The Leadership Quarterly 30 (2019) 59–80

Contents lists available at ScienceDirect

The Leadership Quarterly

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

Review

# The evolutionary anthropology of political leadership

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ABSTRACT

Existing approaches within leadership studies often share a bias towards industrialized societies and lack broader cross-cultural and ethological reference. Meanwhile, cross-cultural and evolutionary approaches within anthropology are actively working to unify research on leadership and followership across the biological and social sciences. This review provides a novel and thorough view of political leadership as investigated by evolutionary anthropologists and highlights the benefits of incorporating findings from the evolutionary social sciences into leadership studies generally. We introduce the anthropological approach to leadership; describe evolutionary anthropology, its subdisciplines (including primatology, paleoanthropology, paleogenetics, human behavioral ecology, and gene-culture coevolution), and its complementary disciplines (particularly evolutionary psychology); review leadership and hierarchy in nonhumans, including our extinct hominid ancestors; review female leadership and sex-differences; and, primarily, discuss the relationships between evolution, ecology, and culture as they relate to the observed patterns of political leadership and followership across human societies. Through evolutionary anthropology's diverse toolkit, a deeper insight into the evolution and cross-cultural patterning of leadership is realized.

## 1. Leadership studies in anthropology

Discussions of leadership within anthropology date to the inception of the discipline. Many early anthropologists identified leadership and followership as critical to understanding human psychology, culture, and social organization (e.g., Firth, 1927; Morgan, 1877; Mumford, 1909; Myres, 1917; Rigby, 1870). Over the next century, anthropologists documented some sort of leadership among every ethnographically studied culture (Brown, 1991; Lewis, 1974), and in many social contexts, including within families and kin groups (Dussart, 2000), in ritual (Singh, 2017), in work groups (Macfarlan, Remiker, & Quinlan, 2012), and in conflicts between groups (Glowacki, Wilson, & Wrangham, 2017).

We focus primarily on political leadership. Political leaders can be described as individuals who have a disproportionate level of influence and decision making power within their communities (Kantner, 2010; Van Vugt, 2006; von Rueden, Gurven, Kaplan, & Stieglitz, 2014). They shape social dynamics directly, through, for example, organizing collective action and enforcing rewards and sanctions, and indirectly, by embodying cultural ideals and modeling successful and appropriate behavior (Henrich & Gil-White, 2001; Keohane, 2010; Price & Van Vugt, 2014; Van Vugt, Johnson, Kaiser, & O'Gorman, 2008). In return, leaders often receive special rewards or privileges (Blader & Chen, 2014; Cheng, Tracy, Foulsham, Kingstone, & Henrich, 2013; Kantner, 2010). Hence, leadership itself is frequently a contested resource that individuals compete to attain and/or maintain. Leadership is distinct from the closely related concepts of high rank, social status, and prestige, which are based on subjective evaluations by the group and involve increased access to contested resources and/or greater deference from others but not necessarily influence over group behavior.

Leadership is a complex, multifaceted phenomenon and researchers and theorists often focus on only a few specific dimensions. It can (1) involve passive influence versus active motivation of group members; (2) be distributed across multiple individuals versus concentrated in a single individual; (3) be based on persuasive reasoning versus coercion; (4) be situational versus institutional; and (5) be achieved on the basis of previous accomplishments or ascribed according to kinship or social identity (Smith et al., 2016; von Rueden et al., 2014). When leadership is ascribed, it also tends to be concentrated, to carry coercive power, and to be institutional, though these aspects of leadership do not necessarily covary (Wiessner, 2010).

A major strength of evolutionary anthropological theories of leadership is the diversity of evidence they tend to incorporate, including (1) evidence of status hierarchies and leadership in nonhuman primates and other animals, (2) paleoanthropological and genetic evidence for the evolution of modern humans from ape and early human ancestors, and (3) a large body of ethnographic reports on leadership across hundreds of different cultures. We first review these sources of evidence, and then discuss classes of theories for the evolution of leadership in humans, some of which also draw on psychological and developmental evidence from Western and non-Western societies.

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https://doi.org/10.1016/j.leaqua.2018.09.001
Received 3 February 2017; Received in revised form 28 August 2018; Accepted 1 September 2018
Available online 22 September 2018
1048-9843/ Published by Elsevier Inc.

## 2. Dominance, knowledge, and leadership in nonhuman animals

To identify features of human leadership that are shared with other animals versus those that are unique to humans, evolutionary anthropologists frequently incorporate findings from ethology and biology. Evolutionary anthropologists tend to focus on processes of leadership among primates because they are close genetic relatives, but also draw on evidence from both social carnivores, because they occupy an ecological niche likely very similar to ancestral humans, and other cooperative breeding species that have similar reproductive challenges and strategies (Burkart, Hrdy, & Van Schaik, 2009; King, Johnson, & Van Vugt, 2009; Schaller & Lowther, 1969; Smith, Swanson, Reed, & Holekamp, 2012).

### 2.1. Dominance hierarchies and leadership

Ethology has a long history of investigating leadership and dominance among various animal species. Based on extensive fieldwork, Allee (1945), an influential American ecologist and zoologist, promoted the view that all social vertebrates living in groups possessed some form of social organization and leadership. The nature of leadership in nonhuman animals however, is highly diverse both within and between even closely related species. A complication of interpreting theoretical models developed from ethological data is determining the distinction between leadership and dominance or social rank. As in humans, leader-follower relationships among nonhuman species may emerge from and contribute to status hierarchy; often leadership and dominance may be synonymous, as in the case of mountain gorillas (*Gorilla beringei beringei*) (Fossey, 1972), but in other contexts dominant individuals are not necessarily leaders, and leadership is distributed across individuals, as is the case among migrating groups of white-faced capuchins (*Cebus capucinus*) (Leca, Gunst, Thierry, & Petit, 2003, and see Section 2.4). Despite conceptual difficulties there is an immense body of ethological literature that can be used to further our understanding of human leadership.

Schjelderup-Ebbe (1935) first described the function of dominance hierarchies based on his research on the social behavior of chickens. Dominance is principally concerned with priority of access to limited resources. Physically fighting over these resources is costly. To avoid paying these costs, many animal species form relatively linear hierarchies based on physical formidability. With an established rank determining access to resources, individuals limit the necessity for employing agonistic tactics (Drews, 1993; Smith & Parker, 1976). In many cases, dominant individuals maintain a strong position of influence within the group until a rival usurps their position through a successful physical attack.

### 2.2. Leadership in primates

In primates, leaders are typically dominant individuals or lineages. Leaders in primate groups tend to control group movement in search of food and shelter, manage the social hierarchy within the group, lead group defense, and represent the group in intergroup interactions (Carpenter, 1963). Among gorillas, for example, a single dominant male, the silverback, guards his harem and controls and directs group movement (Fossey, 1972; Schaller, 1963). There is evidence that in many cases the presence of a successful alpha-leader increases the range of those groups, suggesting an adaptive advantage to leadership in territorial species (Carpenter, 1963).

Primate leadership is often a two-way street though, rather than simply asserting dominance. Leaders benefit from their role, but also depend on having strong social ties to other group members to reach consensus. Research among chacma baboons (*Papio ursinus*) suggests that dominant leaders tend to be individuals who stand to gain the most from group consensus decisions, and followers will fission from the group if costs outweigh the benefits to them (King, Douglas, Huchard, Isaac, & Cowlishaw, 2008). Even within a gorilla dominance hierarchy, a strong social relationship with the reigning leading male as an infant may facilitate leadership later in life (Harcourt & Stewart, 1981).

In chimpanzees (*Pan troglodytes*), males are dominant over females and lower-ranking males will defer spatially to higher-ranking males, voluntarily allowing first access to food resources (Muller, Wrangham, & Pilbeam, 2017; Wilson, 1980). Leaders and alphas among chimpanzees often obtain their positions through alliances and complex sociopolitical maneuvers (Barkow, 1989; De Waal, 1982; Goodall, 1986; Wilson, 1980). The social organization of chimpanzees is fluid and dynamic and groups do not have a single, long-term leader; rather, almost all adult males and females exhibit leadership at some point and there are multiple contexts in which leadership emerges, such as group movements (including mothers leading offspring), within-group conflict resolution, and between-group aggression (Goodall, 1986; Stanford, 1998; Wrangham & Glowacki, 2012). Chimpanzee leaders display a variety of personalities and leadership styles; a calm and tolerant, reluctantly aggressive disposition facilitates leadership, although aggression facilitates leadership as well. If leaders employ aggression, they generally affiliate with their targets afterwards (Goodall, 1986).

Leadership and social hierarchy among bonobos (*Pan paniscus*) differ from chimpanzees in important ways despite commonalities in social organization (Stanford, 1998). Female bonobos are unique among great apes for their high dominance status which is often comparable or superior to males within the group; male offspring of high ranking females seem to inherit their mother's rank (Furuichi, 1997). Female bonobos will occasionally aggressively challenge high and middle ranking males (Furuichi, 1997) and older females often are leaders in group movement (Tokuyama & Furuichi, 2017). The nature of inter- and intra-group male interactions among bonobos is markedly less violent than chimpanzees and the social behavior of female bonobos is suggested to facilitate reduced male conflict (Furuichi, 2011).

### 2.3. Leadership in social carnivores

Archaeological evidence suggests that early humans were probably social hunters and may have competed with and exploited a niche within the social carnivore predatory guild in Sub-Saharan Africa during the Pleistocene (Brantingham, 1998; Jones, 1984; Manuel & Rayne, 2003; Stiner, 2002). Social carnivores therefore also serve as informative animal models for human social organization and leadership given putatively similar ecological niches and selective pressures stemming from aspects of group structure and cooperative hunting (Schaller & Lowther, 1969; Smith et al., 2012). Among wolves (*Canis lupus*), a dominant breeding pair both exhibit leadership, with males directing movement and providing the majority of calories and females leading in defense and caring for young (Mech, 2000). Dominance displays are rare and returns from hunting and important material resources are generally equally distributed among the group; when dominance is displayed or contested it is typically in contests over food (Mech, 1999, 2000; Peterson, Jacobs, Drummer, Mech, & Smith, 2002).

The basic social unit of lions (*Panthera leo*) is the pride, which consists of related females, their offspring, and a few adult males (Heinsohn & Packer, 1995). The leaders of lion prides are responsible for protecting other members of the group. Alpha females will meet potential threats directly, and leaders incur a greater risk of physical harm in territorial defense relative to followers, who lag behind in self preservation (Heinsohn & Packer, 1995).

Among bush dogs (*Speothos venaticus*), leaders prompt individuals to follow with pronounced “rallying” displays, and will actively regroup individuals to maintain coordinated movement; such leaders are less likely than non-leaders to be the recipients of conspecific aggression, and lower ranking individuals behaviorally demonstrate submission via signals of deference (Macdonald, 1996). Leaders among African wild dogs (*Lycaon pictus*), primarily initiate and lead in cooperative hunting

(Frame, Malcolm, Frame, & Lawick, 1979) and leaders are responsible for initiating subsistence efforts (Wilson, 1980).

### 2.4. Leadership based on information and consensus rather than formidability

Dominance hierarchies are not necessary conditions of followership. Menzel (1971) demonstrated that chimpanzees can infer the motivational states of leaders, and that leaders can effectively communicate information on the location, quality, and quantity of resources to the group, supporting the importance of knowledge-based leadership. Horner, Proctor, Bonnie, Whiten, and De Waal (2010) report that deference towards experienced individuals – "prestige" – impacts social learning among chimpanzees, questioning claims that prestige is a uniquely human innovation (also see Chapais, 2015). However, in their analyses they do not distinguish high rank from experience, therefore it is not clear from their data if social learning among chimpanzees is biased towards experienced, "prestigious" individuals or high-ranking dominant ones. Though far from conclusive, other evidence suggests that chimpanzees do strategically bias learning towards both knowledgeable *and* dominant individuals. Tomasello, Call, and Hare (2003) suggest that chimpanzees use cues of visual attention of dominant conspecifics to anticipate competitive behavior, and associate this information with specific individuals. Kendal et al. (2015) provide evidence that naive low ranking individuals prefer observing higher ranking individuals and suggest a 'copy dominant individuals' bias underlying long-established attention structures (Chance, 1967). Kendal et al. (2015) also document a bias to 'copy knowledgeable individuals' among chimpanzees, suggesting that chimpanzees learn from high ranking and knowledgeable individuals. Flexible learning biases would allow individuals to copy the best model in a given context (Kendal et al., 2015), but also facilitate the learning of effective expressions of dominance. Dominance-based attention structures and prestige-based social learning biases may have similar evolutionary origins and may be less distinct than previously suggested (Cheng et al., 2013; Henrich & Gil-White, 2001; Henrich & Henrich, 2007).

