



Full Length Article

Investigating evolutionary models of leadership among recently settled Ethiopian hunter-gatherers



Zachary H. Garfield*, Edward H. Hagen

Department of Anthropology, Washington State University, United States of America

ABSTRACT

Humans are thought to have evolved in small, egalitarian hunter-gatherer societies. Evolutionary theories of leadership, which draw heavily on studies of contemporary hunter-gatherer and other small-scale societies, have proposed numerous traits that putatively characterize leaders in domains of sociality, productivity, reproduction, dominance, and cognition. We investigated many such traits among the Chabu, an Ethiopian population of former hunter-gatherers who now subsist on hunting, gathering, horticulture, and cash crops.

There were strong positive correlations among most traits across domains, which, in turn, were positively associated with elected leader status among both women and men. Measures of prestige and dominance were largely independent, and although both predicted leader status, prestige was more important. Biased social learning was a modest predictor of leader status but a stronger predictor of respect. Revised evolutionary theories of leadership must account for the importance of women leaders and the strong covariation of traits.

Introduction

For the vast majority of human evolutionary history, people lived as hunter-gatherers in small nomadic bands with a stochastic resource base and, based on analogy with contemporary hunter-gatherers, social structures likely characterized by a lack of inherited social distinctions, a cultural ethos of sharing, and a high degree of egalitarianism (c.f., Binford, 2001; Formicola, 2007; Hewlett, 2016b; Kelly, 2013; Lee & Daly, 1999; Marlowe, 2005; Mattison, Smith, Shenk, & Cochrane, 2016; Vanhaeren & d'Errico, 2005). Putatively, it is in this broad socio-ecological context in which any human-specific dimensions of leadership evolved (Von Rueden & Van Vugt, 2015), yet there are few systematic studies of leadership among small-scale societies that share some features with nomadic hunter-gatherers, such as egalitarianism and strong sharing norms.

The literature on small-scale societies has identified many individual qualities that predispose to leadership and other positions of power and prestige. To our knowledge, the relationships between leadership and most of these qualities have never been compared in a single study. The current study aims to determine which of these qualities best characterizes leaders in a contemporary small-scale society with a history of egalitarianism, currently undergoing significant economic, political, and cultural transition. Unlike most studies in both Western and non-Western societies, this study evaluates whether the qualities that characterize male leaders also characterize female leaders.

Leadership and egalitarianism

Anthropologists typically describe populations as having a high degree of egalitarianism when there is relative equality within age and sex classes in access to subsistence and other resources including opportunities for upward social mobility (Kelly, 2013; Lee & Daly, 1999; Mattison, Smith, Shenk, & Cochrane, 2016). Egalitarianism is not an innate feature of human nature or social life. Instead, it is associated with environmental constraints, stochastic resources, and subsistence economies characterized by immediate returns on investments (Cashdan, 1980; Gardner, 1991; Lee & DeVore, 1968; Sahlins, 1972; Woodburn, 1982). It appears to be maintained by cultural values and strict leveling mechanisms promoting sharing, equality, and autonomy, and the active resistance of hierarchy (Boehm, 2008; Peterson, 1993). Yet even the most egalitarian mobile hunter-gatherers have some forms of leadership (Lewis, 1974; Moise, 2014; Von Rueden, 2014).

Leadership in the context of widespread egalitarianism is often ephemeral, context specific, and primarily dependent on mutually beneficial outcomes for leaders and followers (Fried, 1967; Price & Van Vugt, 2014). Leaders typically gain influence through respect and deference for expertise in culturally valued skills, such as subsistence efforts, oratory abilities, shamanism, and through success in warfare or inter-group conflict (Henrich, Chudek, & Boyd, 2015). Influence is generally maintained only to the degree the group permits (Boehm, 1993; Fried, 1967; Service, 1964; Woodburn, 1982). Therefore, the qualities of leaders and the functions they serve are often, but not

* Corresponding author.

E-mail addresses: zachary.garfield@wsu.edu (Z.H. Garfield), edhagen@wsu.edu (E.H. Hagen).

always, prosocial in nature (Henrich, Chudek, & Boyd, 2015; Macfarlan, Remiker, & Quinlan, 2012).

Leaders are commonly responsible for resolving within-group conflicts across many small-scale societies (Glowacki & Von Rueden, 2015). Mechanisms for conflict resolution among egalitarian hunter-gatherers have been debated, however, with some researchers suggesting egalitarian hunter-gatherers generally lack effective cultural institutions and leadership structures to mediate significant conflicts with clashing parties most often choosing to “vote with their feet” and leave the group (Knauf et al., 1991; Wiessner, 2016). Spiritual beliefs and fear of supernatural punishment are also implicated in promoting social cohesion in the absence of more formal mediation (Basedow, 1925; Lewis, 2008). Other scholars have suggested concerted processes of conflict resolution are ubiquitous among egalitarian societies and highlight the senior role of kin group members (Hames, 2015) and the cost of migrations even among highly nomadic populations (Boehm, 1999; Knauf et al., 1991).

Although most studies of leadership in egalitarian societies focus on men (for exception see Von Rueden, Alami, Kaplan, & Gurven, 2018), women in these societies also achieve high levels of prestige and influence (Dahlberg, 1981; Endicott, 1999). It is therefore possible that commonly used definitions of “leadership” downplay or ignore the important roles women play in decision-making within families and residential groups (Brown et al., 1982; Garfield, Hubbard, & Hagen, 2019; Garfield, von Rueden, & Hagen, 2019; Smith, Ortiz, Buhbe, & Van Vugt, In press), as well as their roles in alliances by marriage (Bowser & Patton, 2010). Women are also likely to respect and defer to other women who have large families and have a reputation as high-quality mothers (Brown & Kerns, 1985; Hrdy, 1999). Finally, both sexes are often respected for being good parents and helping family and kinship plays a critical role in political dynamics within many small-scale societies (Barkow, 1989; Hames, 2015; Hrdy, 1999; Walker et al., 2012). The egalitarianism typical of many hunter-gatherer and small-scale societies has had a significant influence on evolutionary theorizing on human leadership.

Leadership and inequalities

Around the same time that anthropologists were emphasizing the egalitarianism of many small-scale societies, James Neel, a major figure in twentieth century genetics and an early collaborator of Napoleon Chagnon, was emphasizing that leaders in such societies are often polygynous and have many more children than other men (Neel, 1980; Neel, Salzano, Junqueira, Keiter, & Maybury-Lewis, 1964). If this pattern characterized human evolutionary history, there would have been strong sexual selection for traits that predisposed to leadership. Based on his observations of headmen in indigenous Amazonian populations, Neel proposed that although physical strength is an asset in campaigns for headmanship, *mental agility* is even more critical. Mental agility would therefore have been under strong sexual selection, contributing to encephalization in *Homo* (Neel, 1970, 1980; Neel & Salzano, 1967).

Neel did not explain how mental agility helped one achieve a leadership role, however, nor why leaders were attractive as mates. Garfield, Hubbard, and Hagen (2019) address these two deficiencies by combining Neel's ideas with the concept of *embodied capital* from life history theory (Kaplan, 1996; Kaplan, Lancaster, Johnson, & Bock, 1995; Lancaster & Kaplan, 2010). Embodied capital includes somatic investment, such as strength and immune function, and skill development, expertise, intelligence, and knowledge. The neuro-cognitive dimensions of embodied capital are referred to as “neural capital” (Kaplan, Mueller, Gangestad, & Lancaster, 2003). We identify Neel's concept of “mental agility” with the Kaplan, Mueller, Gangestad, and Lancaster (2003) concept of *neural capital* (Garfield, Hubbard, & Hagen, 2019). In brief, Garfield, Hubbard, and Hagen (2019) propose that making good decisions for the group and resolving conflicts are cognitively demanding tasks. Men and women who excelled at these tasks were attractive as leaders and mates. The connection between

leadership and intelligence is emphasized by later theories (Boehm, 1993; Van Vugt & Kurzban, 2007) and many empirical studies (e.g., Antonakis, House, & Simonton, 2017; Judge, Colbert, & Ilies, 2004; Lord, De Vader, & Alliger, 1986).

Neel's findings were an early indication that *egalitarian* societies might have more inequality than it seemed at first glance. Smith et al. (2010) assessed the intergenerational transmission of wealth and inequality among a sample of five hunter-gatherer populations. They found that, despite widespread sharing and social leveling mechanisms, wealth disparities are transmitted from one generation to the next, where wealth was broadly defined to include material wealth, in the form of personal property; relational wealth in the form of social and political capital, i.e., alliances and kin/social networks; and embodied wealth, i.e., phenotypic characteristics such as strength, immune function, and expertise (Bowles, Smith, & Borgerhoff Mulder, 2010; Gavrilets & Fortunato, 2014; Mattison, Smith, Shenk, & Cochrane, 2016; Reyes-García et al., 2009). Intergenerational inequality was particularly apparent for relational and embodied wealth but less so for material wealth (Smith et al., 2010).

Research among egalitarian and small-scale societies suggests leaders do in fact have greater access to relational and embodied wealth (Smith, Bliege Bird, & Bird, 2003; Von Rueden, 2014; Von Rueden, Gurven, Kaplan, & Stieglitz, 2014; Wiessner, 2002). A strong social network can be both a path to leadership and a consequence of successful leadership. Followers prefer social partners who serve as leaders, for instance, and leaders therefore often have more allies than non-leaders (Macfarlan, Walker, Flinn, & Chagnon, 2014; Smith, Bliege Bird, & Bird, 2003; Von Rueden, Gurven, & Kaplan, 2008). Leaders typically invest highly in subsistence efforts and convert resources into political capital (Bliege Bird, Coddington, & Bird, 2009; Gurven & Von Rueden, 2006; Wiessner, 2002). Followers balance rewarding prosocial leaders with leveling overly assertive, aggrandizing ones (Boehm, 2008; Price & Van Vugt, 2014). Physically, community leaders tend to be strong, tall, vital men, and fighting ability and demonstrated success in combat are common paths to widespread influence (Glowacki, Wilson, & Wrangham, 2017; Henrich & Gil-White, 2001; Tiger & Fox, 1971; Von Rueden, Gavrilets, & Glowacki, 2015; Von Rueden, Gurven, Kaplan, & Stieglitz, 2014). Leaders are also often highly competent in many culturally revered skills (Barkow, 1989; Henrich & Gil-White, 2001).

It is unclear, though, if male and female leaders systematically differ in some measures of wealth inequality. It is likely that evolved psychological differences (Van Vugt & Spisak, 2008), life history parameters and ecology (Brown & Kerns, 1985; Low, 2005), and cultural history and norms (Goody, 1976; Richerson et al., 2016) shape gender-specific leadership strategies in relationship to material, social, and embodied inequalities.

Paths to leadership: dominance and prestige

Theories of social influence have long highlighted two distinct strategies commonly employed by leaders. Leaders can rely on force, aggression, and coercion to achieve and maintain influence, or, respected individuals may be chosen as leaders based on their expertise, prosociality, and decision-making capabilities (Barkow, 1989; Kracke, 1978; Tiger & Fox, 1971). The aggressive dominance style is commonly thought to be homologous to dominance in the social hierarchies of non-human primates (Barkow, 1989; Chapais, 2015; Henrich & Gil-White, 2001; Tiger & Fox, 1971). The nature of prestige style influence, on the other hand, is a bit of a conundrum (Garfield, Hubbard, & Hagen, 2019). Barkow (1989), like Neel (1980), argued that, in humans, there was sexual selection for traits in men, such as abilities to acquire knowledge and skills, that improved men's ability to attract mates. Henrich and Gil-White (2001) pointed out, however, that this did not explain why men would defer to other prestigious men.

Henrich and Gil-White (2001) instead argued that deference to skilled and knowledgeable individuals was an evolved learning

strategy. Prestigious leaders and other individuals were those with skills/knowledge in valued domains of behavior. Followers competed for access to the highest quality behavioral models, e.g., prestigious individuals, and exchanged deference for the opportunity to carefully monitor and copy their behavior (Cheng, Tracy, Foulsham, Kingstone, & Henrich, 2013; Cheng, Tracy, & Henrich, 2010; Henrich, Chudek, & Boyd, 2015; Henrich & Gil-White, 2001; Richerson & Henrich, 2012). Henrich and Henrich (2007) review the evidence, mostly from laboratory studies in Western populations, that individuals preferentially copy prestigious individuals. According to these authors, followers will pay attention to both dominant and prestigious leaders, but that these two strategies are distinct, and followers will exclusively prefer prestigious individuals, not dominant ones, as models for social learning (Cheng, Tracy, Foulsham, Kingstone, & Henrich, 2013).

Experimental evidence from Western populations supports the distinction between dominance and prestige (Cheng, Tracy, Foulsham, Kingstone, & Henrich, 2013; Cheng, Tracy, & Henrich, 2010). There is also significant cross-cultural evidence that leaders use both dominance and prestige-based strategies to achieve positions of influence (Barkow, 1989; Garfield, Hubbard, & Hagen, 2019; Gurven & Von Rueden, 2006; Kracke, 1978; Tiger & Fox, 1971; Von Rueden, Gurven, Kaplan, & Stieglitz, 2014). Preferences for a dominance-style or prestige-style of leadership might be facultative based on ecological context, such as the intensity of between group conflict or the degree of within group inequality (Laustsen & Petersen, 2017; Ronay, Maddux, & Hippel, 2018; Spisak, Dekker, Krüger, & Van Vugt, 2012). In more egalitarian societies, followers are likely to resist, depose, desert or remove overly assertive dominant leaders, however, and those who are granted a disproportionate level of influence most often attain it through prosocial, prestige-style mechanisms (Barkow, 1989; Boehm, 1993, 2008; Garfield, Hubbard, & Hagen, 2019; Kracke, 1978).

Despite evidence supporting the distinction between dominance and prestige styles of leadership, it is not clear that the prestige style of leadership evolved as a mechanism for enhancing social learning. Extensive analysis of ethnographic accounts of leadership and social learning found little evidence that prestigious leaders served as models for social learning (Garfield, Garfield, & Hewlett, 2016; Garfield, Hubbard, & Hagen, 2019). Yet absence of evidence is not evidence of absence. It could easily be the case that the limited ethnographic evidence for the Henrich and Gil-White (2001) prestige model is simply because ethnographers failed to ask the right questions. The importance and role of prestigious-leader directed learning biases in small-scale societies therefore remains an open question.

Study aims

There are few systematic studies comparing leaders and non-leaders in small-scale societies. Leaders in small-scale egalitarian societies are claimed to gain influence via their expertise in culturally valued skills, and to be generally prosocial by, e.g., playing a key role in conflict resolution. Nevertheless, leadership in these societies is also thought to be associated with disparities in various forms of wealth, including access to mates and social relationships. The dominance-prestige model, which emphasizes disparities in physical formidability and expertise, has not been extensively tested in small-scale societies or compared to other dimensions of leader phenotypes. Finally, most theoretical models of leadership focus on men, raising the question of the extent to which they also explain female leadership.

The current study therefore aimed to investigate, in a contemporary small-scale society with a history of egalitarianism, five general domains of traits that the theoretical literature has identified as predisposing to leadership, one of the few to do so (but see Von Rueden, Alami, Kaplan, & Gurven, 2018; Von Rueden, Gurven, Kaplan, & Stieglitz, 2014; Von Rueden, Gurven, & Kaplan, 2011). The first category was cognitive traits, which included learning and intelligence, expertise, and decision-making abilities. The second category was traits

related to dominance, which included being feared and having a reputation for fighting. The third category was productivity, which included skills in farming, hunting, coffee production, and honey collection. The fourth category was reproductive traits, including spouse quality and parenting skills. The fifth category was social traits, including being respected, number of allies, prosociality, likability, and kin altruism.

Additionally, to our knowledge this study is the first to investigate the learning biases the dominance-prestige model predicts to be associated with prestigious leaders (Cheng, Tracy, Foulsham, Kingstone, & Henrich, 2013; Henrich, Chudek, & Boyd, 2015). Lastly, this study is among the few to investigate sex-differences and female leadership in a small-scale society (but see Bowser & Patton, 2010; Von Rueden, Alami, Kaplan, & Gurven, 2018).

Our specific aim was to determine which of these dimensions of leadership best predicted elected leader status for men and women.

Study population

The Chabu are a population of approximately 2000 forager-horticulturalists who reside in the remote highland forest areas of Southwestern Ethiopia spanning the regional states of Oromia; Southern Nations, Nationalities and Peoples Region (SNNPR); and Gambela (Dira & Hewlett, 2017; Kibebe, 2015). Most scholarly work on the Chabu focused on classifying their language (often mistakenly identified as Shabo or Mekeyir), relying on informants from rural multi-ethnic villages (Bender, 1975; Ehret, 1992; Fleming, 1991; see Kibebe, 2015 for review). More recent linguistic analyses based on forest dwelling informants suggests Chabu is the sole remnant language of a previously undocumented African language phylum (Schnoebelen, 2009; Kibebe, 2015).

The Chabu have only recently been the focus of any systematic or ethnographic research (e.g., Dira & Hewlett, 2016, 2017, 2018; Hewlett, 2016a). The Chabu were mobile hunter-gatherers subsisting on hunted antelope, duiker, warthog and buffaloes as well as various wild yams and collected honey up until the late 1990s (Dira & Hewlett, 2017). Currently, for their primary subsistence, the Chabu at the study site rely heavily on maize, wild and domesticated yams, beans, sugar cane, and some fruit bearing trees such as bananas, avocado, and pineapple. Hunted meat remains an important part of the diet (men reported checking and setting hunting traps 2.29 times per week and spear hunting with dogs 1.82 times per week). Fishing is a seasonal activity influenced by rainfall, but men reported fishing an average of 2.79 times per week during the dry season. Honey, once a staple, is now nearly exclusively an economic product sold at markets (ZG unpublished data; Dira & Hewlett, 2017).

The Chabu are not an officially recognized ethnic group within Ethiopia and have often been mistaken as a clan of the Majang. The Chabu are socially organized into at least 18 patrilineal clans, each with an associated supernatural ability (called *seja*¹) most often associated with specific healing abilities or control over an animal or material (see Dira & Hewlett, 2017). They maintain a relatively egalitarian social structure yet have become increasingly involved in a system of local administration implemented by the Ethiopian government. The Chabu have faced external threats to their culture and territory for decades, but in recent years there has been a marked increase in violent conflict. See Dira and Hewlett (2017) for review.

The Kebele system among the Chabu

The Chabu are actively involved in the Kebele (also qebele) system, the smallest administrative unit of the Ethiopian government that

¹ Chabu words given in International Phonetic Alphabet notation and italicized.

directly couples local communities across the country with the state (James, Donham, Kurimoto, & Triulzi, 2002). This system of neighborhood organization was initiated under the communist Derg regime to promote equality and land reform and has been maintained under the current government (Donham, 1999). Under the Kebele system, local communities elect individuals to various leadership positions to organize development projects and collective activities within the community and to interact with governmental offices (Keller, 1991).

The Chabu adopted a simple version of the Kebele system around 2006, about 10 years prior to the fieldwork reported here, and then gradually increased the number of leadership roles.² The higher-level positions are referred to as the “Kebele leaders” and include seven male positions and four female positions. These leaders oversee a series of nested groups, including a security team; school, elderly peoples', justice, and church committees; and several task forces that each oversee many task groups (known as one-to-five groups). This structure has created what we classify as major leadership positions, minor leadership positions, and elected positions. All residents of the study site can be classified into this scheme, serving as one of these types of leaders, or not being an elected person at all. See Fig. 1.

We also initially intended to include informal leaders in this study, such as elders or respected people who might wield considerable influence despite not occupying a formal leadership position. Extensive interviews with multiple informants revealed, however, that although such informal leadership previously played a key role among the Chabu, it no longer did. Currently, the most influential individuals at the study site are Kebele leaders.

Methods

Data collection occurred during the summer months of 2015 and 2016 in a Chabu village with about 250 residents in Southwest Ethiopia. The study site village has become the largest “medium sized semi-permanent settlement” under the typology of Chabu settlements by Dira and Hewlett (2017). Chabu leaders are actively promoting emigration to the study site village among non-resident Chabu families. Therefore, the study site village is likely a new type of Chabu settlement; the study site is a medium sized permanent settlement, otherwise consistent with the description of medium sized semi-permanent settlements by Dira and Hewlett (2017) (e.g., remote forest location with a dynamic population and high mobility of some residents).

Approval for the current study and data collection was obtained from the institutional review board of Washington State University (IRB #14445); Hawassa University College of Social Sciences and Humanities; the Southern Nations, Nationalities and Peoples' Regional State Office of the President; as well as community elders and leaders.

Sample and data collection

We first identified every major leader, minor leader, and elected individual in the Kebele system at the study site (see Fig. 1). Sixty adult participants (26 women and 34 men) from this village, about half of whom had official positions in the Kebele system, were then recruited using convenience sampling (Bernard, 2011). This sample included many, but not all, of the male and female leaders in this community. Interviews were conducted privately (present company included the participant, a local research assistant, an external research assistant, and ZG), in the Chabu language at the participant's house, at their maize field shelter, or at the house of the researcher's host family.

² The degree of implementation of the Kebele system among Ethiopian minority ethnic groups is highly varied. The Kebele system is present among the pastoral Nyangatom and Hamar, however, it has little to no influence in internal sociopolitical dynamics among the former, and only marginal influence among the latter (Luke Glowacki and Scott Calvert, personal communications).

We collected four sets of data from each participant: (1) self-reported demographic and economic information, (2) anthropometric measures, (3) freelist members of the community who the participant thought would be ideal models from whom to learn important skills, and (4) freelist members of the community who were respected. The demographic self-report structured interview included an estimation of age as well as other sociodemographics and measures of household wealth not used in analyses. Anthropometric data included height and grip strength. In addition, seven participants provided peer-ratings on a set of traits that characterize leaders according to evolutionary theoretical models (Table 1). See Supplementary Information for additional details on data collection procedures.

All participants were instructed to freelist (Quinlan, 2005) anyone in the village who they perceived as a superior model from whom to learn skills in four culturally valued domains: farming, fishing, hunting, and honey collection. Participants provided separate frelists for each domain and could name as few or as many individuals as they chose. We computed *salience scores* for each named individual in each domain as well as a composite *Mentor salience* for each named individual across domains. Participants also freelist the most respected individuals in the village, for males and females separately and we computed a *Respect salience* score for all participants (See Supplementary Information for details).

Ethnographic methods

The first author conducted open-ended and semi-structured interviews (Bernard, 2011) with 25 residents of the study site including 11 adult males, 7 male elders, 5 adult females, and 2 female elders.³ This sample included 3 male Kebele leaders, 2 female Kebele leaders, highly respected hunters, and several highly respected elders. Interviews covered the nature of collective labor and collective hunting, the sexual division of labor, contexts of traditional leadership, qualities of respected people, and the Kebele system and qualities and functions of leaders. During fieldwork, *Ad libitum* sampling observations (Altmann, 1974) of behaviors and interactions of respected elders and Kebele leaders were recorded.

Peer-ratings

Kebele leaders are elected based on a public show of hands vote. Given strong community norms valuing individual autonomy we assume this is an indication of how they are perceived by the community, though other factors could influence voting patterns. We therefore used peer-ratings to assess participants on key traits from the five domains central to leadership identified in the theoretical literature. Participants consented to having a portrait photograph taken for use in a peer-rating procedure. Photographs displayed the participants head and shoulders set against a neutral background. Seven participants (four males, three females) were recruited as peer-raters, based on skill in working with researchers. Peer-raters ranked participants separately for males and females on the 17 traits associated with leadership (Table 1). Five raters (from the pool of seven) ranked each participant (except themselves) on each of 17 traits. These rankings were then converted to relative ranks (*rank/rank k_{max}*). See Supplementary Information for more details.

We computed two composite variables informed by the Dominance-Prestige scale (Cheng, Tracy, & Henrich, 2010). This scale computes *Prestige* based on measures of respect, admiration, success, providing advice, and expertise; and *Dominance* based on measures of coercive control, aggression, forceful personality, and fear. In our data *Prestige*

³ Elders are distinguished from adults on the basis of their estimated age (59 and older) and in considering their social and economic responsibilities; elders do very little if any group work, have limited responsibilities, and generally congregate together in a more isolated social network.

