, leaders who are narcissistic or lack competence may be insulated by an organizational structure in which followers (and shareholders) are unable to effectively observe or regulate upper management. In SSSs, community members differentiate aspiring leaders who are competent and agreeable from those who are merely confident and narcissistic over years of daily interaction. Furthermore, there are fewer social or occupational niches in SSSs in which narcissistic behaviors are rewarded. More often, narcissism results in loss of social support or even ostracism (Boehm, 1999). In SSSs, the benefits of being a leader (and socializing beyond one's family in general) may hinge to a greater degree on one's level of agreeableness (Lukaszewski & von Rueden, 2015). This is supported by the greater covariance between extraversion and agreeableness personality factors found among the Tsimane of Bolivia than in Western samples (Gurven, von Rueden, Massenkoff, Kaplan, & Lero Vie, 2013).

Physical traits

Successful leaders in modern democracies tend to be taller (Ellis, 1994; Stulp et al., 2013) and more masculine in terms of their facial and vocal characteristics (Little, Burriss, Jones, & Roberts, 2007; Tigue, Borak, O'Connor, Schandl, & Feinberg, 2012), which are indications of physical strength (Sell et al., 2009b, 2010). For example, taller US Presidents are more likely to be re-elected (Stulp et al., 2013), and male CEOs with deeper voices manage larger companies and enjoy longer tenures (Mayew, Parsons, & Venkatachalam, 2013). Furthermore, preferences for larger or more masculine leaders may be greater when group members experience more conflict (van Vugt & de Cremer, 1999) or are under threat from out-groups (Blaker & Van Vugt, 2014; Halevy, Chou, Cohen, & Livingston, 2012; Laustsen & Petersen, 2015; Little et al., 2007; Spisak et al., 2011; Tigue et al., 2012). In conjunction with our review of leadership in SSSs, these findings suggest that humans evolved a psychology that trades-off the risk of exploitation by physically dominant leaders with their greater coordination and conflict resolution efficiency in face-to-face interaction with followers (Lukaszewski & von Rueden, 2015; von Rueden et al., 2014a). This tradeoff is more pronounced during situations when free-riding and coordination failure are probable or pose an existential threat to the group, such as during periods of heightened intra- or inter-group conflict. Throughout history, leaders have taken advantage of this psychology by exaggerating risks to the group to legitimate more authoritarian behavior (Tooby & Cosmides, 2010). The context-dependence of leader selection in LSSs is in part the result of a context-sensitive psychology that evolved in SSSs.

In modern nation states, however, the vast majority of citizens never encounter their political leaders face-to-face, and leaders' influence rests on formal institutions to a greater degree than in SSSs. Yet face and body cues of physical formidability continue to shape leadership preferences in LSSs, pointing at the possibility of mismatch. The degree of mismatch may depend on the availability of other information relevant to leader effectiveness. Politically uninformed voters are more likely to attend to face features of political leaders than informed voters (Riggio & Riggio, 2010).

Future research will need to discount alternative explanations to mismatch. For example, body size may reliably signal other traits important to leadership, such as health or intelligence (Blaker & Van Vugt, 2014), or even coalitional support. Larger, more muscular individuals are often preferred as coalition partners (Benenson, Markovits, Emery Thompson, & Wrangham, 2009; von Rueden et al., 2008), but representations of leaders' physical size and coalition size may be entwined even more fundamentally. Recent evidence suggests the mind tends to represent power in any form in terms of body size (Fessler, Holbrook, & Snyder, 2012), because the latter was a primary determinant of success in dominance struggles during and well pre-dating hominid evolution (Archer, 1988). Fessler and Holbrook find that men who are walking in a group estimate the size of a potential foe as smaller compared to when they are walking alone (Fessler & Holbrook, 2013), and members of a threatening out-group are perceived as physically smaller and weaker when their leader's death is made salient (Holbrook & Fessler, 2013). It is possible that observations of aspiring leaders' size and strength generates inferences about their power that extend beyond their physical characteristics, to the strength of their coalition for example.

Leadership as coalitional psychology

How aspiring leaders network and signal their coalitional affiliations is of paramount importance to winning office or ascending the corporate ladder (Bass, 1990; Blau, 1964; Brass, 1984). Leadership competition is a coalitional contest, and evidence from

SSSs and non-human societies suggest this has been true for millions of years of hominid evolution. In chimpanzees, aspiring alpha males may forge coalitions to depose the current alpha (de Waal, 1982), and successful alphas retain allies by sharing mating opportunity (Duffy, Wrangham, & Silk, 2007). In modern human SSSs, social support from kin and other exchange partners and allies is the *sine qua non* of political leadership (Patton, 2005; von Rueden et al., 2008, 2014a).