Sueur and Petit (2008) distinguish unshared consensus decisions, in which a single dominant individual guides group processes, from shared consensus decisions, in which many group members are involved in the decision process. To better understand the role of social structure in influencing the importance of decision processes among groups of primates these authors investigated group consensus in two macaque species: Tonkean macaques (*Macaca tonkeana*), who have only a minimal dominance hierarchy with relatively permissive relationships, and rhesus macaques (*Macaca mulatta*) who maintain a highly rigid and stratified social system. Their results suggest that many individuals contribute to the process of group movement, providing wide support for shared consensus decisions among Old World monkeys. Rhesus macaques, however, displayed a marked increase in unshared consensus decision making relative to Tonkean macaques, with dominant and older individuals occupying leadership roles (Sueur & Petit, 2008). Similar research among white-faced capuchin monkeys suggests that group migrations may be initiated by a number of different individuals and consensus decisions are not determined by a single dominant individual (Leca et al., 2003).

Diverse taxa show evidence of self-organization in group movement in the absence of social hierarchy, global clues, or genetic influences (Krause & Ruxton, 2008); rather, relatively simple inter-individual cognitive mechanisms can explain the emergence of such leadership and followership (Couzin & Krause, 2003). Informed or experienced individuals often function as leaders and facilitate unshared group consensus. Individuals may evoke followership through specialized behavioral signals to uninformed individuals indicating special knowledge, such as the side flops and upside-down lobtails among bottlenose dolphins (*Tursiops truncatus*) (Lusseau & Conradt, 2009).

Couzin, Krause, Franks, and Levin (2005) model the emergence of leadership among nonhuman animal groups and demonstrate that large groups of individuals can achieve consensus in direction of movement relying exclusively on the movements of relatively few informed leaders. Social learning biased towards older, experienced individuals plays a role in some avian migration (Berdahl et al., 2018; Mueller, O'Hara, Converse, Urbanek, & Fagan, 2013). Among elephant species (e.g., *Loxodonta africana*), older matriarchs with special knowledge and experience are the primary decision makers in the group (Payne, 2003) and among killer whales (*Orcinus orca*) post-reproductive females lead foraging movement, especially during times of limited food resources (Brent et al., 2015). In many species, cultural learning and informational asymmetries influence hierarchy formation, beyond the relatively simple heuristic inter-individual cognitive mechanisms (Chapais, 2015; Couzin & Krause, 2003; Sapolsky, 2005).

Garland, Berdahl, Sun, and Bollt (2018) provide a mathematical model of each for the foregoing types of leadership among animals. They model *structural leadership* as the case in which some animals lead as a consequence of rank or hierarchy, *informed leadership* as the case when individuals lead because they have special information, and *emergent leadership* as the case where asymmetric influence comes from social interaction rules.

## 3. Dominance and knowledge across hominin evolution

Based on current fossil and genetic evidence, the last common ancestor (LCA) of humans and chimpanzees, our closest relative, lived sometime between 6 and 12 million years ago (MYA) (Moorjani, Amorim, Arndt, & Przeworski, 2016; Moorjani, Gao, & Przeworski, 2016; Scally & Durbin, 2012). Focusing on only the most phylogenetically conserved traits of African great apes, several researchers have suggested that the social organization of the LCA of humans and apes likely lived in closed social networks with intergroup conflict, males often traveled alone, some males were polygynous, and some males exhibited leadership in intergroup hostility (Chapais, 2017; Duda & Zrzavý, 2013; Hare & Wrangham, 2017; Muller et al., 2017; Wrangham, 1987).

The evolutionary trajectory of the hominins, a group of animals that includes all human ancestors after divergence from the chimpanzee lineage, is complex and seems to have been driven by profound environmental changes. Very roughly, there was an early ape-like phase during the Pliocene and an increasingly human-like phase during the Pleistocene. Morphological features of fossil hominins provide evidence of group size, reproductive patterns, and cooperation in our extinct ancestors (Lippold et al., 2014; Plavcan, 2012a, 2012b) that have implications for patterns of leadership.

The Pliocene, which began 5.3 MYA and ended 2.6 MYA, was marked by a cooling climate, reductions in forest habitats occupied by apes, and expansions of grasslands. During this phase, our ancestors had ape-sized brains and were bipedal, the latter indicating greater adaptation to a terrestrial environment. Social organization, let alone leadership, is difficult to infer from the fossil record. Foley and Gamble (2009) speculate that, based on the shift to patchier and more dispersed plant resources, these early hominins had larger day ranges and feeding parties likely separated and congregated more frequently than forest-dwelling apes. Nevertheless, they conclude that their behavior was well within the normal expectations for ape social behavior and organization, including the presence of dominance hierarchies. Australopithecines, which first appeared around 4 MYA, exhibited substantial sexual body-size dimorphism, indicating male-male physical competition and polygyny (Plavcan, 2012b; Puts, 2010). Hence, the patterns of leadership among ancestral hominins were probably not too dissimilar to those of chimpanzees, gorillas, and baboons described earlier, and therefore were likely based on both dominance and knowledge.

The first members of genus *Homo* appear around the beginning of the Pleistocene, c. 2.6 MYA, which was characterized by a further

cooling of the climate and a transition from patchy, plant-based resources to nutrient dense, predictable animal-based resources (Kaplan, Hill, Lancaster, & Hurtado, 2000; Marean, 2016). Early *Homo* might also have been markedly sexually dimorphic, although the evidence is far from clear (Plavcan, 2012a). Most primates are sexually dimorphic to some degree, however (Kappeler & Van Schaik, 2004). In modern humans, body dimorphism is modest – men weigh about 15% more than women – but this is greater than gibbons and a number of strictly monogamous and polyandrous primate species (Plavcan, 2012b). Human upper body strength, on the other hand, is highly sexually dimorphic and in over 90% of chance encounters between an adult man and woman, the man would have greater upper body strength (Pheasant, 1983; Plavcan, 2012b). Intrasexual contest competition was likely a strong selection pressure on male reproduction across human evolution (Puts, 2010) and at least some polygyny presumably characterized our early hominin ancestors for millions of years. Again, this suggests that male dominance hierarchies, based in part on physical formidability, probably played some role in the social organization of *Homo*, with dominant males often assuming leadership roles.

Multiple lines of evidence suggest the subsistence strategy of Pleistocene hominins centered on cooperative hunting of large-game (Bunn & Ezzo, 1993; Hoppe, 2004; Rodríguez-Hidalgo, Saladié, Ollé, & Carbonell, 2015; Smith et al., 2012). Comparative archaeological analyses of faunal remains at Plio-Pleistocene hominin sites and behavioral studies of contemporary carnivore hunting, suggest that human ancestors exploited a niche within the predatory guild of social carnivores in between top predators and confrontational scavengers (Stiner, 2002), a strategy which may have emerged from adaptations resisting predation of social carnivores (Willems & van Schaik, 2017). The cooperative hunting of contemporary hunter-gatherers has many commonalities with the hunting strategies of social carnivores including cacheing, transportation, systematic processing of carcasses, and widespread sharing within the local group (Brantingham, 1998). Leadership in cooperative hunting likely has deep evolutionary roots with components derived from a primate heritage, adaptation to a social carnivory niche, and human-specific adaptations (Smith et al., 2012; Stiner, 2002).

The earliest known fossil specimen of our species, *H. sapiens*, is dated to about 300,000 years ago in north Africa (Richter et al., 2017). Traditionally, it was thought that there was a punctuated cultural explosion or "revolution" in symbolic material culture, such as decorations, ornamentation, and art sometime after 100,000 years ago (Dunbar, 2007). Contemporary consensus in paleoanthropology, however, suggests a more gradual process of cognitive and cultural development from 300,000 years ago to the expansion of *H. sapiens* out of Africa to Eurasia c. 100,000 years ago, (Foley, Martin, Lahr, & Stringer, 2016; Kimbel & Villmoare, 2016; Mcbrearty & Brooks, 2000); a mixture of punctuated and gradual developments across features of the human phenotype is possible, though (Shultz, Nelson, & Dunbar, 2012).

Given the importance of dominance-based *and* information-based leadership observed among both nonhumans and humans, we can postulate both processes of leader emergence occurred among prehistoric humans. Increases in cognitive capacity and symbolic culture across hominin evolution putatively suggests an increased reliance on informational asymmetries and, consequently, prestige-based leadership, as documented next in the ethnographic evidence.

## 4. Ethnographic evidence

Contemporary and recent historical human societies exhibit substantial variation in size, complexity, and modes of subsistence, ranging from small nomadic bands of about 25 individuals that subsist on hunting and gathering wild foods, to politically autonomous settled communities of 50–150 individuals that subsist on cultivated foods, to societies comprising multiple communities with thousands of individuals practicing intensive agriculture and marked social stratification, to nation states (Bodley, 2011; Service, 1964, 1975). A primary goal of political anthropology is to understand which aspects of leadership vary across these diverse cultural contexts and which are common across cultures. Fried (1967), for example, contrasted leadership among egalitarian societies, ranked societies, and states, and Service (1964) similarly discussed leadership among bands, tribes, chiefdoms and states, both of which contributed to a classification of political variation informed by cultural evolutionary change and the ethnographic record.

Early anthropologists, accustomed to their own highly stratified societies with numerous formal leadership roles, were often struck by the apparent lack of social rank and leadership in small-scale societies. Lewis (1974, p. 4) relates, however, that although "it has long been recognized that the smallest and simplest societies normally lack individuals or groups possessing the power to regularly coerce or control other adults… this discovery evidently blinded ethnographers to the significance of subtler kinds of direction in human affairs, and we are only now becoming truly aware of how important leadership may be in such societies."

This lacuna was soon rectified by ethnographers who provided detailed accounts of leadership and followership in specific non-Western societies (e.g., Fallers, 1964; Hatt, 1974; Kracke, 1978; Lowie, 1948; Ottenberg, 1971), and these accounts were critical in shaping initial theories of political hierarchy (for more recent examples, see Clemmer, 1995; Marak, 1997; Mendoza, 2002). Early reviews such as Hoebel (1954), Cohen and Middleton (1967), and Lewis (1974), discuss ethnographic cases to highlight cross-cultural continuities and notable distinctions in forms of leadership. In the following sections, we summarize the ethnography of leadership across common categories of social organization and subsistence, ranging from the least politically complex to the most politically complex societies.

### 4.1. Leadership among egalitarian hunter-gatherers

Egalitarian societies are those which largely lack inherited status and wealth distinctions, maintain a cultural ethos of sharing, and allow all individuals a relatively equal opportunity to achieve social distinction and high status (Fried, 1967; Mattison, Smith, Shenk, & Cochrane, 2016; Service, 1964). Differences in status, however, still accrue on the basis of age and sex (von Rueden, Alami, Kaplan, & Gurven, 2018). There is immense variation within ethnographically described egalitarian societies, which are commonly nomadic or semi-nomadic hunter-gatherers or small-scale horticulturalists. Most anthropologists contend that the vast majority of human evolutionary history would have been characterized by some degree of egalitarianism (Kelly, 2013; Lee & Daly, 1999) and such societies have played a significant role in political anthropology. Critically, however, egalitarian social structures are not an innate feature of human sociopolitical organization, but rather reliably emerge in the context of environmental instability, difficulty in buffering resource shortages, and a lack of resource accumulation (Cashdan, 1980; Gardner, 1991; Woodburn, 1982) and are culturally maintained (Boehm, 1982, 1984; Knauft et al., 1991; Lee, 1979; Woodburn, 1982).

Contrary to the popular conception that hunter-gatherers live exclusively in small groups, hunter-gatherer societies range in complexity from small nomadic bands of perhaps a half dozen families with few social distinctions other than age, which we refer to as *egalitarian* hunter-gatherers, to large societies with permanent settlements of scores of families (Schalk, 1981) and multiple levels of social stratification, including slaves (Ames, 1994), which we refer to as *non-egalitarian* hunter-gatherers (Kelly, 2013).

Ethnographers have intensely debated the presence and importance of formal positions of leadership among egalitarian hunter-gatherers. Certainly leadership exists among egalitarian hunter-gatherers, but is highly variable, generally dependent upon individual ability and demonstrated success in activities valued by the group, and is often

context specific (Bird & Bliege Bird, 2009; Boehm, 1999; Kelly, 2013). This debate can partly be attributed to often overt cultural institutions and practices among egalitarian societies which eliminate or reduce the need for direct leadership in specific contexts. Among the Aranda in Australia, for example, despite a governing council and formal leaders, cultural models of supernatural punishment in the form of physical indisposition, disease, or death, for disobedience to social norms and antisocial behavior function to maintain much social cohesion without overt leadership (Basedow, 1925). Elaborate cultural taboos also provide a framework for cultural proscription and regulation of behavior, such as the concept of *ekila* among many Congo Basin foragers (see Lewis, 2008). These features of egalitarian society are reflected in models of *substitutes for leadership* from the organizational literature which seek to comprehensively understand leader emergence and effectiveness across diverse social and managerial contexts (Kerr & Jermier, 1978; Podsakoff & MacKenzie, 1997).

The largest groups of hunter-gatherers still practicing a relatively traditional lifestyle are found in the Congo Basin. These populations, who subsist by trading meat and other wild forest products for cultivated foods grown by neighboring farmers, are known for their strong cultural emphasis on individual autonomy (Hewlett, 2014). Putnam (1948, p. 334) explains that among the Mbuti, for example, "there are no chiefs, councils, or any other formal governing bodies in a pygmy camp. In making any decisions concerning the whole camp, two factors are involved. The first of these is respect for older people…secondly,… every man in the camp is entitled to state his own views on any subject." Decisions regarding group movement and hunting ground selection are often based on shared, group-wide consensus, reached after extended, acephalous discussions (Putnam, 1948; Turnbull, 1962, 1965). There are reports of increased deference towards highly respected individuals, however, in addition to respect and deference towards elders (Moïse, 2014).