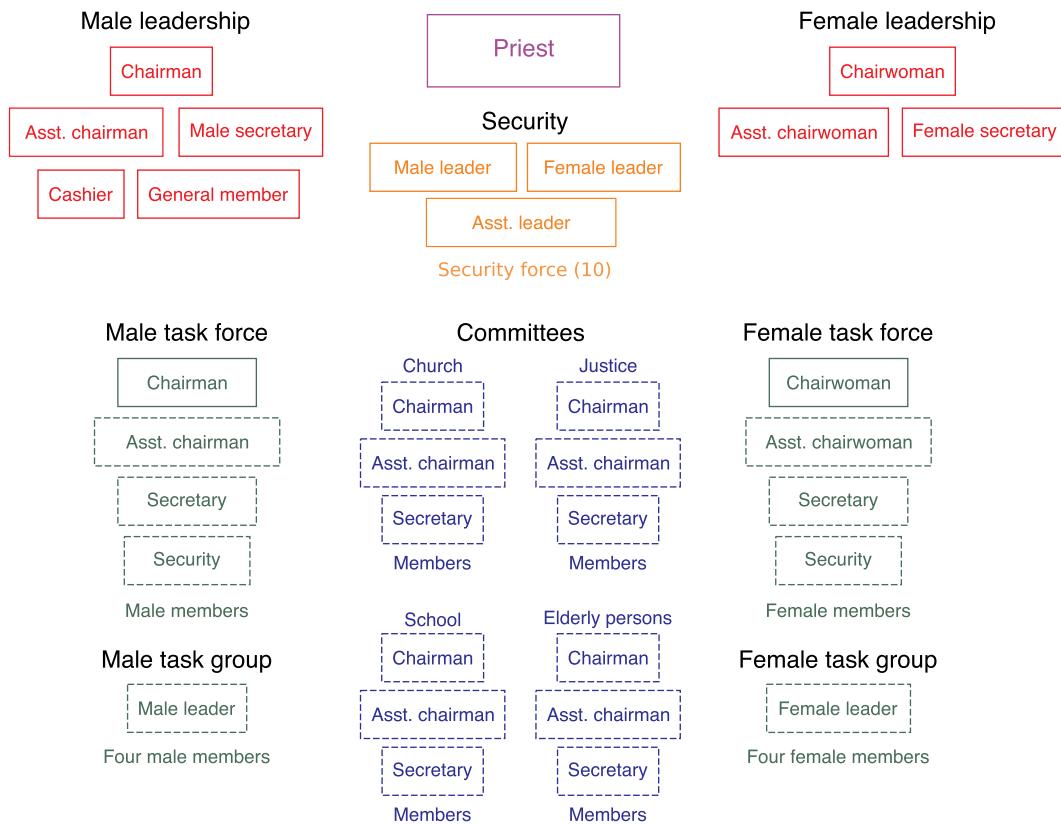


Fig. 1. The Chabu Kebele leadership system. Each box is one leader. Solid border: Major leader. Dashed border: Minor leader.

was the sum of the *Expertise*, *Respect*, and *Likable* relative rankings. *Dominance* was the sum of *Feared* and *Fighting* (see the Supplemental Information for more detail on the *Dominance* variable).

Statistical analysis

Preregistered predictions

We preregistered seven bivariate mean difference tests between leaders and non-leaders (<https://osf.io/ku5wv/>). These tests focused on variables derived from Neel's model and the Dominance-Prestige model, which were the original focus of the study. Specifically, we predicted that leaders would score higher than non-leaders on measures of *Dominance*, *Prestige*, *Spouse quality*, *Mentor salience*, *Fighting*, *Grip strength*, and *Learning and intelligence*. See the Supplemental Information for more detail.

Cluster analysis

To gain a broad overview of our data, we first used hierarchical cluster analysis and heatmaps to explore the entire data matrix and determine if there were distinct groups of peer-rated variables that were highly correlated with one another and if there were distinct groups of participants that had similar peer-ratings on multiple variables. Distance between row vectors (peer-ratings) were computed as $1 - cor$. Distance between column vectors (participants) were computed with the Euclidean metric. Clusters were determined with the Ward agglomeration algorithm.

Elastic net regression

Our main focus was elected leader status, a binary outcome requiring logistic regression, and *Respect salience*, a continuous outcome requiring linear regression. Many of the predictors were highly correlated. Such collinearity can pose severe problems for regression. In a simulation-based evaluation of several methods that address

collinearity, [Dormann et al. \(2013\)](#) found that penalized methods, such as lasso regression and especially ridge regression, worked well. In addition, penalized regression is appropriate when the number of predictors, p , is large relative to the number of cases, n . We had many predictors, yet our data had only 60 cases. We therefore used the `glmnet` package ([Friedman, Hastie, & Tibshirani, 2010](#)) to fit penalized regression models. All variables were centered and standardized by one standard deviation prior to fitting, as required by the elastic net algorithm.

Standard regression models are fit by minimizing an objective function. In ordinary least squares regression the objective function is the residual sum of squares (*RSS*), and in logistic regression it is the negative log-likelihood, $-\loglik(\beta)$. Penalized regression models instead minimize the objective function plus a penalty term based on the magnitude of the coefficient vector ([Le Cessie & Van Houwelingen, 1992; Tibshirani, 1996](#)). For linear regression this is

$$\frac{1}{2} \text{RSS}/n + \lambda * \text{penalty}$$

and for logistic regression:

$$-\loglik(\beta)/n + \lambda * \text{penalty}$$

There are two popular forms of penalized regression: ridge regression and lasso regression. For ridge regression the penalty is $\|\beta\|_2^2 = \sum_{j=1}^p \beta_j^2$, where the β_j are the regression coefficients, and for lasso regression the penalty is $\|\beta\|_1 = \sum_{j=1}^p |\beta_j|$. When $\lambda = 0$, this reduces to the standard estimation. As $\lambda \rightarrow \infty$, the coefficients β_j are "shrunk" to 0. Thus, when λ is small, the β s are relatively unrestricted, which can result in a good fit to the current sample (low bias), but a poor fit on future samples (high variance); roughly, the model will tend to be overfitted. When λ is large, the β s tend to shrink towards 0, which reduces fit on the current sample (high bias), but results in a more stable fit across samples (low variance); roughly, the model will tend to be underfitted. The optimal value of λ is typically found by minimizing

Table 1

Peer-rated variables in five domains, and participant prompts.

Domain	Variable name (short name)	Participant prompt
Cognitive	Consistency in quality decision making (Decisions)	Some people make better decisions than others. Some people's decisions tend to be good for the group, good for themselves, and have positive consequences. Other people tend to make bad decisions. Look at the photos and rank them from those who are the best decision makers, to those who are the worst decision makers, based on their behavior today.
Cognitive	Level of expertise (Expertise)	Some people have more expertise in important skills than others. Some important skills include hunting, farming, fishing, collecting honey, making baskets and mats, making pottery, building houses, cooking, singing, and playing games. Think about all the important skills and rank these people from those with the most expertise to those with the least expertise, considering their skills today.
Cognitive	Learning and intelligence level (Learning and intelligence)	Some people are more intelligent than others. Some people are very intelligent and learn things quickly and easily, others are of average intelligence and some are below average intelligence. Look at the photos and rank them from most intelligent to least intelligent considering their intelligence level today.
Dominance	Feared by others (Feared)	Some people are more feared and intimidate other people more than others. Look at the photos and rank them from most feared to least feared considering how people feel about them today.
Dominance	Fighting involvement (Fighting)	Some people are more likely to get in fights than others. Thinking about both physical and verbal fights, look at the photos and rank them from those most likely to get in fights to those least likely to get in fights today.
Productivity	Coffee production (Coffee)	Some men are better, harder working coffee cultivators than others. Look at the photos and rank them from those who produce the most coffee to those who produce the least.
Productivity	Farming production (Farming)	Some people are better, harder working farmers than others. Look at the photos and rank them from those who produce the most farmed food to those who produce the least, considering their farming production today
Productivity	Honey production (Honey)	Some men are better, harder working honey collectors than others. Look at the photos and rank them from those who collect the most honey to those who collect the least, based on their honey collection today.
Productivity	Hunting returns (Hunting)	Some men are better hunters than others. Some hunt with spears, dogs, traps, or other ways. Thinking about all hunting methods, look at the photos and rank them from those who get the most kills to those who get the least, considering their hunting returns today.
Reproductive	Parental investment (Parenting)	Some people are better parents than others. Some invest a lot of time, resources, and energy in raising children. Look at the photos and rank them from those who invest the most in parenting to those who invest the least.
Reproductive	Spousal quality (Spouse)	Some people have a better spouse than others. Better spouses might be better partners, better workers, better parents, or more attractive. Look at the photos and rank them based on the quality of the individual's current spouse from highest quality to lowest quality.
Social	Number of allies (Allies)	Some people have more close friends and allies than others. In the event of conflict or problems some people would have more people come help them than others. Look at the photos and rank them from those who currently have the most allies in the community to those who have the least.
Social	Conflict resolution skill (Conflict)	Some people are better at resolving conflicts than others and are more likely to get involved to help settle disputes between people who are fighting. Look at the photos and rank them from those who are most effective in conflict resolution to those least effective, based on their behavior today.
Social	Kin investment (Kin)	Some people help their family more than others. Some people help their extended family, not just their household, more than others. Look at the photos and rank them from those who help their family members the most to those who help their family members the least.
Social	Level of likability (Likable)	Some people are more likable and enjoyable to be around than others. Look at the photos and rank them from those most likable to least likable according to how people think of them today.
Social	Prosocial investment (Prosocial)	Some people help others more than other people. Some people do things that are good for the group, not just good for themselves or their family. Look at the photos and rank them from those who benefit the group the most through their actions today to those who benefit the group the least.
Social	Level of respect (Respect)	Some people are more respected than others. Look at the photos and rank them in order from most respected to least respected, thinking about how they are respected today.
(See SI)	Propensity to control others (Control)	Some people are more likely to try to control other people more than others. Look at the photos and rank them from those who try to control people the most to those who do not try to control people, considering their behavior today.

cross-validation error. In cross-validation (cv), which estimates how a model will perform on new data, the data are split into training and test sets, the model is fit on the training set, and prediction error is then measured on the test set. We used 10-fold cv, in which the foregoing is repeated on 10 different splits of the data, and the prediction error is then averaged.

With the lasso penalty, some coefficients might be set to 0, i.e., dropped from the model, which aids interpretation, but when variables are correlated, the lasso might drop some that are genuinely related to the outcome. In ridge regression, in contrast, the coefficients of correlated variables are shrunk to similar values; although the coefficients of some predictors might be very small, all predictors are retained in the model, which can make interpretation difficult.

Elastic net regression (Zou & Hastie, 2005) combines the advantages of ridge and lasso penalties using an additional tuning parameter α , $0 \leq \alpha \leq 1$:

$$\text{penalty} = (1 - \alpha)/2 \|\beta\|_2^2 + \alpha \|\beta\|_1.$$

Thus, $\alpha = 0$ is the ridge penalty and $\alpha = 1$ is the lasso penalty. With intermediate values of α , there is a 'grouping' effect in which strongly

correlated variables tend to enter or leave the model together (i.e., have their coefficients set to 0). We used elastic net regression to fit regression models of leader status and *Respect salience* as functions of all peer-rated variables. Following standard procedure, we used 10-fold cv to find the optimum values of λ and α , i.e., ones that minimized cross-validation error. We also chose a second λ that was the largest value of lambda such that the error was within 1 standard error of the minimum, i.e., one that would increase shrinkage relative to the optimal λ and therefore decrease false positives. For both elastic net regression models we report coefficients from the optimal λ_{min} model and the more conservative λ_{1se} model.

Bayesian regression

Numerous studies have found that prestige and/or dominance are associated with leadership and increased social status (Cheng, Tracy, Foulsham, Kingstone, & Henrich, 2013; Cheng, Tracy, & Henrich, 2010; Gurven & Von Rueden, 2006; Laustsen & Petersen, 2017; Price, 2003; Von Rueden, Gurven, & Kaplan, 2011; Von Rueden, Gurven, Kaplan, & Stieglitz, 2014) which is supported by a rich body of theory and ethnography (Barkow, 1989; Boehm, 1993; Garfield, Hubbard, & Hagen,

Table 2

Prior distributions for coefficients of logistic regression model of leader status as a function of Prestige, Dominance, Sex, and Age. The informative priors for Prestige and Dominance were based on results from previous studies (see text). See also Fig. 4. Values are log odds.

Prior	Intercept	Prestige	Dominance	Sex	Age
Weakly informative Gaussian	$\mathcal{N}(0, 1)$	$\mathcal{N}(0, 1)$	$\mathcal{N}(0, 1)$	$\mathcal{N}(0, 1)$	$\mathcal{N}(0, 1)$
Informative Gaussian	$\mathcal{N}(0, 1)$	$\mathcal{N}(2.63, 0.52)$	$\mathcal{N}(2.01, 0.46)$	$\mathcal{N}(0, 1)$	$\mathcal{N}(0, 1)$

2019; Henrich, Chudek, & Boyd, 2015; Henrich & Gil-White, 2001; Lewis, 1974; Tiger & Fox, 1971). One advantage of Bayesian models is the ability to generate posterior distributions that reflect the impact of new data on results from previous studies (prior distributions).

We therefore fit two Bayesian logistic regression models of leader status as a function of *Prestige* and *Dominance*, each with a different set of prior distributions for these predictor variables (See Table 2). The first model used informative Gaussian priors derived from metanalysis of peer-rated, self-rated, and behavioral measures of dimensions of leadership from Cheng et al.'s experimental studies among North American university students (See Table S6 in the Supplementary Information). We relied on the metafor (Laliberté, 2011) and compute.es (Re, 2013) packages to produce a mean correlation coefficient for *Dominance* ($r = 0.48$) and *Prestige* ($r = 0.58$) and to convert each correlation coefficient to log odds, which produced prior distributions suitable for use in logistic regression for *Dominance* ($mean = 2.01$, $SD = 0.46$) and *Prestige* ($mean = 2.63$, $SD = 0.52$).

The second model did not utilize results from previous studies but instead used "weakly informative" Gaussian priors for each coefficient (Gelman, Jakulin, Pittau, Su, et al., 2008) that are suited to estimate parameters from data with small sample sizes (McNeish, 2016; Schoot, Broere, Perryck, Zondervan-Zwijnenburg, & Loey, 2015). Additionally, these regularizing priors introduce greater conservatism on parameter estimates and have been demonstrated to reduce Type-S error rates relative to frequentist approaches or flat priors (Gelman & Tuerlinckx, 2000; Ghosh, Li, & Mitra, 2018). In this model, the posterior distributions would be heavily influenced by the new data. Both models used weakly informative Gaussian priors for age and sex, which we conceptualized as control variables. See Table 2.

Standard linear regression models assume that the predictor variables are measured without error. Each of our predictor variables, however, was based on several peer ratings that often varied substantially from rater to rater (Fig. S1). We therefore used an "errors-in-variables" model, also known as a Bayesian measurement error model, in which the predictors are a distribution of values with a mean, computed as the mean peer-rating for each trait for each individual, and a standard error of the mean (McElreath, 2018; Stefanski, 2000):

$$\text{Leadership status} \sim \text{Bernoulli}(p)$$

$$\log it(p_i) = \beta_0 + \beta_1 \text{Prestige}_{\text{EST},i} + \beta_2 \text{Dominance}_{\text{EST},i} + \beta_3 \text{Sex}_i + \beta_4 \text{Age}_i$$

$$\text{Prestige}_{\text{EST},i} \sim N(\text{Prestige}_{\text{OBS},i}, \text{Prestige}_{\text{SE},i})$$

$$\text{Dominance}_{\text{EST},i} \sim N(\text{Dominance}_{\text{OBS},i}, \text{Dominance}_{\text{SE},i})$$

We centered and scaled all continuous variables by one standard deviation as required by Markov Chain sampling and then fit both Bayesian models in R (R Core Team, 2017) using Stan and the rstan package (Stan Development Team, 2018). (Unfortunately, the glmnet package does not provide an "errors-in-variables" routine, so we only incorporated measurement errors in the Bayesian analyses.)

Results

Ethnography of Chabu leadership

Very little is known about most aspects of Chabu culture and only recently have they been the focus of any systematic or ethnographic anthropological research (Dira & Hewlett, 2017). This study is the first

to focus on the social organization and political structure of the Chabu. To contextualize our quantitative results, we first report the results of qualitative ethnographic methods conducted at the beginning of this study.

Traditional Chabu cultural models of leadership and respected people

Ethnographic qualitative interviews revealed traditional systems of leadership among the Chabu generally resemble those of many egalitarian hunter-gatherers (Boehm, 1999; Kelly, 2013) and our observations are consistent with Dira and Hewlett (2017). Traditionally, there were no formal leaders or headmen. Leadership emerged facultatively in the context of collective activities. During the building of a new house (*doku*), for example, the owner of the dwelling leads construction, and in clearing land (*áppúr*), the plot owner organizes and directs labor.

Collective spear hunting with dogs (*dirba*) is a form of Chabu hunting for targeting larger game such as pigs and buffaloes and is a generally considered a risky strategy but is an efficient technique for strong and skilled hunters (see Dira & Hewlett, 2016, 2017). *Dirba* hunting is likely the most culturally salient domain of traditional leadership among the Chabu. A collective hunt is organized by the owner of hunting dogs who informs neighbors of plans to hunt the following day. Those interested will join. During the hunt, all hunters may act independently and disperse, radiating from and following the pack of hunting dogs. The hunt leader, however, may also direct and coordinate hunters once the dogs have identified the location of a prey animal. If the animal is first identified by a dog but speared by a hunter other than the hunt leader, the hunt leader has authority over the kill and the distribution of meat. If dogs were not involved in identifying the prey, the hunter who made the kill oversees the distribution of meat. In either case, meat is distributed equally among the hunters, who then share with kin, neighbors, and social partners.

The Chabu show some respect and deference towards elders (*gutare*) and acknowledge that some individuals within age and sex grades are more respected than others. Individuals earn respect by offering effective solutions to community dilemmas, such as resolving conflicts between village members (*sótá*) and serving as a cosignatory for aspiring bridegrooms lacking sufficient bride price capital. Those highly skilled in clan based supernatural powers (*seja*) are also respected. Hosting guests, generosity, and embodying cultural norms of sharing (*appakat*) also garner respect. Mothers also maintain a special position in Chabu society. All mothers are respected and women who have given multiple births and successfully raised many children are especially revered. The Chabu consistently affirm that respected individuals do not enjoy any marked increase in social status per se, but the opinions of these individuals carry more weight and most people accept their advice.

Chabu cultural model of the Kebele system

Ethnographic qualitative interviews and *Ad libitum* observations suggest the Kebele system has either formalized, or perhaps supplanted, the direct influence of more traditional and informal leadership. Kebele leaders maintain a disproportionate level of influence in the community across many aspects of social life. They report, however, that they hold their position only to the degree the community values their service. Kebele leaders are elected by a show of hands vote, based on their high qualities, culturally appropriate behavior, prosocial motivations, and their ability to solve problems. The tenure of leadership positions is not

fixed, but dependent upon the collective value of individual leaders⁴; Woreda (local) officials also play a role in influencing the tenure of Kebele leaders (Dira, personal communication). Kebele leaders expressed that although most people respect them for their service, some do not.

The Chabu mention that good Kebele leaders must be individuals who do not fight with others or spread negative rumors about group members; they should not initiate physical violence if they learn people have spread negative rumors about them. An ideal Kebele leader should be a strong public speaker, they must entertain guests with a positive demeanor, and they should refrain from frequent or excessive alcohol consumption and intoxication. A bad leader is easily angered and displays aggression. In the event of poor leadership, the elders will first advise the leader to improve their leadership. If this intervention proves unsuccessful, the leader will be replaced. Generally, community members appreciate the service of Kebele leaders and view their role as part of a beneficial social structure which has increased their quality of life.

The main function of Kebele leaders includes organizing cooperative labor and enforcing punitive sanctions. For example, in constructing a new church in the village the Kebele leaders delineated the necessary tasks (e.g., collect wood from the forest, clear land and flatten the ground, framing) to various task groups. Critically, the Chabu assert Kebele leaders cannot force them to do anything against their will. This is in contrast with the ability of Kebele leaders to enforce punishments for non-compliance, however, which can include administering fines and incarceration. Unjustified sanctioning by a leader without community consensus and approval of the Justice Committee, however, would most certainly lead to removal from the position.

The Kebele leaders also liaise with the Woreda governmental office as needed. For example, Woreda officials periodically distribute tools, such as machetes or hoes, to rural and ethnic minority populations. In order to receive these resources, Kebele leaders must create a census and collect the names of individuals in the village interested in receiving the tools. Kebele leaders do not receive any direct compensation for their service, often see the role as a burden, and claim they would prefer to focus on their own work rather than community service. Kebele leaders nevertheless recognize their special skills and community respect, and are willing to accept the burden of community leadership in the interest of the group.

Rater agreement

Because most of our leadership traits were inherently subjective and context-specific, we did not expect our raters to closely agree on the extent to which a particular target was, e.g., feared, prosocial, or likable. Accordingly, the standardized Cronbach's α , an index of inter-rater agreement, ranged from 0.42 to 0.9 for the peer-rated variables, with a mean of 0.71. There was the least agreement on female parenting, and the most agreement on male hunting and female fighting. Raters had less agreement on female traits ($\bar{\alpha} = 0.65$) than on male traits ($\bar{\alpha} = 0.75$) and there was greater variability in female ratings. There was also an interesting trend for there to be low agreement on female traits for which agreement on men was high, and vice versa. See Fig. S1 in the Supplementary Information.

Descriptive statistics

The sample included 34 males and 26 females with a mean estimated age of 37.2. Of the 60 participants, 12 were elected to major leadership roles, 11 were elected to minor leadership roles, 13 were elected to non-leadership roles, and 24 were not serving in an elected

⁴We suspect most leadership positions experience succession every one to two years. For example, over the course of approximately 12 years at least five different male chairmen have been elected.

position. Given the distribution of leaders in our sample, for men, we compared major leaders ($n = 9$) to other men ($n = 25$). For women, few of whom were major leaders, we compared major and minor leaders ($n = 5$) to other women ($n = 21$). Leaders tended to marry other leaders: of the 13 participants who were married to leaders, 7 were also leaders. See Table 3 for summary statistics.

Preregistered tests

We tested our seven bivariate preregistered predictions by computing Cohen's D and 95% confidence intervals using the effsize package (Torchiano, 2018) and rejecting the null hypothesis if these intervals excluded 0 (Table 4, Fig. 2A, B). We conducted these comparisons only within sex because some variables, such as grip strength, have known associations with sex. In support of our predictions, *Learning and intelligence*, *Prestige*, *Spouse quality*, *Mentor salience* and *Dominance* (see SI) were significantly higher in male leaders than non-leaders, but contrary to our predictions, *Grip strength* and *Fighting* were not significantly higher (Fig. 2A). In support of our predictions, *Prestige*, *Spouse quality*, and *Mentor salience* were significantly higher in female leaders compared to non-leaders. Only one woman in the sample was mentioned as a potential mentor however, and she was also a leader. Contrary to predictions, the remaining variables were not significantly higher in women leaders, and *Fighting* and *Dominance* trended in the opposite direction (Fig. 2B).

Heatmaps and cluster analysis of peer-rated traits

To gain a broad overview of our data, we created heatmaps of all peer-rated variables. We clustered the rows (variables) and columns (participants) to determine if there were groups of participants who shared similar trait values, and to determine if there were groups of traits that tended to covary across participants. There were several traits for men (e.g., *Coffee*, *Honey*, and *Hunting*) that were not rated for women. We therefore created separate heatmaps for men and women. This was an exploratory analysis, so we do not report *p*-values nor did we formally test for sex differences. See Fig. 3.

It is apparent from the heatmaps that, by and large, the peer-rated traits were all strongly positively correlated, contrary to our expectations. That is, individuals who were rated high on one trait were also rated high on the other traits, and individuals who were rated low on one trait were also rated low on the other traits. The main exception was *Fighting*, which tended to be negatively correlated with the other traits. The median correlation coefficient among all traits except *Fighting* was $r = 0.58$ ($min = 0.075$, $max = 0.95$). See also Figs. S4–S8, in the Supplementary Information.

In both sexes there was a cluster of participants who were highly rated on most traits (red column dendrograms). Among men, all of these highly rated individuals were major leaders. Similarly, 4 of 5 female leaders were also in the high rated cluster (Fig. 3A, B). In men, all major leaders and had above average *Mentor salience* scores, and 5/6 had above average *Respect salience* scores. In women, 5/6 women with above average *Respect salience* scores were in the high rated cluster. Interestingly, highly rated women participants were rated low on *Feared* and *Fighting* (see also Fig. 2).