The primacy of coalitions to the realization of political goals can explain many of the tactics intuitively appealing to leader candidates. For example, aspiring leaders often don symbols of widely supported values (e.g. American flag pins). By doing so, leaders signal their goals as identical to the goals of the community (Tooby & Cosmides, 2010). During political campaigns, candidates denigrate the competence of an opposing candidate, which in part has the function of suggesting that the other candidate's coalition is weak (Petersen, 2015). Without competent leadership, a coalition is less competitive. Perception that a candidate is incompetent may cause their supporters or undecided individuals to turn not to another candidate per se but to an alternative, stronger coalition or political party (Petersen, 2015). Relatedly, leader candidates will often use visual cues to their coalition strength in front of audiences, for example by having a group of supporters stand behind them. These supporters may represent widely held moral values (e.g. a war hero), hold positions of authority, or signal a candidate's coalition strength by virtue of their numbers alone. Even in mass politics where electoral success can be measured in the millions of votes, the presence or absence of a handful of individuals on stage at a rally can affect mental representations of coalitional strength, since our follow-ership psychology evolved at social scales where a change in allegiance of one or two persons was sufficient to determine contest outcomes (Wrangham & Glowacki, 2012).

Gender and race

Consideration of leadership as coalitional psychology has the potential to inform policy regarding the representation of women and other minorities in positions of power. Women may be under-represented as leaders in LSSs not only because of discrimination, an adherence to a traditional division of labor within households, or over-confidence on the part of men (Reuben et al., 2012), but also because of how men and women network and seek influence in groups (Colarelli, Spranger, & Hechanova, 2006; Low, 1992; Van Vugt et al., 2008a). From an early age, boys are more likely than girls to prefer group-level activities over dyadic activities (Benenson, 1993; Lever, 1978), revere each other's competitiveness (Benenson, 2013), and build or join large coalitions of unrelated peers in pursuit of their goals (Benenson, 2013). These average sex differences may in part reflect evolved mating strategies, evident across numerous species, whereby the sex that experiences greater variance in reproductive success (typically males) evolves a psychology that favors risky competition more than the other sex (Benenson, 2013; Daly & Wilson, 1985). However, evolutionary theory also predicts that adoption of particular institutions (e.g. matrilineal inheritance) can increase women's coalition-building and create opportunities for female leadership (Cashdan, 1995; Low, 1992). Better understanding of how sex differences in coalitional psychology are shaped by socio-ecological variation may be a boon for policies aimed at increasing the representation of women in leadership positions.

Aspiring leaders in LSSs are often judged on the basis of their racial identity (Gündemir, Homan, de Dreu, & van Vugt, 2014). In ancestral SSSs, however, individuals of different skin colors were unlikely to meet, which suggests racial prejudice may be a historically recent aspect of coalitional psychology and not the result of a psychology of race per se (Kurzman et al., 2001). Motivated by this logic, recent studies asked participants to observe faces of individuals of different races. When asked to recall particular faces, participants were less likely to confound faces of the same race when participants received information that these faces belonged to individuals of different coalitions (Kurzman et al., 2001; Pietraszewski, Cosmides, & Tooby, 2014). In other words, making racial affiliation orthogonal to coalitional affiliation caused decreased categorization of individuals on the basis of their race. An implication of these studies is that communication of aspiring leaders' *shared coalitional affiliations* with followers may increase the acceptance of racial minority leaders in LSSs.

Leader effectiveness in LSSs

Skill

The influence granted to leaders in LSSs often extends well beyond their domain of expertise, due in part to assumptions that skill in one domain predicts skill in another (Yukl, 2014). Such assumptions may be tied to social learning mechanisms that evolved in SSSs to favor broad imitation of successful individuals (i.e. prestige bias). Broad imitation of a successful individual, a leader, is adaptive because imitators are often unable to identify what particular traits beget a particular skill such as hunting ability (Henrich & Gil-White, 2001). Advertisers take advantage of prestige bias when they pay Michael Jordan to promote underwear or Matthew McConaughey to drive a particular car brand. Prestige bias can have both negative and positive consequences for leader effectiveness in LSSs. On the one hand, broad imitation of leaders can decrease the transaction costs of cooperation in organizations by homogenizing the behaviors of group members with diverse backgrounds (Spisak, O'Brien, Nicholson, & Van Vugt, 2015). On the other hand, failure of business managers is often credited to overly optimistic expectations that they perform a wide variety of duties with equal skill (Hogan & Kaiser, 2005; van Vugt et al., 2008a). Organizations can reduce negative effects of prestige bias by encouraging shared leadership, in which expertise and responsibility are more distributed. At least in work teams facing novel tasks, groups can improve performance when they encourage more equal sharing of ideas and expertise between group members (Woolley, Chabris, Pentland, Hashmi, & Malone, 2010).