Though Congo Basin hunter-gatherers lack an overarching political leader, there are various specialized leadership roles. Among the Aka, for example, these include camp leaders (*kombeti*), older men with greater influence over subsistence activities and movement; elephant hunters (*tuma*), who lead important hunting and seasonal rituals and oversee ritual training of young boys; and traditional healers (*nganga*), who provide a variety of specialized services to the community and maintain a special position of respect and influence (Hewlett, 1988). There is some evidence that these leaders are more likely to be polygynous and have more children (Chaudhary et al., 2016; Hewlett, 1988).

Patterns of leadership among egalitarian hunter-gatherers in other parts of the world are similar to those seen in Congo Basin groups, with some culturally-specific features. Among some San hunter-gatherers of Southern Africa, for example, a headman might have a formidable political role, albeit one that is constrained by powerful social norms against aggrandizement (Bessel, Guenther, Hitchcock, Lee, & MacGeorge, 1989; Guenther, 1996; Lee, 1978, 1979; Marshall, 1960). Among the Tagemiut Eskimos of the Alaskan coast, most leadership is restricted and informal (Weyer, 1967), but coordinated hunting of sea and land mammals requires a skilled and knowledgeable boat owner, an *umialik*, to organize and lead hunting parties (Spencer, 1959). Successful *umialit* have considerable political influence and are in constant competition with rivals to demonstrate competence in hunting, generosity, intelligence, and a reputation for sound decision making (Pospisil, 1964).

In the North American plains, hunter-gatherer leadership systems adapted to increased warfare and colonialism. Traditionally, the Comanche placed great importance on individual freedom and leadership was generally perceived as insignificant (Hoebel, 1954). Yet, the Comanche illustrate the necessity of dual leadership roles. Having adopted a culture of warfare unique among Plains Native Americans, the Comanche successfully displaced the Apaches, deflected advances of Spanish military, and obliterated populations of Pueblos (Hoebel, 1954; Hoebel & Wallace, 1952). In the context of war parties, the leader of the raid assumed absolute control and authority over participants, both in logistic and strategic planning of the attack, as well as the execution (Hoebel & Wallace, 1952).

Lévi-Strauss' (1944) work on leadership among the Nambiquara of Eastern Brazil constitutes an archetypal description of sociopolitical prestige systems in an egalitarian society. The Nambiquara, according to Lévi-Strauss, stand out among hunter-gatherers for their emphasis on political leadership and the presence of multiple competing and cooperating leaders. Nambiquara leaders must compete for, and maintain their position through demonstrated success in culturally revered activities including producing arrow-poison, singing and dancing, territorial knowledge, and oftentimes shamanism. Leaders lack coercive power and maintain their position through quality decision making. In response to valuable leadership, followers bestow respect, trust, and reverence. Polygyny is a benefit nearly exclusive to leaders, yet leaders perceived to have taken too many wives cause unrest among followers (Lévi-Strauss, 1944; for critique, see Price, 1981).

### 4.2. Leadership among egalitarian horticulturalists

Small-scale horticultural societies often actively maintain an egalitarian political structure, similar to egalitarian hunter-gatherers. Leadership among horticultural societies is typified by the headman style. Discussions of Yanomamö headmen provide an important description of leadership systems among egalitarian Amazonian horticulturalists. Yanomamö headmen are political agents who surface in the face of conflict and are easily identified by all members of the village (Chagnon, 1968); headmen can be characterized as a 'first among equals' and are typically skilled hunters, verbose, knowledgeable of tribal lore, accomplished warriors, and polygynous (Neel, 1980). Among the vigorous, verbose, strong warriors, all of which are important assets in campaigns for headmanship, those with "mental agility" are at an advantage (Neel, 1980). Leaders also tend to have large kin networks compared to non-leaders (Hughes, 1988; Kelly, 2013; Walker et al., 2012).

High levels of internal warfare and intervillage raiding requires headmen to lead proactively, considering both offensive and defensive strategies. Leading and participating in successful raids by aspiring warriors can fuel political ascendancy; similarly, failing to anticipate an attack and suffering severe casualties can lead to the disbandment of a village (Chagnon, 1966, 1988). In this environmental and cultural context, the Yanomamö have developed strong values for bravery and ferocity among men and multiple cultural institutions, including competitive displays and ritualized aggression, allow young men to display and develop a warring persona. Yanomamö headmen take on big risks, both in leading and participating in warfare, but also social risks in thwarting political rivals. Leading headmen have great responsibilities and are more likely to face physical dangers related to their social status than are non-leaders.

In contrast, the Tsimane' forager-horticulturalists of lowland Bolivia lack a history of intergroup warfare and leadership is potentiated more by successful negotiation with members of neighboring groups (Huanca, 2008; von Rueden, Gurven, & Kaplan, 2008; von Rueden et al., 2014). Traditionally, shamans maintained important positions of leadership due to their ability to interface with the spiritual dimension of the forest and respected elders were also deferred to (Daillant, 1994). Due to the influences of missionaries and rapid acculturation, Tsimane' shamanism no longer exists. Instead, in response to external political pressures, Tsimane' villages have elected local village leaders (*corregidores*) who serve as representatives to outside bodies, resolve within group disputes, coordinate cooperative activities, and facilitate community meetings (von Rueden et al., 2008, 2014). Much like traditional leaders, *corregidores* lack coercive authority and exert influence over the group through consensus building and persuasion (von Rueden et al., 2014).

In summary, egalitarian societies generally lack leaders with formal powers and authority (Boehm, 1999; Lewis, 1974). Leadership is more likely to emerge facultatively in response to context-specific demands (Fried, 1967; Price & Van Vugt, 2014; Woodburn, 1982) and followers tend to only relinquish autonomy to a leader under the perception of beneficial outcomes to themselves (Henrich, Chudek, & Boyd, 2015). Leaders are typically respected individuals, highly skilled in culturally valued domains, accomplished, have reputations for sound decision making, extroverted, have strong oratory skills, physically formidable, and embody cultural ideals and social norms (Boehm, 1993; Lewis, 1974; Service, 1964; Vaughn, Eerkens, & Kantner, 2010; von Rueden & Van Vugt, 2015; Woodburn, 1982). Consequently, leadership in egalitarian societies is dependent upon directly serving collective interests (Henrich et al., 2015; Macfarlan et al., 2012).

### 4.3. Leadership among non-egalitarian hunter-gatherers

Hunter-gatherers living in favorable, resource abundant environments are not subject to many of the pressures associated with egalitarianism. Ecology, geography, demography, resource availability and particularity, storage, social and informational networks, and cultural variation are all implicated in the lack of egalitarianism among some hunter-gatherers (for review see Kelly, 2013). Non-egalitarian hunter-gatherers are typically sedentary, relatively dense populations, with specialized occupational roles, ownership of resources, food storage, military structure, elaborated prestige systems, and rigid social hierarchy (Ames, 1985; Arnold, 1996; Eerkens, 2010; Hayden, 1996; Keeley, 1988; Wiessner et al., 2002; Woodburn, 1982). Ethnography on leadership from non-egalitarian hunter-gatherers is limited, but includes important descriptions from Pacific Northwest and Northwest Plateau region populations in North America; the Calusa of the Southeastern Gulf coast; Californian populations such as the Chumash; a few Papua New Guinean hunter-gatherers; and the Ainu in Japan.

Leadership among non-egalitarian hunter-gatherers is often based on the ability to accumulate critical resources, including material, symbolic, and social capital, and the conversion of “surplus” into political influence. The Tilingit of southeastern Alaska exemplify this pattern. Traditionally, they relied heavily on a variety of hunted and fished game, gathered roots, berries, and shellfish. Large seasonal hauls from salmon migrations provided an opportunity for long-term food storage (Tollefson, 1997). Within Tilingit society existed three ranked social classes, and populations were organized under overlapping kin-based clans and ritual-based moieties, each containing their own leadership structures with oscillating power asymmetry between them (De Laguna, 1972). Authority was primarily dependent upon wealth-based prestige and high-ranking individuals competed through strategic potlatch ceremonies involving lavish displays, distribution, and destruction of resources, often under the guise of honoring the deceased (Tollefson, 1995).

Some hunter-gatherers exhibit both egalitarian and non-egalitarian features. The Chinookans of the American Northwest, for instance, lived along the Pacific coast and Columbia and Willamette river valleys, areas abundant in marine life, game animals, and plant foods (Beierle, 2004). Wealthy, high-ranking individuals from prominent lineages were able to assume leadership positions and pursue chieftaincy; similarly, warriors and shamans often served as community leaders (Ruby & Brown, 1976). Despite rigid class structure, wealth inequality, ascribed statuses, and slavery, the authority of local chiefs and leaders was nonetheless primarily based on community service and adherence to cultural norms of morally just behavior (Ray, 1975). Ultimate authority resided with the kin group which could replace chiefs and subdue decisions of important leaders. Women also played important leadership roles in group decisions, independently owned property, and served as chiefs when a female candidate was superior to the available male contenders (Ruby & Brown, 1976).

In non-egalitarian hunter-gatherers, leaders also often had important managerial responsibilities. Fixed, coastal fishing economies, such as among the Calusa, present unique challenges for cooperation and competition among fishers, and daily fishing reinforces the need for management and promotes permanent, heritable leadership positions (Widmer, 1988). Leadership facilitates efficient continuous fishing in tropical environments lacking seasonal constraints, and Calusa community members willingly accept hierarchical management. Calusa leaders mediate disputes, plan and manage fair fishing access, and oversee the distribution of returns (Widmer, 1988).

In some non-egalitarian groups, leaders were elected. Among the Ainu, settlements, or small groups of settlements, were politically and economically autonomous and claimed exclusive rights over and defended territories, such as river valleys (Munro, Seligman, & Watanabe, 1963). Village elders elected chiefs and sub-chiefs whose all-encompassing roles included leading in hunting and fishing, leading in inter-village warfare and within-group conflict resolution, managing land rights and division, organizing ceremonies, caring for the ill, leveling sentences on guilty parties, and naming children (Batchelor, 1927). Shamanism also presented male and female experts opportunities for considerable influence within the group (Ohnuki-Tierney, 1981).

### 4.4. Leadership among pastoralists

Pastoralists are populations whose subsistence and economies are heavily, but not exclusively, reliant on herd animals (Borgerhoff Mulder et al., 2010; Rigby, 1985). Their subsistence strategies are highly varied and often include a number of livestock products, hunted or gathered foods, and farmed foods (Jacobs, 1965; Kardulias, 2015; Spencer, 1998). Given the demands of herd management, pastoralists are often nomadic. The degree of nomadism, however, is likely influenced by the need to extract multiple resources from a seasonal resource base (Salzman, 1971; Zarins, 1990).

Current scholarship views key features of pastoralist societies, including their forms of leadership, as shaped by the twin demands of managing a complex resource base while at the same time defending it against numerous competing groups, such as other pastoralists, agriculturalists, and surrounding nation states (Bates, 1971; Galaty & Johnson, 1993; Irons, 1971; Salzman, 1971). Among pastoralists, leadership often involves dimensions of three key features: the emergence of situational and knowledge-based leadership among autonomous households, the promotion of adherence to complex cultural norms, and the presence of age grades or institutionalized hierarchy with significant political and military power ascribed to certain classes.

The Libyan Bedouin who reside in the Sahara's Western Desert, place strong emphasis on personal autonomy. Leader emergence is largely situational and most frequently occurs in decision making on group movement, management of water, and schedules in agricultural work (Peters, Goody, & Marx, 1990). Group leaders (*’aquila*, or “wise man”) also play an important role in conflict resolution but lack coercive authority (Murray, 1935). Much of social control occurs in the absence of individual leadership and is based on firm requirements of social norms and adherence to an “honor code” (Abu-Lughod, 1986).

Among the Sherpa, leaders gained influence as a result of demonstrated wisdom and sound decision making and primarily functioned to lead migrations and establish new settlements (Ortner, 1989). Leaders also relied on supernatural visions of ideal territories to convince followers (Ortner, 1989). In highland Nepal, Khumbu Sherpa pastoralism is household-based, rather than linked to kin groups or clans, and though livestock are privately owned, grazing land is communal and without direct management; nonetheless, residents maintain the local custom was the result of negotiations by an influential political leader (*gebu*) who overturned the previous village-based management system and instituted the policy of household autonomy (Stevens, 1990). The Sherpa case and this cultural model illustrate that autonomous households are willing to defer to a knowledgeable individual with valuable information or a strong leader if they perceive a benefit to their

household.

The contexts and degree to which age-grades and other social structural features facilitate coordination in the absence of more traditional leadership is an important feature of pastoral political systems (Fukui & Turton, 1979; Glowacki & von Rueden, 2015). Among the Maasai of East Africa, for instance, chiefs and shamans maintained authority. The primary political force resided within age-grades of young warriors, however, and chiefs exerted only marginal influence over them (Hollis Sir & Eliot, 1905). Within age-grades, rank emerged based on physical strength and demonstrated bravery, and these individuals serve as leaders in warfare (Merker, 1910). Successful military leaders are treated with great respect and receive a number of privileged adornments to mark their status and accomplishments (Merker, 1910).