In women, the second cluster of participants (green column dendrogram) had intermediate ratings on most variables but high ratings on *Feared* and *Fighting*. In this group, 3/5 women were elderly, and none were leaders. The third and final cluster of female participants (blue column dendrogram) had mostly low ratings on all variables and included a mix of ages and one leader.

In men, the remaining clusters were somewhat less clear-cut. The green column dendrogram were men with intermediate ratings on most variables, but higher ratings on most mentor salience variables. The blue column dendrogram included men with either intermediate values on most variables but low values on mentor salience variables, or men

Table 3
Summary statistics. A: Study variables for male data B: Study variables for female data.

A: Male variables	n	Min	Max	Mean	SD	Gini	Histogram
Age (estimated)	34	18.000	93.000	36.353	16.457	0.221	
Height	34	156.000	177.500	166.691	5.098	0.017	
Grip strength	34	10.100	55.600	38.768	9.216	0.120	
Prestige	34	0.223	0.924	0.515	0.188	0.208	
Dominance	34	0.305	0.928	0.526	0.147	0.155	
Mentor salience	34	0.000	0.273	0.042	0.064	0.705	
Respect salience	34	0.000	0.648	0.093	0.161	0.758	
Allies	34	0.150	0.904	0.515	0.202	0.223	
Conflict	34	0.150	0.922	0.515	0.218	0.248	
Decisions	34	0.186	0.953	0.516	0.212	0.233	
Expertise	34	0.203	0.899	0.515	0.207	0.232	
Feared	34	0.210	0.988	0.516	0.183	0.202	
Fighting	34	0.187	0.904	0.537	0.183	0.194	
Learning and intelligence	34	0.211	0.970	0.514	0.206	0.222	
Kin	34	0.060	0.898	0.480	0.216	0.260	
Likable	34	0.180	0.916	0.517	0.193	0.213	
Parenting	34	0.218	0.985	0.522	0.186	0.196	
Prosocial	34	0.089	0.798	0.487	0.223	0.266	
Respect	34	0.175	0.964	0.515	0.219	0.244	
Spouse quality	34	0.156	0.972	0.527	0.189	0.197	
Farming	34	0.171	0.952	0.513	0.207	0.227	
Honey	34	0.033	0.964	0.504	0.233	0.263	
Hunting	34	0.027	0.982	0.506	0.254	0.290	
Coffee	34	0.060	0.788	0.442	0.200	0.263	
B: Female variables	n	Min	Max	Mean	SD	Gini	Histogram
Age (estimated)	26	18.000	70.000	38.308	14.675	0.213	
Height	26	148.000	169.000	155.654	4.728	0.017	
Grip strength	26	12.100	41.650	29.212	6.954	0.134	
Prestige	26	0.269	0.827	0.526	0.176	0.195	
Dominance	26	0.291	0.891	0.531	0.176	0.188	
Mentor salience	26	0.000	0.004	0.000	0.001	1.000	
Respect salience	26	0.000	0.562	0.078	0.145	0.763	
Allies	26	0.203	0.835	0.526	0.195	0.217	
Conflict	26	0.269	0.837	0.527	0.181	0.195	
Decisions	26	0.157	0.874	0.528	0.221	0.242	
Expertise	26	0.222	0.800	0.524	0.177	0.194	
Feared	26	0.212	0.849	0.517	0.181	0.198	
Fighting	26	0.234	0.976	0.545	0.208	0.220	
Learning and intelligence	26	0.235	0.970	0.527	0.199	0.218	
Kin	26	0.110	0.922	0.525	0.223	0.247	
Likable	26	0.213	0.883	0.530	0.218	0.238	
Parenting	26	0.277	0.881	0.527	0.162	0.175	
Prosocial	26	0.226	0.942	0.526	0.208	0.228	
Respect	26	0.277	0.922	0.524	0.187	0.206	
Spouse quality	26	0.198	0.953	0.531	0.181	0.191	
Farming	26	0.196	0.884	0.524	0.210	0.234	

with low values on most variables, but some higher values on mentor salience variables and especially high values on *Fighting* and *Hunting*.

Turning to patterns among the variables, male variables formed three major clusters. The bottom cluster (red row dendrogram) comprised the mentor salience variables. The middle cluster (green row dendrogram) comprised most productivity measures (*Farming*, *Hunting*, *Honey*) and the dominance measures, *Fighting* and *Feared*. The top cluster (blue row dendrogram) comprised the remaining variables, including all the *Prestige* variables and other social, cognitive, and reproductive measures. Among women, *Feared* and *Fighting* were negatively correlated with the other traits and formed a separate row cluster (the red row dendrogram).

Exploratory elastic net regression of leader status and respect salience

Because our predictor variables were highly correlated (Fig. 3), and because we had a relatively low sample size, we used the *glmnet* package to fit an elastic net logistic regression model of leader status (including both sexes) as a function of all peer-rated variables. Composite variables, i.e., *Prestige* and *Dominance*, were excluded.

In the λ_{min} model *Spouse quality* was the strongest positive predictor of leader status, along with *Respect*, *Feared*, and *Conflict*. Especially weak predictors included *Sex* and *Fighting*. *Age* was the only moderately strong negative predictor. In the more conservative λ_{1se} model, most variables were equally strong positive predictors, consistent with the

Table 4

Results of a priori tests of mean differences between leaders and non-leaders by sex with 95% CI.

Variable	Leader mean	Leader mean SE	Non-leader mean	Non-leader mean SE	Cohen's d	95% CI Lower bound	95% CI Upper bound	Group
Prestige	0.734	0.049	0.437	0.026	2.210	3.171	1.248	Men
Dominance	0.640	0.050	0.486	0.025	1.171	2.014	0.328	Men
Fighting	0.559	0.060	0.529	0.037	0.159	0.952	-0.633	Men
Learning and intelligence	0.772	0.059	0.422	0.024	2.565	3.579	1.551	Men
Spouse quality	0.720	0.067	0.458	0.026	1.739	2.640	0.839	Men
Mentor salience	0.098	0.031	0.022	0.007	1.380	2.242	0.518	Men
Grip strength	42.889	1.090	37.284	2.045	0.622	1.429	-0.184	Men
Prestige	0.695	0.079	0.486	0.034	1.327	2.422	0.232	Women
Dominance	0.447	0.040	0.551	0.041	-0.597	0.444	-1.639	Women
Fighting	0.392	0.034	0.581	0.047	-0.960	0.103	-2.023	Women
Learning and intelligence	0.620	0.094	0.504	0.043	0.581	1.622	-0.459	Women
Spouse quality	0.717	0.091	0.487	0.033	1.438	2.544	0.331	Women
Mentor salience	0.001	0.0009	0.000	0.000	1.095	2.169	0.022	Women
Grip strength	33.260	1.497	28.248	1.591	0.738	1.786	-0.311	Women

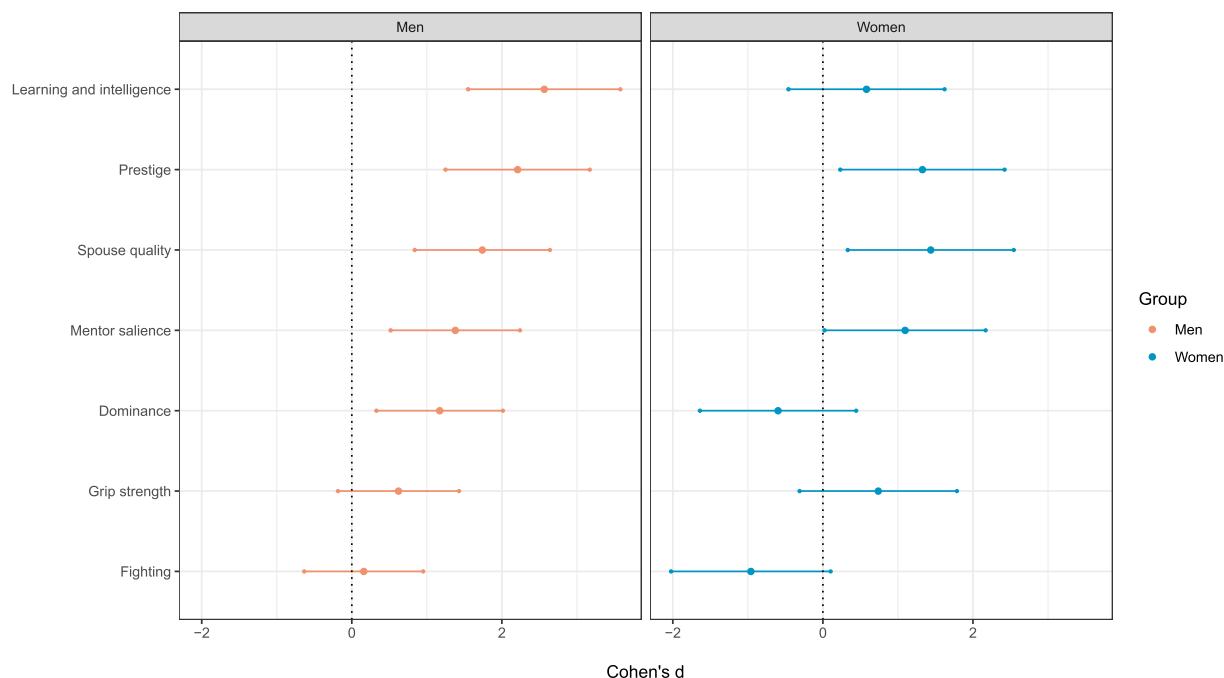


Fig. 2. Preregistered tests. Bivariate comparisons of elected leaders vs. non-leaders on mean values of hypothesized leadership traits. Tested within men only ($n = 34$) and within women only ($n = 26$). Values are Cohen's d; bars represent 95% CI. See Supplementary Information for details on preregistration.

heatmaps (again with the exceptions of *Sex*, *Age*, and *Fighting* which were at or near 0). In this model, the tuning parameter $\alpha = 0$ by cross-validation. This was therefore a pure ridge regression model with no coefficients shrunk completely to 0. See Fig. 4A. For coefficients, see Table S5A in the Supplementary Information.

In the [Henrich, Chudek, and Boyd \(2015\)](#) model, *Mentor salience* plays a central role in leadership, yet in our exploratory model of leader status, Fig. 4A, this variable had an effect only on par with the other cognitive and social variables. It is possible that mentorship abilities and biased social learning play a more important role in prestige and respect than they do in leadership per se.

To explore this idea, we fit a second elastic net model of *Respect salience*, which we interpreted as our most specific measure of respect, as a function of all peer-rated variables (except peer-rated *Respect*). In this model, Fig. 4B, *Mentor salience* was indeed the strongest predictor in the λ_{min} model but was about equal to other social and reproductive variables, *Spouse quality*, *Parenting*, *Likable*, and *Conflict*, in the more conservative λ_{1se} model. Here, the tuning parameter $\alpha = 0.45$ by cross-validation. The coefficients of a block of correlated variables were shrunk to 0, exactly. For coefficients, see Table S5B in the

Supplementary Information.

Prestige and dominance

Currently, one of the most influential evolutionary models of leadership and social status is the Dominance-Prestige model ([Henrich & Gil-White, 2001](#)), which proposes that dominance, based on physical formidability, is distinct from prestige, based on skills, knowledge, and mentorship. Studies of this model in Western populations often rely self-reports and peer-ratings using the Dominance-Prestige scale ([Cheng, Tracy, & Henrich, 2010](#)).

PCA of prestige and dominance

We first conducted a principal components analysis (PCA) of the three peer-rated variables operationalizing prestige (*Respect*, *Expertise*, and *Likeable*), and the three peer-rated variables initially operationalizing dominance (*Feared*, *Fighting*, and *Control*). See Fig. 5.

These results show that the *Prestige* variables loaded primarily on PC1, and the *Dominance* variables on PC2, supporting the view that these are independent qualities of our participants. They also show that

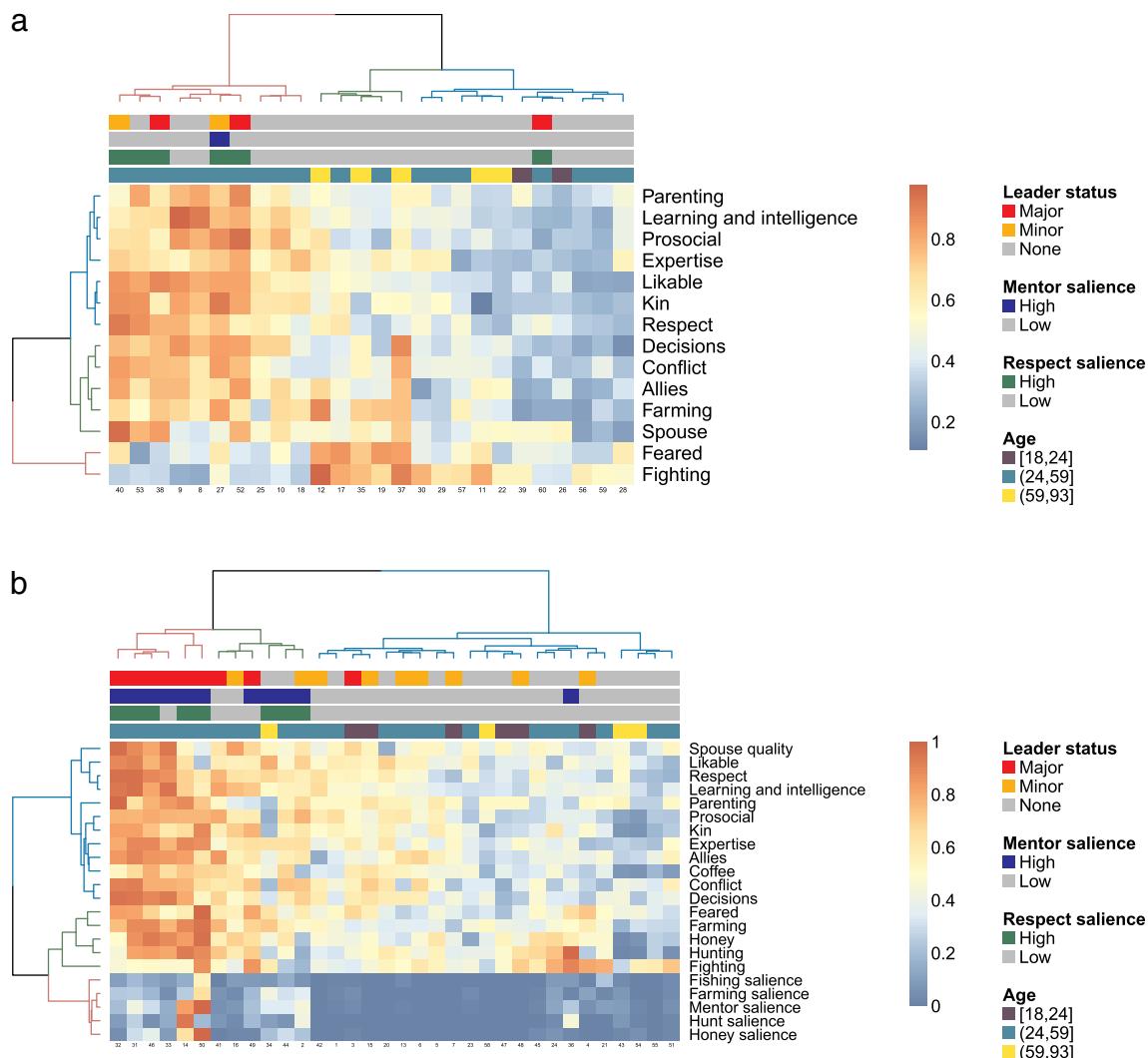


Fig. 3. Cluster analysis of peer-rated leadership traits. A. Female participant ratings. B. Male participant ratings. Colors in each cell represent the mean peer rating of each participant (columns) on each trait (rows). Columns are annotated with each participant's leadership status, mentor salience (above or below average), and age. Distance between row vectors computed with $1 - \text{cor}$. Distance between column vectors computed with the Euclidean metric. Clusters determined with the Ward agglomeration algorithm. (For interpretation of the references to color in this figure legend, the reader is referred to the online version of this article.)

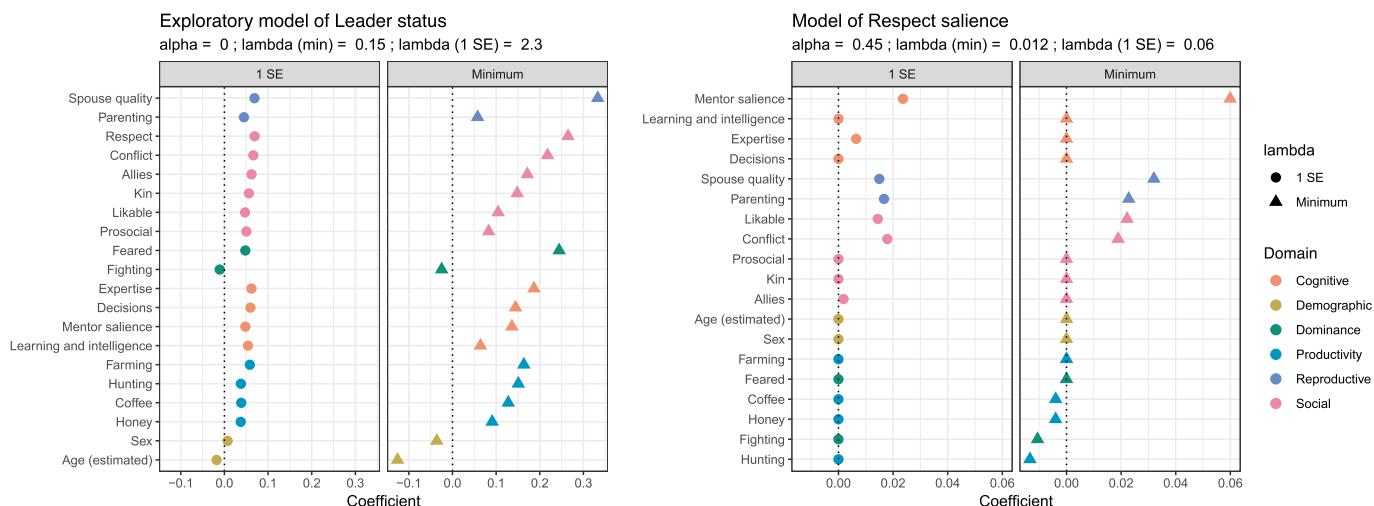


Fig. 4. Elastic net regressions. A. Leader status as a function of all peer-rated variables controlling for age and sex. Coefficients are log odds. B: Respect salience score as a function of peer-rated variables (excluding Respect) controlling for age and sex. Coefficients are standard linear regression coefficients. All variables were standardized prior to fitting. Color-coded variable domains are to facilitate interpretation only; variable domain played no role in the fitting process.

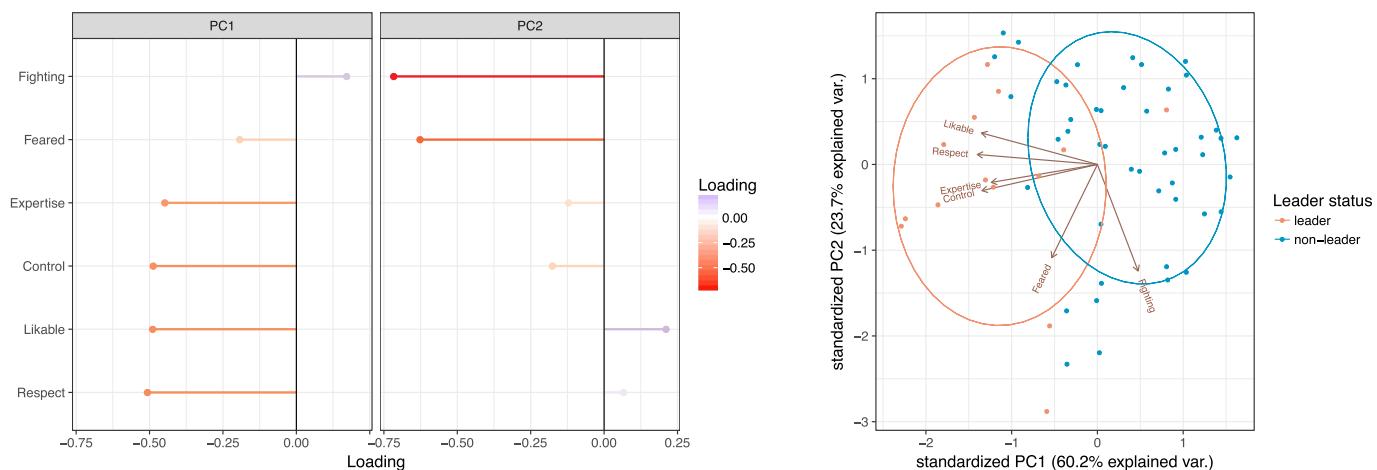


Fig. 5. Variable loadings (left) and biplot (right) of a PCA of the prestige and dominance variables. Variables were centered and scaled by one standard deviation. Each point in the biplot is one participant.

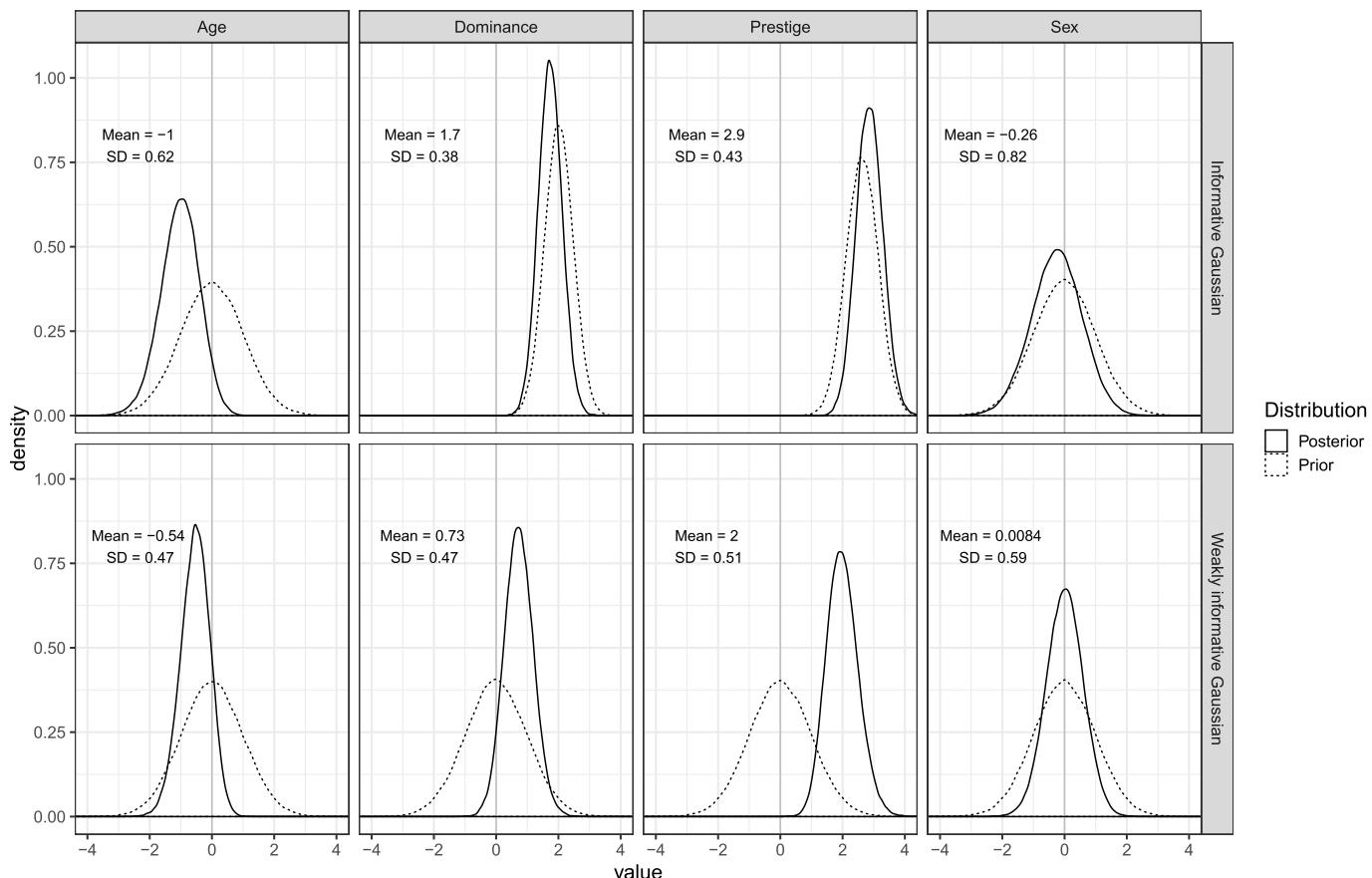


Fig. 6. Posterior distributions (solid lines) under two different sets of prior distributions (dotted lines). All variables were centered and scaled by one standard deviation. Coefficient distributions are log odds.