Integrity and fairness

Leader effectiveness depends not just on competence, but also on perceptions of character. [Blau \(1964\)](#) describes how leaders who are viewed as generous and fair receive the collective approval of group members, which leads to social norms compelling compliance. The GLOBE surveys on leadership in 62 LSS societies show that integrity is a universally highly valued leader trait ([Den Hartog et al., 2002](#)). The perceived integrity of leaders – the correspondence between their words and deeds – can improve firms' bottom line by increasing employee commitment and performance ([Simons, 2008](#)).

This emphasis on integrity and fairness likely reflects a psychology of followership that evolved in egalitarian SSSs to be sensitive to the risk of exploitation by would-be dominants ([Boehm, 1999](#); [Boggild & Petersen, 2015](#); [Smith, Larimer, Littvay, & Hibbing, 2007](#)), and to attend to signals of leader prosociality as evidence that leaders are trustworthy and committed to followers' interests ([Baldassari & Grossman, 2013](#); [von Rueden et al., 2014a](#)). The egalitarianism of SSSs is often misconstrued as an absence of dominance motivations on the part of group members. Rather, egalitarianism is an active leveling of would-be-dominants through norms compelling humility and coordinated punishment of aggrandizers ([Boehm, 1999](#)).

A sensitivity to exploitation can explain why individuals prefer to have a say over who becomes leader ([Tyler, 1994](#)). Elected leadership is typically more effective in maintaining cooperation than exogenously imposed leadership ([Baldassarri & Grossman, 2011](#); [Durham, Knight, & Locke, 1997](#); [Rivas & Sutter, 2011](#)). Sensitivity to exploitation is also revealed in the popularity of media that provides cues to leaders' personalities. People prefer media coverage of politicians' personal lives to coverage of standard political issues ([Trussler & Soroka, 2014](#); [Boggild & Petersen, 2015](#)). Exposés of hypocrisy and selfishness draw inordinate attention, and stories of politicians' humility (e.g. Barack Obama sharing his umbrella with staffers) or self-sacrifice (e.g. Vladimir Putin fighting wildfires) also captivate.

In addition, people attend to anecdotes of leaders' procedural fairness. As opposed to decision outcomes, the process by which leaders make decisions can be more revealing of their character, particularly when some decisions benefiting a group member over the long-term might impose costs on them in the short-term ([Boggild & Petersen, 2015](#); [Van Vugt et al., 2008a](#)). Leaders' procedural fairness in the short-term provide relatively accurate cues to their disposition over the long-term, which can explain why procedural fairness is often critical to leaders' effectiveness in motivating cooperation and to the perceived legitimacy of legal and political institutions in general ([de Cremer & van Knippenberg, 2002](#); [Tyler, 1994](#); [Tyler & Blader, 2000](#)). Furthermore, group members can mobilize around procedural fairness cues when attempting to promote – or demote – leaders ([Boggild & Petersen, 2015](#)).

Organizational structure

Leadership in SSSs tends to operate informally and face-to-face with followers. The success of charismatic and transformational leaders in large modern organizations may result in part from a follower psychology that expects a personal relationship with leaders ([Van Vugt & Ronay, 2014](#)). As physical distance decreases the impact of active leadership influence on followers, organizations must work around this problem to remain effective ([Antonakis & Atwater, 2002](#)). Large, bureaucratic organizations that succeed tend to be structured as nested hierarchies, where leadership at multiple levels preserves the face-to-face leader–follower interaction of SSSs ([Richerson et al., 2003](#); [Van Vugt et al., 2008a](#)). In hunter–gatherer and horticulturalist societies, extended families fission and fuse to form residential groups on the order of 150 individuals ([Dunbar, 1993](#)). Residential groups affiliate sporadically within larger groups to exchange goods, perform religious ceremonies, or cooperate in war ([Hamilton, Milne, Walker, Burger, & Brown, 2007](#)). At these times, a hierarchy of leadership may emerge that is vested with greater authority to overcome coordination and cooperation challenges ([Alberti, 2014](#); [Carneiro, 2000](#); [Johnson, 1982](#)).