Among the Kurds in the Middle East, inter-village warfare and territoriality significantly shaped political systems and created opportunities for leadership. The initiation and successful execution of warfare was the prime pathway to political influence and status mobility (Barth, 1953). Though common people were rarely at risk of true danger, an atmosphere of violence characterized social life and Kurdish chiefs embodied cultural ideals of formidable warriors by being vengeful and courageous, yet generous (Masters, 1953).

### 4.5. Leadership among chiefdoms

As their name suggests, chiefdoms are societies in which there is a formal leader who rules over multiple settlements, each of which usually has its own leader as well. Chiefdoms are characterized by hereditary inequality with at least two social classes (elites and commoners), and significant ascribed leadership roles (Earle, 1997). In chiefdoms, leadership, social rank, and the differentiation of social roles necessarily concern the distribution of resources. There is, however, much diversity in political complexity among chiefdoms. Anthropologists contrast simple chiefdoms, which consist of a dominant community and a number of subsidiary communities under the rule of a single chief, from complex chiefdoms which are collections of simple chiefdoms ruled by a single paramount chief (Earle, 1989; Stanish, 2004).

Among the Maori of New Zealand, each clan (*hapu*) was governed by a chief from the hereditary class of leaders (*rangatira*), and a paramount chief (*ariki*) from the dominant clan was the leader of the chiefdom. Chiefs organized collective labor and controlled property use, oversaw ceremonies, and interfaced with other leaders (Best, 1924a, 1924b; Meijl, 2003). Chiefs were exceptionally wealthy but despite great influence ultimately lacked coercive authority (Firth, 1959).

Polynesian chiefs maintained firm economic control and increased their prestige through perceived generosity which in turn afforded chiefs greater social influence and authority over followers. Among the Tikopia, land was owned by the clan chief and disputes over rights to use land were common among clan members, though only rarely required the chief's involvement, which could involve severe punishment to reach resolution (Firth, 1939b, 1949). Chiefs were more knowledgeable than commoners and youth identified as potential heirs to the chieftainship received special instruction from elders and experts (Firth, 1939a, 1939b). In addition to high social rank, chiefs were expected to be highly technically skilled in activities such as farming and canoe construction (Firth, 1939b). Tikopian chiefs were also exceptionally skilled practitioners of black magic (*tautuku*) and the power of supernatural attack instilled fear among commoners (Firth, 1949). Ultimately, in Polynesia, the greater the productivity and intensification of subsistence, the more economic capital a chief had for distribution, and the greater their influence became (Sahlins, 1958).

The Bemba are the largest ethnic group in northern Zambia. They practice shifting horticulture and are socially organized into chiefdoms of varying size with village, district, and state level political organization. Chiefdoms are under the rule of a hereditary paramount chief (*citimukulu*), from a royal lineage associated with supernatural abilities (Richards, 1940; Roberts, 1973). The Bemba state is not truly politically centralized, however, yet the paramount chief's influence is far from ritualistic (Roberts, 1970). Bemba political structure has been greatly shaped by between group conflict. Warfare between villages is common, succession of chieftainships often involves violent conflict between competing heirs, and the slave trade brought substantial costs to Bemba society (Brelsford, 1944; Richards, 1937). Chiefs were primarily responsible for representing their kin group and ancestors within and between villages (Richards, 1940) and were endowed with absolute coercive authority, in part from their ritual prowess but also stemming from complete economic, military, and social control (Richards, 1939). Male and female ritual leaders who provided important community services also maintained important leadership positions (Richards, 1956). Leadership among the Bemba illustrates an association between intergroup violence and authoritative leadership, while simultaneously providing example of leaders who are respected for their culturally valued skills.

In stratified chiefdoms, the coercive authority of leaders can be drastic and followers, being bound to economic and social systems controlled by a chief, have limited opportunities for recourse. In diverse cultural contexts, chiefs often wielded absolute power over commoners with many subservient followers paying with their lives at the demands of the leader (Burrows, 1937; Richards, 1940).

### 4.6. Ongoing ethnographic research on leadership in small-scale societies

Many ethnographically described societies no longer exist or no longer live as when they were originally described. Research therefore continues among small-scale societies, many of which continue to maintain varying degrees of their traditional cultural and economic livelihoods, but virtually all of which are involved in some way with larger market economies and state governments. Contemporary anthropologists focused on leadership often have an opportunity to investigate how traditional leadership structures are adapting to or being shaped by outside forces. In many cases, previously revered activities associated with leadership lose cultural importance and become negatively perceived as outdated skills, as among Garifuna fisherman in the Caribbean who lost social influence as formal education became more critical and revered (Palacio, 1982). In the face of increasing external political pressure, many small-scale egalitarian societies develop more formal leadership structures. Documenting cultural change and developing theoretical models using ethnographic data from small-scale egalitarian populations as they navigate greater outside political pressure will be of enormous benefit to political anthropology (von Rueden & Van Vugt, 2015). We outline our ongoing systematic and ethnographic research on leadership in small-scale societies.

Garfield and Hagen (2019) focus on elected leadership among the Chabu, a population of recently settled hunter-gatherers in the highland forests of Southwest Ethiopia. The Chabu currently rely on hunted game, gathered and cultivated plant foods, and cash crops for their primary subsistence and economic base. They remain largely egalitarian in many ways and exhibit characteristics of horticultural societies, consistent with their increasing population density, intensifying subsistence base, greater market integration, and more complex sociopolitical organization (Dira & Hewlett, 2016, 2017; Garfield & Hagen, 2019; Hewlett, 2016).

Leadership among the Chabu takes traditional and non-traditional forms. In many traditional activities, leadership is ephemeral, based on individual skill, and specific to certain tasks, such as house construction or group hunting (Dira & Hewlett, 2018). The Chabu are involved in the state-mandated Kebele system, however, under which they elect individuals to formal leadership positions, defer to their authority, and can be punishing for failing to do so. Leaders nevertheless reflect the egalitarian ethos in that they are respected for their knowledge and

skills and avoid the use of aggression (Garfield & Hagen, 2019).

von Rueden and colleagues have systematically investigated leadership and determinants of social status among the Tsimane' forager-horticulturalists in Bolivia. Tsimane' households are autonomous units and do not frequently engage in large-scale collective action. Villagers occasionally hold meetings to discuss projects or resolve disputes, however, and they elect a leader to coordinate these meetings and to represent the community to outsiders. Elected village leaders and other influential villagers tend to be physically dominant, in possession of more material wealth, and perceived as more generous — traits whose effects on influence appear to be mediated by larger social networks (von Rueden et al., 2008, 2014). Such leaders are not rewarded a greater share of returns of cooperative activities but may benefit from greater social support when in need. Increasing integration with a market economy means market-related acumen is replacing traditional skills like hunting ability as a source of influence (von Rueden et al., 2008). Villages closest to the market town experience higher frequency of conflict and greater inequality in political influence (Glowacki & von Rueden, 2015), and influence associates with more extra-marital affairs and surviving offspring (von Rueden, Gurven, & Kaplan, 2011).

Glowacki and colleagues describe the emergence of leadership among the Nyangatom, a population of nomadic pastoralists in East Africa and provide a rare quantitative assessment of leadership in inter-group warfare among a small-scale society. Most Nyangatom live in mobile encampments or semi-permanent villages, however environmental harshness and the threat of conflict can force relocation or disbandment of populations. The Nyangatom frequently engage in warfare with several neighboring populations and leaders emerge in the organization of large battle raids and are active participants in planning and executing attacks (Glowacki & Wrangham, 2015). Leaders who are highly experienced raiders and are central in a large social network are critical in raid initiation (Glowacki et al., 2016). Raid participation is associated with greater lifetime reproductive success among elders. Over the short-term, though, raiding is not associated with more wives or children, and current battle leaders do not have more children than non-leaders (though small sample sizes and increased mortality may play a role) (Glowacki & Wrangham, 2015).

Smith et al. (2016) systematically compared leadership in a small sample of small-scale human societies to leadership in various non-human social species. Commonalities in human and nonhuman leadership included that leadership is largely achieved rather than inherited, and the fitness benefits of leaders and followers are not substantially different. In within-group conflict resolution and between-group interactions, power tends to be concentrated in a few individuals, whereas in other domains, such as movement, it is more diffuse. One difference is that in humans, food acquisition is more often a group activity involving leaders but in nonhuman animals is usually an individual activity without leaders, and another is that human leaders tend to lead in only one domain but nonhuman leaders typically lead in multiple domains.

## 5. Theoretical forerunners to evolutionary models of leadership

The rich body of ethnography from the first half of the 20th century led anthropologists to identify general patterns of leadership that then influenced later evolutionary theories. One important distinction was that between achieved statuses, which are attained through individual skills and competition, and ascribed statuses, which are assigned to individuals based on predefined qualities including age, sex, marriage, and kinship (Linton, 1936). Achieved leadership positions are more common in small, autonomous, kin-based societies, and therefore have been more influential on evolutionary theories of leadership, whereas ascribed positions are more common in larger, more complex societies (Lewis, 1974), and therefore are often thought to reflect cultural evolutionary processes (Johnson & Earle, 1987).

### 5.1. Big Men: force & persuasion

Mead (1935) defined leaders in small-scale societies as "Big Men," and suggested that social hierarchy emerged from aggression and intimidation coupled with respect and admiration. Among the Arapesh of Papua New Guinea, Mead (1935, p. 33) describes, "against the really violent man the community had no redress. Such men fill their fellows with a kind of amazed awe; if crossed they threaten to burn down their houses, break all their pots and rings, and leave that part of the country forever."

Sahlins (1958, 1963) further developed the Big Man model, describing ascendancy to the social role among Melanesian chiefdoms as result of a political machinations, competitive displays in culturally salient skills, and developing patterns of indebtedness through strategic generosity. Using Machiavellian cunning and superior expertise, aspiring Big Men develop a following and expand their influence. The Big Man model of leadership is consistent with much of the ethnographic record and is suggested to be a precursor to marked social stratification and inequality. For further review, see Roscoe (2000).

Kracke (1978), synthesizing his work with Amazonian indigenous groups as well as the ethnographic research of many others, proposed a bipartite theory of leadership that is very similar to the dominance versus information distinction described in nonhuman animals and the Big Man model developed by Mead and Sahlins, and which influenced later evolutionary theories of leadership. Kracke argued that dominance, based on coercive force, and persuasion, based on interpersonal trust and mutual benefit, were distinct strategies employed by leaders. Persuasion-style leader-follower relations in small-scale societies are fundamentally rooted in an emotional connection between individuals, an idea that parallels findings from some studies in Western societies that leaders tend to have superior emotional intelligence (Côté, Lopes, Salovey, & Miners, 2010; Humphrey, 2002; for discussion, see Antonakis, Ashkanasy, & Dasborough, 2009). Leaders in small, traditional societies are often a central focus of social life and actively unify followers through their exceptional abilities, extroverted personalities, and abilities to provide direct benefits to followers. Kracke (1978) claims an emotional bond built on mutual benefit and trust is a universal component of human leadership and allows leaders to maintain and expand their influence relying primarily on persuasion. Kracke's model de-emphasizes dominance and suggests that persuasion is necessary for followers to truly commit, on an emotional-psychological level, to cooperative engagement.

### 5.2. Chiefs: capital & control

Many theoretical approaches to leadership in egalitarian societies suggest that fluctuating circumstances such as increases in group size, resource accumulation and scarcity, inter-group conflict, and inter-group negotiation can relax community norms of autonomy, increase inequality, and increase community support for the emergence of more authoritarian, centralized leadership as found in chiefdoms (Ames, 2010; Bendix, 1974; Cashdan et al., 1983; Cashdan, 1980; Kent, 1989; Knauft, 1990; Mattison et al., 2016; Murphy & Steward, 1956; Powers & Lehmann, 2014; Price & Feinman, 2014). Lowie (1948) provides a framework for reconciling the variation in political authority across indigenous groups in the Americas, suggesting that egalitarianism recedes along a continuum in the wake of increased population pressure, military threat, and in association with supernatural powers increasingly bestowed to individual leaders.

One argument for the increased function and hierarchy of leadership among sedentary, non-egalitarian hunter-gatherers is that in these communities leaders provide a benefit in controlling the efficient flow of information concerning the temporal availability of critical resources and ensuring resources are appropriately distributed throughout the group (Ames, 1985). These models suggest that even among hunter-gatherers with an ethos of autonomy and egalitarianism, followers will

willingly relinquish some degree of individual autonomy when they perceive a benefit to themselves. This includes functions of economies of scale (Henrich & Boyd, 2008), seasonal variation influencing political hierarchy (Wengrow & Graeber, 2015), collective action in larger groups (Hamilton, 2000), and in the context of defensible resources (Smith & Choi, 2007). These models speak to the nature of leadership among hunter-gatherers and, in part, explain the gradations of leadership from egalitarian bands, to non-egalitarian complex hunter-gatherers, to more stratified non-foraging populations.