Control loaded with the other *Prestige* variables on PC1, justifying our *Dominance* variable that excludes *Control* (see Supplementary Information).

PC1 distinguished elected leaders (who were highly rated on the *Prestige* variables) whereas PC2 did not, suggesting that dominance does not play a large role in leadership among the Chabu. However, male leaders were highly peer-rated on *Feared*, as were older women (Fig. 3). Multiple studies, including among Western populations and small-scale societies, have found that dominance is associated with leadership. It is therefore possible that after controlling for sex and age, dominance and

prestige would both predict leadership.

Bayesian dominance-prestige regression model

To compare the relative value of prestige and dominance in predicting elected leader status after controlling for age and sex, we fit Bayesian measurement error models. Models employed four Markov chains using Stan's Hamiltonian Monte-Carlo sampling algorithm. All chains converged and demonstrated high mixing across 40,000 iterations following a burn in of 20,000 iterations. For all parameters across both models (weakly informative Gaussian priors and informative

Gaussian priors), the number of effective samples was 80,000, (with values of 26,889 and 30,675 for the log-posteriors, respectively) the convergence measure $R > 1.000$, and no observations exerted undue influence on posteriors.

We then used leave-one-out-cross-validation (LOO) from the loo package (Vehtari, Gabry, Yao, & Gelman, 2018) to evaluate the relative predictive accuracy of each model. The informative prior model had a marginally lower LOOIC value than the weakly informative prior model (smaller values are better; see Table S7 in the Supplementary Information). The informative prior model had a Bayes R^2 value of 0.57 (Gelman, Goodrich, Gabry, & Ali, 2017), and a Tjur's D of 0.56, compared to an R^2 value of 0.44 and Tjur's D of 0.44 in the weakly informative prior model.

The posterior probability distribution of the *Prestige* coefficients was entirely positive under the informative and weakly informative priors and the distribution means were similar. The posterior probability distribution of the *Dominance* coefficients were also entirely positive for the model with the informative prior, but a small fraction of the distribution was negative for the model with the weakly informative prior (94.5% of estimated values > 0). The mean value of the *Dominance* posterior distribution under the weakly informative prior is approximately 1 unit value lower (on log odds scale) than under the informative priors, demonstrating that although *Dominance* is positively associated with leader status after controlling for *Prestige*, *Age*, and *Sex*, this effect is more sensitive to the prior probability distribution than it is for *Prestige*. See Fig. 6.

Anthropometrics and leadership

The bivariate tests found that leaders were not significantly stronger than non-leaders. We therefore conducted several exploratory analyses to understand the relationship between our anthropometric variables, grip strength and height, and dominance and leader status. Since there are large sex differences in grip strength and height, we conducted these analyses separately by sex (only one woman was freelistened as a mentor, so we removed *Mentor salience* from the female analyses). Cluster analyses (Fig. 7) found that, in men, the anthropometric variables clustered with the dominance variables (*Feared* and *Fighting*) as well as with the productivity variables (*Coffee*, *Honey*, *Hunting*,

Farming). In women, height clustered with the dominance variables (*Feared* and *Fighting*), but all other variables were in a separate cluster. We assessed the uncertainty in these clusters using the pvcust package (Suzuki & Shimodaira, 2015). Whereas several of the lower level clusters were strongly supported by the data, the top-level clusters were weakly supported by the data. See Fig. S9 in the Supplementary Information for more detail.

We discovered one other interesting pattern. Whereas the most feared men were in the upper distribution of grip strength, the most feared women, with two exceptions, were generally either young with high grip strength, or old; alternatively, the most feared women had the highest grip strength for their age. See Fig. 8.

Discussion

From these results we draw two primary conclusions. First, there is a strong positive correlation among most of the peer-rated leadership traits — individuals who were rated high on one trait were rated high on the other traits, and individuals who were rated low on one trait were rated low on the other traits. Those with high values on these traits tended to be leaders (Fig. 3).

Our more conservative elastic net regression model of leader status, λ_{1se} (Fig. 4A) found that the coefficients of most predictor variables were of similar positive magnitude. The less conservative model, λ_{min} , however, found that *Spouse quality*, *Respect*, *Conflict resolution*, and *Feared* had larger coefficients than other variables. The latter result supports the roles of reproductive success and mating inequalities among leaders, as emphasized by Neel (1980), as well as dimensions of both dominance and prestige (being feared and respected), and prosocial community service (conflict resolution) (Cheng, Tracy, Foulsham, Kingstone, & Henrich, 2013; Henrich & Gil-White, 2001; Price & Van Vugt, 2014), consistent with egalitarian social structures.

Nevertheless, the strong positive covariance among almost all leadership traits, which were chosen from multiple evolutionary models of leadership, means that our results do not clearly favor some theoretical models or domains of traits over others. The strong covariance of traits could indicate a correlation with some underlying trait, such as health or intelligence (McDermott, Lopez, & Hatemi, 2016; Von Rueden,

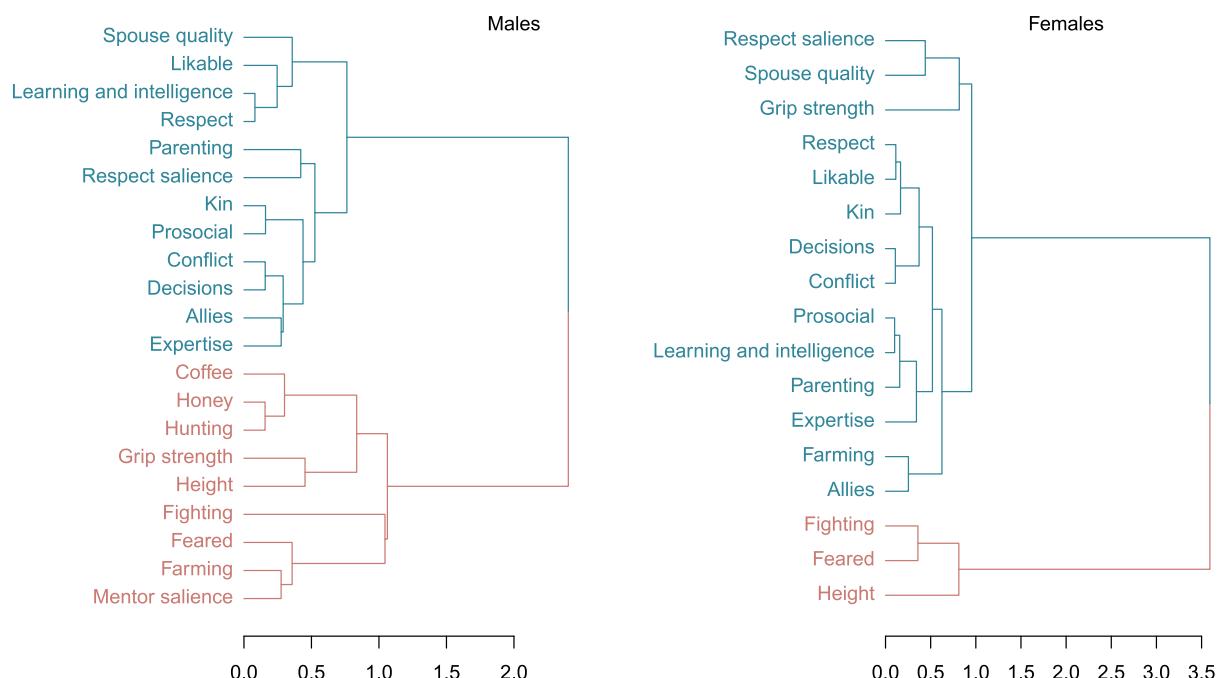


Fig. 7. Hierarchical cluster analyses of grip strength, height, and peer-rated variables. Distance was $1 - \text{cor}$. Clusters agglomerated with the Ward algorithm.

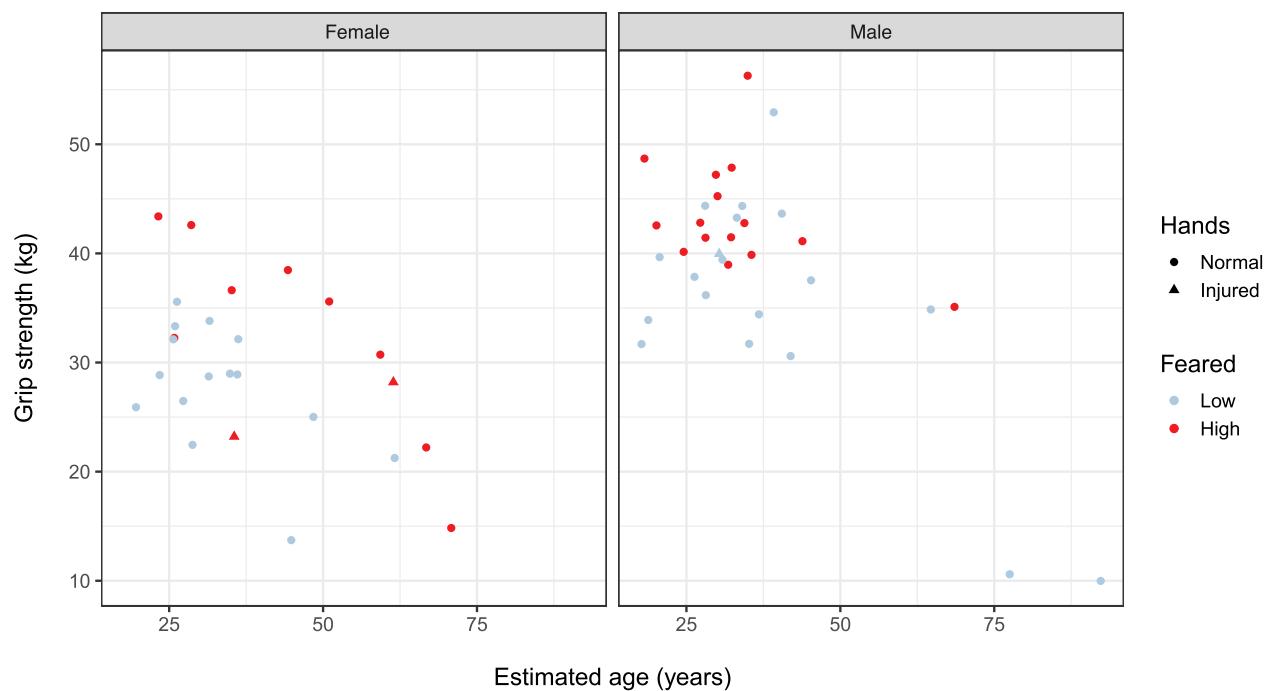


Fig. 8. Feared (greater or less than the mean) vs. age and grip strength, by sex. Three individuals had injuries to their right hands and were therefore tested using their left hands only. A small amount of jitter was added to distinguish overlapping points.

Gurven, & Kaplan, 2008; Von Rueden, Gurven, Kaplan, & Stieglitz, 2014). It is also possible that this covariance reflects a property of rater psychology, e.g., that raters either perceive the value of some underlying trait, and then assign that value to many other traits (a “halo effect”; Nisbett & Wilson, 1977), or that raters perceive social status, and assign values to traits that correspond to individuals’ social status (but see Reyes-García et al., 2016 for validation of peer evaluation methods). Our peer-rating methodology, however, is consistent with other anthropological field research (see Supplementary Information).

The main exception to the positive covariation of traits was *Fighting*, which tended to be moderate or low among leaders, especially female leaders, who were also low on *Feared*. *Fighting* was also negatively associated with female leaders (albeit not significantly so; see Fig. 2). This corresponds with the Chabu cultural model that women leaders serve to *resolve*, rather than cause, intragroup conflicts, and that good leaders of both sexes should be individuals skilled in conflict resolution who do not fight with others or spread negative rumors.

Our second main conclusion is that, other than the distinction in *Feared*, female and male elected leaders share similar phenotypic profiles. Both male and female leaders are respected individuals, they tend to score high on most peer-rated leadership traits (see Fig. 3), and they both score significantly higher than non-leaders on prestige. Moreover, after controlling for other variables, sex was a very weak predictor of leader status in both our elastic net models (Fig. 4) and our Bayesian models (Fig. 6). These results should encourage the incorporation of women into evolutionary theories of leadership. Garfield, Hubbard, and Hagen (2019) argue that the traits that predispose to leadership within communities, such as expertise, high quality decision-making, conflict resolution, and kin investment, apply equally to leadership within families (See also Hagen & Garfield, 2019). The key role that women likely played as leaders within families, especially given the importance of alloparenting in human evolution (e.g., Meehan, 2005), appears to have been overlooked in most of the literature on leadership (Garfield, von Rueden, & Hagen, 2019; Smith, Ortiz, Buhbe, & Van Vugt, In press; Vandermassen, 2008). In this sample, male and female leaders were often married to one another. These “power couples” warrant future study.

Dominance-Prestige model

Our results provided mixed support for the Dominance-Prestige model. In support, dominance and prestige loaded on separate components in the PCA (Fig. 5), verifying the distinction between prestige and dominance (Barkow, 1989; Cheng, Tracy, Foulsham, Kingstone, & Henrich, 2013; Henrich & Gil-White, 2001; Kracke, 1978). Prestige and dominance were both positive predictors of leader status in our multiple regression models, as also seen in the Tsimane’, another small-scale society (Von Rueden, Gurven, Kaplan, & Stieglitz, 2014). Inspection of a scatter plot indicated that whereas female leaders were high on prestige but low on dominance, male leaders were high on both prestige and dominance (Fig. S10 in the Supplementary Information), associations supported by our preregistered bivariate tests (Fig. 2).

In our Bayesian logistic regression model, the posterior distributions of coefficients for *Dominance* and *Prestige* were almost entirely positive under both weakly informative and informative priors. Posterior distributions under informative priors are consistent with Cheng et al.’s experimental results; the *Prestige* posterior distribution suggests a slightly greater positive effect than the informed prior distribution, whereas the *Dominance* posterior distribution suggests a slightly greater negative effect than the informed prior distribution (Tables 5A and 5B and Fig. 6), possibly reflective of greater egalitarianism among the Chabu relative to Western populations. These results support the importance and independence of both constructs and suggest Chabu leaders may rely on prestige, dominance, or both, consistent with many

Table 5A

Weakly informative Gaussian prior model posteriors in log odds. All variables were centered and scaled by one standard deviation.

	Mean	Standard deviation	2.5%	97.5%
(Intercept)	-1.74	0.492	-2.73	-0.81
Prestige	2.00	0.509	1.06	3.05
Dominance	0.73	0.467	-0.16	1.67
Age	-0.54	0.470	-1.51	0.33
Sex	0.01	0.593	-1.16	1.17
Log-posterior	-83.09	7.922	-99.57	-68.68

Table 5B

Final informative Gaussian prior model posteriors in log odds.

	Mean	Standard deviation	2.5%	97.5%
(Intercept)	-2.07	0.558	-3.19	-1.00
Prestige	2.86	0.428	2.04	3.72
Dominance	1.74	0.381	1.00	2.50
Age	-1.03	0.624	-2.31	0.13
Sex	-0.26	0.819	-1.89	1.33
Log-posterior	-79.49	7.905	-95.88	-64.87

theories and empirical findings in both large-scale and small-scale societies (Barkow, 1989; Chapais, 2015; Cheng, Tracy, Foulsham, Kingstone, & Henrich, 2013; Henrich & Gil-White, 2001; Kracke, 1978; Price & Van Vugt, 2014; Tiger & Fox, 1971; Von Rueden, Gurven, & Kaplan, 2011; Von Rueden, Gurven, Kaplan, & Stiegitz, 2014).

In support of biased learning towards leaders, a unique prediction of the Henrich and Gil-White (2001) model, *Mentor salience* was clearly associated with leadership in the bivariate test (Fig. 2) and cluster analysis heatmaps (Fig. 3), was a positive predictor of leadership in the exploratory elastic net model (Fig. 4A), and was the strongest predictor of *Respect salience* in the less conservative λ_{min} elastic net model (Fig. 4B). *Respect salience* involved freelistng respected individuals, arguably our most specific measure of respect, which supports the role of mentorship in achieving status among the Chabu (see Dira & Hewlett, 2016 on learning to hunt).

Against the dominance-prestige model, although *Mentor salience* was a predictor of leader status, it was no better than many other variables (Fig. 4A), which does not support the special role of biased learning towards prestigious leaders as suggested by Henrich and Gil-White (2001), Cheng, Tracy, Foulsham, Kingstone, and Henrich (2013), and Henrich, Chudek, and Boyd (2015). Furthermore, Fig. 3 suggests leaders who score high on *Mentor salience* also score high on the dominance measures, especially among men, contrary to the predictions of Henrich and Gil-White (2001) and Cheng, Tracy, Foulsham, Kingstone, and Henrich (2013).

Chabu leaders are not physically stronger than non-leaders nor are they more likely to fight with others (Fig. 2), contrary to predictions of the dominance model, and inconsistent with Von Rueden, Gurven, Kaplan, and Stiegitz (2014). Our *Fighting* variable is based on peer-rated propensity for verbal and physical fighting, however, whereas Von Rueden, Gurven, Kaplan, and Stiegitz (2014) measured peer-rated ability to win physical fights. The consistent negative association of fighting with leader status indicates that followers are resistant to overly aggressive individuals – another defining feature of egalitarian leadership (Boehm, 1993; Knauf et al., 1991). Chabu leaders are nevertheless often feared, which Chapais (2015) argues is more closely linked with respect and prestige than admitted by Henrich and Gil-White (2001). In men, greater grip strength is associated with being feared, whereas in women older age also plays a role (see Fig. 8). We failed to find any effect of height associated with leadership (consistent with Von Rueden, Gurven, Kaplan, & Stiegitz, 2014) or being feared.

Although dominance appeared to be independent of prestige, some evidence suggests dominance may be confounded with economic productivity, in that these variables clustered together in men (Figs. 3 and 7). Horticulture requires considerable manual labor, and taller height and greater strength could be associated with greater physical work capacity (Nystedt, Lundborg, & Rooth, 2009; Spurr, 1983). Therefore, our results support Von Rueden et al.'s (2014, p.562) informed speculation that, "it may be less the fighting ability of physically dominant individuals than their productive ability, confidence, extraversion, ability to attract attention, and dissuasion of free-riding that makes them valuable leaders" (emphasis added).

For females, dominance is not associated with leadership. Women who score high on *Fighting* and *Feared* are not leaders and tend to have moderate scores on other leader traits; that is, women who are feared

and are more likely to engage in conflict appear to only be perceived as moderately respected, intelligent, and socially supported, and none are elected leaders. This sex difference is consistent with psychological studies among Western samples (e.g., Buss, 1981), and with what psychologists have described as *backlash* against dominant females in positions of leadership and high status (Williams & Tiedens, 2016); dominant women may experience many negative social outcomes in response to assertive behavior, including being less liked (in these data the correlation between *Dominance* and *Likable* for females is -0.37). Our results suggest, even among a relatively gender-egalitarian population, dominant women are less preferred as leaders than non-dominant women.

Limitations and future research

Our study had a cross-sectional design that assessed correlations between perceived traits and elected leader status. Our predictors were endogenous, imperfectly operationalized, and imperfectly measured. We therefore cannot determine cause and effect. We also did not measure actual decisions or instances of leadership. All participants belonged to a single large Chabu community. Our results therefore might not generalize to smaller Chabu communities, particularly the small extended family settlements (Dira & Hewlett, 2017). The strong correlation among most of our variables along with a relatively small sample size limited our ability to clearly discriminate which variables best predicted leader status. Finally, although leaders tended to be married to other leaders, we did not investigate the relationship between marriage and achieving leader status. These political couples warrant further research.

Our analysis of sex differences might have been biased because female leader status included major and minor leaders, whereas male leader status was limited to major leaders. Our decision to operationalize leaders status as such was based on (1) heatmaps in Figs. 3, which revealed female major and minor leaders largely clustered together whereas male major and minor leaders largely clustered apart, (2) informal observations that female "minor leaders" had considerable influence and respect in the community (relative to the average male "minor leader"), and (3) given the relatively fewer elected leadership positions available for females, "minor leader" positions are more significant. An advantage of this decision is that we have a slightly larger sample of female elected leaders and can more confidently evaluate sex differences. A disadvantage is that it we cannot compare major and minor leaders within or between the sexes, and our results may be influenced by this methodological decision. We initially developed the major/minor classifications from the social structure of the Kebele system and a few interviews and observations. From these data, including the total of our interviews and observations, we suggest a revision to our initial classification (as we have done in our analyses) recognizing the Kebele positions classifiable as "major" leadership roles are sex-specific. In summary, in considering the degree of community influence and respect and the traits of individuals classified as major or minor leaders, males and females appear distinct and the operationalization of our outcome measures (leader status) follows this perspective.

Our limited support for the role of prestige-biased learning in leadership could be due to the fact that we only measured some forms of social learning and mentoring and likely omitted important domains; specifically, pottery, collecting wild yams, and food processing are important female activities to investigate in future research. The Chabu also recognize clan-specific supernatural abilities that vary among individuals, which might require cultural transmission and play an important role in both prestige and attainment of leadership positions.

Future research should include longitudinal investigations of leadership trajectories that include objective measures of leader influence, leadership within households and kin groups, positive assortative mating of leaders, and broader conceptions of culturally valued skills.

We also aim to assess the importance of clan and variation in clan-based supernatural abilities in predicting elected leadership. Lastly, future research will investigate the importance of the Kebele system and investigate other more traditional systems of leadership among smaller, less sedentary Chabu settlements.

In subsistence horticultural societies, dominance and economic productivity are both enhanced by physical strength. Hence, the relationship between physical formidability and leadership is confounded with higher productivity. Future research should disentangle the relationships between physical strength, productivity, and leader status.

Conclusion

The study reported here is among the few to systematically investigate leaders in a small-scale society and among even fewer to compare male and female leaders. It is notable there are several female leadership positions and women maintain autonomy in many domains, despite a male bias in leadership roles. Generally, female and male leaders display similar phenotypic profiles including high peer-ratings on cognitive, social, productivity, and reproductive traits. The one clear exception is aggressiveness, which characterizes male elected leaders, whereas a lack of aggressiveness characterizes female elected leaders. Despite a history and relative persistence of egalitarianism, including gender-egalitarianism, Chabu women face constraints in their ability employ dominance-based leadership strategies that men do not, a pattern consistent with broader political institutions cross-culturally, especially among Western societies (Low, 2005; Williams & Tiedens, 2016). These results suggest women and men may rely on dominance in sex-specific ways, with differences potentially related to life history (Brown, 1985) or variation in social, embodied, and material capital (Hess & Hagen, 2006, 2017; Von Rueden, Alami, Kaplan, & Gurven, 2018). More generally, the evolutionary importance of women's leadership has been overlooked by most theorists, perhaps because of a failure to recognize the importance of leadership within families (Garfield, Hubbard, & Hagen, 2019; Garfield, von Rueden, & Hagen, 2019; Smith, Ortiz, Buhbe, & Van Vugt, In press), a key topic for future research.

Although dominance and prestige are both associated with elected leaders among the Chabu, prestige is clearly more critical. Our data do support a general distinction between dominance and prestige, but we also find that the components of dominance – being feared and being aggressive – are also distinct. Established dominance hierarchies limit the need for physical aggression in contest competition. Evidence suggests humans are equipped with psychological mechanisms to assess variation in strength and fighting ability from visual, vocal, and other cues (Sell et al., 2010, 2009). Individuals who are feared may be able to achieve dominance-based influence without relying on direct aggression. We suggest there is likely significant overlap between at least some components of dominance and some components of prestige within human social and political hierarchies. A possible mechanism of this overlap may be the necessary connections between, (1) the association of physical formidability and social dominance, (2) the physical demands of economic productivity, and (3) the high degrees of respect often bestowed towards physically formidable individuals well-equipped to provide group benefits, such as conflict resolution, facilitating cooperation, and sharing surpluses of critical resources (Chapais, 2015; Lukaszewski, Simmons, Anderson, & Roney, 2016; Von Rueden, Gurven, Kaplan, & Stiegitz, 2014).

We provide the first evidence of leader-directed social learning biases supporting theories linking prestige-biased learning and leadership, but also find learning biases include dominant individuals and do not strongly predict leader status relative to other traits, presenting new challenges to such theories.