The average residential group size in SSSs of approximately 150 or less is mirrored in the average size of basic military units historically and cross-culturally ([Dunbar, 1993](#)). Also, effective organizations, like Toyota and Virgin devolve decision-making to managers of business units of 50 to 150 employees ([van Vugt et al., 2008a](#)). Such similarity in the organization of cooperation by large- and small-scale societies (1) provides evidence that humans possess cognitive constraints on the ability to successfully coordinate face-to-face beyond a group size of roughly 150 ([Dunbar, 1993](#)) and (2) predicts that large organizations improve performance when leadership is decentralized and leaders interact directly, and more personally, with followers ([Antonakis & Atwater, 2002](#); [van Vugt et al., 2008a](#); [Richerson et al., 2003](#)). Decentralizing leadership may reduce “groupthink” and is shown to increase employee satisfaction and motivation ([Wassenaar & Pearce, 2012](#)).

Leader status and compensation

The rewards to successful leaders in LSSs are unparalleled in SSSs, and they contribute to tremendous levels of wealth inequality in modern society. In the U.S., average citizens vastly underestimate the extent of wealth inequality ([Norton & Ariely, 2011](#)). This misconception may be due in part to optimistic perceptions of social mobility ([Norton & Ariely, 2011](#)). Underestimations of wealth inequality may also result from the concentration of wealthy and poor into different communities, limiting face-to-face interaction across wealth levels ([Dawtry, Sutton, & Sibley, 2015](#)). Much evidence suggests that the status comparisons most consequential for happiness and psychosocial stress are typically among individuals who are in geographic proximity or who occupy the same social network ([Anderson, Kraus, Galinsky, et al., 2012](#); [Norton, 2013](#); [Wood, Boyce, Moore, et al., 2012](#)). People tend to be happier when they are richer than their neighbors ([Blanchflower & Oswald, 2004](#); [Frank, 1999](#); [Luttmer, 2005](#)), and worker satisfaction correlates better with relative rather than absolute income levels ([Clark & Oswald, 1996](#); [Groot & van den Brink, 1999](#)). Those living just above the poverty line may resent welfare for those living just below it ([Kuziemko, Buell, Reich,](#)

& Norton, 2011), and a millionaire may envy a multimillionaire more than she envies a billionaire. Executive compensation is a positional arms race (Frank, 1999), where the most sought-after leaders feel entitled to salaries that dwarf the compensation of leaders slightly lower in the hierarchy.

The importance of these relative status perceptions to human psychology has its roots in SSSs, where rewards of status tend to be zero-sum and are contested among individuals who interact frequently. Among the Tsimane of Bolivia, where leadership tends to be informal and carries little material benefit, men who have more informal political influence produce more surviving offspring (von Rueden et al., 2011) and experience less stress and better health (von Rueden et al., 2014b). These benefits result in part from influential individuals' relatively greater access to social support, which acts as a buffer against risks of food shortage, illness, or conflict. Similar findings have been reported in LSSs in samples of managers in the public and private sectors. The higher is their position in the organizational hierarchy, the lower their stress levels and the better their health, due in part to a greater sense of control over life events (Marmot, 2004; Sherman et al., 2012). We care about our position relative to others, independent of our absolute levels of wealth, because relative status had consequence throughout our evolutionary history, even in the most egalitarian of SSSs (von Rueden et al., 2014b). The role of relative status in human motivation suggests that reductions in

Table 1

Determinants of leader emergence and effectiveness, in evolutionary perspective.