Johnson and Earle (1987), building on Fried and Service's schemes for classifying cultures based on social complexity, demonstrate through ethnographic and archaeological data that changes in sociopolitical organization and leadership structures across levels of cultural complexity are ultimately rooted in increased population pressures linked to subsistence intensification. Chiefdom level societies are of particular importance in understanding the development of leadership roles across cultural evolution as they represent an important transition from more egalitarian social structures to hereditary systems of social stratification. Earle (1997), building on his pioneering work on the relationship between social stratification and cultural complexity (Johnson & Earle, 1987) provides a four-fold model of how chiefs come to power that is grounded in the pursuit of prestige and dominance by some individuals within a group. Earle's (1997) model suggests that chiefs use strategies based in economic, military, spiritual, and social control to promote their interests and maintain influence over the group. The source of a chief's power has implications for the scope and stability of their leadership. Earle notes the importance of heritable social rank among chiefdoms, but emphasizes that each individual is at the center of their own kinship network and these networks can overlap significantly. Some individuals, however, are more effective at manipulating their kin network to leverage political power. Economic control is the most critical source of power within chiefdoms, yet often requires military force to facilitate and ideological systems to culturally legitimize power asymmetries. Earle (1997) insists no source of power can solely promote the emergence and stability of political institutions; however, economic control carries more weight and provides a more stable source of political power that facilitates other sources of power. This model provides an important connection between the anthropological literature on leadership in small-scale egalitarian societies to political anthropology and more general theoretical models concerning leadership in large-scale stratified societies.

The dichotomy of achieved versus ascribed positions of leadership and status is an oversimplification of political hierarchy and sociopolitical dynamics of inequality. In all societies, some egalitarian cooperative institutions can be found, and among both highly egalitarian and highly stratified societies, social structural features offer advantages to certain individuals along the lines of social, informational, or material benefits (Wiessner, 2010). Nevertheless, the predominance of achieved leadership roles in small-scale societies has had a substantial influence on evolutionary theorizing.

## 6. Evolutionary theories of human leadership

Most theories of leadership developed outside of anthropology are based on a relatively 'thin slice' of human diversity, i.e., historical or contemporary nation states (Bass & Stogdill, 1990; Keohane, 2010). Leadership in such societies can differ dramatically from patterns of leadership seen in non-state societies (von Rueden & Van Vugt, 2015). Evolutionary anthropologists aim to rectify this deficiency by developing and testing models of leadership using the entire range of cultural diversity (e.g., Garfield, Hubbard, & Hagen, 2019). Nevertheless, because humans evolved in small, politically autonomous societies of close kin, evidence from such societies plays an outsized role in most evolutionary theories of leadership.

Early 'evolutionary' theories of human societies posited a linear evolution from 'primitive' simple (and non-European) societies to 'advanced' European states (e.g., Morgan, 1877; Spencer, 1860; Tylor, 1871). This approach was rejected by most anthropologists in the twentieth century. One replacement, termed *cultural ecology*, held that social organization and social complexity culturally evolve in response to local socioecological conditions (e.g., Fried, 1967; Service, 1964; Steward, 1955; White, 1959), a theoretical approach that heavily influenced later evolutionary anthropologists (e.g., Boyd & Richerson, 1985; Smith & Winterhalder, 1992).

Modern evolutionary anthropologists combine the modern synthesis in biology (e.g., Dobzhansky, 1974; Hamilton, 1964; Mayr, 1961; Williams, 1966) that is used by animal behavioral ecologists with quantitative anthropological field methods (e.g., Borgerhoff Mulder et al., 1985; Chagnon & Irons, 1979; Cronk, Chagnon, & Irons, 2000; Hames, 1979; Hill & Hurtado, 1995; Kaplan & Hill, 1985; Smith & Winterhalder, 1992). As in animal behavioral ecology and cultural ecology, evolutionary anthropologists attempt to understand the relationship between behavior and local socioecological conditions. The main presumptions of evolutionary approaches to leadership are that the behavior of leaders and followers are likely to be explained by decision rules or psychological mechanisms that genetically evolved because they maximized the biological fitness of leaders and followers in ancestral socioecological conditions, and continue to work well in many circumstances. Leaders and followers are not necessarily distinct genetic morphs but rather share genes that promote either leader or follower behavior given the situation and the attributes of individuals. Some leader-follower patterns, however, might be better explained by cultural evolutionary approaches somewhat similar to those proposed by cultural ecologists (Richerson et al., 2016; Richerson & Henrich, 2012).

### 6.1. Are human leaders alpha males in a dominance hierarchy?

Tiger and Fox (1971), drawing on results from the relatively young field of primatology (e.g., Kawamura & Kawai, 1956; Washburn & DeVore, 1961a, 1961b), were among the first anthropologists to theorize about human behavior as a type of primate behavior. Specifically, they identified human status hierarchies and leadership as homologous with nonhuman primate status hierarchies. For them, human politics are a "breeding system" (p. 25). Leaders are dominant, and typically older males, who command "attention" (Chance, 1967), control the distribution of resources in the group, and have greater access to females (see also Tiger, 1970). Much ethnographic evidence supports their perspective. In societies ranging from egalitarian hunter-gatherers to complex chiefdoms, leaders tend to be physically formidable, influence the distribution of resources, and have more wives and children than other men (Earle, 1997; Fried, 1967; Henrich & Gil-White, 2001; Johnson & Earle, 1987; Lewis, 1974; von Rueden & Jaeggi, 2016; von Rueden & Van Vugt, 2015). In addition, the sexual dimorphism in upper body strength suggests the importance of male-male physical competition in human evolutionary history (although it might also indicate sex-specific evolution in the context of a sexual division of labor) (Dediu & Levinson, 2018; Puts, 2010; Puts, Hodges, Cárdenas, & Gaulin, 2007; Shipley & Kindscher, 2016).

Boehm's (1993) Reverse Dominance Hierarchy theory challenges this view. Boehm contends that whereas primate societies are characterized by a linear dominance hierarchy with priority of access to resources and social control vested in high ranking alphas, the social systems of egalitarian humans are characterized by systems of control with power ultimately vested in the group. Despite social hierarchy, norms and leveling mechanisms limit the coercive ability of individuals. Faced with overly assertive leaders, followers have the freedom and ability to disband, depose leaders, or in extreme circumstances assassinate undesirable leaders (Boehm, 1993, 1999, 2008). Boehm's theory is informative to the degree it also accurately describes patterns in the ethnographic record. The causative mechanisms, however, are problematic. For Boehm, followers maintain the egalitarian ethos purposefully

(also see Boehm, 1982; Lee, 1979; Woodburn, 1982), which implicitly downplays the social and environmental conditions underlying egalitarianism. In focusing on the maximum costs followers are willing to accept from poor leadership, his theory overlooks the complexity of social trade-offs and the mutual benefits received by leaders and followers (Price & Van Vugt, 2014; von Rueden et al., 2014). Finally, there are circumstances within egalitarian societies where a dominance hierarchy model may be more applicable. Gusinde (1937), for instance, reports of powerful Ona shamans in Tierra del Fuego who lacked officially sanctioned positions of leadership, yet were able to control large groups of followers through the threat of ritual attack and sporadic displays of intense physical aggression. The Reverse Dominance Hierarchy theory has nevertheless been influential within anthropology and other fields (e.g., Hogan & Kaiser, 2005).

### 6.2. Human leadership based on intelligence, knowledge, and skills

Another challenge to the dominance model, which parallels emerging views about animal leadership and much of the ethnographic record, is that human leadership relies more on information than on physical formidability. James Neel, based on his work with South American horticulturalists in collaboration with anthropologist Napoleon Chagnon, focused on the role of headmen (see Section 4.2) (Chagnon, 1968; Neel, 1970, 1980; Neel & Salzano, 1967). Because headmen are typically skilled hunters, verbose, knowledgeable of tribal lore, and are accomplished warriors, Neel (1980) suggests that although physical strength is an asset in campaigns for headmanship, *mental agility* is even more critical. Neel proposed an *index of innate ability*, "a quantitative trait certainly related to intelligence, based on the additive effects of alleles at many loci" (Neel, 1980, p. 285). Neel's index of innate ability is closely related to what many evolutionary anthropologists now refer to as embodied capital, defined as an organism's investment in its own physical and cognitive capabilities via growth, development, and learning (Kaplan, 1996; Lancaster & Kaplan, 2010), or, more specifically, neural capital, the cognitive and neural components of embodied capital (Kaplan, Mueller, Gangestad, & Lancaster, 2003).

Many scholars have discussed the importance of intelligence and knowledge in leadership (e.g., Cavazotte, Moreno, & Hickmann, 2012; Connelly et al., 2000; Henrich et al., 2015; Judge, Colbert, & Ilies, 2004; Roscoe, 2007; Van Vugt & Kurzban, 2007; Wilson, Near, & Miller, 1996). Neel's contribution is his early recognition that because leaders in traditional societies tend to have more wives and children than other men, there would be strong sexual selection on traits that predispose to leadership, i.e., his index of innate ability, or important aspects of embodied capital (Neel, 1970, 1980; Neel & Salzano, 1967). Neel's ideas therefore implicate leadership dynamics in the dramatic increase in brain size over human evolution (encephalization) (Garfield et al., 2019).

Neel's theory was only loosely constructed, and he never specified exactly how mental agility predisposed to leadership, or why leaders were attractive as mates. Garfield et al. (2019) operationalize Neel's theory by combining the concepts of embodied and neural capital (Kaplan, 1996; Kaplan, Lancaster, Johnson, & Bock, 1995; Kaplan et al., 2003; Lancaster & Kaplan, 2010; von Rueden, 2014) with sexual selection and reproductive skew (discussed further in the following section) (Betzig, 1986; Darwin, 1871; Johnstone, 2000; Kokko & Jennions, 2003; Vehrencamp, 1979). Garfield et al. (2019) then fill the two gaps in Neel's model. First, ascending to a leadership position often depends on developing a reputation for high-quality decision-making that benefits the group, and such decision-making is a cognitively demanding task. Hence, individuals with greater embodied capital, especially neural capital, are more likely to become leaders. Second, in humans, a male and female cooperate for decades to raise their mutual offspring, and individuals who choose good decision-makers as mates would benefit with higher rates of success in the cooperative childrearing endeavor. Hence, individuals who develop a reputation for high-quality decision-making that benefits others will tend to be chosen as leaders and mates. For details, see Garfield et al. (2019).

Barkow et al. (1975), working independently of Neel, directly critiqued the Tiger and Fox (1971) dominance model, similarly arguing that in human social hierarchies, culturally acquired skills and knowledge play more important roles in acquiring status and competing for resources and mates, and physical formidability and aggression play less important roles than in ape social hierarchies. Specifically, men who mastered complex, culturally transmitted skills were able to acquire more resources and therefore were able to use these resource to attract more mates (Barkow, 1989).

In support of Barkow (1980), complex symbolic material culture appears in the paleoanthropological record after the appearance of modern *H. sapiens*, suggesting that this might be a unique feature of our species (there is little consensus on whether our sister species, *H. neanderthalensis*, was capable of complex symbolic culture, although there is increasing evidence that they were) (d'Errico et al., 2016; Foley, 2016). Barkow's critique and reformulation is also well-supported by the ethnographic evidence. In most egalitarian societies, aggressive leaders are strongly disfavored; leaders are instead respected for important skills such as hunting, healing, warfare, and ritual knowledge (Boehm, 1993, 1999; Fried, 1967; Garfield et al., 2019; Henrich & Gil-White, 2001).

### 6.3. Contemporary genetic evidence for sexual selection

The theories of Tiger and Fox (1971), Neel (1980), and Barkow (1980) all predict that leaders attract more mates and have more children than other men. In support, the association of high status and leadership positions with greater reproductive success, particularly for men, is an incredibly robust finding (von Rueden & Jaeggi, 2016). Biased reproduction, also referred to as *reproductive skew*, is observed in high-ranking males in many nonhuman species as well (Kokko, 2003; Shen & Reeve, 2010; Vehrencamp, 1983).

These theories rest not only on the relative reproductive success of leaders in contemporary societies, however, but on the biased reproduction of some men over hominin evolution. Recent genetic evidence indicates a long evolutionary history of male-biased reproductive skew in humans (Batini & Jobling, 2017; Hammer, Mendez, Cox, Woerner, & Wall, 2008; Heyer, Chaix, Pavard, & Austerlitz, 2012; Jobling & Chris, 2017). By comparing variation in mtDNA (inherited from mothers only) to non-recombining Y chromosomal regions (inherited by sons from fathers only) in a large multi-regional sample of genomes, both Lippold et al. (2014) and Karmin et al. (2015) conclude that, pre-dating the migration of modern humans from Africa, there was a consistent bias in favor of female effective population size over that of males (i.e., relatively fewer males reproduced). This could indicate either a long evolutionary history of polygyny and/or sex-specific migration, and/or matrilineality (Oliveira et al., 2018).

Tentatively interpreting the results from Karmin et al. (2015) as evidence of male reproductive skew (Fig. 1), there were approximately 3 reproducing females for every reproducing male from 140 to 30 thousand years ago (KYA), with some fluctuation during the expansion of out Africa c. 80–50 KYA. This ~ 100 KYA time span might have been sufficient for sexual selection to have acted on the evolution of the psychological mechanisms underlying prestige, mating, and leadership-followership, especially if the pattern seen here extended even further into the past.