The high collinearity of the diverse traits measured here suggests that each of the domains of leadership traits that we investigated — cognition, sociality, productivity, reproduction, and dominance — are

potentially important in understanding variation between leaders and non-leaders. To systematically overlook any of these domains may be a severe methodological limitation and this strong positive covariation of most leadership traits warrants further investigation.

Acknowledgements

We are deeply grateful to the Chabu community for their generous hospitality and support of this research. Several Chabu research assistants and families made great efforts to accommodate the research team. Dr. Kibeb Tsehay Taye served as the external research assistant and his strong Chabu language skills and experience at the study site were invaluable components of this research. We thank our colleagues and fellow Chabu researchers Barry Hewlett, Bonnie Hewlett, Samuel Jilo Dira, and Richard Berl for important insights and feedback on the manuscript as well as Erik Ringen and Robert Boyd for comments during the review process. Joey Cheng provided helpful unpublished data for use in developing Bayesian priors. We thank Amalo Sooge from the University of Hawassa for facilitating university and governmental support. This project has benefited from guidance and feedback from the first author's Ph.D. committee members Barry Hewlett, Robert Quinlan, Anthony Lopez, and Leslie New. We also thank the co-editors of the special issue and three anonymous reviewers for thorough review and helpful comments. Lastly, we thank Washington State University Vancouver's College of Arts and Sciences and backers on experiment.com (project DOI: 10.18258/3735) for funding. Partial funding from the United States National Science Foundation Division of Behavioral and Cognitive Science awards #1628509 and #1823324.

Appendix A. Supplementary data

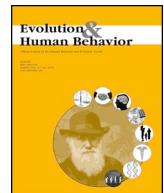
Supplementary data to this article can be found online at <https://doi.org/10.1016/j.lequa.2019.03.005>.

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Universal and variable leadership dimensions across human societies

Zachary H. Garfield^{a,b,*}, Kristen L. Syme^b, Edward H. Hagen^b



^a Institute for Advanced Study in Toulouse, Université Toulouse 1 Capitole, 1, esplanade de l'Université, 31080 Toulouse Cedex 06, France

^b Washington State University, Department of Anthropology, College Hall 150, PO Box 644910, Pullman, WA 99164-4910, United States of America

ARTICLE INFO

Keywords:

Cross-cultural
Leadership
Non-WEIRD
Shamanism
Universals
Cultural variation

ABSTRACT

Many researchers have turned to evolutionary theory to better understand diversity in leadership. Evolutionary theories of leadership, in turn, draw on ethnographic cases of societies thought to more closely resemble the smaller-scale, face-to-face communities in which humans evolved. Currently, though, there is limited systematic data on the nature of leadership in such societies.

We coded 109 dimensions of leadership, including costs and benefits relevant to evolutionary models, in 1212 ethnographic texts from 59 mostly nonindustrial populations in Human Relations Area Files (HRAF). We discovered evidence for both cultural universals in leadership, as well as important variation by continental region, subsistence strategy, group context, and leader sex. Candidate universals included that leaders were intelligent and knowledgeable, resolved conflicts, and received material and social benefits. Evidence for other leader dimensions varied by group context (e.g., there was more evidence that leaders of kin groups were older and tended to provide counsel and direction), subsistence (e.g., hunter-gatherers tended to lack leaders with coercive authority), and sex (e.g., female leaders tended to be associated with family contexts). There was generally more evidence of benefits than costs for both leaders and followers, with material, social, and mating benefits being particularly important for leaders, and material and other benefits important for followers.

Shamans emerged as an important category of leaders who did not clearly conform to influential models that emphasize two leader strategies: using knowledge and expertise to provide benefits to followers vs. using physical formidability to impose costs. Instead, shamans and other leaders with supernatural abilities used their knowledge to both provide benefits and impose costs on others. We therefore propose a modified scheme in which leaders deploy their cognitive, social, material, and somatic capital to provide benefits and/or impose costs on others.

1. Introduction

Anthropologists and sociologists realized early on that leadership and followership were critical to understanding human psychology, social organization, and culture (e.g., Firth, 1927; Morgan, 1877; Mumford, 1906; Myres, 1917). Leaders are documented among every ethnographically observed society (Brown, 1991; Lewis, 1974), and in diverse contexts, such as kin groups (Dussart, 2000), ritual (Singh, 2017), economic groups (Macfarlan, Remiker, & Quinlan, 2012), conflicts between groups (Glowacki, Wilson, & Wrangham, 2017), and nonindustrial political groups (Cohen & Middleton, 1967). For review, see Garfield, von Rueden, and Hagen (2019).

Despite decades of scholarship on leadership, to our knowledge there is no systematic investigation of leader functions and qualities, and the costs and benefits of leadership and followership, across a

representative sample of nonindustrial societies. Moreover, outside of anthropology, most scholarship on leadership is based on data from Western or Westernized, postindustrial societies (von Rueden & Van Vugt, 2015).

There is now a broad consensus on the importance of data from the full range of human cultural diversity. Since Henrich et al.'s (2010) seminal WEIRD people paper, many social scientists have sought data from "non-WEIRD" populations. Dichotomizing populations, their psychologies, or social dynamics as WEIRD or non-WEIRD, however, is a mistake.¹ As anthropology has conclusively demonstrated, there is enormous diversity across societies that does not remotely resemble a dichotomy. Conversely, anthropology has been criticized for essentializing diverse "Others" as part of its colonial history (Abu-Lughod, 2008; Said, 1979). In this regard, Abu-Lughod (2008) noted that the concept of culture operates much like its predecessor – race.

* Corresponding author at: Institute for Advanced Study in Toulouse, Université Toulouse 1 Capitole, 1, esplanade de l'Université, 31080 Toulouse Cedex 06, France.
E-mail address: zachary.garfield@iast.fr (Z.H. Garfield).

¹ A Google Scholar search for "non-WEIRD" produced over 1000 results.

There is potentially more diversity within “non-WEIRD” populations than WEIRD ones, and there is also substantial overlap of the behaviors all people (Brown, 1991). Henrich et al. (2010) in their critique of the over-reliance on WEIRD samples emphasized a holistic approach to cultural diversity within and across “telescoping” levels of societies. Comparative research must assess cultural variation without assuming that all members within a population are essentially similar, and without putting undue emphasis on either the between-population differences or similarities.

Evolutionary scholars typically define leaders as individuals who maintain disproportionate influence over group decision-making (von Rueden & Van Vugt, 2015), whatever the group may be. One outstanding question is the degree to which theoretically important dimensions of leadership vary between cultures and across social contexts. Leadership studies have focused on community and political leaders, often overlooking leadership across contexts and levels of social organization, such as among kin and informal social groups. A second outstanding question is what benefits and costs leaders and followers incur. While the benefits leaders accrue have received substantial attention – fitness benefits in particular – the costs of leadership and followership have been relatively under-investigated (but see Cheng, 2019; Glowacki & von Rueden, 2015; Price & Van Vugt, 2014; von Rueden, Gurven, Kaplan, & Stiegitz, 2014).

1.1. The functions of leadership across cultures and contexts

Roscoe (2009) proposed leadership in small-scale societies is structured by the joint demands of within-group conflict resolution and cooperation, and signaling coalitional strength to rival groups. Among many small-scale societies, which generally lack institutionalized political structures, community leadership is typically informal and emerges in response to group demands (Boehm, 1993; Kantner, 2010; Lewis, 1974; von Rueden & Van Vugt, 2015). Theoretical literature suggests these demands most commonly arise in the contexts of collective actions, resolving conflicts between families, and punishing norm violations (e.g., Gavrilets, Auerbach, & Van Vugt, 2016; Glowacki & von Rueden, 2015; Henrich, Chudek, & Boyd, 2015; Hooper, Kaplan, & Boone, 2010; von Rueden, Gavrilets, & Glowacki, 2015). Leaders also play important roles in ritual and religious contexts (Singh, 2017; Winkelman, 2020), facilitating marriages (Walker, Flinn, Ellsworth, & Hill, 2011), and organizing feasts (Wiessner & Schiefenhövel, 1996). Leadership in between-group conflict and cooperation is also common across nonindustrial societies, including hunter-gatherers (Apicella, Marlowe, Fowler, & Christakis, 2012; Glowacki et al., 2017; Hames, 2019; Richerson et al., 2016).

Stronger authority of community leaders, leadership beyond the community, and institutionalized managerial roles are associated with sedentarization, defensible resources, and social stratification (Ames, 1985; Johnson, 1982; Johnson & Earle, 1987; Kaplan, Hooper, & Gurven, 2009). Among horticulturalists and agriculturalists, managerial leadership can promote more efficient use of shared resources such as water reserves and cooperative labor (e.g., von Rueden et al., 2014). Pastoralists and coastal populations often face similar pressures concerning grazing lands and fishing access (e.g., Stevens, 1990; Widmer, 1988). Defensibility of resources creates increased opportunities for resource management and is often associated with increased territoriality and inter-group conflicts (Glowacki et al., 2017). Community leaders among populations more reliant on domesticated plant foods, livestock, and specific territories are often required to manage military operations (Lopez, 2017).

1.2. The qualities of leaders across cultures and contexts

Intelligent and knowledgeable individuals (e.g., Antonakis et al., 2017; Antonakis, Simonton, & Wai, 2019; Judge, Colbert, & Ilies, 2004; Neel, 1980), elders, and respected individuals tend to have greater

influence over community decisions across cultures, including among egalitarian hunter-gatherers, stratified chiefdoms, and nation-state organizations (Bass & Stogdill, 1990; Garfield, von Rueden, & Hagen, 2019; Silverman & Maxwell, 1978; Tooby, Cosmides, & Price, 2006). Leaders also tend to have large social networks (von Rueden, 2014; von Rueden et al., 2014; Walker et al., 2012), and embody the qualities most respected by the group (Collier & Rosaldo, 1981; Henrich & Gil-White, 2001; Low, 1992a; Roscoe, Chacon, Hayward, & Chacon, 2019; Van Vugt, 2006). Leaders across multiple contexts tend to be taller and more physically formidable, which might facilitate resolving inter- and intra-group conflicts (Lukaszewski, Simmons, Anderson, & Roney, 2016; von Rueden et al., 2014). Charisma and oratory skills are common properties of leaders when they must rely on persuasion to influence community members (Grabo & Van Vugt, 2016).

Leadership and status are similar but not identical. Leaders have disproportionate influence, whereas status is often conceptualized as a relative indicator of the social value of the individual by the group and of their relative access to contested resources (e.g., Blader & Chen, 2014; von Rueden, 2014). Although leaders are generally expected to be high status (e.g., Buss et al., 2020; Cheng, 2019; Van Vugt & von Rueden, 2020; von Rueden & Van Vugt, 2015), the causal relationship between the two is likely to be context-specific and driven by underlying correlates (e.g., Blader & Chen, 2014; Cheng, 2019; von Rueden, 2014).

Substantial evidence suggests a near universal male-bias in community leadership (Low, 1992b; Sanday, 1981; Whyte, 1978), as well as across diverse nonhuman social species (Smith et al., 2020; Tiger & Fowler, 1978). Sex, however, is confounded with factors such as social network size, economic specialization, and education, that are also associated with leadership. After controlling for these factors, some studies have found that sex is not a strong predictor of community leadership (Garfield & Hagen, 2020; von Rueden, Alami, Kaplan, & Gurven, 2018; Yanca & Low, 2004).

In the context of institutionalized social stratification, such as among chiefdoms, community leadership is often highly influenced by heredity and class structures (Earle, 1997; Redmond, 1998; Stanish, 2004). Managerial elites maintain influence over community decisions and are endowed with privileged social status (Stanish, 2010). Within state-level societies, including nonindustrial kingdoms, leadership positions are proscribed and institutionalized. Ruling classes, parties, or political bodies monopolize political influence and maintain control through a variety of mechanisms including military force, ideologies, and control of information (Bodley, 2011).

1.3. The benefits and costs of leadership across cultures and contexts

Evolutionary models generally assume that, on average, the fitness benefits of leadership outweigh the fitness costs. The costs, however, have received less attention. Fulfilling group responsibilities and mediating conflicts can be physically and socially costly, and some decisions will upset some followers (Wiessner, 2010). In the absence of institutionalized authority, all group members are equipped to challenge leaders directly or indirectly using a variety of leveling mechanisms including physical aggression, gossip, and ridicule (Boehm, 2008; Hess & Hagen, 2017). Physically formidable individuals with strong social networks are better equipped to manage these costs than others (Glowacki & von Rueden, 2015).

Leadership positions are also commonly associated with numerous social, material, and reproductive benefits (Cheng, Tracy, & Anderson, 2014; Grammer, 1996; von Rueden, 2014; von Rueden, Gurven, & Kaplan, 2008). Leaders and high-status individuals are more likely to be the recipients of social support and material benefits in times of need (Gurven, Allen-Arave, Hill, & Hurtado, 2000; Sugiyama, 2004; von Rueden, 2014). Many leadership positions in industrialized societies are associated with increased financial compensation (Tsui, Enderle, & Jiang, 2017). High social status, wealth, intelligence, and leadership

status are also generally viewed as sexually attractive, particularly to women (Buss, 2006; Stanik & Ellsworth, 2010). Most measures of reproductive success are positively associated with male social status, independent of subsistence type or status measure (von Rueden & Jaeggi, 2016).

Although, empirically, leadership is associated with benefits, evolutionary models require that leaders cause or generate benefits. Potential mechanisms include that leaders (1) facilitate collective actions that yield net benefits to themselves or close kin; (2) claim a fee or greater share of returns for their services; (3) receive reciprocal exchange in other currencies; or (4) gain other social or reproductive benefits by signaling their high qualities (von Rueden & Van Vugt, 2015). Leaders can also promote policies that either align with their individual interests or that are not especially costly for themselves, their kin, or their social partners (Garfield, Hubbard, & Hagen, 2019; Hagen & Garfield, 2019; Kantner, 2010).

2. Study aims

We seek to provide a systematic and near comprehensive view of the qualities and functions of leaders, and the costs and benefits of leadership and followership, from a representative sample of nonindustrial populations. We then explore how these dimensions of leadership vary within populations across social contexts and across populations with different subsistence strategies, as well as by leader sex and continental region. We aim to identify features of the qualities and functions of leaders (e.g., do particular qualities or functions tend to covary or cluster together?). Such features might lend support to existing theories; for instance they might correspond to qualities associated with “prestige” or “dominance” (Henrich & Gil-White, 2001) or functions associated with conflict or cooperation (Gavrilets, 2015; Glowacki et al., 2017; Hooper et al., 2010). Finally, we hope to synthesize empirically-derived features of leadership with evolutionary theories of social organization to propose essential elements of leadership.

Our approach was exploratory. Whereas previously we used the ethnographic record to conduct *a priori* tests of leadership theories (Garfield, Hubbard, & Hagen, 2019), here we aim to let the ethnographic record of leadership “speak for itself.”

3. Methods

3.1. Ethnographic sample and coding

We use the database of 1212 ethnographic paragraphs (termed text records) on leadership, described in Garfield, Hubbard, & Hagen (2019) (<https://doi.org/10.5281/zenodo.2541999>), to code entirely new variables on the functions and qualities of leaders and the costs and benefits of leadership and followership. The text records were extracted from the 60-culture Probability Sample Files (PSF) of the electronic Human Relations Area Files (eHRAF) (Naroll, 1967). The PSF, which comprises over 212K pages of digitized text, aims to mitigate Galton’s problem of cultural non-independence by randomly sampling one culture with high quality ethnographic coverage from each of 60 regions.

The function and quality variables were not operationalized *a priori*. Instead, we used an iterative process whereby ZG and KS made multiple passes through the database, identifying leader functions and qualities (see Table S1). In contrast, operationalizations of the costs and benefits of leadership were developed *a priori* based on theoretical literature (Garfield, von Rueden, & Hagen, 2019) (see Table S2). ZG and KS then coded all text records for the presence (1) or absence (0) of evidence for each variable, which we henceforth refer to as leadership dimensions. Some of the costs and benefits (e.g., mating) were similar to leader qualities (e.g., polygyny). The distinction is that costs and benefits were transactional whereas qualities were descriptive (e.g., leaders obtain wives vs. have wives). ZG then created a measure of group context (see Table 1). ZG and KS coded all text records for group context. Finally,

the sex of each leader was coded as male, female, both, or unknown.

ZG and KS discussed every instance of disagreement between their respective coding on all leadership dimensions and group context variables to produce a consensus database. See the *Coding example* section of the supplementary information (SI). Finally, each culture was coded for continental region, total pages of ethnography for that culture in the eHRAF, and subsistence strategy.

3.2. Data analysis

Our data comprised one row for each text record. For all 109 leadership dimensions, each row was coded as 1 if there was evidence in the text record for that dimension, and 0 otherwise. Because absence of evidence is not evidence of absence, our data only inform the extent to which there is evidence for the operationalized leadership dimensions.

Our first goal was to assess if discovery of evidence for each leadership dimension was biased by publication date, total pages of ethnography for a culture, and sex of the ethnographer(s). Our second goal was to assess the proportion of text records and cultures that provided evidence for each coded dimensions. We computed the proportion of text records supporting each dimension, and their 95% confidence intervals (CIs), using intercept-only logistic mixed effects models with random intercepts for document authors nested within cultures, using the lme4 package (Bates, Mächler, Bolker, & Walker, 2015). We then computed the proportion of cultures with at least one text record with evidence for each dimension, with 95% CIs computed using a cluster bootstrap.

Our third goal was to assess variation in each leadership dimension by four theoretically important factors for which we had data for all rows: group context, subsistence strategy, continental region, and leader sex. We again fit logistic mixed effects models using the lme4 package, with each leadership dimension as an outcome, all four factors as predictors, and author nested within culture as random intercepts. To investigate which words were associated with particular leadership dimensions, or which dimensions predicted evidence for other dimensions, we used elasticnet regression from the glmnet package (Friedman, Hastie, & Tibshirani, 2010). Elasticnet models are penalized regression models that are useful when the number of predictors is large relative to the number of observations. We used the “lasso” penalty ($\alpha = 1$), which will often set many coefficients to 0, thereby selecting the most important predictors.

Our fourth goal was to explore lower dimensional representations of these data that might reveal informative “features.” These included hierarchical cluster analysis, logistic PCA, and minimal spanning trees and k-nearest neighbors (mst-kNN). See the SI for additional details. Our fifth goal was to assess variation in our lower-dimensional features by group context, subsistence strategy, continental region, and leader sex, using logistic mixed effects models fit with the lme4 package. Our sixth goal was to evaluate the features in light of evolutionary theories of leadership. Guided by empirically derived features, we aimed to construct “elements” of leadership that corresponded to elements of influential theories, examining intersections of these elements across all text records.

The analyses computing levels of evidence for each dimension used the entire set of text records. Analyses investigating lower dimensional representations used a smaller set that omitted rows with no evidence for any dimension (i.e., all zeros), and dimensions with very little evidence (almost all zeros).

Throughout, we compare regression models of the same outcome variable using the Akaike information criterion (AIC). $AIC = 2k - 2\ln(\hat{L})$, where k is the number of model parameters and \hat{L} is the maximum likelihood. AIC increases as model complexity increases, and decreases with improved fit. Hence, a model with a lower AIC value is considered to be superior.

All analyses were conducted with R version 3.6.1 (2019-07-05).

Table 1
Operationalization of the group context variable.

Group context	Description
Residential subgroup	Informal groups of co-residents, social groups, age-based groups, or performance groups
Kin group	Groups based on kin relationships, such as lineages, phratries, and clans
Economic group	Subsistence groups, market groups, and other groups with primarily economic goals
Military group	All groups related to inter-group conflict
Religious group	Groups formed for spiritual or supernatural purpose
Political group (community)	Political groups at the level of the community, i.e., political leaders, such as village headmen, can potentially interact directly with most community members
Political group (supracommunity)	Political groups that encompass multiple residential communities, such as complex chiefdoms, regional political leaders, and kings or state-level leaders

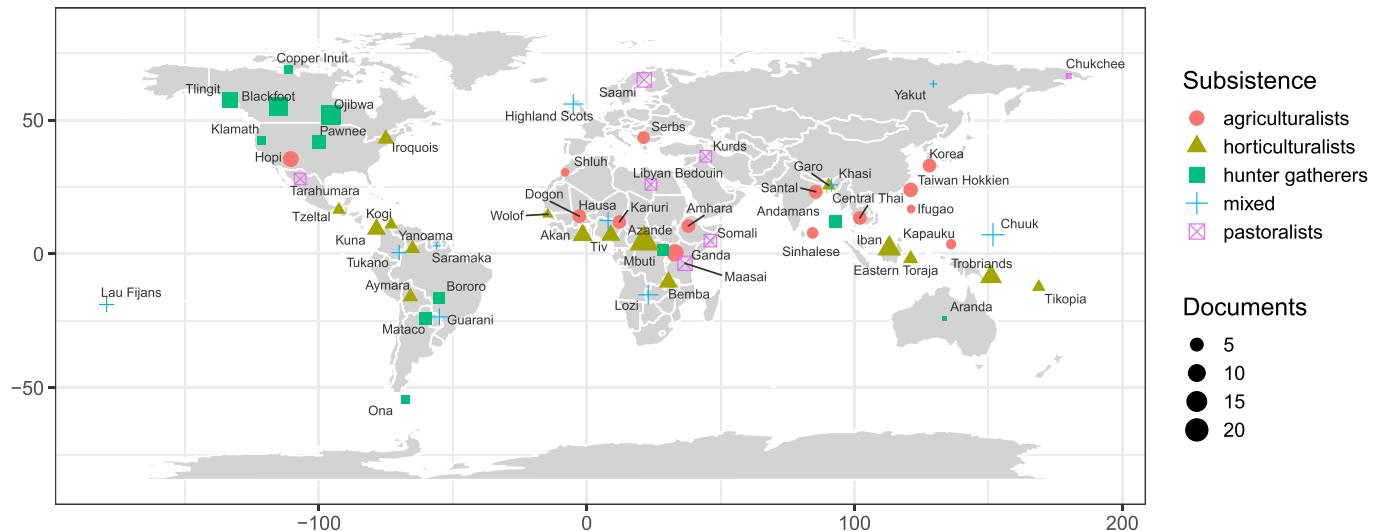


Fig. 1. The geographical distributions of cultures in this analysis. Symbol shapes indicate subsistence strategy and symbol size indicates the number of documents available for that culture. Axes are degrees latitude and longitude.

4. Results

The geographic distribution of the culture sample is displayed in Fig. 1 (see also Fig. S1). The database comprised 1212 text records from 321 documents describing 59 cultures.

Subsistence strategy, group context, and continental region were confounded. Hunter-gatherer text records often referred to residential and kin leadership, but rarely to supracommunity leadership; agriculturalist text records rarely referred to residential leadership but often referred to supracommunity leadership. Community-level political groups were frequent across all subsistence types. African text records were predominantly from horticulturalists whereas North American text records were predominantly from hunter-gatherers. See Figures 2 and S1, and Table S3.

The majority of text records discussed male leadership (88.1%) and very few discussed female leadership (2.5%), with the remaining records not sex-specific (Table S3). There were female leaders in almost all contexts, however, except military and religious. Female leaders did tend to lead within kin and residential subgroups, though: 26.7% of female leaders led at the residential subgroup level, compared to 6.65% of male leaders. The majority of text records which exclusively described female leaders were from horticulturalists (63.3%) (Table S4).

We investigated if there were biases in the discovery of evidence for any of our 109 leadership dimensions by document publication date, female gender of any author or co-author, or total pages of ethnography from each culture. We found minimal evidence of bias, and therefore do not control for bias variables in subsequent analyses. For details, see the *Bias* section of the SI.

4.1. Evidence for leader functions and qualities

For all 109 coded dimensions (Tables S1 and S2), we computed the proportion of text records (95% CI) that provided support and computed the proportion of cultures with at least one text record providing support for that dimension (see Methods section). See Fig. 3 and Table S9.

The most common leader functions, documented in over 70% of cultures, were resolving conflicts, providing social functions, organizing cooperation, and providing counsel or direction to followers. In about half of cultures sampled here leaders punished group members and managed economic systems. Controlling group movement and immigration were notably rare functions.

The most common leader qualities were having high social status (over 90% of cultures), being experienced or accomplished, and being knowledgeable or intelligent (approximately 80% of cultures). Notably rare qualities included physical formidability, having many social contacts, and being feared (approximately 35% of cultures) and charisma and fairness (approximately 20% of cultures).

The random intercepts indicated that support for many variables did vary modestly by author and culture. Most of the standard deviations of the random author and culture intercepts for each model were between 0 and 1, on the scale of the linear predictor (Figures S13 and S14). In a few cases, one or the other was exactly 0, which can occur in models like ours that have many random effect levels (e.g., 312 authors) and a relatively small data set (Bates et al., 2015).