Category	Description	Evolutionary explanation	Implication for leadership practice
Personality	Frequent emergence of extraverted and over-confident leaders.	In SSSs, extraversion and confidence are more likely to co-vary with agreeableness and competence, respectively, because individuals have years to vet each other.	Change recruitment or election procedures to differentiate aspiring leaders who are merely extraverted and confident from those who are also agreeable and competent. More protection and encouragement of whistle-blowing.
Physical traits	Preferences for tall or physically masculine leaders, particularly when groups are under threat.	Followers in SSSs trade-off risks of exploitation by physically large leaders with increased coordination efficiency large leaders provide, particularly when groups face existential threats.	Anticipate that evaluation of leaders' competence can be affected by their size or appearance. During periods of threat or organizational challenge, expect increased susceptibility to a physical size preference in leaders.
Coalition strength	Competition for political leadership involves competition over whose coalition is stronger.	In SSSs, individuals who forge the most social ties within the community are afforded more leadership opportunity, in part because their coalitional strength signals their ability to coordinate and achieve consensus.	Critically evaluate whether displays of coalition strength by aspiring leaders accurately reflect skill in consensus-building. Political candidates will use media largely to signal their coalition strength (relative to opponents).
Gender	Women less likely to emerge as leaders in politics and business.	Women and men evolved different mating strategies that affect sex differences in physical size, propensity for over-confidence, as well as investments in large coalitions for political gain.	Removing overt discrimination and achieving sex parity in childcare may not equalize leadership opportunity across the sexes. Limit the extent to which promotions hinge on "old boys club" networking and create more formal opportunities for women to promote their accomplishments.
Race	Racial minorities less likely to emerge as leaders in politics and business.	Racial prejudice is driven by coalitional psychology, not a psychology of race per se.	Aspiring leaders should communicate shared goals and a coalitional affiliation with followers to decrease attention to their race.
Skill	Broad imitation of and deference to leaders in domains outside their expertise, sometimes resulting in leader failure.	Evolution favored broad imitation of prestigious individuals, because imitators are often unable to identify what particular traits beget a prestigious individual's skill.	To avoid groupthink, facilitate more sharing of expertise and observations, among managers and between managers and employees.
Integrity and fairness	Followers are attracted to cues of leader integrity and procedural fairness, even where hypocrisy or unfairness does not directly affect organizational performance.	In SSSs, group members gossip about each other's integrity and fairness to identify and punish selfish leaders or to nominate generous leaders. Cues to leader integrity and procedural fairness predict how leaders will treat followers over the long-run, more than the success of any single collective action.	Leaders who reinforce their stated goals with public but humble acts of generosity and procedural fairness increase employee performance and motivation.
Organizational structure	Information flow and follower motivation are more difficult in large bureaucracies.	In SSSs, leaders and followers typically interact face-to-face. Follower psychology may expect a personal relationship with leaders involving reciprocal exchange of ideas.	Large organizations improve employee performance and motivation by implementing nested hierarchies, in which leaders at multiple levels maintain personal relationships with followers, decentralize decision-making, and involve employees in leader recruitment.
Compensation	Executive compensation is sky-rocketing due to a positional arms-race among organizations to attract and retain the best leaders.	Humans care about relative position, not just absolute wealth, because relative status had consequence throughout our evolutionary history in SSSs.	Reductions in executive compensation within and across industries can be a collective good that provides employees with more of the fruits of economic growth, while maintaining the incentives to executives associated with higher relative income.

the absolute income of executives may not unduly harm their incentives, because executives remain relatively well compensated. Most US citizens, liberal and conservative, want more income parity (Norton & Ariely, 2011), and executives may be willing to lower their incomes so long as all executives do the same.

Conclusion

Explanation of any behavior is incomplete without consideration of its proximate determinants as well as its evolutionary origins (Scott-Phillips et al., 2011). By studying leadership in SSSs, we gain insight into the conditions that shaped the evolution of our social psychology of leadership and followership. We improve our understanding of why leaders and followers act as they do in any society, including the effect of context (e.g. group size, external threat) on leader and follower behaviors. An evolutionary perspective complements existing leadership theory, while explaining aspects of leadership that are either unexplained or only partially explained by existing theory (Van Vugt & Ahuja, 2011). Furthermore, an evolutionary perspective generates novel predictions about leader and follower behaviors, and offers suggestions for the kinds of policies that may ultimately improve leadership and organizational performance.

Table 1 lists several determinants of leader emergence and effectiveness and, for each, notes how an evolutionary perspective rooted in study of SSSs can inform leadership practice. Each of these determinants and their implications for leadership practice are described more fully in the preceding sections. However, our review sacrifices much depth for breadth. Furthermore, Table 1 is not nearly representative of all that has been published on leadership from an evolutionary perspective, nor exhaustive of the implications of our evolution in SSSs for leadership practice. Indeed, we have only scratched the surface of the potential implications.

We hope this review inspires research in both SSSs and LSSs that tests our claims, since many of them are provisional and supported by only a handful of studies. More quantitative research on leadership emergence and effectiveness in SSSs has tremendous importance, for its contribution to evolutionary theories of leadership and for its practical relevance to the political challenges faced by modern SSSs. The remaining SSSs on the planet are fast-disappearing due to incorporation into state-level societies, and in the process they are experiencing much exploitation and cultural loss. Enabling effective leadership in SSSs is critical to guarding their human rights and smoothing their transition to a global, market economy.

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