The dramatic increase in this ratio starting after the glacial maximum c. 20 KYA, peaking at > 16 in the early-to-mid Holocene, has been attributed to a combination of a transition to patrilineal social organization coupled with intensive warfare that would have killed many men in some patrilineages, leading to extinction of their Y-chromosome lineages, and hence low Nm. Women, on the other hand, would not have been killed but instead would have joined the victors'

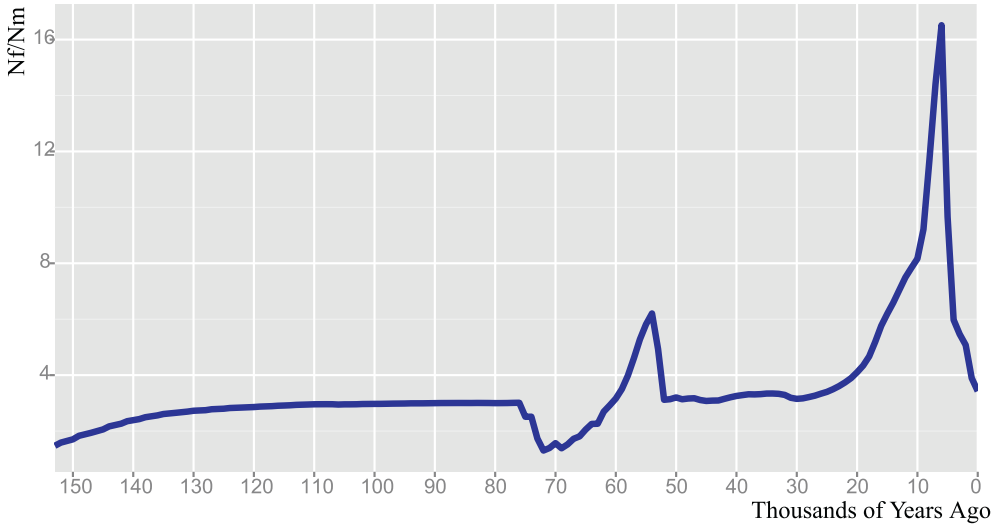


**Fig. 1.** The temporal dynamics of the ratio of female (Nf) and male (Nm) effective population size in the last 140 KY. The ratios of the global accumulative Ne estimates of mtDNA (Nf) and Y chromosome (Nm) are plotted against the time (in thousands of years) back from the present (0). The BSPs estimates of Ne were obtained in BEAST using a piecewise-linear coalescence model. Source: Figure and caption from Karmin et al. (2015).

patrilineages (Zeng, Aw, & Feldman, 2018). These factors, combined with other sociocultural factors such as the emergence and expansion of inequality, concentrations of power and wealth, and social prestige have likely contributed to increased variance in reproduction among human males in the last 10,000 years (Heyer et al., 2012; Karmin et al., 2015; Webster & Wilson Sayres, 2016). The potential impact of sexual selection over this much shorter time period, however, is less clear.

These analyses are consistent with the robust finding that male polygyny is common across a diverse range of both egalitarian and socially stratified traditional societies (Low, 1988; Murdock, 1967), and, importantly, is often limited to those of high social status and those in positions of leadership (Cronk, 1991; Fieder & Huber, 2012; Gurven & von Rueden, 2006; Irons, 1979; Marlowe, 2005; von Rueden & Jaeggi, 2016). Many factors can impact estimates of effective population size, however, and there are numerous technical challenges to investigations of sex-biased demography using genetic variation (Webster & Wilson Sayres, 2016), so these interpretations must be treated with caution (Batini & Jobling, 2017).

### *6.4. Theories on leadership in the context of the evolution of collective action*

Humans, as a species, are reliant on high levels of coordination and cooperation among groups of individuals who are often either distant relatives, or non-relatives. The evolution of cooperation in such settings faces well-known barriers, such as free-riding and coordination (Axelrod & Hamilton, 1981; Olson, 1965). Many researchers have proposed that leadership might have evolved, at least in part, to solve such collective action problems by monitoring individual behavior, sanctioning free-riders, rewarding contributors, and solving coordination problems (Gavrilets & Fortunato, 2014; Glowacki & von Rueden, 2015; Hooper, Kaplan, & Boone, 2010; Price & Van Vugt, 2014; Ruttan & Borgerhoff Mulder, 1999; Tooby, Cosmides, & Price, 2006; Van Vugt & Kurzban, 2007). The main idea is that leaders will assume the costs of leadership to the extent they are compensated by followers or receive positive reputations that attract future aid and mating opportunities (e.g., Glowacki & Wrangham, 2013; Hooper et al., 2010; Smith & Choi, 2007). According to human behavioral ecology – the evolutionary ecology of human behavior – how adaptive decision-making at the individual level leads to political institutions will also vary in the degree to which it results from conflict versus cooperation (Boone, 1992).

Variation in the qualities of leaders, followers, and group structure can significantly impact the likelihood that cooperative collective action will succeed. Evidence from small-scale societies suggests that social structural features such as age-grades and formalized roles can facilitate collective action in large groups. Coordination and sanctioning will also be enhanced by, and be less costly for, leaders who possess specific phenotypic qualities such as strength and height, as well as social capital including large social networks, allies, and a large kin group (Glowacki & von Rueden, 2015; von Rueden, Gavrilets, & Glowacki, 2015). Additionally, followers may prefer, and be selectively adapted, to engage in cooperation and collective activities when leaders possess a reputation for prosocial investments (Henrich et al., 2015; Macfarlan & Lyle, 2015). Some authors have highlighted increasing group size, e.g. “scalar stress,” role specialization, e.g. “managerial mutualism,” and resource base limitations as important factors in the transition from egalitarianism to hierarchy within groups and societies (Boone, 1992; Eisenstadt & Roniger, 1980; Johnson, 1982; Kaplan, Hooper, & Gurven, 2009; Mattison et al., 2016; Service, 1975; Smith & Choi, 2007).

Gavrilets and Fortunato (2014) proposed an alternative involving competition among leaders of different groups. In this model, if dominants (e.g., leaders) within groups gain a disproportionate share of the public benefits of between-group competition, then the dominants will pay the cost to compete with other groups even though some of their fellow group members free ride. Thus, in the absence of between-group conflict, humans might prefer more egalitarian social organization, as observed in most extant foragers, which would reduce the importance of leaders in collective actions. In the presence of between-group conflict, however, humans might prefer more hierarchical social organization, which would increase the importance of leaders in collective actions against other groups. Doğan, Glowacki, and Rusch (2018) provide some empirical support for this model using experimental economic games among participants from three Ethiopian populations and find that both the nature of between-group relations and the distribution of resources from between-group conflict influence individual motivations to pursue violent between-group conflict. These results suggest that when a high-ranking leader is highly incentivized they will likely pursue offensive strategies independent of the interest of the group.

The political inequality of particular human societies, relative to more egalitarian hunter-gatherer ancestors, are often shaped by rates of inter-group violence over the society's history (Johnson & Earle, 1987; Kaplan et al., 2009; Mattison et al., 2016), though hunter-gatherers engage in warfare (see Glowacki et al., 2017). In larger groups, particularly those facing greater internal or external conflict, encompassing larger territories, and relying on defensible resources, group members may willingly cede greater decision-making and sanctioning authority to leaders, given the functional benefits of leader-follower relationships in such contexts (Glowacki & von Rueden, 2015; Hooper et al., 2010;

Service, 1964). Among pastoralists, for example, cross-cultural evidence suggests a high degree of intergenerational transmission of material wealth, owing to kin-based control and inheritance of herds, positive assortative mating between wealthy kin groups, and benefits from economies of scale in herd management and labor (Borgerhoff Mulder et al., 2010). The defensibility of material resources, such as herds, grazing grounds, and water access, facilitates institutionalized leadership structures and heritability of economic and political influence (Glowacki & von Rueden, 2015). Such conditions are also often associated with high rates of inter-group conflict. Warfare has likely been a recurrent threat over human evolutionary history (Glowacki et al., 2017; Lopez, 2016) and represents a collective action dilemma often associated with strong leadership (Chagnon, 1988; Glowacki & Wrangham, 2013; Otterbein, 1997).

Kaplan et al. (2009) integrate several of the foregoing ideas. They suggest that certain universal features of human social structure, such as the inheritance of various forms of wealth, food sharing, cooperation, and risk-pooling, are a consequence of adaptations to a human-specific foraging niche involving the social learning of complex skills targeting high return but highly variable food sources, such as large game (see also Kaplan et al., 2000). The resource base in different subsistence systems will vary in their economies of scale – which promote various forms of managerial leadership – and in their defensibility – which promotes various forms of dominance hierarchies and social stratification. See Table 1.

### 6.5. Gene-culture coevolutionary theories of leadership based on information, skills, and experience, and implications for human cooperation

Henrich and Gil-White (2001) agreed with Tiger and Fox (1971), Kracke (1978), and Barkow (1980) that human status hierarchies are based on both dominance and prestige. They disagreed, however, that Barkow (1980) provided a convincing evolutionary account of human prestige: why should men defer to other men who are better able to provide resources to women? Henrich and Gil-White (2001) draw on a large body of research, often referred to as gene-culture coevolutionary theory, that suggests social learning – culture – is one of the key traits that distinguishes humans from other primates (Boyd & Richerson, 1985). This unique human trait then explains unique aspects of human status hierarchies. Culture involves individuals learning from other individuals (Cavalli-Sforza & Feldman, 1981; Cavalli-Sforza, Feldman, Chen, & Dornbusch, 1982). This raises the question: is it better to learn from some people than others? Henrich and Gil-White (2001) argue that, due to differential skill levels in culturally learned behaviors, less-skilled individuals would benefit by learning from the most-skilled individuals. By showing deference to those with greater knowledge and skills, the less knowledgeable and skilled can gain access to them so as to acquire their knowledge and skills. Once common, such patterns of deference could then be utilized by new learners to decide from whom to learn, i.e., copy the most 'popular' or prestigious members of the group (Henrich & Gil-White, 2001). Thus, like the theories of Neel and Barkow, this theory has strong parallels with the information-based theories of animal leadership (c.f., Chapais, 2015).

Henrich et al. (2015) extend the foregoing model by mathematically modeling how group members can become more cooperative by copying cooperative leaders, which can then drive natural selection on leaders to be even more cooperative. Their Big Man Mechanism suggests that cooperation is often rooted in prestige-based leadership, prestige-biased learning, and positive assortment of leaders and followers. In the Henrich et al. (2015) models, cooperation can emerge from emulation biases and, unlike some of the collective action models reviewed above, can be maintained in the absence of punitive sanctions if followers are preferentially modeling their behavior after prosocial leaders. Leaders whose influence stems from information-based prestige can expand their influence via other strategies, including dominance and non-informational prestige (Henrich et al., 2015).

Many studies in Western populations provide evidence that learners preferentially copy, and direct attention to, prestigious individuals and those that are high in the social hierarchy (Cheng et al., 2013; Cheng, Tracy, & Henrich, 2010; Foulsham, Cheng, Tracy, Henrich, & Kingstone, 2010; Henrich & Henrich, 2007; Maner, DeWall, & Gailliot, 2008; Richerson & Henrich, 2012), which could indicate that variants in human culture facilitate cultural group selection for human cooperation, through, for example, social learning mechanisms and biases (including conformism and prestige biases), social norms and institutions, symbolic markers of groups and individuals, and complex social institutions (Richerson et al., 2016). According to this perspective, leadership stands to play a significant role in cultural group selection

**Table 1**
Cultural variation in dimensions of social organization, including leadership, summarized by categorization by subsistence base reproduced from Kaplan et al. (2009).

| subsistence system (resource base) | intergenerational relations | male–female relations | scale of cooperation, leadership | inequality |
|---|---|---|---|---|
| *foragers* (mobile prey and widely distributed gathered resources) | intergenerational provisioning, little inheritance | predominant monogamy, bride service | cooperative production and risk reduction, small-scale leadership | relative egalitarianism |
| *stratified foragers* (concentrated and predictable foraging sites) | intergenerational provisioning, inheritance of foraging sites | some polygyny, bride capture | cooperation and leadership in production and warfare | stratification, slavery, unequal access to prime foraging sites |
| *horticulturalists* (labour-limited cultivation) | intergenerational provisioning, little inheritance | some polygyny, bride capture | cooperative field labour, big men manage conflict over land | relative egalitarianism |
| *pastoralists* (livestock) | intergenerational provisioning, inheritance of herds | significant polygyny, bride wealth and bride capture | cooperative husbandry, chiefs manage conflict over herds and grazing land | significant inequality in herd-based wealth |
| *agriculturalists* (concentrated, high-quality land) | intergenerational provisioning, inheritance of land, primogeniture | significant polygyny, female claustration and dowry | cooperation and leadership in large-scale warfare and public works | stratification, slavery, high inequality in land-based wealth |

models as leaders can greatly facilitate the adoption of successful cultural norms, attract group members and promote prosocial behavior; these models also suggest that egalitarian social norms may facilitate large-scale cooperation in the absence of formal leadership roles (Henrich et al., 2015; Richerson et al., 2016).