4.2. Benefits and costs of leadership and followership

Evidence for leader and follower costs and benefits were estimated

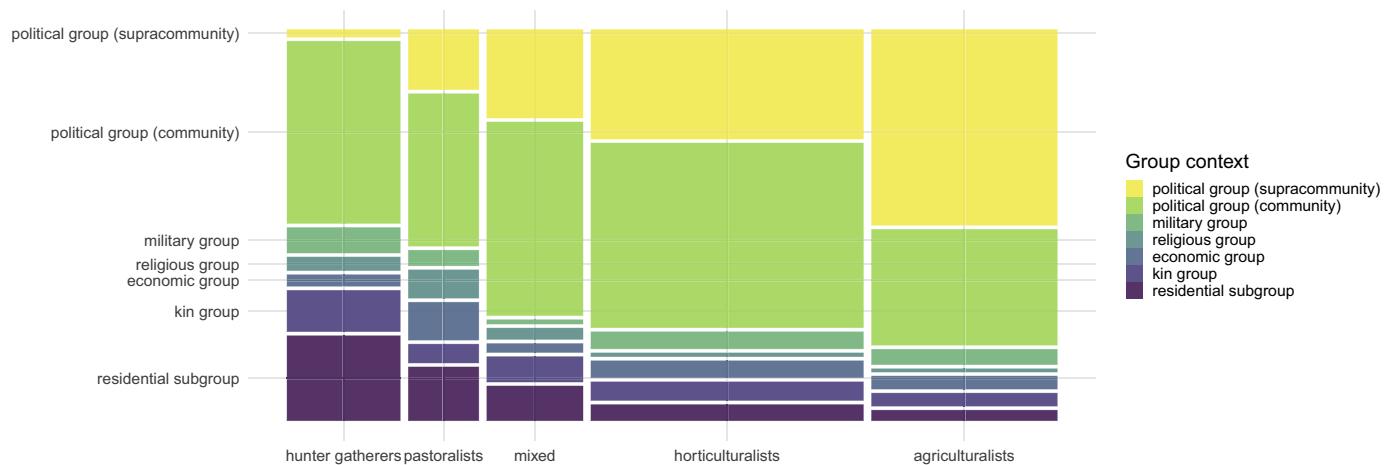


Fig. 2. The distribution of text records by subsistence and group context. Areas of the bars are proportional to the number of text records in that category.

similarly to the leader qualities and functions described above. Common leader benefits included greater access to material resources and increased social status (documented in 69.5% and 66.1% of cultures, respectively). Evidence for mating benefits and social services benefits was also relatively common. In general, the costs tracked the benefits. Leaders were often described as losing their high social status and greater access to resources (documented in 45.8% and 39% of cultures, respectively). See Fig. 4.

Followers on the other hand most commonly benefited from leadership systems by receiving material resources (documented in 47.5% of cultures) but otherwise by receiving social services (documented in 35.6% of cultures). Evidence of mating and fitness benefits was relatively rare for followers. Followers were most frequently described as incurring costs in the form of material resources lost and in providing social services (documented in 37.3% and 25.4% of cultures, respectively). See Fig. 4.

Leadership and followership can evolve when their benefits exceed their costs. Our data did not allow us to compare benefits and costs. Instead, we compared levels of evidence for benefits vs. costs for each leader and follower benefit/cost dimension. Specifically, we fit a mixed effects logistic regression model of evidence (0/1) as a function of the leader dimension (e.g., *Mating*, *Food*), a binary term indicating if the evidence was for a benefit or cost, and their interaction, with random intercepts for author nested within culture. We fit separate models for leaders and followers. These two models allowed us to estimate the relative evidence for, e.g., leader mating benefits vs. leader mating costs, and follower mating benefits vs. follower mating costs, etc. For leaders, the odds ratio that a text record would provide evidence for a benefit vs. a cost (averaging across all benefit/cost dimensions), was $OR = 3.2$, and for followers, was $OR = 1.8$. Hence for both leaders and followers, there was more evidence of benefits than costs.

Within benefit/cost dimensions, there was relatively more evidence for mating and territory benefits than costs for both leaders and followers, and equal levels of evidence for protection from harm vs. risk of harm. For leaders compared to followers, there were noticeably higher odds ratios for mating, inclusive fitness, material resources, and social services. See Fig. 5.

4.3. Universality in leadership dimensions

We investigated four possible sources of variation in evidence for our 109 leadership dimensions: group context, subsistence strategy, continental region, and leader sex. Specifically, we fit separate multiple logistic mixed effects regression models of each leadership dimension as a function of these four factors, with random intercepts for author nested within culture. We then compared the AIC value of each model

to a model with only the fixed and random intercepts. Models whose AIC values were at least two less than the intercept-only models were deemed to outperform the intercept-only model (Burnham & Anderson, 2002).

We first examined the leadership dimensions with the most evidence, i.e., the 15 for which evidence was found in at least 60% of cultures. Of these, 9 dimensions did not meaningfully vary by continental region, subsistence strategy, group context, or leader sex, and are therefore candidates for universal human leadership dimensions. See Table 2.

4.4. Variation by group context, subsistence strategy, continental region, and leader sex

We then examined the 20 (out of 109 total) leadership dimensions that exhibited important variation by one or more of our four factors, i.e., whose AIC values indicated improved fits over intercept-only models (Tables S5 and S6). To determine which factor contributed to improved fit, we dropped each factor in turn and computed the change in AIC. For most of these 20 varying leadership dimensions, one factor had a noticeably bigger effect on fit than the others. Variation in group context, in particular, was associated with variation in almost half of the dimensions (Fig. 6).

For each of our four factors, we then investigated which levels of the factor were associated with higher or lower levels of evidence for the leadership dimension. For instance, there were three dimensions in which subsistence strategy played an important role: *No coercive authority*, *Provide subsistence*, and *Distribute resources* (see Fig. 6). Hunter-gatherers had particularly high levels of evidence for *No coercive authority*, relative to other subsistence strategies (and averaging over levels of the other three factors), and pastoralists had relatively low evidence for *Distribute resources* (see Fig. S10). For group context, region, and leader sex see Figures S9, S11, and S12.

4.5. When do leaders have high status?

High status was the most frequently identified leader quality (32.3% of text records and 91.5% of cultures provided evidence of high status leaders). To explore factors that distinguished these records from those with no evidence for high status, we first created a document-term matrix (DTM) of all “informative” words in our corpus of texts and the frequency with which they occurred in each text record (see SI for details). We then fit an elasticnet logistic regression model (with the lasso penalty, $\alpha = 1$) of *High status* (0/1) as a function of the frequencies of all 9656 words. Words that were strong positive predictors epitomized the semantic content of the text records which provided evidence

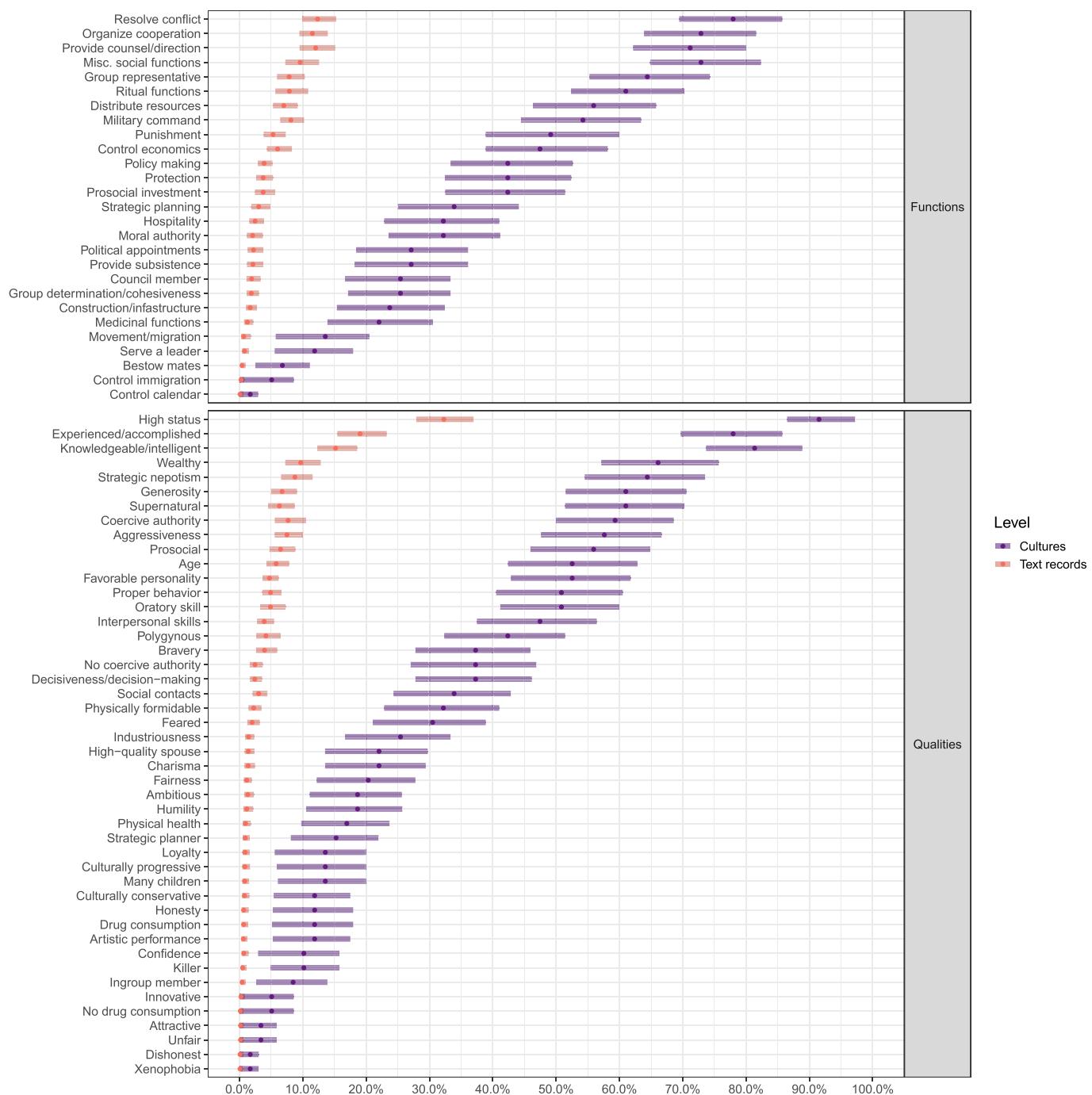


Fig. 3. Evidence for each coded dimension of leader functions (top) and qualities (bottom). Red (lower values): percent of text records with evidence of support (95% CI computed with intercept-only binomial mixed effects models with random intercept for author nested within culture). Purple (higher values): percent of cultures with evidence of support (95% CI computed with a cluster bootstrap).

of high status leaders. These included *respect*, *prestige*, *status*, *reputation*, *honor* and *rank*, which were the strongest predictive terms. Notable weak-predictor terms included, *influence*, *authority*, *headman*, and *chief*, and *economic* was a negative predictor. See Fig. 7A.

To determine which leader quality and function dimensions were associated with evidence for high status leaders, we fit an elasticnet logistic model of *High status* as a function of all quality and function dimensions, (with the lasso penalty, $\alpha = 1$). The non-zero coefficients indicated that *Punishment*, the only identified function, was a negative predictor, whereas *Wealthy*, *Strategic nepotism*, *Age*, *Experienced/accomplished*, and several other qualities, were positive predictors. See Fig. 7B.

High status meaningfully differed by levels of group context, subsistence strategy, continental region, and leader sex, with the most important factors being region followed by group context (see Fig. 6). Examining the estimated marginal means, South America and East Eurasia had relatively high levels of evidence compared to Africa and North America, and kin and religious groups had relatively high levels of evidence compared to political groups. Nevertheless, the differences were quite modest. See Fig. S11.

4.6. When do leaders have coercive authority?

Coercive authority was documented in 59% of cultures. Unlike other

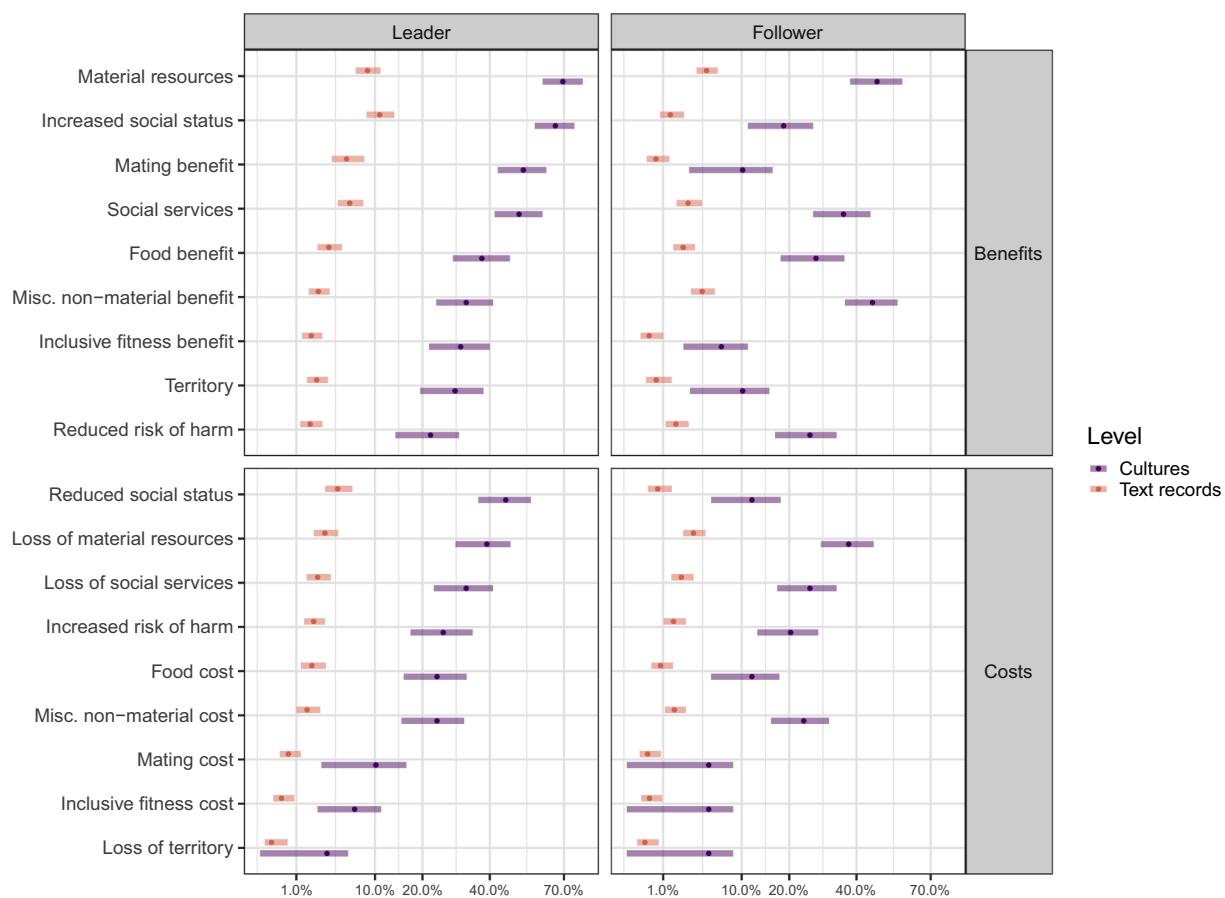


Fig. 4. Support for each coded dimension for the costs and benefits of leadership and followership. Red (lower values): percent of text records with evidence of support (95% CI computed with intercept-only binomial mixed effects models with random intercept for author nested within culture). Purple (higher values): percent of cultures with evidence of support (95% CI computed with a cluster bootstrap). X-axis on the square root scale.

more frequent leader qualities, which were generally positive or pro-social traits, *Coercive authority* was the most frequent negative or dominance-style quality. Additionally, it was one of the few dimensions with a complementary dimension, *No coercive authority*, which was documented in 37% of cultures (Fig. 3). *No coercive authority* demonstrated variability by subsistence strategy, with hunter-gatherers providing relatively higher levels of evidence. See Fig. S10.

We therefore chose to perform additional exploratory analyses with

Coercive authority and *No coercive authority* as the outcomes in logistic elasticnet regression models similarly as described above for *High status* (see Fig. 8).

Words that were strong predictors of leaders with coercive authority included, unsurprisingly, *power* and *authority*, as well as *territory*, *chief*, and *control*; the word *leadership* was the only strong negative predictor. Words that predicted no coercive authority tended to be those that indicated either hunter-gatherers, such as *band* and *Mbuti* (Congo Basin

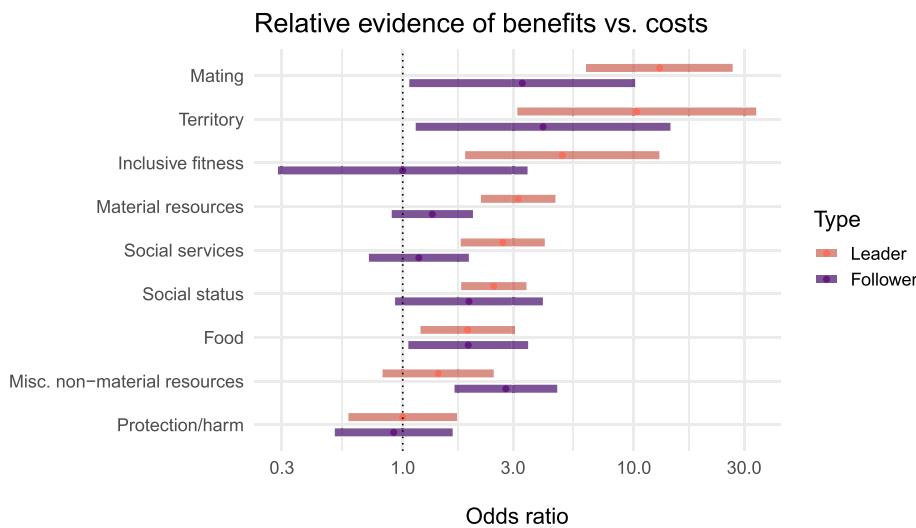


Fig. 5. Odds ratios of finding evidence of a benefit vs. a cost in a text record for leaders and followers, by each dimension of benefits and costs. Odds ratios estimated using a mixed effects logistic regression model of evidence (0/1) as a function of each dimension (e.g., Mating, Food), a term indicating if the evidence was for a benefit or cost, and their interaction, with random intercepts for author nested within culture. Separate models were fit for leaders and followers. X-axis is on a log scale.

Table 2

Candidate universal leadership dimensions. These dimensions were common in the ethnographic record (appearing in at least 60% of cultures) and did not appear to meaningfully vary by continental region, subsistence strategy, group context, or leader sex.

Variable	Type	Percent of cultures
Knowledgeable/intelligent	Qualities	81.4
Resolve conflict	Functions	78.0
Misc. social functions	Functions	72.9
Material resources	Leader Benefits	69.5
Increased social status	Leader Benefits	66.1
Wealthy	Qualities	66.1
Group representative	Functions	64.4
Strategic nepotism	Qualities	64.4
Generosity	Qualities	61.0

foragers), or kinship and residential-level contexts, such as *lineage*, *house*, *clan*, and *village*. See Figures 8A,C.

Using all other quality and function dimensions as predictors identified *Punishment* as the strongest predictor of evidence for *Coercive authority*. *No coercive authority* was most strongly predicted by *Humility*. See Figures 8B,D.

4.7. Dimension reduction

Our qualities and functions data comprised sparse 1212×46 and 1212×27 matrices of binary data, respectively. Most data reduction methods did not find strong or stable evidence of structure in the data. We therefore explored reduced matrices that removed uninformative rows with no evidence for any dimension, and dimensions with only a few rows with evidence. Stable clusters emerged with 796×42 and 633×27 matrices for qualities and functions, respectively.

Here we report the cluster analysis of dimensions that used the correlation distance metric ($1 - cor$), and the Ward agglomeration algorithm (for results from other methods, see the SI). Fig. 9A displays a dendrogram from the cluster analysis of the 46 leader quality dimensions and Fig. 9B a dendrogram from the cluster analysis of the 27 leader function dimensions. Each cluster analysis includes two estimates of significance for how strongly each cluster within the dendrogram is supported by the data. We rely on the AU (Approximately Unbiased) p values, which are computed by multiscale bootstrap resampling and represented as percentages (e.g., clusters with AU values > 95 are strongly supported, and the top-level clusters are automatically highlighted by rectangles).

The leader quality cluster analysis (Fig. 9A) identified two top-level clusters, one that comprised mostly dimensions related to prosocial

qualities and one that comprised other individual-level qualities which were not necessarily prosocial. Within the latter top-level cluster we identified two interpretable and strongly supported subclusters: *Social, reproductive, and material success* and *Competencies*. Within the first top-level cluster, we also identified two subclusters, one of which contained measures related to group-level pressures (*Cultural conformity*) and one which contained the prosocial traits (*Prosocial competencies*); these subclusters were moderately supported.

The leader functions cluster analysis (Fig. 9B) also identified two top-level clusters; the larger of which we identified as a management cluster and the smaller of which we identified as a *Prosociality* cluster. Within the management cluster, we identified two moderately supported subclusters: *Strategize* and *Organize*.

We identify these seven named subclusters as “features” of leadership dimensions in the ethnographic record. In naming these features, we gave extra weight to dimensions that were strongly supported empirically (Fig. 3), therefore not all dimensions within these clusters were clearly related to the themes of each feature. These features correspond fairly well to major elements of evolutionary theories of leadership, with the possible exception of *Competencies*, a single feature that included at least two important theoretical elements: dominance and prestige. Because features were aggregated dimensions, they are more common at both the text record and culture level (see Fig. 10).

There were modest or no correlation between features (see Fig. S22). We fit separate logistic mixed effects models of each of the 7 features as a function of group context, subsistence strategy, continental region, and leader sex, reported in the SI.

4.8. Shaman leaders and competencies

The *Competencies* feature combined dimensions of prestige-style leadership, such as knowledge and experience, with dimensions of dominance-style leadership, such as aggressiveness and feared. It also included supernatural qualities. The MST-kNN analysis similarly clustered leaders with ritual and medicinal functions, which rely on special knowledge, with those who had supernatural, feared or killer qualities (see Fig. S21).

Shamans and leaders with supernatural qualities were surprisingly common. Of our 1212 text records, 33 used the word “shaman”, 77 provided evidence for supernatural qualities, and 95 provided evidence for one or both (7.84% of all text records). We term the latter variable *Shamanism*. We fit a logistic elasticnet model of *Shamanism* as a function of all leadership dimensions (minus *Supernatural*). This model revealed that shaman leaders combined dimensions of dominant leaders (*Feared*) with dimensions of prestigious leaders (*Medical functions*, a form of knowledge or expertise, and *Experienced/accomplished*). See Fig. 11.

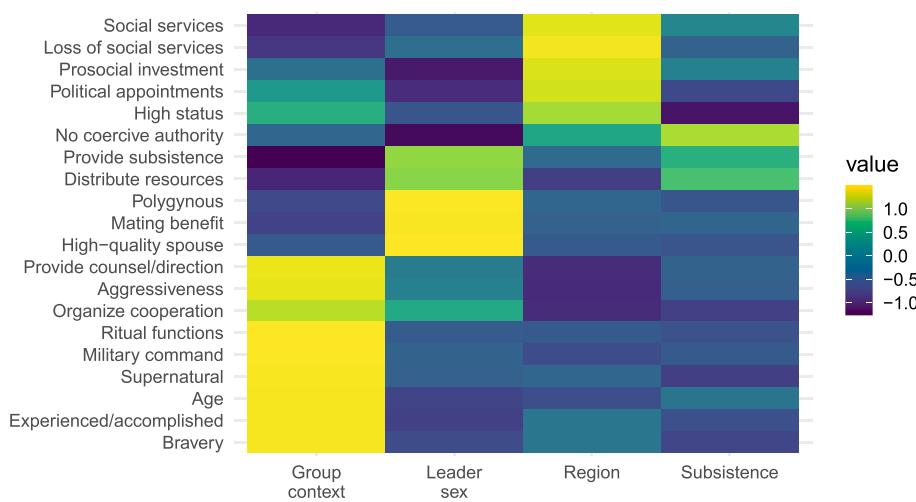


Fig. 6. Leadership dimensions that, according to a decrease in AIC relative to intercept-only models, varied by group context, subsistence strategy, continental region, and/or leader sex. Colors represent the relative change in AIC value after dropping that factor from a multiple logistic mixed effects regression model. Yellow: dropping factor substantially increased AIC relative to other factors. Black: dropping factor did not substantially increase AIC relative to other factors. For display purposes, delta AIC values were standardized by rows, and therefore can only be compared within rows.