The prestige-biased learning model does not directly account for the increased mating success of prestigious leaders, however, nor the pronounced male-bias in leadership, and examples of adults copying prestigious leaders are relatively rare in the ethnographic record (Garfield, Garfield, & Hewlett, 2016; Garfield et al., 2019). See commentary in Richerson et al. (2016) for thorough discussion and critiques of gene-culture co-evolutionary models of cooperation and leadership.

## 7. Evolutionary psychological approaches to leadership

Studies of leadership in evolutionary anthropology, which mostly involve observations of behavior in real-world settings, inform, and are informed by, experimental work on leadership in evolutionary psychology. Building on observations by anthropologists that leadership is a universal trait of human groups, evolutionary psychologists have claimed that there are universal psychological decision-rules that emerge across development and facilitate leader-follower interaction. These psychological adaptations evolved over our species' evolutionary history because they facilitated the resolution of recurrent adaptive problems such as coordination and collective action problems (Tooby et al., 2006; Van Vugt, Hogan, & Kaiser, 2008; Van Vugt & Ronay, 2014; Van Vugt & Tybur, 2014).

### 7.1. The ontogeny of leadership

Evolutionary developmental psychologists have extensively investigated status hierarchies and social dominance among children, often in collaboration with anthropologists. Children face at least two challenges concerning social hierarchy: they must learn the existing patterns of hierarchical social relationships, i.e., the intergenerational social hierarchy of adults, and they must be prepared to contribute to and strategically navigate the emerging social hierarchy of their peers, i.e., the intragenerational social hierarchy of children. Evidence for the development of leadership behavior include (1) adaptations for cooperation in infants, (2) the impact of cultural variation in childcare on social behavior, social learning of cultural norms and selective trust, and (3) strategies of resource control, social dominance, and leadership among children.

Leadership often stems from cooperation among leaders and followers. Comparative psychologists have looked for unique components of human cognition related to cooperation, prosociality, and social norms (Tomasello & Gonzalez-Cabrera, 2017). Infants as young as 18 months demonstrate capacities for cooperation including commitment to a joint goal, understanding their unique role, and providing assistance to fellow cooperators (Moll & Tomasello, 2007). In experimental games, chimpanzees are skilled in manipulating social relationships and information to receive an individual payoff, as are human children. Unlike chimpanzees, however, human children are able to engage in true cooperation by encouraging other individuals to cooperate, identifying their unique role in a cooperative task, and deferring or leading as necessary to maintain a cooperative activity (Warneken, Chen, & Tomasello, 2006). This suggests that learning the complex nature of nested spheres of cooperation and deference, which are central to leader-follower dynamics, constituted a strong selective pressure in the human lineage since the LCA with chimpanzees.

Building on attachment theory (Bretherton, 1992; LeVine & Norman, 2008), anthropologists have documented an effect of cultural variation in infant-caregiver relations on the development of selective trust and social relationships. Leadership necessarily involves the relinquishing of autonomy by followers (freely or coerced), a process often rooted in the trust of leaders by followers. The intimate nature of social life and child rearing among hunter-gatherers, which includes increased physical contact between caregivers and infants relative to small-scale farming communities and industrialized populations, is suggested to shape internal models of trust and social relationships (Hewlett, Lamb, Leyendecker, & Schölmerich, 2000). Across development, children are not indiscriminately trusting of social superiors, but selectively trust those who have previously provided reliable information and those who behave in ways more consistent with group-level norms (Harris & Corriveau, 2011). In support of the importance of social developmental environments, research within managerial contexts suggests that leaders who were undermined within the family through, for example verbal abuse, are more likely to exhibit abusive supervisory behaviors (Kiewitz et al., 2012). Parental figures are the first leaders children follow and these early experiences can impact behavioral models. Comparative analyses of social learning among hunter-gatherers suggest that parents actively teach children specific cultural values, including sharing norms and age-graded social distinctions (Garfield et al., 2016). This also suggests that social dominance and patterns of deference might function to facilitate informational exchange. For infants and children, learning the nuances of social hierarchy quickly and efficiently is critical. Also, such psychological processes suggest that the benefits of maintaining group cohesiveness, a function of leader-follower dynamics, are significant. Features of the social environment of children across development may ultimately perpetuate the degree of community egalitarianism and provide children with cues of existing patterns of deference, ultimately influencing leadership and followership.

Research on leadership among children primarily focuses on social dominance, which is defined as variation in the ability to acquire and control resources in a social group and is known to emerge early in development (Hawley, 1999). Early approaches to social dominance investigated similarities between children and nonhuman primates. Behavioral markers of social dominance from ethology (e.g., physical attacks, threat gestures, and object/position struggles), when used individually, proved reliable in assessing dominance among children. Different markers yielded different rankings among children, however, suggesting that ephemeral coalitions, contextual factors, and social learning create a more dynamic social hierarchy among human children than among nonhuman primates (Savin-Williams, 1976; Strayer & Strayer, 1976).

Developmental psychologists have repeatedly documented that males have stronger, more salient dominance hierarchies (Hold-Cavell, 1996; McGrew, 1972), and have often portrayed young girls as lacking expressions of dominance and overt aggression (Lorenz, 1966). Some developmental psychologists have claimed female children lack dominance hierarchies entirely (McGrew, 1972). Patricia Hawley has been a leading proponent suggesting that a more complete understanding of social dominance among children and adolescents should incorporate both coercive and prosocial behaviors (Hawley, 1999). Evidence from Western preschoolers suggests that socially dominant children employ both coercive and prosocial strategies in resource control and children prefer dominants who do so as partners in play (Hawley, 2002, 2003). Despite male-biases in direct aggression and coercive strategies, boys and girls are perceived as equally skilled in resource control when both prosocial and coercive strategies are taken into account (Hawley, Little, & Card, 2008). Hawley's works suggest that social dominance among children is more complex than among primates, but, when prosocial and coercive strategies are considered, the nature of social hierarchy observed across development is similar in functionality compared to nonhuman primates despite distinct behavioral profiles, such as a reduction in the importance of physical dominance as children mature.

There is very little evidence on social dominance and leadership among children in small-scale societies. In one study comparing children from an industrialized and a hunter-gatherer setting, high status individuals initiated activities and organized collective behavior. Among hunter-gatherers, however, lower ranking children were more

likely to initiate collective activities and to engage in physical contact with others compared to lower ranking children in industrialized populations (Hold, 1980).

More research on leadership and social dominance among children in small-scale societies is needed. What remains unclear is how and if attention structures in dominance hierarchies among children translate into social hierarchy and leadership among adults. Subordinates may preferentially pay attention to dominants both out of fear and respect. Cross-cultural evidence does suggest that being the center of attention in a group, rather than having the attention in dyadic relationships, is associated with leadership among children, and children often gain this attention through initial aggressive displays, even when later leadership strategies include prosocial and persuasive techniques (Hold-Cavell, 1996). Children are keenly aware of relative positions in a social hierarchy and direct attention to dominant individuals; dominant individuals utilize biased attention to employ a range of leadership styles.

In summary, the ontogeny of social dominance among children has clear parallels with, and is best understood in the context of dominance hierarchies among nonhuman primates, but also diverges from primate patterns in important ways. Both coercive and prosocial behaviors are important among children, and the later likely equalizes status asymmetries between the sexes. Children demonstrate evidence of psychological adaptations for hierarchy within their age-grade and also in preparation for joining the existing social system of adults. To date, no theory of dominance or leadership addresses the relationship between the ontogeny of social dominance and inter-individual differences in attention structure and leadership style, though many theories are engaging and developing these concepts. For further review, see Redhead, O'Gorman, and Cheng (2018).

### 7.2. Evolved leadership psychology in adults

Evolutionary psychology has produced evidence for universal adaptations related to leadership and followership in adults. A species-typical leader-follower psychology, including multiple distinct psychological mechanisms, is suggested to have evolved from an ancestral primate psychology, shaped by natural selection over the course of human evolutionary history (Tooby & Cosmides, 1992; Tooby et al., 2006; Van Vugt & Grabo, 2015; Van Vugt et al., 2008). Therefore, the traits of, and preferences for leaders today, will often relate to the conditions recurrently faced by our evolutionary ancestors.

Psychological mechanisms related to leadership include preferences for leaders based on physical characteristics and reputations for fairness and prosociality. Across diverse organizations, male leaders are often taller than non-leaders (Hamstra, 2014; McCann, 2001; Stulp, Buunk, Verhulst, & Pollet, 2013), suggesting that physical height has been an adaptive characteristic of male leaders across evolutionary history. Biases towards physically formidable leaders may stem from dominance-based leadership, or the ability of taller, stronger leaders to promote within group cooperation (Lukaszewski, Simmons, Anderson, & Roney, 2016; von Rueden et al., 2014). Followers also consistently demonstrate preferences for fair and prosocial leaders, suggesting that follower psychology is designed to assess the degree to which relinquishing personal autonomy to a leader will result in individual and group benefits (Bøggild & Petersen, 2016; Petersen, 2015a, 2015b). Individuals are highly cognizant of the quality of potential coalitionary partners and people prefer individuals with capacities for leadership, skills in strategic planning, physical strength, and the ability to motivate others as allies (Sugiyama, 2005; Tooby et al., 2006). Furthermore, we possess psychological adaptations for assessing several of these features based on physical appearance or individual reputations (Hawley, 1999; Puts et al., 2007; Sell et al., 2010, 2009). These and other preferences are often theorized and found to be facultative, dependent for example upon the intensity of within or between group conflict or the distribution of wealth inequality (Laustsen & Petersen, 2015, 2017; Ronay, Maddux, & von Hippel, 2018; Spisak, Blaker, Lefevre, Moore, & Krebbers, 2014).

Drawing on the near universality of prestige-based leadership across cultures, Price and Van Vugt (2014) suggest that elaborated prestige systems are the result of adaptations promoting reciprocal exchange between leaders and followers. In this model, followers voluntarily forfeit some degree of autonomy by accepting the influence of a leader. Leaders provide services for the group, such as monitoring free riders, enhancing group protection, and punishing individuals who break social norms. In return, followers collectively provide prestige to individuals who display quality leadership (Price & Van Vugt, 2014, 2015). This model frames leader-follower relations as a series of costs and benefits and suggests that human prestige systems are a solution to collective action problems. The system is held in balance as long as followers have bargaining power over leaders and can resist tendencies towards dominance. Several predictions follow from this service-for-prestige theory of leadership. Specifically, disrespectful followers of good leaders should be targeted by the group and punished; additionally, followers that do not express punitive sentiment towards bad leaders should be targeted by the group and punished (Price & Van Vugt, 2014).

The underlying psychological tools used to interact with leaders are likely functioning in similar ways to that of our hunter-gatherer ancestors. The adaptations described by evolutionary psychologists, however may or may not be associated with effective leadership in contemporary contexts (Van Vugt & Ahuja, 2010). Despite potential for mismatch, adaptations for leadership and followership are nonetheless illustrative of the ancestral selection pressures which shaped the design features of our species' leader-follower psychology.

## 8. Female leadership and sex differences in leadership

In recent decades, a focus on female leadership has emerged in anthropology and across the social sciences (e.g., Appelbaum, Audet, & Miller, 2003; Arvey, Zhang, Avolio, & Krueger, 2007; Garfield & Hagen, 2019; Garfield et al., 2019; Low, 2005; Ross, 1986; Van Vugt & Spisak, 2008; von Rueden et al., 2018). We review anthropological analyses focusing on gender differences in leadership and social influence, many of the influential theories, and evidence for sex-specific leadership styles.

### 8.1. Gender differences in leadership in the ethnographic record

A male bias in leadership is a near cross-cultural universal and in a large sample of non-industrial societies, political leadership positions were exclusive to men in approximately 88%. Among the 10% of societies in which women did occupy leadership positions they were either less numerous or less powerful than their male counterparts (Whyte, 1978). Female leadership has traditionally been under-investigated across the social and biological sciences, however (e.g., Lewis, 1974; Stogdill, 1948), and the political lives of women have been grossly overlooked in the ethnographic record as well (Low, 2005; Rosaldo, 1974; Roscoe, 2000). Early ethnographers, at least on occasion, denigrated the cultural domains in which women were the primary agents (Reiter, 1975) in favor of focusing on the more public and aggrandizing politics of men in small-scale societies (Rosaldo, 1974). Additionally, much of the ethnography on the lives of women has been filtered through male informants and composed by male ethnographers, leading some feminist scholars to discount much of the ethnographic record of women generally (Reiter, 1975), though other scholars are critical of this position (Whyte, 1978). Hence, the male bias in leadership could, at least in part, represent a bias on the part of ethnographers.

Egalitarian societies, which are often characterized by increased gender equality, do allow for increased female leadership relative to more socially stratified societies (Dahlberg, 1981; Dyble et al., 2015; Endicott & Endicott, 2008; Leacock, 1978). Draper (1975) documented

that women among more mobile !Kung bands had greater political influence compared to more sedentary populations. Nevertheless, even in most egalitarian societies men tend to occupy positions of political leadership (Collier & Rosaldo, 1981). Women's political influence appears to be restricted by the demands of motherhood and female work. Among the Mekranoti-Kayapo in the Brazilian Amazon, increased investments in child care are negatively associated with group level influence in that mothers with greater parenting demands are less influential than women with less or no parenting demands (Werner, 1984). Brown (1970) suggests that the division of labor and the local political structure in traditional societies are similarly shaped by maternal demands. The subsistence activities of women are more likely to be those that are more compatible with childcare (Brown, 1970; Pasternak, Ember, & Ember, 1997). Such qualities include tasks that are located close to home and are compatible with frequent interruptions from needy children. While these activities prioritize successful parenting, they also serve to restrict women's ability to play a larger and more active role in local politics, at least while women are in their child rearing years.

Though motherhood and domestic responsibilities seem to limit female leadership, postmenopausal changes are often associated with increased status opportunities, prosocial investments, and wider political influence. Brown (1985) outlines three reasons for women's middle age status mobility and increased leadership in small-scale societies. First, the end of their reproductive careers often provides women freedom from culturally specific restrictions (for example, menstrual customs) and the constraints of childcare, giving them the opportunity to maximize their social influence and enjoy greater mobility. Next, middle age grants a woman administrative authority over her juniors; she has the right to delegate tasks and organize the labor of her younger family members and also exert greater influence in important matters concerning youths' eligibility for initiation and marriage. Brown (1985) concludes that middle age provides women with avenues for extra-domestic recognition through the pursuit of special status positions such as curer, midwife, or ceremonial leader. Ethnography reveals status competition and prosocial expressions of dominance in the context of cooperative breeding can yield dividends later in life when high status women emerge as major political leaders in many small-scale societies.

### 8.2. Gender differences in leadership styles

Determining which aspects of leadership we observe in males and females are attributable to a sex-specific psychology versus sociocultural constraints and expectations is a difficult challenge and politically contentious. Our Western stereotype suggests that women will tend to lead in an interpersonally oriented style while men will tend to focus on task-oriented leadership styles (Eagly & Johnson, 1990). Results from empirical studies have been mixed, with some identifying sex-differences in leadership (Buss, 1981; Helgesen, 1995; Hennig & Jardim, 1978) and others suggesting that there are more similarities between male and female leaders than differences (Bass & Stogdill, 1990). Buss (1981) suggests that the expression of dominance among men is more likely to serve immediate individual level goals whereas for women dominant behavior is more likely to increase within-group cohesion; women do engage in dominant behavior, but tend to do so in a gendered way.

Eagly and Johnson (1990) conducted a meta-analysis of organizational, laboratory, and assessment leadership studies and found that women and men do in fact lead in gender specific ways, however these patterns do not fit standard stereotypes consistently. In organizational datasets, males and females did not differ largely in terms of their leadership styles. However, in laboratory and assessment based studies, women tended to employ a more democratic style of leadership and men a more autocratic style (Eagly & Johnson, 1990). Eagly's work provides the most robust findings and makes connections between mainstream managerial research and biological-evolutionary theory, however, major mainstream reviews on female leadership have overlooked this research (e.g., Appelbaum et al., 2003).

### 8.3. Theories on female leadership

Much theoretical work on sex differences in leadership seeks to explain the near universal male bias in political leadership. Some early biologically deterministic approaches suggested that leadership was an innate, sex-linked trait exclusive to males (reviewed in Bass & Stogdill, 1990). Anthropological theories, however, have implicated cultural-ecological factors which constrain female leadership and promote male leadership. One theory suggests that because males travel more than women they have greater knowledge of the outside world including neighboring groups, which gives those males with high mobility an advantage in developing alliances, addressing threats from potential rivals, and access to wider economic opportunities (Pasternak et al., 1997).

Another group of theories propose that because males are nearly universally exclusively involved in warfare (Glowacki et al., 2017; Rosen, 2009; Whyte, 1978) and much of leadership concerns decisions regarding between group conflict, it may be optimal to have those with experience in warfare, e.g. male warriors, occupy the highest level political positions (Pasternak et al., 1997). Therefore, male political power may be in part a result of male participation in warfare. Experimental data from Western undergraduate students suggests that part of our leader-follower psychology encourages the acceptance of male leaders in cases of intergroup competition and female leaders in cases of intragroup competition (Van Vugt & Spisak, 2008).

Some evolutionary psychologists have suggested that women are less interested than men in status attainment and leadership positions due to adaptations promoting individual safety and limited indirect, agnostic competition (for review, see Björkqvist, 1994). There is ethnographic evidence, however, indicating women do pursue positions of influence and benefit from leadership roles (Brown & Kerns, 1985; Endicott & Endicott, 2008; Goodale, 1971). Other evolutionary scholars have therefore worked to identify the female-specific evolutionary psychology and biology of leadership roles and status competition (Campbell, 1999, 2002; Duque-Wilckens & Trainor, 2017; Hess & Hagen, 2006a, 2006b; Vandermassen, 2008).

Although some scholars, primarily focused on post-industrial societies, have downplayed the importance of motherhood in social rank for women (Castro, 1990), evolutionary feminist scholars have suggested that intrasexual competition, deference, and respect (e.g., leadership) among women will often revolve around motherhood and domestic skills (Brown & Kerns, 1985; Hrdy, 1999, 2011). An evolutionary theoretical perspective suggests that female coalitions will function to maximize offspring survival by eliciting paternal investment, investing strategically in allomaternal care, and cooperating within the kin group rather than the larger community (Low, 1992). These aims are likely best met through social networks of information sharing (Hess & Hagen, 2006b). When women do directly pursue political leadership positions, they should involve domains which allow them to receive reproductive benefits to themselves or their kin group. Most critically, an evolutionary perspective on female leadership suggests that men and women will differ in their political strategies, and that while for men within-group cooperation may be most beneficial for enhancing between-group competition and achieving leadership positions, for women, within-group cooperation is likely to be more circumscribed and focused on recruiting allomaternal care (Vandermassen, 2008).

von Rueden et al. (2018) suggest that sex differences in leadership are a product of sexual selection, sexual division of labor, and their interaction. Sexual selection on body size and the demands of pregnancy and motherhood privilege male leadership (e.g., Eagly & Johnson, 1990), and sexual selection may have shaped status-striving

motivation among men, more so than women, to involve violent competition (Daly & Wilson, 1988), large coalition building (Benenson, 2013; Low, 1992), and risky economic pursuits (Gurven & von Rueden, 2006; Hawkes, 1991). These sex differences in physiology, obligate parental investment, and motivation contribute to culturally-transmitted sexual divisions of labor that impose opportunity costs on women's ability to pursue political leadership. Among the Tsimane', for example, gender *per se* does not strongly predict political leadership; instead, the male bias in leadership is due to a male bias in body size, access to education, number of cooperation partners, and contribution to the latter from the sexual division of labor (von Rueden et al., 2018).

As discussed earlier, Garfield et al. (2019) propose that high quality decision-making that benefits others is a critical element of prestige-style leadership. The male bias in leadership might therefore stem, in part, from a research bias in which leadership is defined as *political leadership* at higher levels of social organization, such as the residence group (e.g., a band or settlement) or political units comprising multiple settlements, but which ignores leadership within and between families. For the reasons outlined above, men more often lead at the higher levels of social organization but women more often lead within and between families within a residence group, making daily decisions for their children and the family as a whole. From this perspective, a greater proportion of women than men might occupy leadership roles. Systematic evidence reveals that autonomous decision making by mothers in a small-scale society was positively associated with better nutritional outcomes in offspring (Starkweather & Keith, 2018) and greater executive functioning and emotional control of mothers in a Western population was associated with positive outcomes among children (Crandall, Ghazarian, Deater-Deckard, Bell, & Riley, 2018). In fact, since high levels of parental investment in offspring from infancy until early adulthood 20 years later is one hallmark of the human species, with mothers (and fathers) making numerous decisions for their children, it might be the case that mothering (and fathering) is one of the evolutionary origins of human leadership.

## 9. Conclusion

The evidence reviewed here suggests that, in diverse species, including humans and human ancestors, leaders help solve problems of competition over resources, coordination, movement, and social behavior using both asymmetries in physical and social formidability (dominance) and asymmetries in information and skills. This undermines claims that the evolution of prestige-style leadership is rooted in the evolution of cumulative culture that is unique to humans (e.g., Barkow, 1989; Henrich & Gil-White, 2001). Instead, prestige-style leadership among humans might be an elaborated form of leadership based on informational and skill asymmetries that are seen in many species. Thus, in humans and other animals, leaders sometimes engage in dominant behaviors that often benefit themselves at the expense of the group, and sometimes provide information- and skill-based services that benefit both themselves and the group. A single leader can, of course, use both types of strategies.

The deep evolutionary roots of leadership strongly implies that all humans, including adults and children of both sexes, possess universal psychological mechanisms for both leadership and followership. These mechanisms, which evolved among small, kin-based, hunter-gatherer societies – similar to those reviewed here – now shape leader and follower behavior in organizations, communities, and nations with hundreds, thousands, or even millions of members.

### 9.1. The path forward

We highlight two major implications of this evolutionary perspective that we believe would benefit future research on leadership. First, evolutionary anthropologists and psychologists investigating dimensions of group living, including cooperation, aggression, and mating, have often overlooked the critical role of leadership in each of these domains. An integrated perspective of leadership and followership stands to bring new insight to the nature of group living.

Unlike the 70% of mammalian species that do not live in groups (Wilson & Reeder, 2005), humans could not survive or reproduce without belonging to a group. And unlike many species that do live in groups but do not engage in complex cooperative behaviors, such as many herd species, humans must cultivate elaborate, often lifelong cooperative relationships with multiple members of both sexes to raise offspring, produce food, and defend territory. Because these different goals require cooperation at different scales, humans live in groups with complex structures, such as families nested within food-producing communities nested within regional political entities, such as chiefdoms or states, but also including groups, such as religions, that cut across other groups. Understudied, especially from an evolutionary perspective, is the extent to which leader-follower dynamics *define* these groups – who belongs, and who does not (Hogg, van Knippenberg, & Rast III, 2012) – and the extent to which these dynamics establish group goals (Grabo & Van Vugt, 2016). Leadership might therefore turn out to play an unexpectedly large role in shaping group structure, the very basis of human survival and reproduction.

Also, leadership and mating are probably more deeply intertwined than is recognized by either mainstream or evolutionary theorists. Other than Barkow (1989), who argued that leaders and other prestigious men can offer more resources to mates, and Neel (1980), who argued that the reproductive success of leaders resulted in strong sexual selection on intelligence, few theorists have attempted to synthesize theories of sexual selection with theories of leadership, despite the overwhelming evidence that in most human societies leaders and other prestigious men have increased reproductive success (Glowacki & Wrangham, 2015, 2013; von Rueden et al., 2011; von Rueden & Jaeggi, 2016). Given that leadership within families, the primary social unit of reproduction, has also been almost entirely ignored, and that women might often fill the family leadership role, it is likely that there are some unexpectedly deep connections between leadership by both men and women, and their relationships with the opposite sex. Garfield et al. (2019), for example, argue that the computational and other services leaders of both sexes provide to groups, including the family group, might be valuable to both sexes when choosing mates. Hence, there would be sexual selection for these computational abilities in both males and females.

The second major implication of an evolutionary approach to leadership is that in larger societies especially, some qualities we are evolved to value in leaders might increasingly be mismatched to the actual challenges leaders and their followers face. Many possible mismatches are provided by Van Vugt (2008), von Rueden and Van Vugt (2015), and Giphart and Van Vugt (2018). The relationships between leadership, physical formidability, and mating provide particularly clear examples. Leaders are often tall (Hamstra, 2014; Stulp et al., 2013), for instance, which suggests that physical formidability is a desirable leader quality even in organizations in which physical fighting plays no role and leader-follower relationships are rarely face-to-face. There also is likely an evolved male psychology that seeks to take advantage of leadership roles to pursue mating opportunities (Barkow, 1989; Schmitt, 2015; Tiger & Fox, 1971). In most small-scale societies, polygyny is socially acceptable and most group work is divided between the sexes. In Western societies, however, monogamy is the law of the land, there is less sexual division of labor, sexual relationships among members of the same organization can create huge conflicts of interest, and unwanted sexual attention can be devastating. Increasingly strong institutions and social norms might therefore need to be put in place to regulate consensual relationships within organizations and prevent unwanted sexual attention. In general, historically successful cultural institutions and norms are often those that help mesh evolved leadership and followership intuitions with the collective action problems of very large societies and organizations (Richerson &

Henrich, 2012).

The social sciences are placing greater value on consilience. For the study of leadership, we see tremendous benefits to integrating diverse sources of evidence from studies of animal behavior, paleoanthropology, ethnography, psychology, political science, and other social sciences. The challenge will be to identify and explain universal patterns of human leadership systems while still doing justice to their diversity.

## Acknowledgments

We thank the first author's Ph.D. committee, Barry Hewlett, Robert Quinlan, Anthony Lopez, and Leslie New, for comments on early drafts of this manuscript, as well as Luke Glowacki and Shyamalika Gopolon for comments on specific sections. We also thank Sergey Gavrilets and an anonymous reviewer for valuable comments and suggestions.

This work was funded by National Science Foundation Division of Behavioral and Cognitive Sciences award 1628509.

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