Predictors of High status

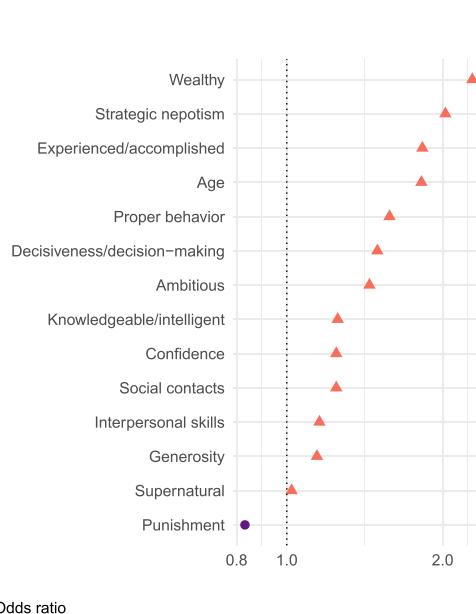
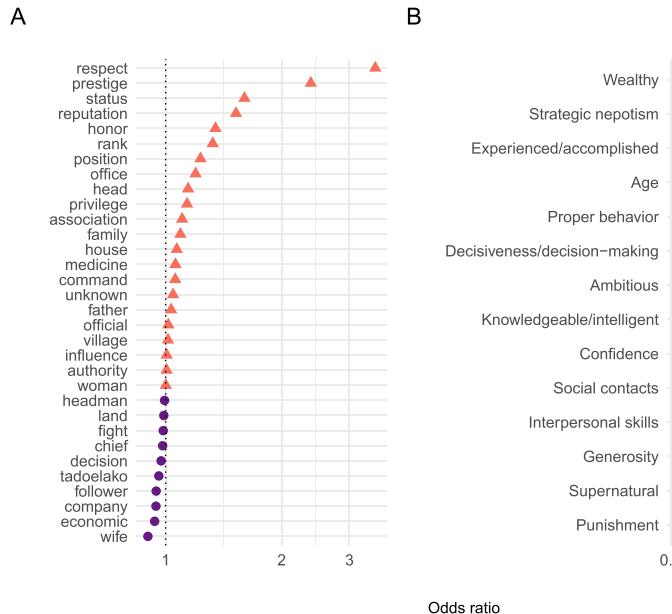
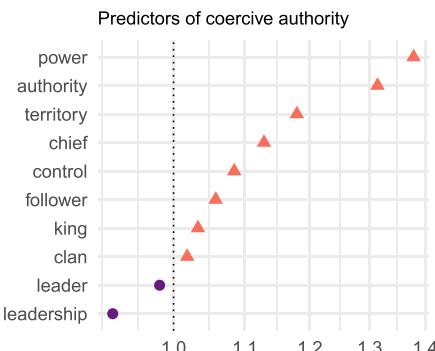
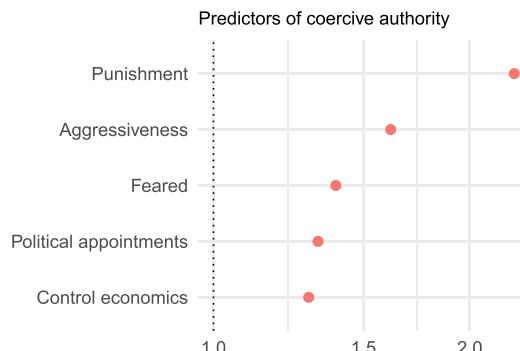


Fig. 7. Coefficients of logistic elasticnet regression models of evidence for High Status. A: Coefficients indicate the words whose frequencies in each text record best predicted evidence for High status in each text record. B: Non-zero coefficients of all quality and function dimensions that best predicted evidence for High status. Both models used the lasso penalty ($\alpha = 1$), with λ_{1SE} chosen by cross-validation (1 SE from λ_{\min}). Red values are positive predictors; purple values are negative predictors. Predictors with coefficients = 0 not displayed. X-axes are odds ratios on a log 10 scale.

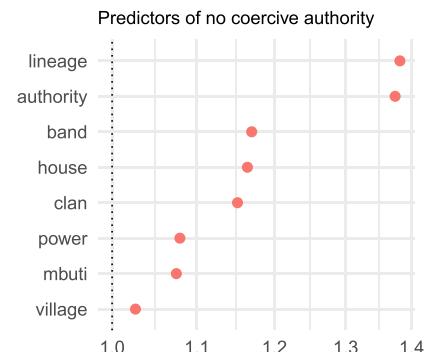
A



B



C



D

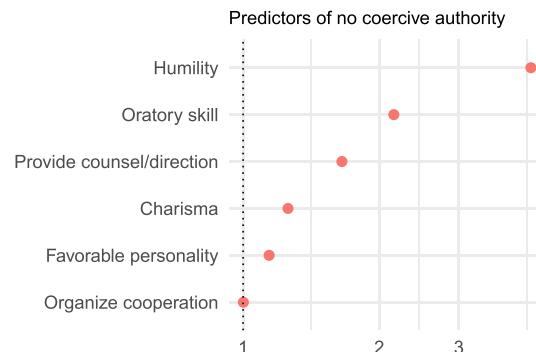


Fig. 8. Coefficients of logistic elasticnet regression models of evidence for Coercive authority and No coercive authority. A, C: Coefficients indicate the words whose frequencies in each text record best predicted evidence for Coercive authority and No coercive authority, respectively, in each text record. B, D: Non-zero coefficients of all quality and function dimensions that best predicted evidence for Coercive authority and No coercive authority, respectively. All models used the lasso penalty ($\alpha = 1$) and chosen λ_{1SE} by cross-validation (1 SE from λ_{\min}).

There were no text records that described shamans or leaders with supernatural qualities who were exclusively female. However, there were 3 text records describing such leaders of both sexes. There was also more evidence of shamans and leaders with supernatural qualities in the Americas compared to other regions. See Fig. S8.

4.9. Cognitive, social, and somatic capital

Motivated by our feature analysis, and the apparent importance of shaman leaders, we tentatively advance a scheme, similar to von Rueden (2014) (and inspired by Kaplan, Lancaster, & Robson, 2003;

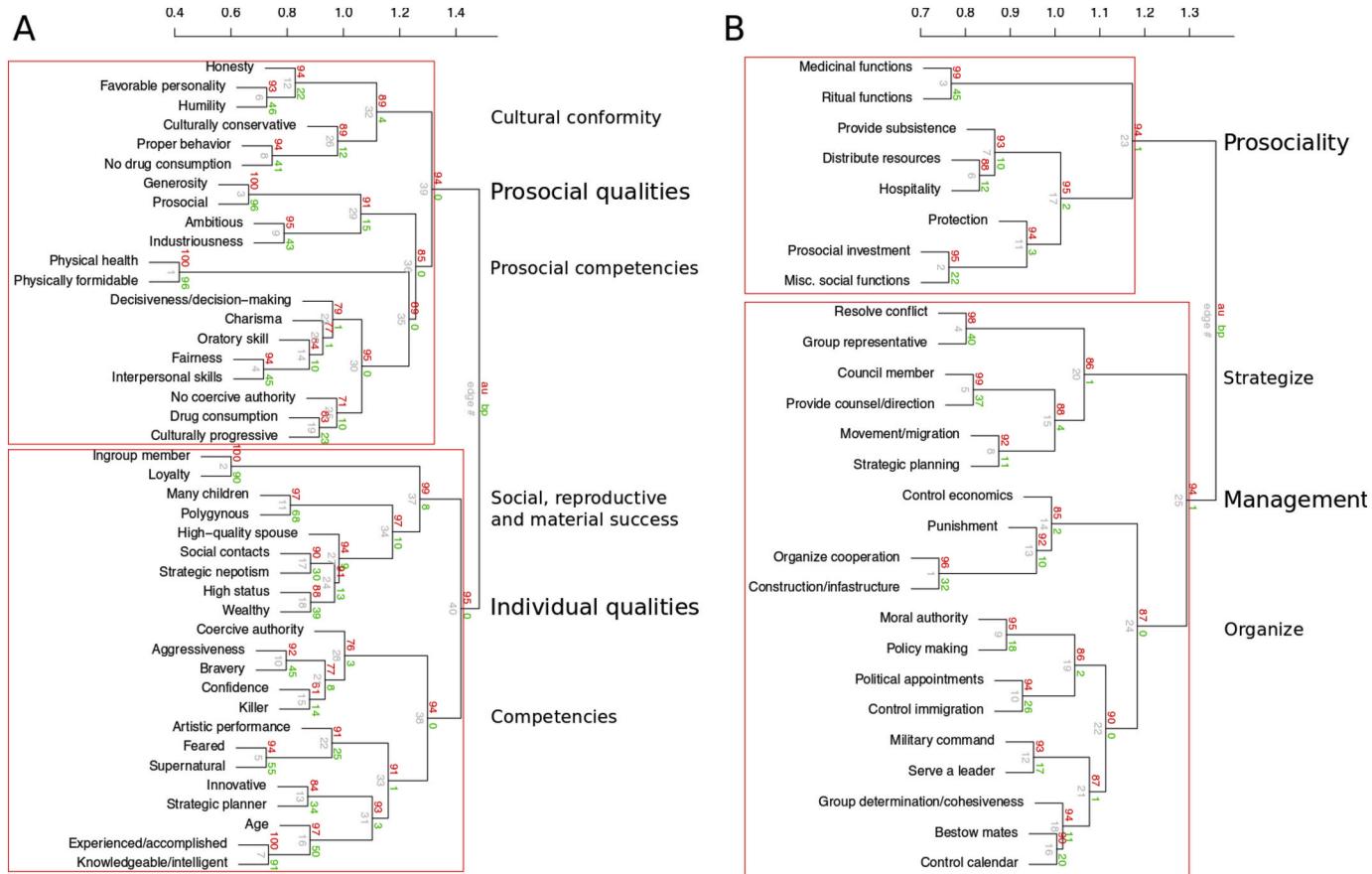


Fig. 9. Cluster analysis of (A) leader quality dimensions and (B) leader function dimensions. Distances were $1 - \text{cor}$. Ward agglomeration method. AU p-values (red) computed with 10,000 bootstrap samples using the *pvclust* package (Suzuki & Shimodaira, 2015).

Kaplan et al., 2009; Borgerhoff Mulder et al., 2009), whereby leaders possess some combination of cognitive, social, material, and somatic capital that they deploy to provide benefits and impose costs (for further justification, see the Discussion). Hence, we should be able to find examples of leaders with various combinations of these six elements.

To test this idea, we operationalized the six elements using the leadership qualities cluster analysis (Fig. 9A) as guidance (for variable operationalizations, see Table S7). About half of the text records (58%) had evidence for one or more of the six elements, in heterogeneous combinations. See Fig. 12. In particular, not all leaders have evidence for high *Social capital*, leaders with *Cognitive capital* provide benefits and impose costs, and *Somatic capital* is rarely mentioned, but when it is, it is associated with providing benefits as well as imposing costs. Shamans

are associated with evidence for *Cognitive capital* and imposing costs.

5. Discussion

This exploratory study systematically evaluated ethnographic evidence for 109 leadership dimensions from a diverse sample of 59 largely nonindustrial cultures. Results revealed universal dimensions of leadership as well as important variation by group context, subsistence type, continental region, and leader sex.

5.1. Universal dimensions of leadership

We found strong evidence that several leadership dimensions were

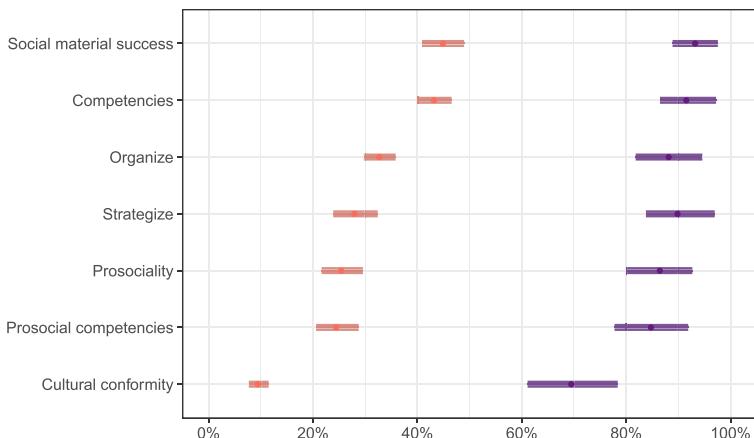


Fig. 10. Support of each feature variable at the levels of text records and cultures. Feature support at the text record was defined as the adjusted proportion of text records with evidence for at least one underlying dimension in the feature. Feature support at the culture level was defined as the proportion of cultures with evidence for the feature in at least text record in the culture.

Predictors of Shamanism

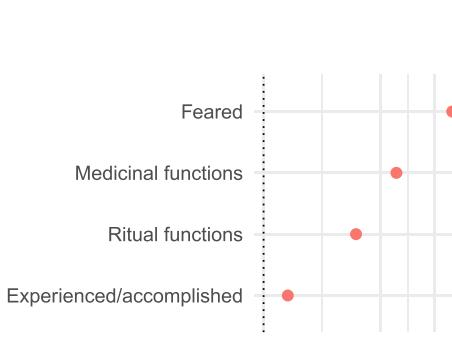
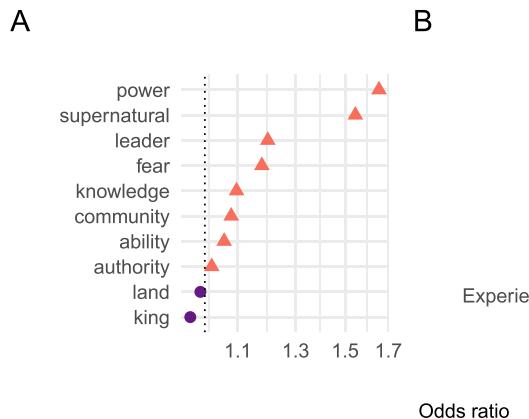


Fig. 11. Coefficients of logistic elasticnet regression models of evidence for Shamanism. A: Coefficients indicate the words whose frequencies in each text record best predicted evidence for Shamanism in each text record. B: Non-zero coefficients of all quality and function dimensions that best predicted evidence for Shamanism. Both models used the lasso penalty ($\alpha = 1$) and chose λ_{1SE} by cross-validation (1 SE from λ_{\min}). Red values are positive predictors; purple values are negative predictors. Predictors with $coefficients = 1$ not displayed. X-axes are odds ratios on a log 10 scale.

universal across cultures and across contexts within cultures. Leaders are seen as high status, knowledgeable or intelligent, and experienced or accomplished in about 80% or more of cultures, and function to resolve conflicts, organize cooperation, and provide counsel or direction in over 70% of cultures (Fig. 3). Leaders benefited materially, reproductively, or socially in 50% or more of cultures (Fig. 4).

Some common leadership dimensions were also relatively invariant across group context, subsistence strategy, continental region, and leader sex. These dimensions included the qualities, knowledgeable/intelligent, wealthy, strategically nepotistic, and generous; and functions, resolving conflicts and representing the group. These dimensions are therefore candidates for universal dimensions of human leadership. By “universal” we do not mean all leaders have all these traits. Instead, we mean there is evidence for these traits across a solid majority of cultures that do not vary much by key measures of population or group variation (i.e., the four factors) (Table 2 and Fig. 3).

The leadership features we derived by clustering leadership dimensions were represented across most cultures. Leaders performed three broad functions: providing prosocial services, strategizing, and organizing collective actions. Regarding characteristic traits, leaders possessed some combination of individual competencies, many of which are prosocial, conformed to cultural norms, and received various benefits (Fig. 10).

These potentially universal dimensions of leadership correspond to several evolutionary theories that have drawn on select ethnographic cases (Garfield, von Rueden, & Hagen, 2019). They partially correspond to the prestige model (Henrich et al., 2015; Henrich & Gil-White, 2001), which emphasizes knowledge, skill and generosity, but they do not include a key feature of that model: emulation of prestigious leaders. We labeled one of our leader quality features “cultural conformity”, however, in which leaders are culturally conservative and exemplify desirable traits such as honesty, humility, and “proper behavior” (Fig. 9). This feature corresponds in part to leaders who serve as models for followers (see also Garfield & Hagen, 2020).

The universal dimensions also partially correspond to the service-for-prestige model (Price & Van Vugt, 2014, 2015) in which leaders receive special status in exchange for providing services, but that model does not emphasize the concrete material benefits seen here. The absence of *High status* and *Aggressiveness* on this list of universals corresponds to the reverse dominance hierarchy model (Boehm, 1993), which emphasizes knowledge, conflict resolution, generosity, and status leveling mechanisms among largely egalitarian societies.

Our candidate universal dimensions appear in the computational services model (Hagen & Garfield, 2019), in which knowledgeable and intelligent individuals provide computational (cognitive) services (e.g., conflict resolution, strategizing) to group members in exchange for a variety of fitness benefits (see also Garfield, Hubbard, & Hagen, 2019).

This model emphasizes mating benefits, however, which appear in 52.5% of cultures, below our arbitrary 60% threshold for “universality” (Fig. 4). But there was evidence for the *Social, reproductive, and material success* feature, which included polygynous leaders, having a high-quality spouse, and having many children, in more cultures (93.2%) than other features (Fig. 10). Interestingly, the computational services model highlights women’s family leadership role, and there was proportionally more evidence for the *Social, reproductive, and material success* feature among females leaders than male leaders (Fig. S24), with the caveat that there were few text records on female leaders in our sample.

Pawnee chiefs illustrate leadership involving several of the universal dimensions, including intelligence, conflict resolution, and generosity (Murie & Parks, 1989):

...a chief was a regulator, not an absolute ruler or tyrant. Although chiefs had considerable authority, their decisions were generally based on a consensus of opinion rather than arbitrary whim. The chief, like his celestial forebear, was supposed to be a guardian of the people, always mindful of their wishes and needs. And even though the office was hereditary in certain families, the man chosen to fill it had to demonstrate humility, generosity, and sagacity, because a jealous or aggressive temperament was considered unbecoming a chief.

Evidence of coercive authority is common in the ethnographic record of leadership and does not vary by any of our four factors, yet did not quite make the 60% cutoff for our candidate universals. This dimension features in several evolutionary models of leadership involving dominance hierarchies (Barkow, 1989; Cheng, 2019; Henrich & Gil-White, 2001; Tiger & Fox, 1971; Van Vugt & Smith, 2019) and the role of punishment in promoting cooperation (e.g., Marlowe et al., 2008; Boyd & Richerson, 1992; J. Henrich, Ensminger, et al., 2010; Henrich et al., 2006). Indeed, we found that coercive authority among leaders was associated with enforcing punishment, aggressiveness, being feared, and also with controlling economics, which evokes “resource holding power,” a concept from the behavioral ecology of dominance hierarchies (Fig. 8). The authority of Trobriand chiefs is illustrative (Pospisil, 1993, pp. 64–65):

Power implies not only the possibility of rewarding, but also the means of punishing. This in the Trobriands is as a rule done indirectly, by means of sorcery. The chief has the best sorcerers of the district always at his beck and call....If anyone offends him, or trespasses upon his authority, the chief summons the sorcerer, and orders that the culprit shall die by black magic....As the natives are very deeply and genuinely afraid of sorcery, the feeling of being hunted, of imagining themselves doomed, is in itself enough to doom them in reality. Only in extreme cases, does a chief inflict

direct punishment on a culprit.

5.2. Variable dimensions of leadership

There was substantial cross-cultural variation in evidence for most leadership dimensions: 83 of 109 leadership dimensions had evidence in less than 50% cultures (Figures 3 and 4). There was systematic variation in 20 leadership dimensions by group context, subsistence strategy, continental region, and/or leader sex, factors for which we had complete data for all text records.

These four factors were confounded. Evidence for leadership in residential subgroups and kin groups was relatively more common in hunter-gatherer and pastoralist societies, populations more likely to experience high residential mobility (Kelly, 2013; Rigby, 1985; Wild et al., 2019). Evidence for supraregional political leadership was more common in horticultural and agricultural societies, which tend to rely heavily on cultivated land and maintain fixed, defensible territories (Figures 2 and S4). These patterns support perspectives suggesting restricted residential mobility and subsistence intensification are associated with increasing complexity of sociopolitical organization (Johnson & Earle, 1987; Powers & Lehmann, 2014; Steward, 1938). Perhaps as political structures become more institutionalized and economic systems transcend the household, leadership within households and residential groups diminishes.

The clearest pattern to emerge from analyses of systematic variation is that, not too surprisingly, many leadership dimensions are context-specific: aggressiveness and bravery were associated with military leadership, supernatural qualities and ritual functions were associated with religious leadership, organizing cooperation and being experienced or accomplished were associated with economic-group leadership, and providing counsel and older age were associated with kin-group leadership (Fig. S9). (Six leadership dimensions varied by continental region; Fig. S11. We do not have clear theoretical interpretations of this variation, so we treat region simply as a control variable.) These results underscore recent trends in evolutionary approaches to leadership that emphasize the context-dependency of leader emergence and evolutionary selection pressures (Hagen & Garfield, 2019; Smith et al., 2016; Smith & Van Vugt, 2020).

Four leadership dimensions varied by subsistence strategy. There was more evidence that hunter-gatherer leaders lacked coercive authority compared to others, supporting much theory and ethnography discussing egalitarianism and the resistance of hierarchy among hunter-gatherers (e.g., Boehm, 1999, 2008; Woodburn, 1982). Reliance on a mobile and stochastic resource base is suggested to promote social norms of sharing (Cashdan, 1980; Peterson, 1993) and shape resource transfers and partner preferences (c.f., D. Smith et al., 2018; K.M. Smith, Larroucau, Mabulla, & Apicella, 2018). There was more evidence that both hunter-gatherer and pastoralist leaders generated food surpluses, but less evidence that pastoralist leaders distributed food and other resources. Thus, systematic ethnographic evidence supports the important role of provisioning resources by influential males among foragers (Alger, Hooper, Cox, Stieglitz, & Kaplan, 2020; Gurven, 2005; Gurven et al., 2009; Wood, 2006). However, there was more evidence that leaders in communities with mixed subsistence strategies distributed resources, lending support to males using economic productivity as an influence-seeking strategy (Hawkes & Bird, 2002; Hawkes, O'Connell, & Coxworth, 2010).

5.3. The rarity of some important leadership dimensions

Evidence for several theoretically important leadership dimensions was relatively rare in the ethnographic record. The nonhuman animal leadership literature, for example, commonly focuses on group movement (Couzin, Krause, Franks, & Levin, 2005), and “movement” was one of four leadership dimensions Smith et al. (2016) compared

between small-scale human societies and nonhuman animal societies, yet movement or migration was identified as a leader function in only 13.6% of cultures, of which the vast majority (71.4%) were hunter-gatherers.

Several theories of leadership also emphasize the moral authority of leaders (e.g., Bøggild & Petersen, 2016; Henrich et al., 2015; Henrich & Gil-White, 2001; Richerson & Henrich, 2009; Tietjen & Walker, 1985), yet evidence for leaders as sources of moral authority or “fair” was found in only a minority of cultures (32.2% and 20.3% of cultures, respectively). The dominance theory of leadership (e.g., Chapais, 2015; Cheng, Tracy, & Henrich, 2010; Henrich & Gil-White, 2001; Tiger & Fox, 1971) emphasizes leaders’ ability to instill fear, but in only 30.5% of cultures was there evidence that leaders were feared. Finally, a large literature on leadership in industrialized societies highlights the physical attractiveness of leaders (e.g., Altemeyer & Jones, 1974; March & Weil, 2009; Sinclair, 1995), but evidence that leaders were attractive was found in only 3.4% of the nonindustrial cultures sampled here.

5.4. Benefits and costs of leadership and followership

Leadership often involves the provisioning of a public good at an individual cost, raising the question of how the individual benefits of leadership outweigh the costs. Followership, on the other hand, involves relinquishing individual decision-making to a leader who might or might not act in the follower’s interest. The benefits of followership (and by extension, group living) must also outweigh the costs for leadership to evolve and be maintained (e.g., Bastardoz & Van Vugt, 2018; Garfield, von Rueden, & Hagen, 2019; Gavrilets & Fortunato, 2014; Hagen & Garfield, 2019; Hooper et al., 2010; Price & Van Vugt, 2014).

Leaders were widely reported to receive material benefits, social status, and mating benefits but loss of material resources and social status were also widely reported, suggesting leadership to be a high-risk, high-return strategy (Fig. 4). Nevertheless, for most dimensions of benefits and costs, there was more evidence of benefits than costs (Fig. 5), and the same was true averaging across all benefit/cost dimensions ($OR = 3.2$). Additionally, several positive leader qualities indicating social, reproductive, and material success clustered together (bottom cluster Fig. 9A). These results are consistent with much theoretical literature that links leader benefits to their capacities to provide prosocial benefits (e.g., resolving conflicts, organizing collective actions, and generosity) and/or impose social costs (e.g., punishing and aggressiveness) (e.g., Bowles, Smith, & Mulder, 2010; Gavrilets & Fortunato, 2014; Glowacki & Wrangham, 2013; Hooper et al., 2010; Price & Van Vugt, 2014; Smith et al., 2016; von Rueden & Jaeggi, 2016).

Among the Trobriand horticulturalists in Papua New Guinea, Irwin (1983, p. 47) describes relationships between polygynous marriages, increased wealth, and widespread social contacts:

Chiefs managed unusually large quantities of resources and it is agreed that the basis of such wealth was polygamy. Rank was quite directly expressed in the number of wives. The chief of Omarakana had 16 wives in Malinowski’s time, while his predecessor Enamakala had 19....In traditional Trobriand society it seems that all leaders of village clusters of guyau status became polygamists. An emerging leader might also expect to be given wives by traditional allies outside the cluster while he might demand them from traditional rivals of subordinate subclans....

Followers similarly benefited from increased material and social resources, but also often lost these resources. Followers were not reported to receive mating benefits, relative to leaders or other benefit types.

For both leaders and followers, individuals stood to lose what they were able to gain (Fig. 4). Hauptman (1981, p. 183) describes Laura Cornelius Kellogg (also known as Minnie and Wynnogene, 1880–1947), a land-claims activist, writer, and perhaps the most famous Iroquois

female leader, whose life exemplified the risks to both leaders and followers:

Despite her exceptional gifts – a brilliant mind, beauty, self confidence, unusual oratorical abilities, and her educational attainments – Kellogg is also the most controversial Iroquois leader of the twentieth century. It is clear from her many bizarre involvements that she misused her prodigious talents and/or was incapable of carrying out all the massive designs she had for her people's betterment. Although acknowledged today as a major force and brilliant person, she is accused by many Iroquois elders of swindling them out of hundreds of thousands of dollars in her abortive efforts to bring their land claims to fruition and of creating debilitating factionalism that impeded tribal development for decades. Unfortunately, because of her questionable ethics and her inability to carry out what she espoused, Kellogg is blamed today for all that went wrong in Iroquois history in the interwar period. Consequently, her life story had the feel of a Greek tragedy: she wanted to use her extraordinary abilities to help her people but ended up accused by them of being a common outlaw.

5.5. Female leadership and sex differences

Only 30 of the 1212 text records discussed female leaders exclusively, and another 11 explicitly discussed both female and male leaders. Leader sex was only associated with variation in seven of our 109 leadership dimensions (Fig. S12), and one feature variable (Fig. S24), indicating that most dimensions of leadership probably characterize leaders of both sexes.

When ethnographic texts described female leaders exclusively, they were relatively more likely to be described as married to a high-quality spouse in a polygynous marriage, and the recipients of various mating benefits (Fig. S12). Female leaders also had higher levels of evidence for the *Social, reproductive, and material success* feature (Fig. S24). Evidence for female leaders was also more likely to be found in kin and residential subgroups. This suite of characteristics supports discussions of high status first-wives who gain and maintain social influence across the lifespan by leveraging their extended kin and social networks (Brown & Kerns, 1985; Goodale, 1971; Yanca & Low, 2004). Garfield and Hagen (2020) similarly found evidence of positive assortative mating of high status leaders in a small-scale society with relative gender-egalitarianism. Our results are also consistent with theoretical arguments emphasizing women as leaders of families (e.g., Garfield, Hubbard, & Hagen, 2019; Hagen & Garfield, 2019).

5.6. Disentangling the relationship between leadership and high status

Although leadership and high social status often covary, leaders are not always high-status individuals, nor are high status individuals always leaders (see Cheng & Tracy, 2020; Garfield, von Rueden, & Hagen, 2019; Van Vugt & Smith, 2019; von Rueden, Redhead, O'Gorman, Kaplan, & Gurven, 2019). Because individuals maintain multiple social "statuses," social context is critical (see Wiessner, 2010). In many cultures, for example, communities form work-groups and appoint "chiefs-for-a-day" who manage the work but have little status or authority otherwise (e.g., Macfarlan et al., 2012). Garfield, Hubbard, & Hagen (2019) found that leader organization dimensions clustered separately from leader prestige dimensions, suggesting a distinction. Garfield and Hagen (2020) found that some leaders among recently settled hunter-gatherers had organizing responsibilities but unexceptional levels of respect. Some older individuals, on the other hand, were highly respected but had little influence or authority.

Our results (Figures 3 and 4) support the importance of high social status for leader emergence (Cheng & Tracy, 2020). Nevertheless, over two thirds of our text records on leadership did not mention status, and it was not one of our candidate universal leadership dimensions, with

more evidence for high status from South American cultures (Fig. S11).

The words and leadership dimensions predictive of high status leaders (Fig. 7) resemble "Big men" (Garfield, von Rueden, & Hagen, 2019): wealthy, accomplished, older men who are respected for their decision-making abilities, knowledge and intelligence, and who favor their kin. These associations implicate leadership in the evolution and emergence of inequality (c.f., Sanday, 1981; Borgerhoff Mulder et al., 2010; Bowles et al., 2010; Mattison, Smith, Shenk, & Cochrane, 2016; Price & Feinman, 2010; Shenk, Kaplan, & Hooper, 2016). Our results did not strongly implicate high status leaders with particular functions, with the exception that punishment was modestly negatively associated with evidence for high status. The word "economic" was a negative predictor of high status, hinting that organizational roles might not be high status.

Smith and Van Vugt (2020) speculate that, "leadership may...be more strongly correlated with high status in large, complex organizations, such as in corporations and governments (p. 2)." Evidence for high status leaders, however, did not substantially vary by group context, which included levels of social organization ranging from sub-residential to supracommunity (Fig. S7). This null result fails to support this hypothesis.

5.7. Beyond dual models of leadership

Our results support many aspects of influential evolutionary theories of leadership, but offer new directions for expansion and synthesis.

5.7.1. Dominance and prestige

Leadership styles have long been described as based on either force and strength (i.e., dominance) or respect and expertise (i.e., prestige) (see Barkow et al., 1975; Bernstein, 1976; Kracke, 1978; Lewis, 1974; Mead, 1935; Sahlins, 1963; Tiger, 1970). Barkow (1980; 1975), synthesizing the ethological evidence of primate dominance hierarchies with ethnographic evidence, distinguished human prestige from dominance, suggesting the evolution of human prestige was linked to intra- and inter-sexual selection of culturally acquired competencies. Henrich and Gil-White (2001) introduced this important distinction to social science disciplines outside of anthropology, agreeing with Tiger (1970) and Barkow (1980; 1975) on a primate heritage of dominance, but offering an evolutionary account of prestige rooted in social rather than sexual selection for culturally acquired competencies. Henrich and Gil-White (2001) inspired much subsequent work across the behavioral sciences (e.g., Cheng, Tracy, Foulsham, Kingstone, & Henrich, 2013; Garfield, Hubbard, & Hagen, 2019; Halevy, Chou, Cohen, & Livingston, 2012; Maner, 2017; Suessenbach, Loughnan, Schönbrodt, & Moore, 2019; Van Vugt & Smith, 2019).

Our analyses supported the cross-cultural importance of leader aggression and coercion (dominance), as well as culturally acquired competencies (prestige). Our logistic PCA analysis of leader qualities, for instance, indicated that dominance qualities, such as coercive authority and aggressiveness loaded positively on PC1 and PC2, whereas prestige qualities, such as knowledge, experience, and high status loaded negatively on PC1 and PC2. See Fig. S19. But our analyses also indicated that some important modifications are required.

5.7.2. Leader competencies, shamanism, and the use of knowledge to impose costs

The individual competencies cluster (Fig. 9A) comprises dimensions associated with dominance-based leadership, including coercive authority and aggressiveness, as well as qualities associated with prestige-based leadership, including knowledgeable/intelligent and experienced/accomplished. These dimensions are among the most strongly supported in the ethnographic record (Fig. 3).

Shamanism appears to be a distinct form of leadership that combines a strategy of inducing fear, similar to the dominance strategy, but

is based on knowledge and expertise, similar to the prestige strategy. The *Competencies* feature included supernatural and feared dimensions (Fig. 9). The MST-kNN analysis similarly clustered leaders with ritual and medicinal functions, which rely on special knowledge, with those who had supernatural, feared or killer qualities (Fig. S21). Our *Shamanism* variable (which was not one of our original leadership dimensions) was predicted by words that evoke both dominance and prestige, such as *supernatural, power, fear, and knowledge* (Fig. 11A), and by four other leadership dimensions that also overlap with the dominance and prestige constructs: *Feared, Medicinal functions, Ritual functions, and Experience/accomplished*.

[Winkelman and White \(1987\)](#) found that in societies sampled from the HRAF ($n = 43$) shamans provided decision-making services within judiciary, economic, military, or political domains in 44% or more of societies, and held charismatic leadership roles in 19% of societies. [Winkelman \(1992\)](#) emphasized the influential positions of leadership shamans attain through their charisma, social unification, healing abilities, and use of supernatural powers to cause harm. Artistic performance is also implicated in this style of leadership, and ceremonial, artistic performances by shamans are common displays which often incorporate superhuman abilities ([Singh, 2017](#)). Earlier we quoted [Pospisil \(1993\)](#) on Trobriand chiefs' use of sorcerers to punish. Here, [Bishop \(1974\)](#) describes Ojibwa shaman leaders:

Leadership was vested in the heads of the co-residential groups who held their position through their hunting abilities and supernatural power as shamans. Shamans had the ability to foresee future events and the ability within certain limits to control them. These men were feared as well as respected and prior to 1900, most leaders were polygynists.

The potential evolutionary theoretical importance of shaman leaders (which in our data includes all leaders with supernatural qualities), highlights the importance of evidence on leadership from nonindustrial and non-Western populations. Shaman leaders, with their abilities to provide valuable benefits and impose severe costs, can play an outsized role in nonindustrial populations in numerous domains ([Winkelman & White, 1987](#)). The WEIRD notion of secular nationalism, which separates the religious and temporal spheres ([Juergensmeyer, 1993](#)), can perhaps blind scholars raised in this tradition from recognizing how weird this separation is.

5.7.3. Prosociality

The prosocial cluster (Fig. 9A), comprising prosocial competencies such as generosity and charisma, along with cultural conformity, generally corresponds to a charismatic style of leadership that has been identified in industrialized settings and widely discussed in sociology and evolutionary psychology ([Den Hartog, House, Hanges, Ruiz-Quintanilla, & Dorfman, 1999](#); [Grabo, Spisak, & Van Vugt, 2017](#); [Grabo & Van Vugt, 2016](#); [Howell & Shamir, 2005](#); [Weber, 1978](#)). The importance of leader prosociality also supports the [Henrich et al. \(2015\)](#) Big-man mechanism by which positive assortment of followers to prosocial leaders can facilitate the evolution of cooperative social norms and prestige-based leadership.

We also found leader functions often involve prosocial investments in group welfare (Fig. 9B). The prosociality feature of leader functions included distributing resources and providing protection, which are commonly highlighted in the anthropological leadership literature ([Boehm, 1993, 1999](#); [Johnson, 1982](#); [Johnson & Earle, 1987](#); [Sahlins, 1963](#); [Service, 1975](#)). In the absence of institutionalized leadership roles, leaders often maintain social influence via continued community investment and the demands of followers can shape leadership functions to meet local needs.

5.7.4. Leaders are managers

Our results (Fig. 9B) correspond very closely to what [Van Vugt and Kurzban \(2007\)](#) define as *strategic leadership*, where leaders increase the

pay-offs of another individual's behavior, thereby incentivizing followership, versus *coordinating leadership*, where individuals must effectively organize collective effort. There is also a history within managerial studies among industrial populations of contrasting *leaders from managers* ([Zaleznik, 1977](#)).

Leaders, possibly drawing on their special competencies, devise and implement strategic solutions to group problems including resolving conflicts and providing counsel (strongly supported functions), as commonly noted in the literature ([Boehm, 1999](#); [De Cremer & Van Vugt, 2002](#); [Knauft et al., 1991](#); [Wiessner, 1982, 2019](#)). The *Organize* feature aligns with many evolutionary theories that emphasize the role of leaders in organizing collective actions (e.g., [Glowacki et al., 2016](#); [Hooper et al., 2010](#); [Perret, Hart, & Powers, 2020](#); [Pietraszewski, 2020](#); [Van Vugt & Kurzban, 2007](#)).

5.8. Leadership and cognitive, social, material, and somatic capital

In our view, the dominance-prestige and "dual-model" theories of leadership, while advancing the discipline, cannot easily account for shaman leaders nor "chiefs-for-a-day" (managers). Critically, these models have conflated the ability to provide "benefits" with knowledge and expertise, and the ability to impose "costs" with physical formidability. [Van Vugt and Smith \(2019\)](#), for instance, state that the source of deference for prestige-style leadership is "Information asymmetry", and for dominance-style, "Power asymmetry" (their Table 1). Instead, as shaman leaders demonstrate, knowledge and expertise can both provide benefits and impose costs, and the same goes for physical formidability. The use of knowledge to impose costs is widely recognized by many social scientists. The role of gossip and other forms of indirect aggression in social dominance, for instance, has been extensively investigated in industrial populations (e.g., [Hawley, 1999](#); [Hess & Hagen, 2006, 2017](#)) and also among hunter-gatherers ([Hess, Helfrecht, Hagen, Sell, & Hewlett, 2010](#)).

Our revised model, inspired by [von Rueden \(2014\)](#) and others, proposes that leaders deploy cognitive, social, material, and somatic capital to provide benefits and impose costs on followers. If their abilities to do so are similar to other groups members, as in "chiefs-for-a-day", they acquire little status, but if their abilities are exceptional relative to others, they gain status via biological market mechanisms ([Garfield, Hubbard, & Hagen, 2019](#); [Hagen & Garfield, 2019](#); [Hammerstein & Noë, 2016](#); [Pietraszewski, 2020](#)). There was strong evidence for cognitive and social capital, with cognitive capital associated with both providing benefits and imposing costs, particularly among shaman leaders (Fig. 12).

6. Limitations

Our results are conditional upon the content ethnographers chose to discuss, the way they discussed it, and the way we interpreted and coded their texts. There was a general male bias, which could reflect a male bias in community leadership or a more systemic bias of the ethnographic record (see [Mukhopadhyay & Higgins, 1988](#); [Rosaldo, Lamphere, & Bamberger, 1974](#)). These data are also biased towards cultural models of leadership (rather than particular cases) and community leadership; descriptions of kin and residential group leadership were less frequent. The high proportion of text records discussing political leaders could be attributable to our broad search strategy or the content of the ethnographic record of "leadership." Our sample of cultures and text records by continental region and subsistence strategy is also unbalanced. We also detected bias in evidence by date of publication for nine of our 109 leader dimensions (see Fig. S6).

Another limitation lies in our ability to interpret the absence of evidence. The cross-culturally frequent measures discussed here are strongly represented in the ethnographic record and hence very likely to represent broad cross-cultural patterns. We cannot strongly conclude, however, that the relatively infrequent measures identified are

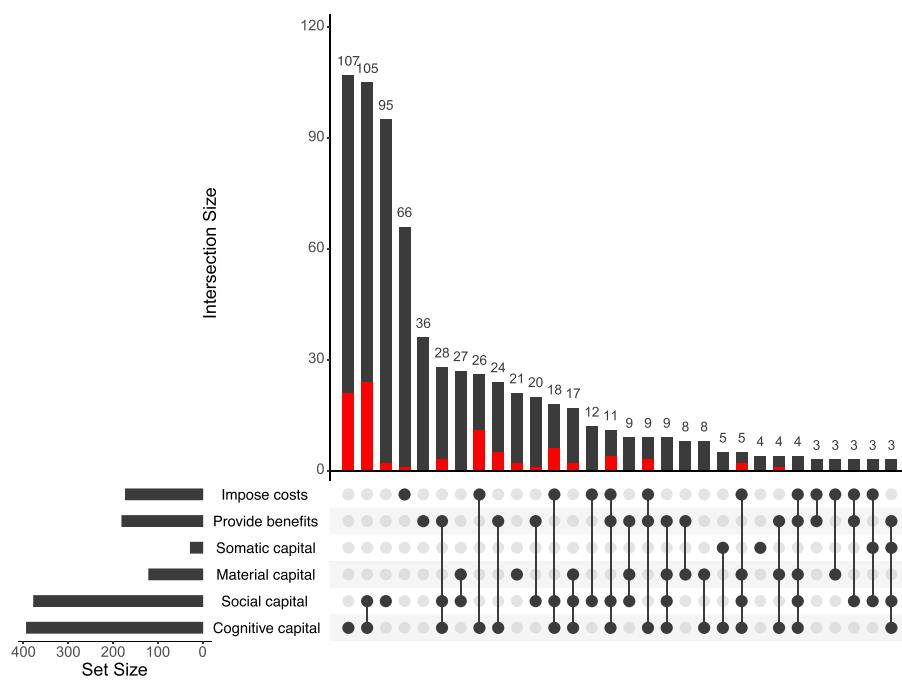


Fig. 12. The intersections of evidence for our six basic elements of leadership among all text records (an ‘upset’ plot) (Gehlenborg, 2019). Horizontal bars (left): The total number of text records in each element. Black dots: has evidence. Gray dots: does not have evidence. Vertical bars (top): The number of text records in that intersection (with lower limit set at 3). Red: The number of text records involving shamans or leaders with supernatural qualities.

truly infrequent dimensions of human behavior and culture, only that they are relatively less frequent in the ethnographic record.

This is an exploratory study. Our analyses were driven by data rather than by *a priori* hypotheses. This has the advantage that unexpected patterns can be discovered, such as the role of shaman leaders, but the disadvantage that some random variation can, and almost certainly will, be misinterpreted as meaningful patterns. In particular, our cluster analysis of leader qualities (Fig. 9A) was sensitive to the choice of different clustering algorithms and inclusion or exclusion of dimensions with little evidence.

7. Concluding remarks: Beyond the non-WEIRD

The WEIRD people problem in behavioral science cannot be remedied simply by a “non-WEIRD” solution. Our results, and much of anthropology, clearly demonstrate enormous diversity among populations that are now often categorized as “non-WEIRD”, “traditional”, or “small-scale.” Anthropologists have often made the opposite mistake in essentializing diverse “others” and failing to recognize deep similarities among peoples of all cultures (Brown, 1991; Reyes-García, Zurro, Caro, & Madella, 2017; Said, 1979).

Our results support important, potentially universal dimensions of leadership, as well as systematic variation in other dimensions, especially by the specific context in which leadership occurs. We found leaders in the ethnographic record are widely portrayed as generally prosocial, equipped with special competencies such as knowledge and expertise, resolve conflicts and organize cooperation, and receive material, social, and reproductive benefits. Cross-cultural evidence also supports a dominance style of leadership involving coercive authority, punishment, aggression, and control of resources. These results generally provide broad cross-cultural support for several influential theories, such as the dominance-prestige model, the service-for-prestige model, the computational services model, and numerous collective action models (for review, see Garfield, Hubbard, & Hagen, 2019).

Shamans emerged as an important category of leaders that are rarely discussed in the evolutionary literature (but see Singh, 2017). Supernatural qualities were among the top ten leader qualities across cultures (Fig. 3). Shamans share qualities with prestige-style leaders, such as having specialized knowledge and abilities, yet appear, at least at times, to use their knowledge to instill fear, similar to dominance-

style leaders. We therefore suggest moving beyond dichotomous or “dual” models of leadership, which have tended to conflate knowledge and expertise with providing benefits. Instead, our data indicate that leaders deploy cognitive, social, material, and somatic capital to provide benefits and impose costs (Fig. 12). This view aligns with the theoretical framework developed by many scholars that emphasizes the importance of embodied capital (neural and somatic) and social and material capital in the evolution of human social organization (Bowles et al., 2010; Kaplan et al., 2009; Kaplan, Lancaster, & Robson, 2003; Kaplan, Mueller, Gangestad, & Lancaster, 2003; von Rueden, 2014).

Leaders across cultures rely on a range of individual competencies, including cognitive, supernatural, material, social, and physical endowments, to organize group members, implement strategic actions, provide prosocial services to the group, and impose costs, all while conforming to cultural norms. Currently, no single theoretical perspective has yet captured the ethnographic reality of human leadership.

Acknowledgements

We thank the co-editors of the special issue, Joseph Henrich, Coren Apicella, and Ara Norenzayan; Christopher von Reuden; and an anonymous reviewer for their valuable comments. This research was funded by National Science Foundation Division of Behavioral and Cognitive Sciences award [1628509]. Zachary H. Garfield acknowledges IAST funding from the French National Research Agency (ANR) under the Investments for the Future (Investissements d’Avenir) program, grant ANR-17-EURE-0010.

Data availability

The data associated with this research are available at <https://doi.org/10.5281/zenodo.2541999>.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.evolhumbehav.2020.07.012>.

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Review

The evolutionary anthropology of political leadership

Zachary H. Garfield^{a,*}, Christopher von Rueden^b, Edward H. Hagen^a

^a Washington State University, United States of America

^b University of Richmond, United States of America



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, & Stiegartz, 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.

* Corresponding author.

E-mail addresses: zachary.garfield@wsu.edu (Z.H. Garfield), cvonrued@richmond.edu (C. von Rueden), edhagen@wsu.edu (E.H. Hagen).

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 socio-political 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 Boltt (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). Intrexual 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; Knaft 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 (Moise, 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 Tagemiat 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 *umialik* 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 co-operating 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 Tlingit 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 Tlingit 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 chiefs 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 socio-political 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; Knauf, 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 socio-political 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 socio-political 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; Connolly 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-followerhip, 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’

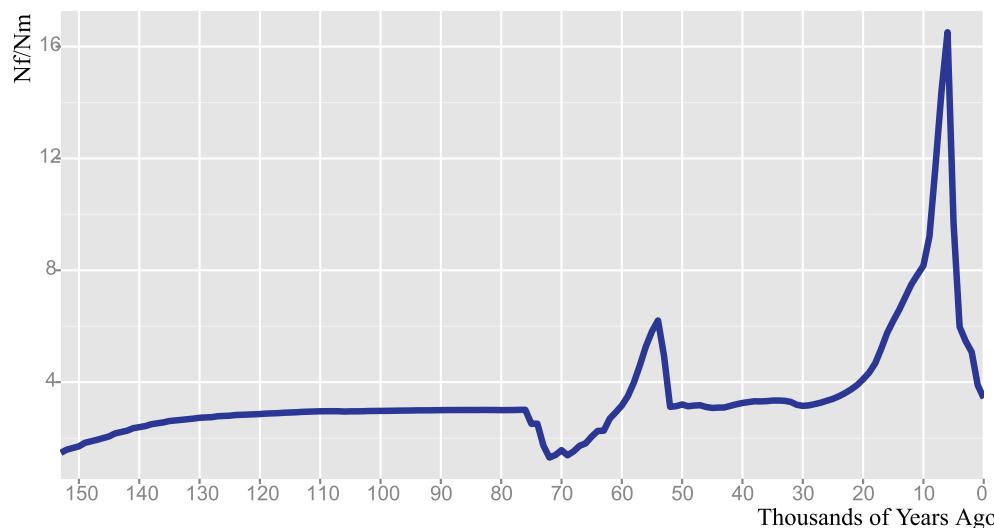


Fig. 1. The temporal dynamics of the ratio of female (N_f) and male (N_m) effective population size in the last 140 KY. The ratios of the global accumulative N_e estimates of mtDNA (N_f) and Y chromosome (N_m) are plotted against the time (in thousands of years) back from the present (0). The BSPs estimates of N_e 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 (Batin & 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
<i>foragers</i> (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
<i>stratified foragers</i> (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
<i>horticulturalists</i> (labour-limited cultivation)	intergenerational provisioning, little inheritance	some polygyny, bride capture	cooperative field labour, big men manage conflict over land	relative egalitarianism
<i>pastoralists</i> (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
<i>agriculturalists</i> (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 & Grabs, 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 socio-cultural 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 alloparental 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 alloparental 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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